

Physical and biogeochemical gradients and exchange processes in
Nyanza Gulf and main Lake Victoria (East Africa)

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Nyanza Gulf is a large, shallow and long river-influenced embayment located in northeastern Lake Victoria. The gulf opens to the main lake through the narrow and deep Rusinga Channel, the exchange zone between the two ecosystems with different physical chemical and biogeochemical conditions. The main goals of this study are to characterize physicochemical and nutrient gradients along the gulf-main-lake transect, characterize and quantify the water and nutrient fluxes between the gulf and the main lake, and assess the response of phytoplankton community and photosynthesis to the spatially varying physical and nutrient conditions along the study transect. Between March 2005 and March 2006, measurements of physicochemical profiles as well as nutrient and the phytoplankton community analysis were conducted monthly along the study transect. Additionally, analysis of different surficial sediment phosphorus fractions was done in order to assess the potential role of bottom sediment in contributing to phosphorus enrichment in the lake water column. A box mass balance model was used to calculate the exchange of water and nutrient fluxes between different zones along the study transect and to estimate ecosystem metabolism in the gulf and the channel.

Spatial variability in physicochemical and biogeochemical conditions was observed along the study transect, especially between the shallow and river-influenced inner-gulf, the deep and physically active Rusinga Channel, and the main lake, mainly in response to river inputs and varying morphometry along the study transect. The gulf had significantly higher electrical conductivity (EC), turbidity, total nitrogen (TN), and dissolved reactive silica (DRSi) but the levels declined monotonically along the channel in response to mixing with the main lake water. The channel and the main lake had, respectively, significantly higher dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) compared to the gulf. Spatial variability in morphometry and exposure to varying wind forcing lead to differential mixing and differential heating and cooling along the transect, resulting in density driven fronts and horizontal exchange of water and nutrients between the gulf and the main lake. Upwelling and downwelling maintained mixing conditions in the channel which

consequently influenced nutrient recycling, the light environment and hence affecting phytoplankton community composition and productivity.

The net residual water flow from the gulf to the main lake was $36 \text{ m}^3/\text{s}$ but the mixing flux was approximately 20 times higher and both fluxes accounted for a gulf exchange time of 1981 days. The advective and mixing fluxes between the gulf and the main lake resulted in net export of dissolved inorganic phosphorus (DIP; 400 kg P/d) from the main lake into the gulf and net export of DRSi (10 t Si/d) from the gulf into the main lake. In the deep, narrow and physically active Rusinga Channel there was net production of dissolved nutrients whereas in the gulf there was net consumption of dissolved nutrients, which helped to maintain high net ecosystem production (NEP; $566 \text{ mg C/m}^2/\text{d}$) in the gulf in contrast the channel which showed net heterotrophy. The high NEP in the gulf and the associated high nutrient demand coupled with possibly low SRP to DIN supply ratio lead to P limitation of algal growth in the gulf as indicated by all indicators of nutrient status. This has important implications for management since increased P input into the gulf will translate into increased algal blooms in the gulf and therefore compromise water quality.

Spatial variability in physical conditions and nutrient status along the study transect influenced phytoplankton community composition and photosynthesis. The shallow and turbid gulf was dominated by cyanobacteria but diatoms dominated in the channel in response to reduced turbidity and increased physical mixing and nutrient availability (DRSi, SRP). In the main lake seasonal stratification and deep mixing depth favoured both cyanobacteria and diatoms. The phytoplankton community in channel had a higher photosynthetic capacity (F_v/F_m , P_{Bm}) compared to both the gulf and the main lake.

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Chapter 1

General Introduction

Lake Victoria is a large and shallow (surface area 68000 km²; mean depth 40m) saucer shaped freshwater body located along the equator between 0.5°N and 2.5°S and between 32°E and 34°E at an elevation of 1134 m asl and has a large catchment (195,000 km²), which lies on an uplifted plateau between the eastern and western rift valleys of eastern Africa (Asnani, 1993; Spigel & Coulter, 1996). The lake has a convoluted shoreline with numerous gulfs and bays (Fig. 1.1), some of which are semi-closed and are recipient of riverine inflows and municipal and industrial discharges from the adjacent urban centers and give heterogeneity to this meso-eutrophic lake. The hydrology of the lake is dominated by precipitation and evaporation with riverine input contributing only 30% (20 km³ yr⁻¹) of the water budget, with the same amount leaving through river Nile, the only outflow (Piper et al., 1986). The timing of rainfall and synoptic wind patterns are influenced by the movement of the Intertropical Convergence Zone (ITCZ), with the main rainy seasons occurring between March to May (long rains) and between November and December (short rains) and the strongest winds occur between April and May and are southwesterlies (Asnani, 1993; Stager et al 2005).

The lake is an important source of water and fish protein to the riparian population and is of high economic value to the riparian countries through its multimillion dollar fishery, besides its cultural, aesthetic, and global ecological value. However, due to water quality and ecological changes that have occurred in the lake in the last 5 decades (Ogutu-Ohwayo, 1990; Ochumba & Kibaara, 1989; Hecky, 1993; Hecky et al, 1994; Kling et al. 2001), the socioeconomic and ecological value of the lake has been negatively affected. Increased nutrient and sediment input from the catchment has resulted in increased eutrophication of the lake, an associated increase in occurrence of algal blooms and more persistent hypolimnetic hypoxia which have compromised water quality and reduced fish habitat (Witte et al 2005). The algal population has changed from one dominated by diatoms 50 years ago (Talling, 1965) to the present one which is dominated by bloom-forming and potentially toxic cyanobacterial species (Kling et al, 2001). In the nearshore areas, where direct input

from the catchment occurs, increased turbidity associated with fluvial sediment input and algal blooms has resulted in reduced water transparency, therefore affecting fish feeding and production in these important breeding areas (Witte, 2005), while compromising drinking and recreational water quality. The proliferation of the exotic floating weed, water hyacinth (*Eicchornia crassipes*), in the inshore areas of the lake has become a management problem through its blockage of water intakes, fishing grounds and water transport (Twongo, 1996; Mailu, 2001; Williams et al, 2005).

The nutrient budget of Lake Victoria is dominated by direct atmospheric input, which contributes about 55% of TP loading (Tamatamah et al, 2005) and more than 65% of TN loading (LVEMP, 2002). However, nutrient input from the catchment through surface runoff and from industrial and municipal sources has continued to increase and exert direct impact on the nearshore areas, especially the numerous semi-closed embayments as is evidenced through increased algal blooms and recent proliferation of the water hyacinth (Ochumba & Kibaara, 1989; Twongo, 1996; Mailu, 2001). This is the case for Nyanza Gulf, which receives about 56% of its TP and TN from non-point sources and Murchison Bay which receives about 85% of TP and 76% of TN from municipal and industrial sources (LVEMP, 2002). The inshore areas of Lake Victoria serve vital ecological and socioeconomic roles as they are important fish refugia and breeding grounds and are main sources of drinking water for several major cities (e.g. Nyanza Gulf for Kisumu City, Murchison Bay for Kampala and Mwanza Gulf for Mwanza) and it is therefore imperative to understand physical and biogeochemical processes in order to be able model and predict the impact of inputs from the catchment on the immediate environment and on the lake as a whole.

Physicochemical and biogeochemical gradients between inshore and offshore areas of Lake Victoria have been observed and attributed to both internal and external factors including external inputs of dissolved and particulate matter to the nearshore areas (Lungayia et al, 2005; LVEMP, 2002), hypolimnetic phosphorus release and denitrification in the seasonally stratifying offshore areas (Hecky, 1993; Gikuma-Njuru & Hecky, 2005) and morphological differences between the deep offshore and shallower inshore areas. These lead to differential mixing, and therefore influence light conditions, nutrient recycling and the

phytoplankton assemblage and productivity (Lehman et al. 1998; Kling et al. 2001; Mugidde et al. 2003). Total nitrogen and soluble reactive silica concentrations are reportedly higher inshore compared to offshore areas whereas soluble reactive phosphorus concentration is higher offshore compared to inshore waters (Mavuti & Litterick, 1992; Mugidde, 2001; Gikuma-Njuru & Hecky 2005). In addition to physical and nutrient gradients, and as a consequence, phytoplankton community and productivity has been observed to vary between the two lake zones with the inshore areas having higher algal biomass and integral primary productivity (Mugidde, 1992) and this causes lower Si except in Nyanza Gulf which is P limited.

The inshore and offshore areas of lake ecosystems are linked by physical processes through mixing and exchange of water and associated dissolved and particulate constituents (MacIntyre & Melack, 1995; Talling, 2001). Wind shear and density gradients resulting from differential heating, differential cooling and differential mixing are the main forces driving physical processes in lakes (Imberger & Parker, 1985; Monismith et al. 1990). The inshore-offshore interaction result in the flushing of the inshore areas and act to transport and disperse materials and energy from the inshore areas to the rest of the lake. It is therefore important to understand and characterize the inshore-offshore exchange processes in order to model and predict the impact of catchment inputs to the lake ecosystems. Nutrients and energy transported from inshore areas can contribute to increased offshore primary and secondary production as has been observed in some estuarine and coastal marine ecosystems (e.g. Sutcliffe, 1983; Dronkers, 1988). Similarly upwelling from the deep offshore waters can be an important source of nutrients and energy for primary and secondary production in inshore areas (e.g. Schelske et al. 1971; Verburg, 2003).

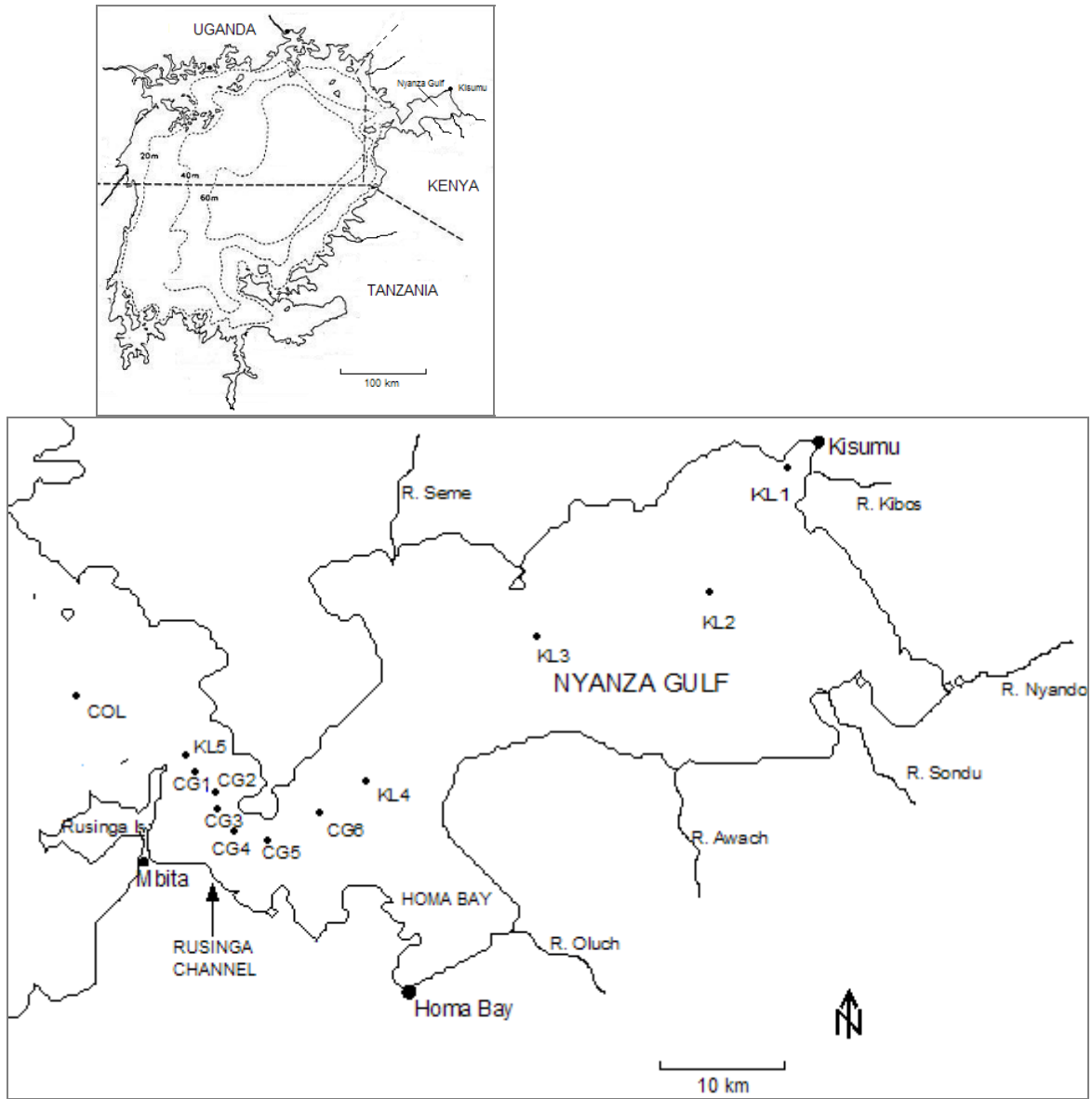


Figure 1.1 Lake Victoria (inset) and a detailed map of the study area, showing the location of sampling stations and river tributaries

The purpose of this study is to contribute to the understanding of physicochemical and biogeochemical gradients in Lake Victoria, the exchange dynamics between inshore and offshore waters and the role of hydrological and physical processes in influencing nutrient availability and light climate and consequently influencing phytoplankton assemblage and production. The study was conducted in the northeastern part of Lake Victoria along a transect between Nyanza Gulf (also known as Winam or Kavironondo Gulf) and the main lake (Fig. 1.1). Nyanza Gulf is a large and shallow embayment (surface area 1400 km²; mean depth 10 m), 70 km long and with a maximum and minimum width of 30 km and 5km respectively (Mavuti & Litterick, 1991 and Crul, 1995). The gulf is wide and shallow in the eastern part but narrow and deep in the western areas as it opens into the main lake to the west. The gulf is a recipient of riverine inflows, with rivers Sondu and Nyando contributing the bulk of the input and is also a recipient of industrial and municipal effluents from urban centers and agro-based industries located in the catchment (Calamari et al, 1995; Lungayia et al 2001). The study was done between March 2005 and March 2006 along a transect extending from the eastern end of the gulf to the main lake (Fig. 1.1). Twelve stations were established to represent the different morphometric and limnological zones along the transect. Four stations (KL1, KL2, KL3 and KL4) are within the main gulf area, which is wide, shallow and with high riverine and urban influences and characterized by high inorganic turbidity, high algal biomass and daily mixing of the water column (Gikuma-Njuru and Hecky, 2005). Seven stations (CG1 to CG6 and KL5) are located along the narrow and deep Rusinga Channel, the area of exchange between the gulf and the main lake and one station (COL) is in the main lake, which is relatively deep and experiences seasonal stratification (Talling, 1957; Ochumba, 1996). The stations KL1, KL2, KL3, KL4 and KL5 are part of the existing Lake Victoria Environmental Management Project (LVEMP) water quality monitoring sampling network and were adopted for this study in order to make use of the existing historical data and to contribute to the long term data acquisition and knowledge base of the gulf environment. The stations between KL5 and CG6 are spaced between 2 and 5 km apart and were established in order to study the gradients and exchange dynamics along the channel. COL represent the main lake conditions and was chosen to be near the long-term

monitoring station 32 (Ochumba and Kibaara, 1991) but also to fall along the Rusinga Channel transect. The stations KL1 and KL2 were only sampled during the study of the surficial sediment phosphorus. The mean depths and geographical locations of the stations are presented in Table 1.1.

Table 1.1 Mean depths and geographical locations of sampling stations. The mean depths are based on monthly measurements done between March 2005 and March 2006

| | Mean Depth | Latitude | Longitude |
|-----|------------|--------------|---------------|
| COL | 34.1 | 0° 18.542' S | 34° 08.776' E |
| KL5 | 21.8 | 0° 21.102' S | 34° 14.320' E |
| CG1 | 14.9 | 0° 21.988' S | 34° 14.885' E |
| CG2 | 12.1 | 0° 22.945' S | 34° 15.459' E |
| CG3 | 27.1 | 0° 23.952' S | 34° 16.095' E |
| CG4 | 20.8 | 0° 24.975' S | 34° 16.927' E |
| CG5 | 23.5 | 0° 25.148' S | 34° 18.090' E |
| CG6 | 14.0 | 0° 23.969' S | 34° 20.621' E |
| KL4 | 12.1 | 0° 22.728' S | 34° 22.903' E |
| KL3 | 5.3 | 0° 15.301' S | 34° 31.188' E |
| KL2 | 3.3 | 0° 13.324' S | 34° 39.787' E |
| KL1 | 2.5 | 0° 07.205' S | 34° 43.295' E |

1.1 Study objectives

This thesis consists of 4 independent, but related, data chapters each written as a separate manuscript for publication in a scientific journal. The first chapter lays the foundation for the other three chapters as the knowledge of physical processes from this chapter is pertinent in the study of nutrient dynamics in the water column and sediments (Chapters 3 and 4) and phytoplankton dynamics (Chapter 5). Similarly, the results on nutrient status from Chapter 3 are used in chapter 5. The objective of the first data chapter (Chapter 2) was to characterize the spatial and temporal variability in physicochemical conditions along

the transect between the Nyanza Gulf and the main Lake Victoria and characterize and quantify the exchange processes between different zones along the transect. The hypothesis was that river inputs into the eastern gulf area together with varying morphometry and meteorological conditions along the gulf-main-lake transect result in spatial variability in physicochemical conditions along the transect and drive the exchange between the gulf and the main lake. Physicochemical profiles were taken along the transect over a 13 month period, between March 2005 and March 2006. Spatial cross-section plots of temperature, dissolved oxygen (DO) and electrical conductance (EC) were used to trace mixing and transport along the transect. A mass balance mixed model was used to calculate advective water flow between different zones and to calculate the mixing fluxes using conductivity as a conservative tracer (Gordon et al. 1996).

The first objective of Chapter 3 was to characterize the spatial and temporal variability in concentration in the water column of different nutrient fractions along the gulf-main-lake transect and to quantify the exchange fluxes of soluble nutrient fractions between different zones along the transect. This was accomplished through monthly sampling and analysis for dissolved and seston nutrient fractions along the study transect, between March 2005 and March 2006. The second objective was to calculate net nutrient fluxes (production) and ecosystem metabolism in the gulf and the Rusinga Channel, the exchange zone between the gulf and the main lake. The model used in Chapter 2 was expanded to include a nutrient component and used to calculate nutrient exchange fluxes and net fluxes (production) of dissolved inorganic and organic phosphorus (DIP, DOP), dissolved inorganic and organic nitrogen (DIN, DON) and dissolved reactive silica (DRSI) and ecosystem metabolism.

The main objective of Chapter 4 was to characterize different phosphorus fractions in the surficial sediments along the study transect, in order to assess the potential role of sediment phosphorus in contributing to the increasing P concentrations in Lake Victoria. A secondary objective was to assess the factors determining the spatial variability in the concentration of different phosphorus fractions and metal elements in the sediment. A sequential acid-base extraction method was used to characterize and quantify different phosphorus fractions and X-ray diffraction was used to analyze different metal elements in

the sediment. Phosphorus in the sediment can occur in different forms of associations, which determine its availability for biological uptake in the water column (Bostrom et al., 1988; Levy and Schlesinger 1999).

The primary objective of Chapter 5 was to assess the role of spatially changing nutrient and physical conditions along the study transect in influencing phytoplankton assemblage, biomass and productivity. Phytoplankton community composition and productivity is normally determined by the relative availability of different nutrients (N, P, micronutrients) and light climate and it was therefore hypothesized that the changing nutrient status and light climate along the study transect will result in spatial variability in phytoplankton assemblage and productivity, especially between the shallow and turbid inner gulf area, the deep and physically active channel and the main lake. Measurements of phytoplankton community composition, biomass and photosynthesis along the study transect were carried out and their spatial and temporal variability related to the findings of Chapters 2 and 3.

Chapter 2

Spatio-temporal variability in physicochemical variables and water flux along a transect between Nyanza Gulf and the main lake

2.1 Introduction

The spatial and temporal variability of physico-chemical conditions in lakes can be associated with a number of internal and external factors including inflows and outflows, meteorological conditions, physical processes and biogeochemical processes. Inflows bring materials (dissolved and suspended) from the drainage basins into the receiving waters and outflows act to export materials and heat out of the system (Kalff, 2002). Precipitation may introduce solutes or dilute the water body (Lesack & Melack, 1991) and evaporation acts to concentrate solutes and modify thermal conditions in the water column (Talling, 2001). Solar irradiance introduces thermal energy and acts to set the tempo for physical dynamics (mixing and transport processes) and wind stress initiates turbulence leading to water movement and mixing of heat, solutes and particulate matter, and evaporative cooling (Lewis, 1983; MacIntyre & Melack, 1995). The importance of any one or a combination of these factors will vary for lakes of different sizes, morphometry and latitude (Wetzel, 2001). The large surface area of Lake Victoria (68000 km²) and its tropical location makes it responsive to prevailing meteorological conditions although, in the numerous semi-closed inshore areas of Lake Victoria, inputs from the catchment can have a disproportional influence on the physical and chemical conditions (Lung'ayia et al. 2001; Gikuma-Njuru & Hecky, 2005).

In tropical lakes, where summer is “endless” (Kilham and Kilham 1989), small temperature differences have disproportionately large influence on physical processes due to the rapid change in the density of water at high temperature (Talling, 1957) and therefore any differential heating or differential cooling in the lake will have significant influence on the physical processes. Spatial variability of temperature mainly results from differential heating and differential cooling in different parts of a lake and usually occurs when a lake is exposed to spatially varying wind stress, varying absorption of solar irradiance associated with

variability in turbidity or weather conditions or under varying lake morphometry (Imberger & Parker, 1985; Monismith et al., 1990). Spatial variability of water temperature resulting from differential heating and differential cooling leads to differential mixing and density driven fronts, which result in exchange of water and associated matter between different lake zones (MacIntyre & Melack, 1995). Talling (1966) observed markedly different water column thermal structures in the sheltered inshore and offshore regions of Lake Victoria, which he suggested might play an important role in the exchange between these two lake zones. Diel measurement of temperature profiles in Pilkington Bay, northern Lake Victoria, showed development of density fronts associated with differential heating and differential cooling in the Bay and the adjacent Buvuma Channel (MacIntyre et al. 2002).

Wind energy causes mixing and evaporative cooling and can lead to differential cooling and differential mixing in a lake with variable morphometry or exposed to variable wind speed (Monismith, 1985; Imberger & Parker 1985). Wind can also cause horizontal displacement of surface water and compensational underflow of bottom water and therefore leading to exchange of water and materials between different lake zones. Worthington (1930) observed the diurnal changes of wind along the Nyanza Gulf and the displacement of water in and out of the gulf in response to the wind patterns. Newell (1960) observed wind-driven inshore-offshore exchange of water in northern part of Lake Victoria and reported currents of between 6 and 24 cm/s in the channels. Episodic wind storms have been observed in Lake Victoria and have been associated with local upwelling (Kitaka, 1972) and development of swift currents (Ochumba, 1996).

The existence of physical and chemical gradients between inshore and offshore waters of Lake Victoria has been recognized since the early days of the lake research (Worthington, 1930; Fish, 1952, Newell, 1960; Talling, 1966). However, due to the high pollution input associated with increased human population and land degradation and the resultant water quality changes (Ochumba & Kibaara, 1989; LVEMP, 2005; Witte et al, 2005) it has become increasingly necessary to characterize the physical and chemical gradients and understand how the inshore and offshore areas interact. Short term studies of the physical dynamics in Pilkington Bay (MacIntyre et al, 2002) and in Nyanza Gulf

(Romero et al, 2005) have shed light on some physical processes in the inshore areas of Lake Victoria. However, fuller understanding of the factors that contribute to the inshore offshore gradients in Lake Victoria and the processes that drive the interaction between the two lake zones is required in order to further understand the fate and impact of the lake catchment input and pollution on the immediate inshore areas and the lake as a whole.

This study explores spatial, temporal and seasonal variation of physico-chemical variables in the northeastern Lake Victoria and the gradients and water fluxes along the exchange zone between the Nyanza Gulf and the main lake and how the exchange influences and is influenced by the physical and meteorological forcing.

2.2 Methods

2.2.1 Study area

The study area was in the northeastern part of Lake Victoria along a transect lying between the Nyanza Gulf (also known as Winam Gulf) and the main Lake Victoria (Fig. 2.1). Nyanza Gulf is a large and shallow embayment (surface area 1400 km²; mean depth 10 m), 70 km long and with a maximum and minimum width of 30 km and 5km respectively (Mavuti & Litterick, 1991 and Crul, 1995). The gulf is wide and shallow in the eastern part but narrow and deeper in the western areas as it opens into the main lake to the west. The gulf is a recipient of riverine inflows, with rivers Soundu and Nyando contributing the bulk of the input and is also a recipient of industrial and municipal effluents from urban centers and agro-based industries located in the catchment (Calamari et al, 1995; Lungayia et al 2001).

Before 1983, the gulf had two openings into the main lake; one through Mbita channel to the south of Rusinga Island and the other through the Rusinga Channel to the east of the Island, but the Mbita Channel was blocked in 1983 through back-filling during the construction of the Mbita Causeway, which now connects the mainland with the Rusinga Island (Fig. 2.1). The Rusinga Channel begins west of Homa Bay and is characterized with complex morphology being narrow and deep relative to the rest of the gulf and main lake,

having a change of orientation from southwest to northwest, and containing several markedly deeper areas (holes) which contribute to its physical heterogeneity and influence the dynamic exchange between the gulf and the main lake ecosystems. The depth of the channel is uneven and at its narrowest area, near the bend from southwest to northwest, a few meters drift on the surface can be related to a change in depth of more than 10 meters (Personal observation). Towards the opening to the lake there are shallow sills of about 12m separating depths of about 30m on each side (Fig 2.1). The Bridge Island, west of the channel in the main lake, are a surface expression of this underwater topography.

Ten sampling stations were established along the gulf and in the main lake in a way to represent the different morphometric and limnological zones along the transect. Two stations (KL3 and KL4) are within the main gulf area, which is wide, shallow and with high riverine and urban influences and is characterized with high inorganic turbidity, high algal biomass and daily mixing of the water column (Gikuma-Njuru and Hecky, 2005). Seven stations (CG1 to CG6 and KL5) are located along the narrow and deep Rusinga Channel, the area of dynamic exchange between the gulf and the main lake (Antenucci et al, 2006), and one station (COL) is in the main lake, which is relatively deep and experiences seasonal stratification (Talling, 1957; Ochumba, 1996). Three stations (KL3, KL4 and KL5) are part of the existing Lake Victoria Environmental Management Project (LVEMP) water quality monitoring sampling network and were adopted for this study in order to make use of the existing historical data and contribute to the long term data acquisition and knowledge base of the gulf environment. The stations between KL5 and CG6 are spaced between 2 and 5 km apart and were established in order to study the gradients and exchange dynamics along the channel. COL represent the main lake conditions and was chosen to be near the long-term monitoring station 32 (Ochumba and Kibaara, 1991) but also to fall along the Rusinga Channel transect.

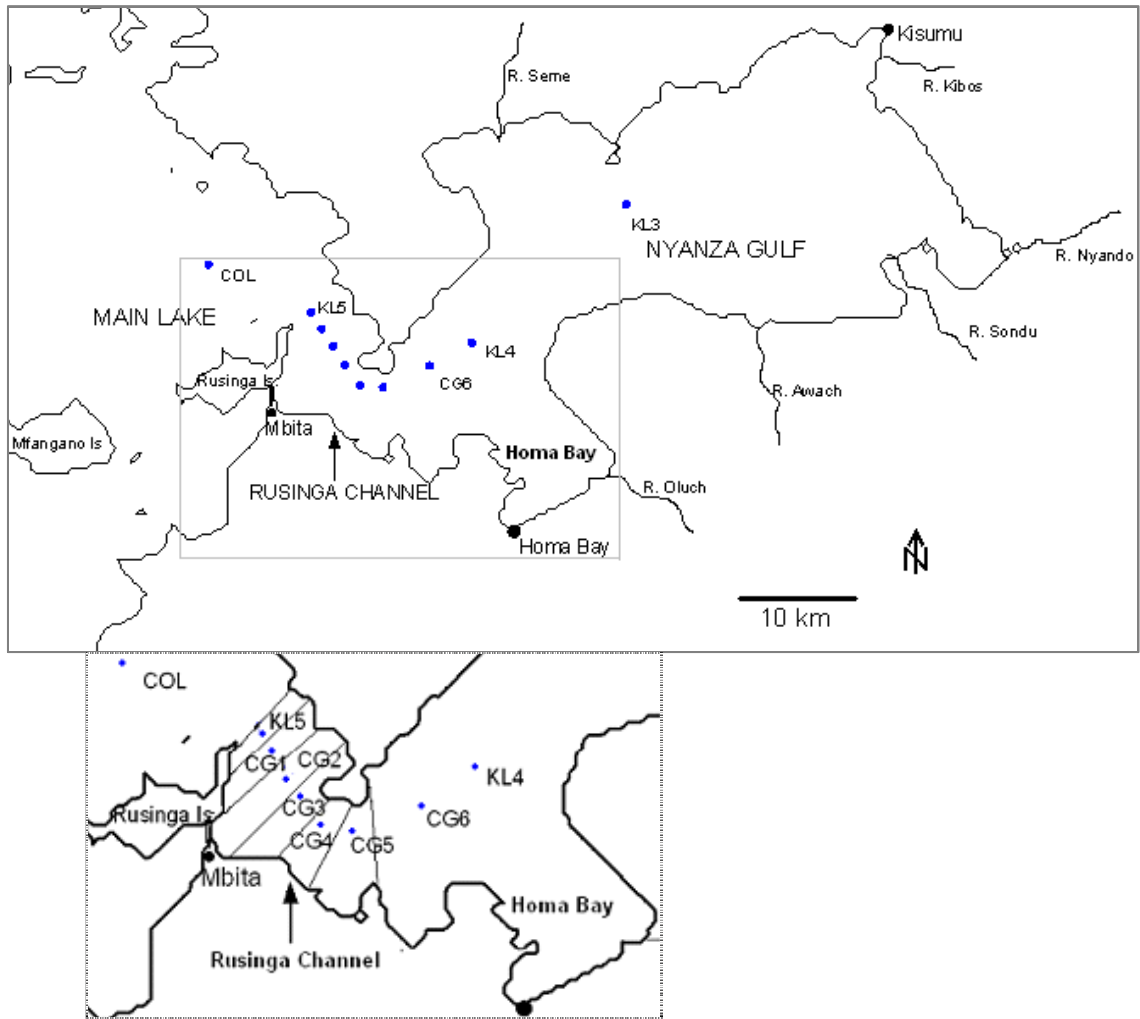


Figure 2.1 Map of northeastern Lake Victoria including Nyanza Gulf and showing the location of the sampling stations and the river tributaries. The inset shows the details of the sampling stations and study segments along the Rusinga Channel: the transect lines between sampling stations separate different study segments, each identified with the station between two transect lines. The gulf segment is represented by stations KL3, KL4 and CG6.

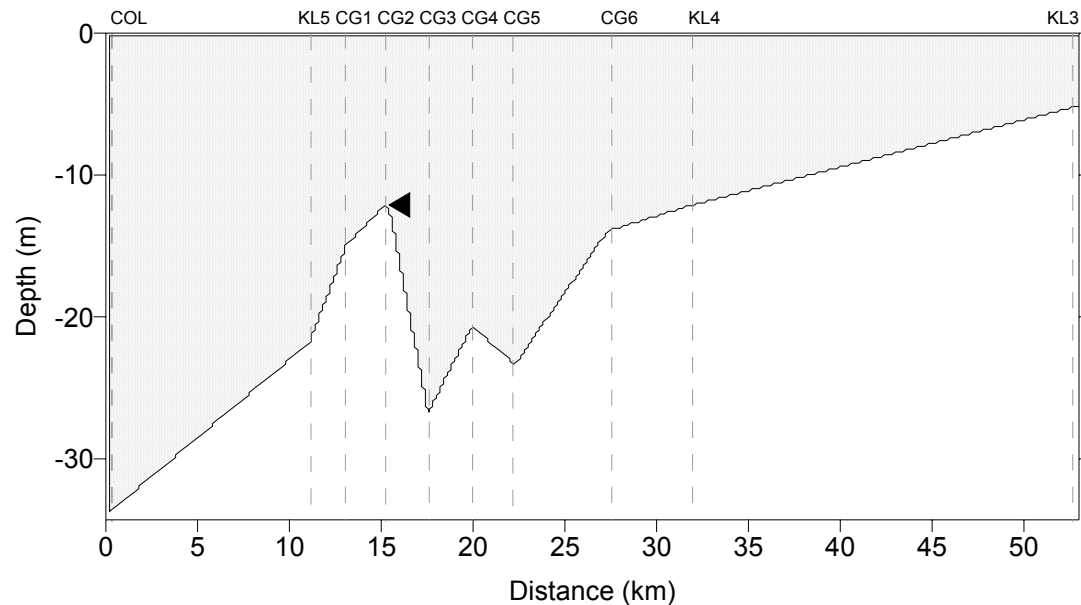


Figure 2.2 Vertical cross-section along the sampling stations, from the main lake station (COL) along the Rusinga Channel into the mid gulf station (KL3). The lower x-axis show the distance from COL and y-axis is the water depth. The vertical broken lines indicate the locations of the sampling stations as indicated in the upper x-axis. Note the fluctuating depth along the Rusinga Channel and 12 m sill (indicated by the arrow head), separating deeper channel areas (>20m) and the main lake (>34m).

The cross-section of the bathymetry along the study transect and the approximate distance between stations is shown in Figure 2.2. For the purpose of this study, the gulf is divided into two morphologically distinct zones namely the inner-gulf (KL3, KL4), which consists of the gulf area minus the channel and is hereinafter referred to as the gulf and the Rusinga Channel (KL5, CG1 to CG6), the narrow and deep area between the inner-gulf and the main lake (COL).

2.2.2 Field measurements

The study was carried out between March 2005 and March 2006 with field measurements done monthly during the study period. The Kenya Marine and Fisheries Research Institute (KMFRI) *RV Utafiti* was used during the study, except for a few occasions when it was not available and other available boats were used. Temperature, dissolved oxygen (DO), electrical conductance (EC) and pH profiles were measured using a Hydrolab

Sonde[®] multiprobe with a Surveyor 4a[®] data display. Calibration of the EC and pH probes was done each morning in the field against known standard solutions and the DO probe was calibrated using ambient air but was occasionally compared with Winkler's titration of dissolved oxygen. Profiles for turbidity in the water column were measured using a YSI probe, which had been calibrated in the laboratory using known standards and a Hach[®] bench turbidimeter. Underwater light climate and extinction was measured using a Li COR underwater quantum sensor and meter (Li-COR 1000), which measured photon flux density of PAR (400-700 nm). Light attenuation coefficient (k_d , m^{-1}) was taken as the slope of the regression of depth (z) on $\ln(I_z)$, where I_z is the down-welling PAR at depth z . Water transparency was estimated using a 25cm black and white Secchi disk. A hand held anemometer, Mini Environment Quality (Sper Scientific 850070), was used to measure wind speed, air humidity and air temperature and wind direction was estimated using a cloth flag on top of the boat and a navigation compass. StowAway Tidbit temperature loggers were occasionally deployed for short periods to measure temporal changes in water temperature at fixed depths in the water column with a logging time width of 30seconds.

2.2.3 Historical data acquisition

Historical meteorological data for Kisumu was obtained from the Ministry of Water and Irrigation, Kisumu office and that of the area near the Rusinga Channel was obtained from the International Centre for Insect Physiology and Ecology (ICIPE) weather station. Rivers' discharge data was obtained from the Ministry of Water and Irrigation, Kisumu office.

2.2.4 Calculations

The water fluxes in different segments along the study transect were estimated using a box model approach, initially developed and formalized as a standard protocol for an international research program called the Land Ocean Interactions in the Coastal Zone (LOICZ) and is described by Gordon et al (1996). The model protocol has been used to characterize water and salt exchanges in estuarine environments such as the Tomales Bay,

California (Smith and Hollibaugh, 1997) and San Francisco Bay (Smith and Hollibaugh, 2006). The different model segments are shown in Figure 2.1 and include the gulf area up to CG6 and 6 other segments along the channel, each including a sampling station. The morphometric details for the different segments are presented in Table 2.1. The delineation of boundaries for the segments along the channel was done in such a way as to include a sampling station and be approximately perpendicular to the hydrographic flow.

The fluxes calculated are the residual flow (V_R), which is the quantity of water flow to or from a particular segment that must occur to balance the water budget in the segment and the mixing flux (V_X) which represents the tidal-like short-term exchange of water and associated solutes between the study segment and the end member (the adjacent segment or the main lake). The water exchange (residence) time (τ) between different segments has also been calculated.

Table 2.1 Morphometric data for different segments (Fig. 2.1) used in the budget model. Surfer® software was used to estimate surface area, volume and mean depth from a bathymetric map (Silsbe, 2003).

| | Gulf | CG5 | CG4 | CG3 | CG2 | CG1 | KL5 |
|---------------------------------|--------|------|------|------|------|------|------|
| Surface Area (km ²) | 1333.1 | 24.8 | 11.4 | 21.9 | 21.0 | 12.4 | 4.6 |
| Volume (km ³) | 6.07 | 0.23 | 0.19 | 0.24 | 0.24 | 0.18 | 0.10 |
| Mean Depth (m) | 4.6 | 9.3 | 16.8 | 11.1 | 11.3 | 14.6 | 22.1 |

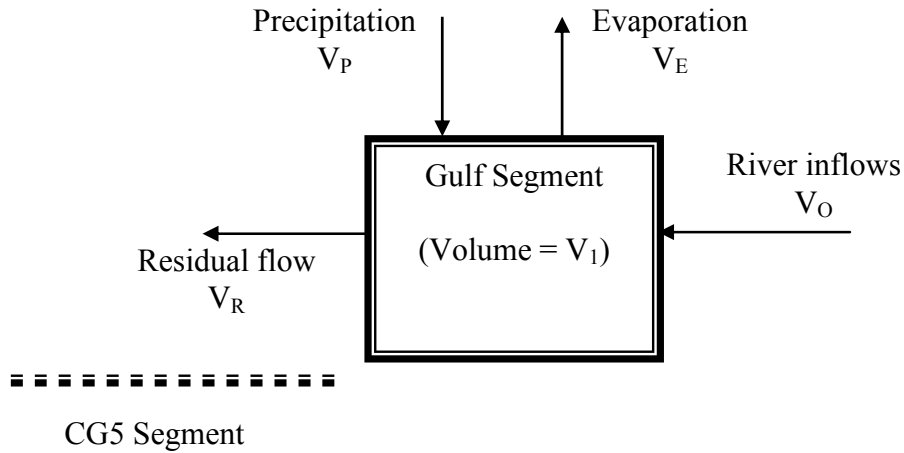


Figure 2.3 Conceptual model of water budget for the gulf segment (adapted from Gordon et al (1996)). Water flux variables (V_O , V_R , V_E and V_P) are in units of volume per unit time and the gulf volume (V_1) is in units of volume. V_O represents the rivers' discharge into the gulf. The arrows indicate the water flow associated with each process.

Figure 2.3 shows a conceptual water budget model for the gulf segment and the processes are related as follows (Gordon et al, 1996):

$$\frac{dV_1}{dt} = V_O + V_P + V_R + V_E \quad (1)$$

Where dV_1/dt is the time dependent change in gulf volume and V_O , V_P , V_E , and V_R represents the water flux terms associated with river inflows, direct precipitation, evaporation and residual flow respectively. The water flux from groundwater and urban runoff are considered insignificant compared to the river inflows and are therefore not included in the budget.

Assuming change in gulf volume to be negligible (i.e. steady state conditions; $dV_1/dt = 0$) then equation 1 can be rearranged to solve for the unknown flow, V_R (Eq. 2):

$$V_R = -V_O - V_P - V_E \quad (2)$$

The water level in the gulf and the channel has been observed to vary with a periodicity of about 6 to 12 hours (Romero et al, 2005) and therefore the assumption of the steady state conditions can be assumed to be valid over a 24 hour period or longer within a

season. The same budget model was applied on the other segments in the channel with the residual flow (V_R) of the preceding segment taken as the inflow (V_O) for the next segment (e.g. V_R for the gulf was V_O for CG5).

After calculating the V_R , the mixing flux (V_X) can be calculated using a conservative material as a tracer. In estuaries, salinity is used as a conservative tracer of the exchange of inflowing freshwater and the high saline oceanic water (Gordon et al, 1996). In the current study, salinity was not measured and therefore electrical conductivity (EC), which is a measure of total dissolved substances, was instead used as a surrogate for salinity in tracing the mixing fluxes along the channel. As will be discussed in the results section, a strong EC gradient between the gulf and the main lake was observed which makes it a suitable tracer of the exchange between the two ecosystems. An equation similar to equation 1 can therefore be written for the EC budget in the segment (Eq. 3):

$$\frac{V_1 dC_1}{dt} = V_O C_O + V_R C_R + V_X (C_1 - C_M) \quad (3)$$

Where C_1 , C_O , C_M and C_R represents the conductivity in the gulf segment, river inflows, end member, and the residual flow. C_R is taken as the conductivity at the boundary between the segment and the end member and is equal to $(C_1 + C_M)/2$.

Rearrangement of Eq. 3 for steady state conditions, where volume and conductivity in the channel are constant, gives an estimate of exchange flux, V_X (Eq. 4).

$$V_X = \frac{V_O C_O + V_R C_R}{C_1 - C_M} \quad (4)$$

From equations 2 and 4 the exchange time (or residence time) τ can be calculated (Smith and Hollibaugh, 2006):

$$\tau = \frac{V_1}{V_X + |V_R|} \quad (5)$$

The morphological details of the study segments are presented in Table 2.1 and in Table 2.2 the hydrological and meteorological data used in the water flux model are presented.

The buoyancy frequency $N = (g/\rho \, d\rho/dz)^{1/2}$, a measure of water column stability, was calculated as in Imberger and Peterson (1990): where ρ is density, g is gravity and z is the

depth. Density (ρ) at each depth was calculated from salinity (derived from conductivity) and temperature following the equation described by Chen and Millero (1977, 1986).

2.3 Results

2.3.1 Hydrology and meteorological conditions

The annual precipitation measured near Kisumu was higher than that measured at Mbita near the Rusinga Channel and similarly evaporation was higher in Kisumu compared to that measured at Mbita (Table 2.2). Precipitation from both locations had two peaks, a major peak in April and a minor peak in November and evaporation was lowest between May and August. The mean river discharge during the study period was $70.3 \text{ m}^3/\text{s}$ and followed the same seasonal trend as that of precipitation (Table 2.2).

Relative humidity ranged from 32.8 to 86.6% during the study period and was higher in the main lake (mean $63.3 \pm 17.3\%$), compared to the gulf and the channel, mean 55.1 ± 11.6 and $59.4 \pm 9.8\%$ respectively. Air temperature ranged from 20.9 to 33.0°C (mean $26.4 \pm 2.0^\circ\text{C}$) in the gulf, 23.4 to 32.6°C (mean $27.1 \pm 3.6^\circ\text{C}$) in the channel and 22.4 to 29.7°C (mean $26.2 \pm 2.7^\circ\text{C}$) in the main lake. Photosynthetic active radiation (PAR) measured between 11:00 hr and 14:00 hr over the study period ranged from 270 to $1874 \mu\text{E m}^{-2} \text{ s}^{-1}$ (mean $1409.5 \pm 323 \mu\text{E m}^{-2} \text{ s}^{-1}$) with low values measured during cloudy and overcast days and high values during cloudless days.

Table 2.2 Hydrological and meteorological data for Kisumu and Rusinga and river discharges into the gulf. The last column shows average discharge and total precipitation.

| | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec | Jan | Feb | Mar-06 | Av/Tot. |
|-------------------------------------|-----|-----|-----|-----|-----|-----|------|-----|-----|-----|-----|-----|--------|---------|
| River Discharge (m ³ /s) | 46 | 83 | 183 | 133 | 67 | 119 | 165 | 51 | 25 | 12 | 10 | 8 | 13 | 70 |
| Precipitation (mm) - Kisumu | 135 | 222 | 176 | 73 | 60 | 81 | 85 | 100 | 153 | 95 | 82 | 93 | 135 | 1490 |
| Precipitation (mm) - Rusinga | 143 | 130 | 305 | 105 | 20 | 113 | 137 | 57 | 30 | 0 | 87 | 105 | 150 | 1382 |
| Evaporation (mm) - Kisumu | 217 | 172 | 148 | 143 | 146 | 161 | 175 | 201 | 185 | 227 | 222 | 218 | 158 | 2373 |
| Evaporation (mm) - Rusinga | 178 | 148 | 142 | 133 | 146 | 156 | 164 | 169 | 160 | 168 | 173 | 163 | 178 | 2078 |

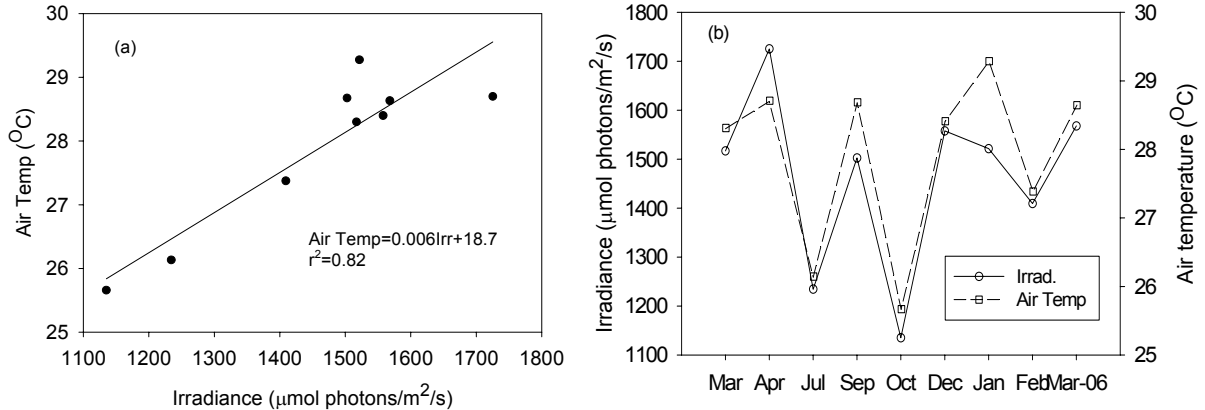


Figure 2.4 (a) dependence of air temperature on irradiance and (b) seasonal variation of surface light irradiance and air temperature. Temperature and irradiance values are monthly means of measurements taken between 1200 and 1400hr. Note June, August and November values are not included for both irradiance and air temperature due to lack of air temperature measurements

Surface irradiance and air temperature, measured between early and mid-afternoon, showed strong dependence (Fig. 2.4a) but values measured during morning and late afternoon hours showed no dependence. Both irradiance and air temperature showed seasonal variation with high values recorded in April and January and low values recorded in July and October (Fig. 2.4b).

2.3.2 Water column temperature

Water column temperature during the study period varied over the spatial scale among different stations and depths (Fig 2.5) but on average a defined pattern along the study transect was observed (Fig. 2.6). Average of all temperature profiles for depths $\leq 5\text{m}$ increased along the study transect from an average value of 25.64°C in KL3 to 25.81°C in KL4, then decreased to a lowest value of 25.63°C in CG4 and CG3 before increasing to a highest average value of 26.24°C in KL5 and then decreasing to 25.82°C in COL. Averages for the whole water column varied with the same spatial trend but were lower than averages for depths $\leq 5\text{m}$. Comparison between stations showed no significant difference (ANOVA; $P = 0.05$) between stations, except KL5 which was significantly warmer than the other stations (excluding neighboring CG1; Table 2.3).

Seasonal variation of water column temperature was observed for different zones and over the whole study area (Fig. 2.5). The lake was warmest between March and April and coolest between July and August. Between September and October, the column temperatures increased but cooler water persisted in the lower depths of the main lake. By December, warming had occurred in the whole water column of the main lake but in the channel and parts of the gulf cooling had occurred, with temperature decreasing from about 25.6 °C (in October) to 25.2 °C in the channel. Warming took place between January and March 2006, from a mean range of 25.44 to 25.62 °C to that of 25.98 to 26.38 °C. Interannual variability was observed between March 2005 and March 2006 with March 2005 having a higher temperature range of 26.20 to 26.55 °C compared to a range of 25.44 to 25.62 °C recorded in 2006.

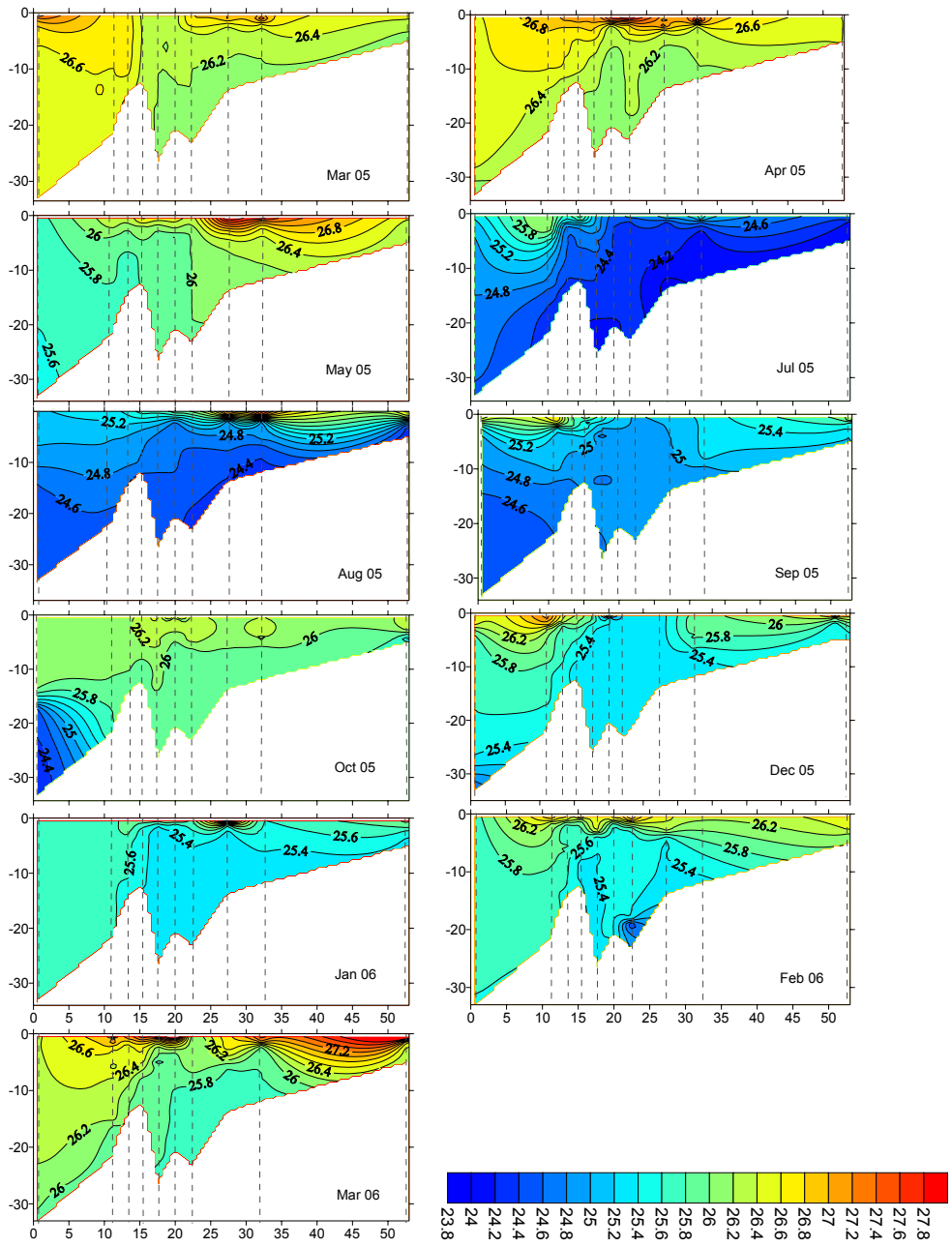


Figure 2.5 Spatial variation of temperature along the gulf-main lake transect for different dates between March 2005 and March 2006. The x-axis is the distance from the open lake station (0m), y-axis is the depth and the sampling stations are indicated with the vertical dotted lines and the order is as shown in Figure 2.1. The isotherm distance is 0.2 oC.

Table 2.3 Pair wise ANOVA comparison of temperature (left section) and dissolved oxygen (right section) between stations for profiles measured between March 2005 and March 2006. Only values for depths $\leq 5\text{m}$ were considered since the shallowest station (KL3) had depth of 5.5m. Values for top most 1m were not included in the analysis in order to minimize the influence of short-term meteorological variation due to time of the day the measurements were done. The highlighted P-values are for stations which are significantly different at 95% confidence.

| | KL3 | KL4 | CG6 | CG5 | CG4 | CG3 | CG2 | CG1 | KL5 | COL | | |
|-------------|-----|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|------------------|-------------|
| Temperature | KL3 | 1.00 | 0.50 | 1.00 | 1.00 | 0.04 | 0.00 | 1.00 | 0.00 | 0.00 | Dissolved oxygen | |
| | KL4 | 1.00 | 1.00 | 0.00 | 0.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | |
| | CG6 | 1.00 | 1.00 | 0.00 | 0.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | |
| | CG5 | 1.00 | 1.00 | 1.00 | 1.00 | 0.00 | 0.00 | 0.12 | 0.00 | 0.00 | | |
| | CG4 | 1.00 | 1.00 | 1.00 | 1.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.00 | | |
| | CG3 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | |
| | CG2 | 0.44 | 1.00 | 1.00 | 1.00 | 0.62 | 0.50 | 1.00 | 0.22 | 1.00 | | 1.00 |
| | CG1 | 0.09 | 1.00 | 1.00 | 1.00 | 0.16 | 0.12 | 1.00 | 1.00 | 0.03 | | 0.01 |
| | KL5 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.07 | 1.00 | | 1.00 |
| | COL | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.00 | | 1.00 |

The channel area between CG5 and CG3 seemed to be a cooler water region compared to other study areas and the structure of the isotherms indicated underflow of this cooler water into the deeper zones of the main lake and a compensational overflow of warmer surface water into the channel (Fig. 2.5). Down-welling and upwelling were frequently observed in the channel area between CG3 and CG5 (e.g. Mar, April, and October 2005, February 2006 and March 2006 in Fig. 2.5). The higher rate of vertical circulation in the channel (around CG3, CG4 and CG5) prevented formation of stable warm surface waters compared to other lake stations: whole water column mixing was frequently observed in this area even when strong diurnal stratification developed in adjacent areas (Fig. 2.5).

Water density estimated from temperature and salinity (derived from EC; Chen & Mellero, 1977 & 1986) varied spatially along the study transect following a trend approximately opposite that of the temperature (Fig. 2.6b). KL3 had highest average water density whereas KL5 had the lowest average value. The channel area between CG6 and CG3 had similar average density for averages taken over depths $\leq 5\text{m}$ but for averages taken over the whole water column CG3 had relatively higher average value compared to the rest of the

channel and the main lake. In contrast to the temperature, which decreased with depth (Fig. 2.6a), water density increased with depth.

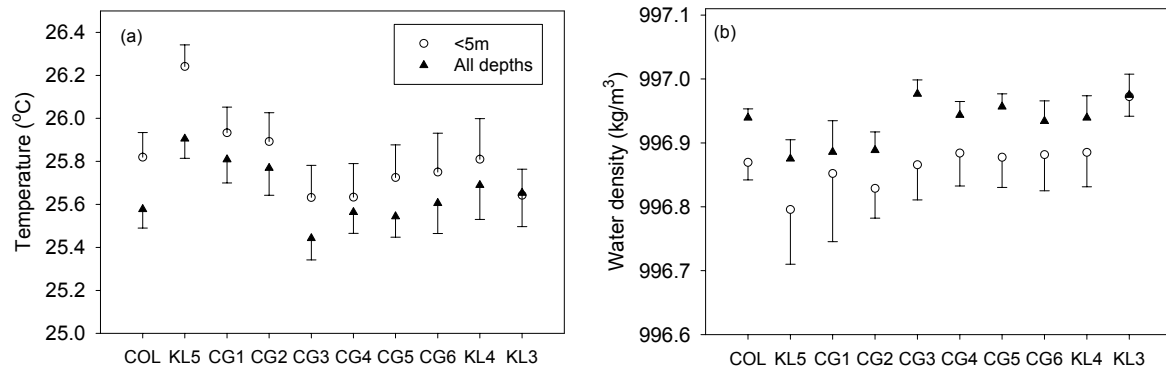


Figure 2.6 Spatial variation in (a) water column temperature and (b) water density averaged over the whole column and ≤ 5 m depths for profiles taken between March 2005 and March 2006. Values for top most 1m were omitted in order to minimize the influence of short-term meteorological variation due to time of the day the measurements were done. The errors bars are the 95% confidence intervals.

2.3.3 Thermal stratification and mixing regimes

Strong diurnal stratification (Brunt Vaisala Frequency N between 26 and 60 cph) was observed between late morning and mid afternoon hours during periods of high solar insolation and low winds. Increased wind action and reduced insolation during late afternoon and early evening lead to breakdown of stratification and in the shallow gulf areas (<10m deep) whole water column mixing occurred by early morning. 24-hr deployment of thermistors (6 in total, deployed at different depths) at KL3 (depth 5.5 m) showed development of thermal stratification after 1100 h and total mixing of the water column occurring by 1800 h. In the deeper Rusinga Channel, diurnal stratification and mixing was observed, but mixing may be attributed to both wind action and upwelling and intrusion processes, which were observed to take place in this dynamic zone (Fig. 2.5). Thermistors deployed at CG1 (depth 14m) showed development of strong thermal stratification by 1300 h, onset of mixing at 1500 h and total water column mixing at 0300 h.

In the main lake, seasonal thermal stratification was observed to take place between March and April and between September and December (Fig. 2.7a) at COL (maximum depth 34m). Lack of stratification in January and February at COL maybe observed while deeper waters of the larger Lake Victoria (maximum depth 70m) are still stratified at depths >35m (Hecky et al. 1994). The strongest stratification was observed in October (N, 42 cph) with a thermocline at 15m and a temperature difference between epilimnion and hypolimnion of 1.83 °C. In November, two thermoclines were observed, at 15 m and 20 m and in December deeper mixing was observed with single thermocline at 30m. Mixing of the whole water column at COL took place between January and February but stratification started to develop in March 2006, with a thermocline at 22m. Differences between years were observed, with whole water column mixing observed in March 2005 (N, 0 cph) whereas in March 2006 slight thermal stratification was observed (N; 28.9 cph).

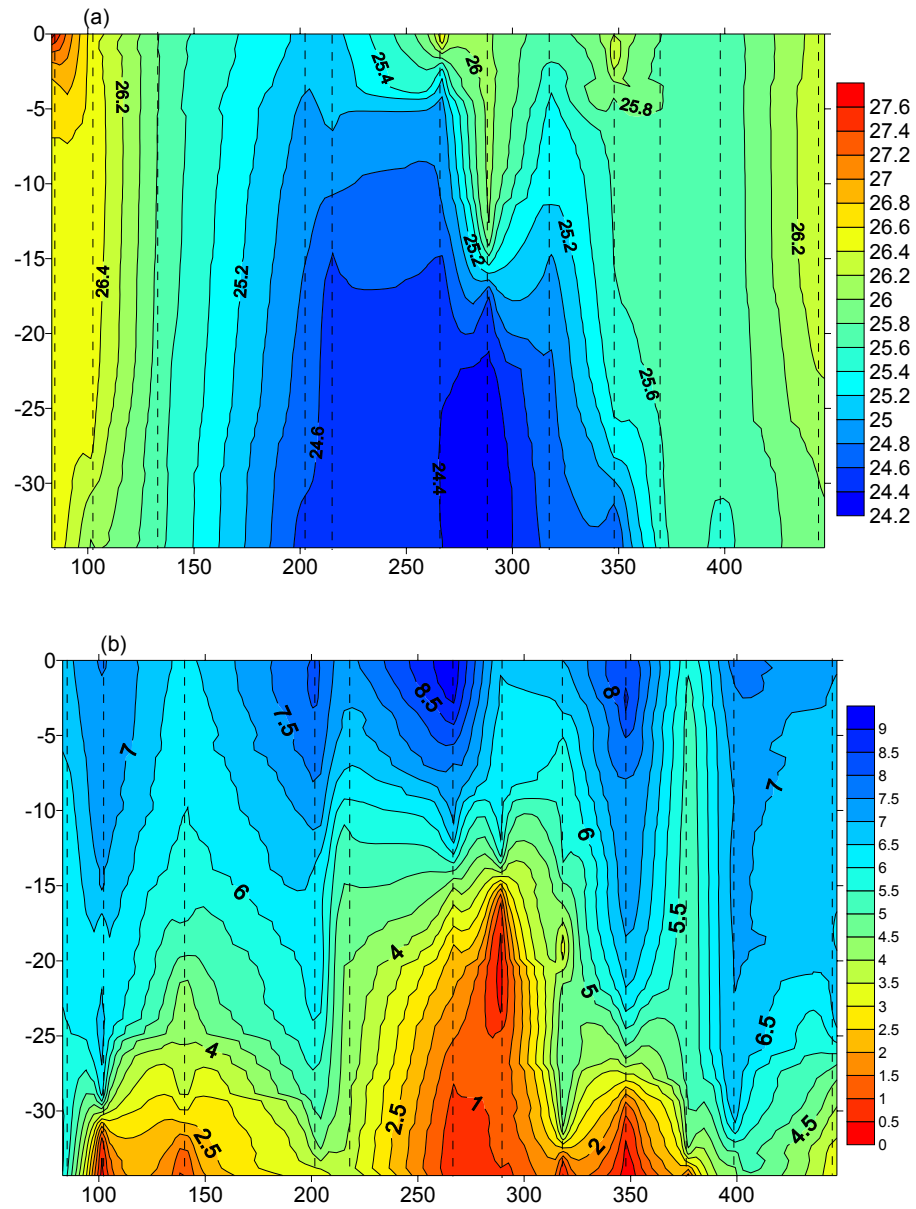


Figure 2.7 Temporal variation of temperature (a), and (b) dissolved oxygen in the open lake station (COL) for the period between 25th March 2005 and 22nd March 2006. The x-axis is the Julian days and y-axis is water column depth. The vertical broken lines fall on the dates the profiles were taken (Mar 25, Apr 11, May 20, Jul 22, Aug 12, Sep 23, Oct 15, Nov 15, Dec 15 2005 and Jan 13, Feb 2, Mar 22 2006)

2.3.4 Dissolved Oxygen (DO)

Dissolved oxygen (DO) concentration ranged from 0.1 to 10 mg/L during the study period and showed spatial and temporal variation between stations and column depths (Fig. 2.8 & Fig. 2.9). The shallow gulf zone was well oxygenated, with concentrations always above 5 mg/L, but as the depth increased towards the Rusinga Channel lower concentrations were observed. The area between CG3 and CG5 had significantly lower DO concentration (ANOVA; $P < 0.05$) compared to the other study zones (Table 2.1), although concentration was always above 3.5 mg/L even in the lower depths. In the main lake DO concentration varied seasonally and with depth and, during strong stratification, anoxic conditions were occasionally observed below the thermocline (e.g. in October DO concentrations < 1 mg/L were observed at 18m; Fig. 2.7b). Flow of low oxygen water from the main lake into the Rusinga channel was observed (e.g., August, September and October; Fig. 2.9), although the 12m 'sill' near CG2 (Fig. 2.2) prevented the inflow of anoxic water, which occurred below 18m depth in September and October 2005, into the channel. Intrusion of anoxic water was observed to take place below the metalimnion (about 20m) during strong stratification in October (Figs. 2.7b and 9). Deep water column mixing resulted in distribution of dissolved oxygen to the deeper depths in the main lake as was observed in March 2005 and January and February 2006 (Fig. 2.7b).

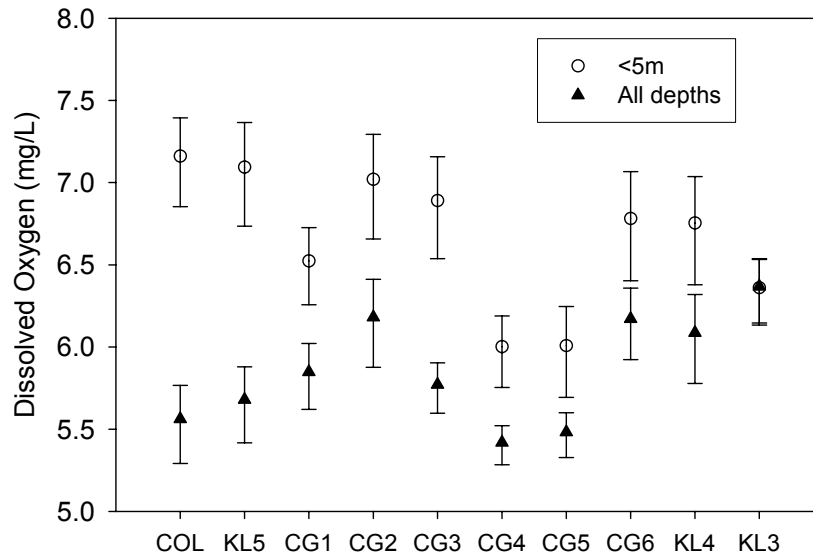


Figure 2.8 Spatial variation in dissolved oxygen (DO) averaged over the whole column and depths ≤ 5 m. The profiles were taken monthly between March 2005 and March 2006 excluding June and November 2005. The error bars are the 95% confidence intervals.

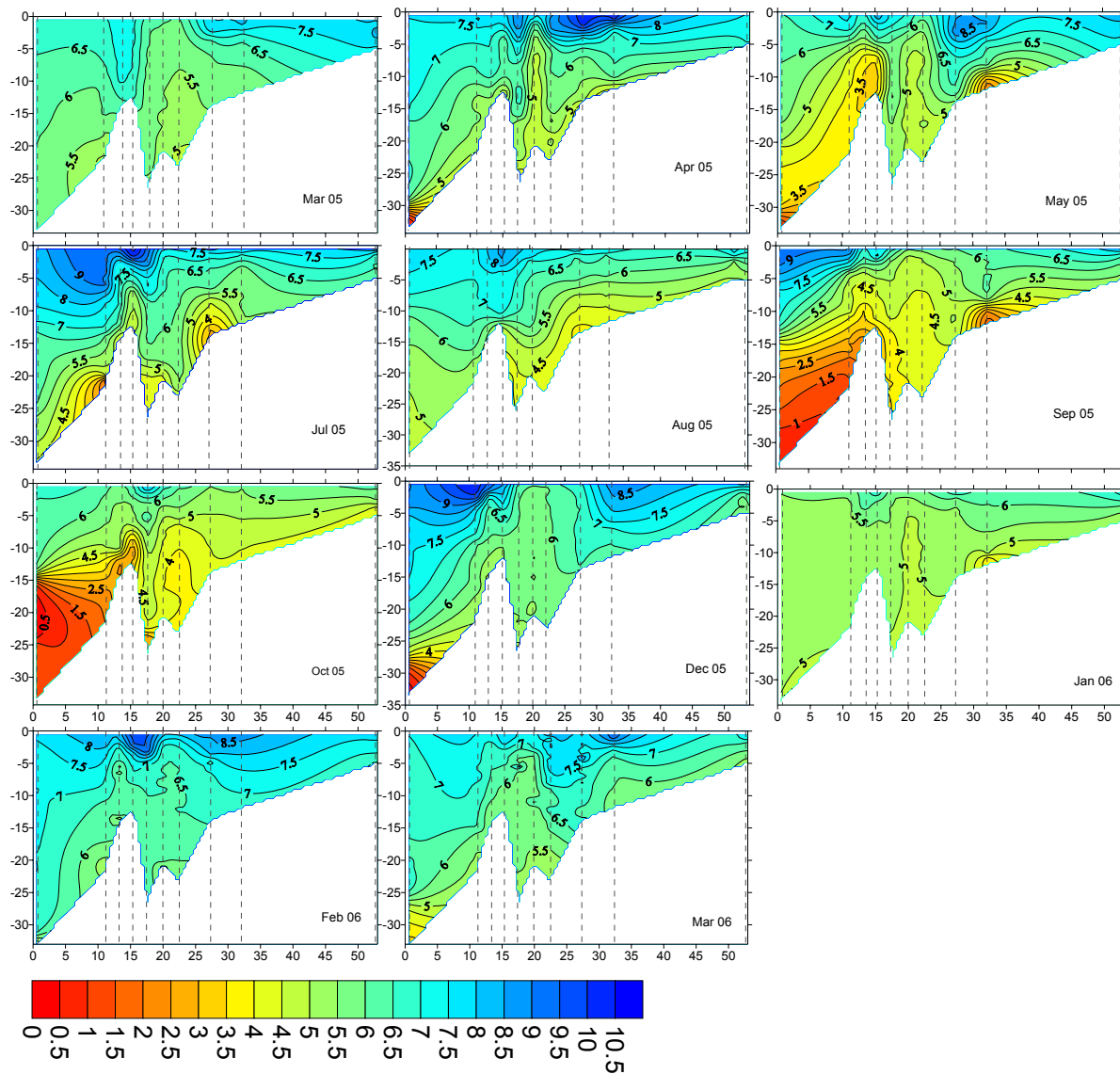


Figure 2.9 Spatial variation of dissolved oxygen (DO) along the gulf-main lake transect for different dates between March 2005 and March 2006. The x axis is the distance from the open lake station (0m), y-axis is the depth. The vertical dotted lines indicate location of the sampling stations and the order is as shown in Figure 2.1. The isopleth distance is 0.5 mg/L

2.3.5 pH and alkalinity

pH values in the water column ranged from 8.24 ± 0.72 to 8.83 ± 0.50 and varied with a defined spatial trend along the study transect (Fig. 2.10). Average values increased between KL3 and CG6 and then decreased to minimum value in CG5 and then followed an increasing trend towards the main lake. pH decreased with depth, although maximum values were normally observed slightly below the surface. Statistical comparison between stations showed no significant difference between most stations, except CG5 which had significantly lower pH (ANOVA; $P < 0.05$) compared to the other stations (Table 2.4). Alkalinity decreased consistently along the study transect, from 1.35 meq/L in KL4 to 0.76 meq/L in the main lake (Fig. 2.10).

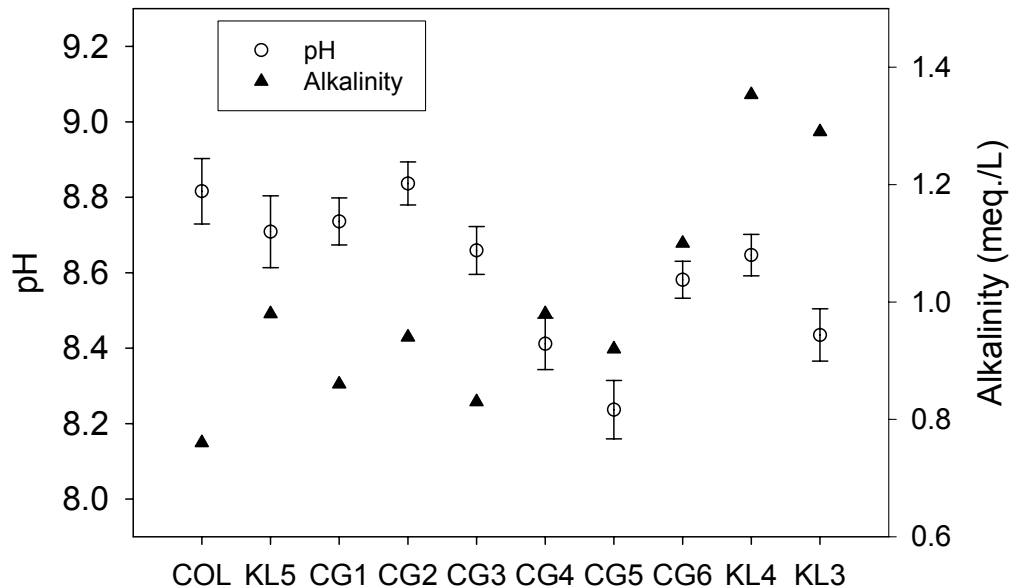


Figure 2.10 Variation of water column pH and alkalinity along the gulf-main-lake transect. pH values are averages of measurements taken between March 2005 and March 2006 for depth $< 5\text{m}$ and alkalinity values are for surface samples collected in October and December 2005. The pH error bars are the standard errors.

Table 2.4 Pair wise ANOVA comparison of electrical conductivity (EC; left section) and pH (right section) between stations for profiles measured between March 2005 and March 2006. Only values for depths $\leq 5\text{m}$ were considered since the shallowest station (KL3) had depth of 5.5m. The highlighted P-values are for stations which are significantly different at 95% confidence.

| | KL3 | KL4 | CG6 | CG5 | CG4 | CG3 | CG2 | CG1 | KL5 | COL | |
|----|-----|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|----|
| EC | KL3 | 1.00 | 1.00 | 1.00 | 1.00 | 0.87 | 0.00 | 0.08 | 0.14 | 0.00 | pH |
| | KL4 | 0.00 | 1.00 | 0.01 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | |
| | CG6 | 0.00 | 0.00 | 0.05 | 1.00 | 1.00 | 0.80 | 1.00 | 1.00 | 1.00 | |
| | CG5 | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | |
| | CG4 | 0.00 | 0.00 | 0.00 | 0.00 | 0.82 | 0.00 | 0.09 | 0.16 | 0.01 | |
| | CG3 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 1.00 | 1.00 | 1.00 | |
| | CG2 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 1.00 | 1.00 | |
| | CG1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 1.00 | |
| | KL5 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | |
| | COL | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | |

2.3.6 Electrical Conductivity (EC)

Electrical conductivity (EC) was high in the gulf ($150\text{-}180 \mu\text{S cm}^{-1}$) and decreased along the Rusinga Channel towards the main lake, where it ranged from 95 to $105 \mu\text{S cm}^{-1}$ (Fig. 2.11 and Fig. 2.12). Vertical variation of EC was occasionally observed in the channel and main lake stations (Fig 2.12). Comparison between stations showed that there was significant difference (ANOVA; $P < 0.05$) between all the stations (Table 2.4) congruent with the observed decreasing trend along the study transect. A strong EC gradient was observed along the Rusinga Channel, with EC decreasing from 141 ± 6.5 to $112 \pm 7.6 \mu\text{S cm}^{-1}$ over a distance of 11 km, between CG5 and KL5. The gradient followed a regression line ($r^2 = 0.98$) with conductivity, $C = 2.3d + 84.4$ (Fig. 2.11b), where d is distance from COL. The negative intercept indicates that after KL5 the gradient is discontinued and the main lake environment starts to dominate. The gradient is traced by the approximately vertical isopleths in Fig. 2.12. Towards the main lake the isopleths are distorted but in a defined pattern indicating patterns of the exchange between the low conductivity main lake water and the relatively high conductivity water from the gulf. The pattern of the isopleths shows evidence of outflow and underflow (April, July and August), upwelling and downwelling (May, Sep and October)

processes between the channel and the main lake. During the strong stratification that was observed in October and September in the main lake, flow from the channel into the main seem to be more pronounced as evidenced by the relatively high EC above the thermocline in COL (compare Fig. 2.5 and Fig. 2.12). Conductivity had a strong relationship with alkalinity ($r^2=0.76$, 2.11c).

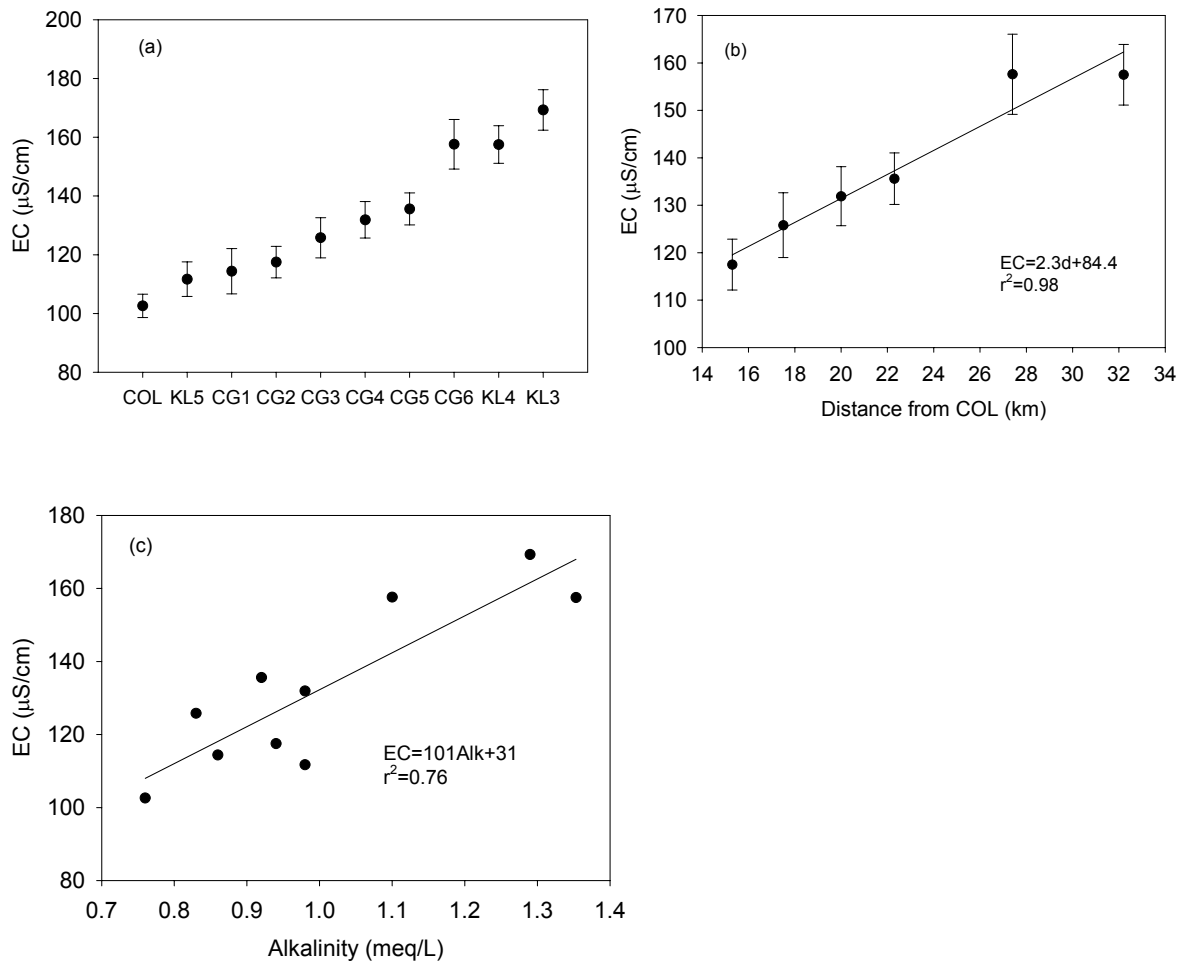


Figure 2.11 Spatial variations in Electrical conductivity, EC (a) and linear relationship between EC and distance from COL for channel stations KL5 to CG5 (b) and between EC and alkalinity measured in all the stations (c). The EC values are the mean of profiles taken between March 2005 and March 2006 and the error bars are the standard deviation.

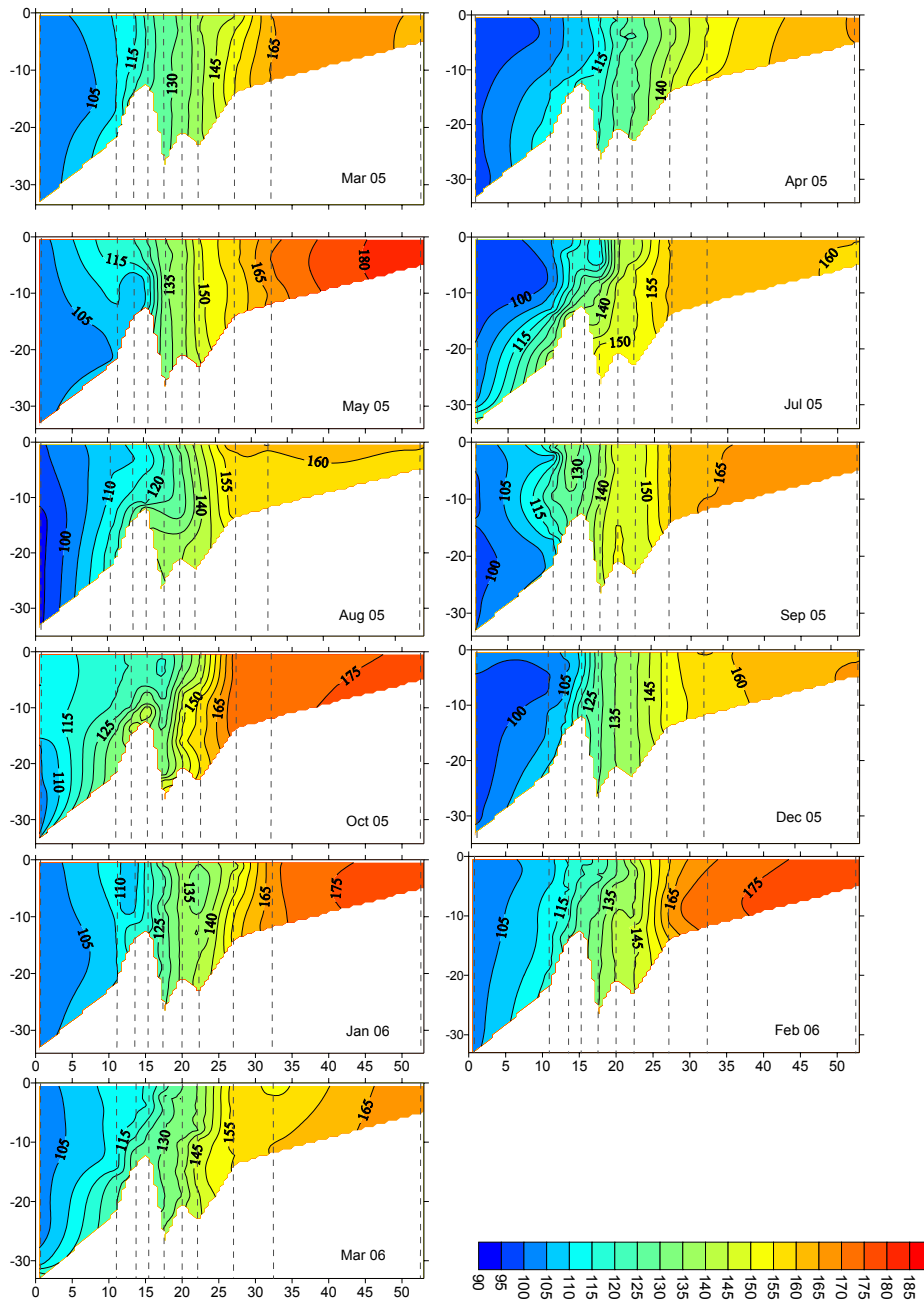


Figure 2.12 Spatial variation of electrical conductivity (EC) along the gulf-main lake transect for different dates between March 2005 and March 2006. The x axis is the distance from the open lake station (0m), y-axis is the depth and the sampling stations are indicated with the vertical dotted lines and the order is as shown in Figure 2.1. The isopleth distance is 5 $\mu\text{S}/\text{cm}$

2.3.7 Turbidity and underwater light climate

Turbidity decreased along the study transect from a mean value of 15.8 ± 2.8 NTU in KL3 to a mean value of 2.8 ± 1.2 NTU in the main lake station, COL (Fig 2.13a). The high turbidity in the gulf is associated with fluvial input and resuspension of suspended particulate matter from river tributaries to the southeast of the gulf (Fig. 2.1), although occasionally heavy algal blooms were observed and contributed to the turbidity. During the rainy season, a turbidity plume (>70 NTU) develops in the eastern part of the gulf, which subsequently flows westward to the channel where it undergoes dilution through dynamic mixing with the low turbidity main lake water. This movement of turbidity from eastern gulf area to the Rusinga Channel can take several weeks and usually follows a characteristic anti-clockwise pattern along the eastern gulf end and then along the northern part of the inner gulf (Fig. 2.14). Turbidity in the Rusinga Channel was also locally influenced by the highly turbid and shallow Homa Bay and by direct surface runoff from the land surrounding the channel.

Underwater light climate varied spatially along the study area with light extinction coefficient (k_d) decreasing along the gulf-main-lake transect from 2.5 ± 0.7 (m^{-1}) in KL3 to 0.60 ± 0.16 (m^{-1}) in COL (Fig. 2.13a). Secchi depth (a measure of water transparency) showed an opposite trend to that of turbidity and light extinction coefficient, and increased along the gulf-main-lake transect from 0.65 ± 0.23 m (KL3) to 2.1 ± 0.68 m (COL). Both light extinction coefficient (k_d) and secchi depth were strongly correlated with turbidity (Fig. 2.13b). The ratio between particulate carbon (PC) and total suspended sediments (TSS) in the water column followed an increasing trend from KL3 to COL (Fig. 2.15), providing evidence for the settling of inorganic sediment along the east-west transect and perhaps increasing production of organic matter by primary production..

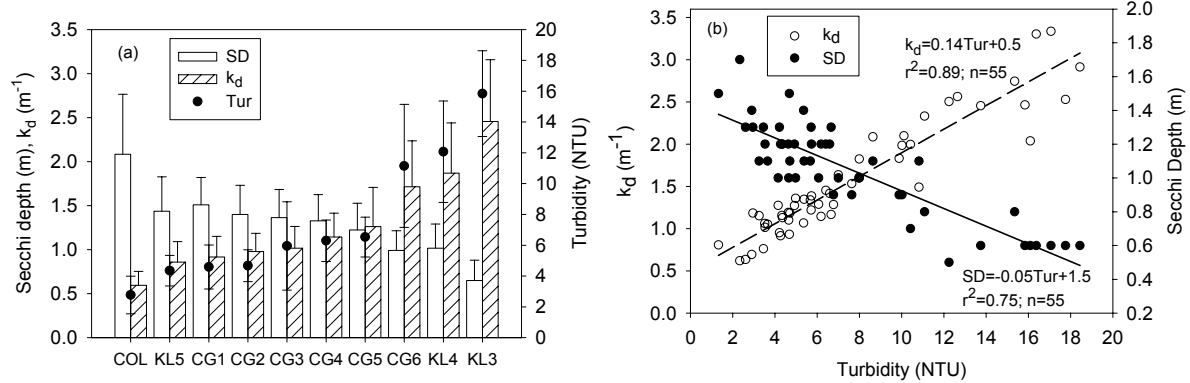


Figure 2.13 (a) Spatial variation in Secchi depth (SD), light extinction coefficient (k_d) and turbidity along the transect between Nyanza Gulf and main lake and (b) relationship between turbidity and light extinction coefficient (k_d) and water transparency (Secchi) for values measured monthly between March 2005 and March 2006 (Secchi and k_d) and between September 2005 and March 2006 (turbidity). The error bars in (a) are standard deviations



Figure 2.14 Satellite image of Nyanza Gulf, showing turbidity flumes in the eastern area and in Homa Bay. The image was taken on 8th June 2005 from Modis

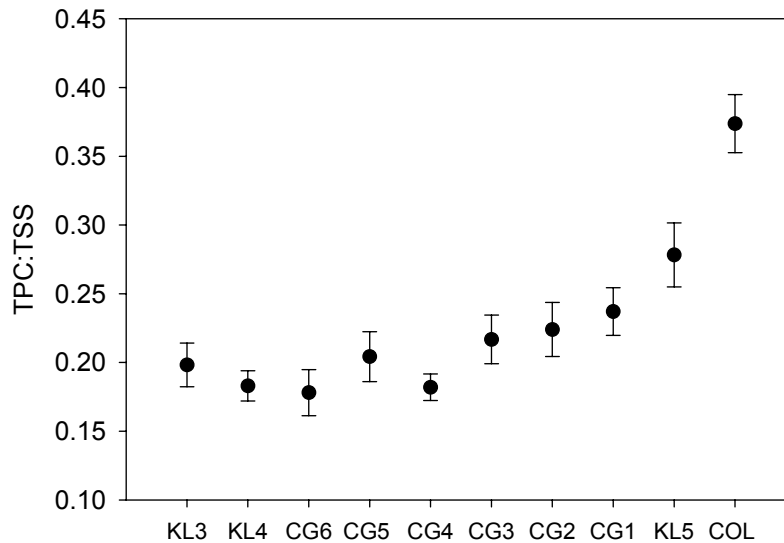


Figure 2.15 Spatial variation of the ratio between particulate carbon (TPC) and total suspended solids (TSS) along the gulf-main-lake transect for surface samples (approximately Secchi depth). Error bars are standard errors.

2.3.8 Horizontal Water flux and mixing along the Rusinga Channel

Dynamic exchange between and within different lake zones was observed. Development of a density gradient between the relatively cool channel and the warm main lake led to underflow of the channel water into the deeper depths of the main lake in several months (Fig. 2.5; April, July, August and December 2005 and March 2006). The dynamic exchange between the channel and the main lake is more evident in Figure 2.12 as EC, which is a conservative tracer, seems to resolve more clearly the complex dynamics of the exchange. In the channel area downwelling and upwelling were common (Fig. 2.5; March, April, October and February and Fig. 2.12; May, July and September) and maybe responsible for whole water column mixing which was frequently observed in the area between CG5 and CG3, relative to other study zones (Fig. 2.5). The density gradient between the gulf (KL3) and the channel (Fig. 2.6b) may have played a role in the flow of cooler and high EC water from the gulf into the channel area around CG6 (e.g. March, July and December 2005 and January 2006; Fig. 2.5).

The horizontal exchange of water across the channel was characterized and calculated as the residual flow, V_R and the mixing flux, V_X (Fig. 2.16; Table 2.5). The average residual flow (V_R) over the study period was towards the main lake and was the same (about $35 \text{ m}^3/\text{s}$) for all the study segments (Fig. 2.16). However, between October 2005 and March 2006 relatively low river discharges lead to net residual flow from the main lake into the gulf (Table 2.5). The mixing flux (V_X) was substantially higher (>20 fold) than V_R and varied spatially along the channel but with no defined trend. The gulf had the lowest V_X value of $747 \text{ m}^3/\text{s}$ whereas the highest value of $1890 \text{ m}^3/\text{s}$ was observed in CG4. The total water exchange time (τ) for the gulf segment was 1981 days whereas the total τ for the channel was 171 days (Table 2.5). However, the average τ values for both the gulf and the channel were heavily weighted by the relatively high values for March and October 2005 and March 2006 when precipitation and river discharges were low (Tables 2.2 & 2.5).

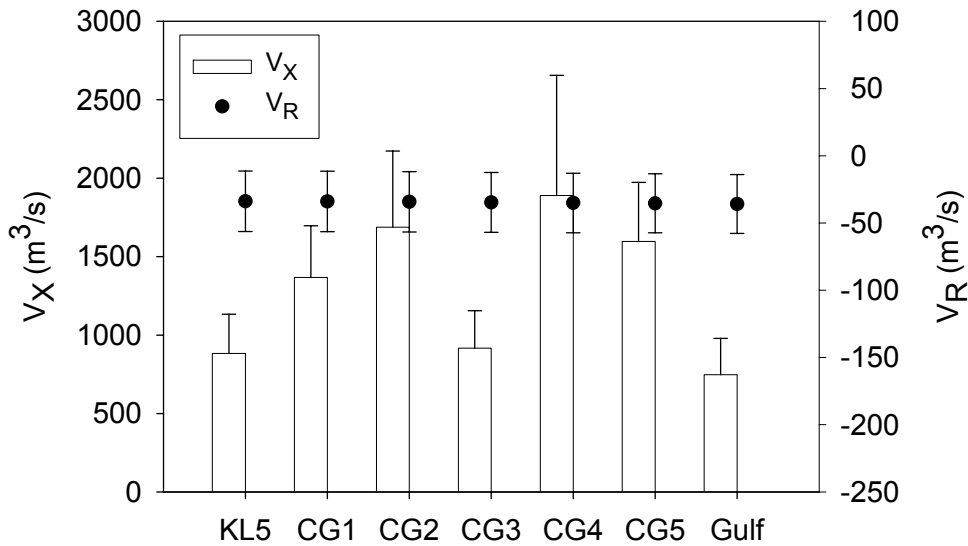


Figure 2.16 Averages and standard errors of water residual and mixing fluxes (V_R , V_X) between different segments in the gulf and along the channel for the period between March 2005 and March 2006. The segments are as shown in Figure 2.1.

Table 2.5 Monthly averages of residual water flow (V_R) and mixing flux (V_X), residence time (τ) for the gulf and the channel. The channel V_R and V_X is that of the KL5 segment and channel (τ) is the sum of values for all the channel segments.

| | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec | Jan | Feb | Mar-06 | Average |
|-----------------------------------|------|------|------|------|-----|------|------|------|------|------|------|-----|--------|---------|
| V_R (m ³ /s)-Gulf | 5 | 109 | 197 | 97 | 24 | 79 | 118 | 1 | 8 | 4 | 9 | 1 | -2 | -36 |
| V_R (m ³ /s)-Channel | -4 | -108 | -203 | -96 | -20 | -78 | -117 | 3 | -3 | 60 | 62 | 64 | -1 | -34 |
| V_X (m ³ /s)-Gulf | 51 | 1121 | 3020 | 1220 | 286 | 1082 | 1321 | 5 | 47 | 535 | 588 | 417 | 16 | 747 |
| V_X (m ³ /s)-Channel | 38 | 2069 | 2898 | 1218 | 189 | 459 | 976 | 57 | 39 | 1375 | 1439 | 720 | 11 | 884 |
| τ (days)-Gulf | 1524 | 70 | 25 | 63 | 269 | 70 | 59 | 6539 | 1826 | 120 | 109 | 148 | 4937 | 1981 |
| τ (days)-Channel | 178 | 6 | 5 | 8 | 39 | 12 | 7 | 1181 | 176 | 13 | 12 | 10 | 576 | 171 |

2.4 Discussion

The sampled transect, from the eastern Nyanza Gulf to the main lake, covers a distance of over 52 km with varying bottom bathymetry consisting of the wide and shallow gulf area, the deep and narrow channel area and the deep and open waters of the main lake (Fig. 2.1), which together with the varying meteorological conditions along the transect (Asnani, 1993) acts to create spatial thermal and physical variability. Average water temperature over the study period varied spatially between different areas (Fig. 2.6), an indication of varying conditions and influencing factors along the study transect. Lake morphometry plays an important role in determining the water column thermal status and structure through its influence on solar heat capture and storage and therefore the net water column temperature (Wetzel, 2001). During day time, the shallow lake zones capture and store less heat energy and therefore cool faster during the night time compared to the deeper zones, which result in differential heating and differential cooling in a lake with varying morphometry. Monismith et al (1990) observed large horizontal temperature gradients between a sidearm and a reservoir in Western Australia and attributed it to differential daytime heating and nighttime cooling which they associated with the difference in water depth between the shallow sidearm and the deeper lake. Morphometry also influences water column mixing and stability and therefore influences the oxygen condition. However, together with morphometry, other factors including wind stress, turbidity and river inflows may have contributed to the observed spatial variability of physicochemical conditions.

2.4.1 Differential heating and cooling and spatial variability of temperature

Spatial variability in wind stress results in differential heating and differential deepening in a water body and therefore influences the water column structure and physical dynamics (Imberger and Parker, 1985). The varied morphometry and shoreline topography over the study area resulted in variability of wind stress and therefore led to differential mixing and differential cooling and heating of the water column. The channel area between CG2 and KL5 is surrounded by the Ulambwe Hills to the south and the hilly Rusinga Island

to the west, which together with the elevated land mass to the north shelters this area from prevailing wind conditions, and therefore reduces evaporative cooling. This area (CG2 to KL5) was relatively warmer than the rest of the study area (Fig. 2.6), and KL5 had significantly higher water temperature (ANOVA; $P < 0.05$) compared to the other stations (Table 2.3). In contrast, the channel area between CG3 and CG5 had the lowest average temperature compared to other study areas and mixing of the whole water column was normally observed (Fig. 2.5 and Fig. 2.12). This area is relatively more exposed and strong winds were observed to occur between early and late afternoon and in the morning hours after midnight, therefore resulting in enhanced differential mixing and evaporative cooling. MacIntyre et al (2002), working in Pilkington Bay, northern Lake Victoria, found that surface heat losses contributed to more than 70% of the energy for the surface layer deepening 82% of the time. Flow of cooler water from shallow nearshore areas, with enhanced nocturnal cooling, into this deep channel area (CG3-CG5) could also be occurring and contributing to the observed relatively cooler water pool. McIntyre observed similar differential cooling in the shallow areas of Pilkington bay and associated underflow of cooler water into the deeper parts of the bay, leading to downwelling and upwelling.

In the inner-gulf area (KL3), greater wind fetch allows for increased turbulence and mixing, which keep this wide and shallow area well mixed and oxygenated, possibly enhancing water turbidity through increased resuspension of bottom sediment while also increasing evaporative cooling. The river inflows, to the southeast of the gulf, may also influence the water temperature depending on the average temperature of the inflows relative to that of the lake. River Sondu, which contributes over 60 % of riverine inflow to the gulf (LVEMP, 2001), normally has water temperature lower than that of the rest of the lake as it flows down from higher elevations on the escarpment to the south and it is therefore likely that the observed relatively low average water column temperature in KL3 (Fig. 2.6) may also be due to the influence of river inflows.

Spatial variability of turbidity and suspended particulate matter result in differential heating of the water column, because suspended matter absorbs solar energy more than water and in contrast increased turbidity reduces the penetration of solar energy in the water

column and also increases albedo (Kling 1988; MacIntyre and Melack, 1995). The observed turbidity gradient from the eastern gulf area near the river inflows towards the main lake (Fig. 2.13a) may have contributed to the observed spatial variability of water column temperature along the study transect including the observed relatively low temperature in KL3 (e.g., Coates and Patterson, 1994).

2.4.2 Water exchange and mixing across the Rusinga Channel

Spatial temperature differences along the study transect resulted in the development of density gradients (Fig. 2.6b), which can lead to dynamic density-driven exchange of water between different zones along the study area. The cold water from the channel area between CG3 and CG5 flowed under the warmer water in the area between CG1 and KL5 into the lower depths of the main lake and compensational flow of warm surface water into the gulf took place (Fig. 2.5 & Fig. 2.12). MacIntyre et al (2002) observed development of density fronts on a spatial scale of kms within the Pilkington Bay due to differential heating, differential cooling and wind mixing and Imberger and Parker (1985) observed similar density flows in a lake exposed to variable wind field.

In addition to density driven currents, the water exchange across the Rusinga channel is also driven by wind generated currents related to reversal of lake-land winds over a diel cycle (Worthington, 1930) and by pressure gradients due to water level changes. Daily water level changes of 5 to 10 cm and water current speeds of 20 to 40 cm/s in and out of the channel, with a periodicity of 12 to 24 hrs, were observed near station CG5 in May and August 2005 (Romero et al 2005). This daily flow in and out of the gulf resulted in relatively high mixing component (V_X) compared to the residual flow (V_R) across the Rusinga channel (Fig. 2.16; Table 2.5), leading to the development of a well-defined physicochemical gradient along the Rusinga channel (Fig. 2.11). Newell (1962) observed similar water flow in the Buvuma channel, northern Lake Victoria, with currents of between 6 and 24 cm/s, which he associated with accumulation of water northward in response to southerly winds.

The downwelling and upwelling, which was observed in the channel (Fig. 2.5 & Fig. 2.12) can be associated with wind action and may have contributed to the whole water

column mixing frequently observed in the channel area between CG3 and CG5 (Fig. 2.5) and associated resuspension and entrainment of bottom sediment. The area around CG5 has been observed to have no fine sediment but only bare rock and gravel in the bottom (Personal observation), an indication that vertical mixing and horizontal transport processes play important role in sorting and transport of sediment and associated nutrients in the lake (Chapter 4). According to MacIntyre and Melack (1995) resuspension of living and non-living particles from the sediments can reseed phytoplankton to the upper layers and alter rates of nutrient supply or scavenging of pollutants. The observed gradient of different phosphorus fraction in the sediment between the Nyanza Gulf and the main Lake has been attributed to sorting and transport of lighter sediment during dynamic flow of water between the gulf and the main lake (see Chapter 3).

2.4.3 Conductivity and pH gradients

Conductivity was relatively high in the gulf compared to the channel and the main lake (Fig. 2.11 and Fig. 2.12). Electrical conductance (EC) of water is a surrogate for a measure of dissolved ionic content and a proxy indicator of total dissolved solids (TDS). TDS concentration in the lake can be influenced by the inflowing rivers, evaporation and precipitation and biogeochemical processes in the sediment and water column (Lesack & Melack, 1991). The river tributaries had on average lower EC ($139 \mu\text{S}/\text{cm}$) compared to the gulf ($150\text{-}180 \mu\text{S}/\text{cm}$) and therefore riverine input cannot alone account for the observed high EC in the gulf. The calculated gulf residual outflow into the main lake was about $36 \text{ m}^3/\text{s}$ (Fig. 2.16), implying that approximately half of the water input from the tributaries ($70 \text{ m}^3/\text{s}$; Table 2.2) was lost through evaporation and therefore leading to the concentration of solutes in the water column. The observed daily mixing in the gulf may also contribute to the TDS by enhancing the release of dissolved solutes from the sediments.

The channel behaved like an estuarine tidal area but in the latter the density gradients are associated with salinity (Cloern et al 1989) whereas in the Rusinga Channel density gradients were associated with temperature (Fig. 2.6). The conductivity range in the lake is too low to create any noticeable water density differences but as a conservative tracer it was

useful in characterizing the structure of exchange and mixing between the channel and the main lake (Fig. 2.16).

pH values over the study period were moderately alkaline, ranging from 8.24 ± 0.72 to 8.83 ± 0.50 and varied over the study area and across the water column (Figure 2.10). In highly productive eutrophic systems like Lake Victoria, pH is normally influenced by algal primary production, when withdrawal of CO_2 and HCO_3^- results in a rise in pH. pH changes of up to one unit can occur in waters with high algal biomass ($>30 \mu\text{g Chl/L}$) and low to moderate alkalinity such as Lake Victoria (Kalff, 2002). The observed spatial variation of pH in the study area may be related to differences in algal biomass along the study transect, which has been observed to vary along the transect (Gikuma-Njuru et al, 2005) and the observed low pH in the lower depths can be associated with metabolic processes in the lower water column and in the sediments (e.g. Davis, 1974; Lampert & Summer, 1997). This hypothesis is reinforced by the lower pH in the physically active channel area between CG3 and CG5 associated with the mineralization of resuspended organic matter, which also resulted in relatively low oxygen conditions (Fig. 2.8 & Figure 2.9). pH can play an important role in phosphorus recycling in water bodies. Increase of pH in water in contact with sediment decreases the P-binding capacity of iron and aluminum compounds through ligand exchange reactions in which hydroxide ions replace orthophosphate (Bostrom et al. 1982; Jensen & Andersen, 1992; Kalff, 2002). James and Barko (1991) observed a linear increase of phosphorus release from sediment with pH. In Lake Victoria, the role of pH in phosphorus biogeochemistry is currently unknown.

2.4.4 Biogeochemical relevance

The observed mixing and exchange of water masses across the Rusinga Channel can act as an important physicochemical and biogeochemical link between the gulf and the main lake. Physical processes in lakes link littoral, benthic and pelagic habitats through resuspension and transport of nutrients and biological components (McIntyre and Melack, 1995, MacIntyre & Jellison, 2001; Talling, 2001). The highly predictable and persistent gradient of electrical conductance (Fig. 2.11) across the Rusinga channel can be used to

evaluate the gains and losses of non-conservative components such as suspended sediments, nutrients and chlorophyll using a similar model as used for water exchange (Fig. 2.3) with a non-conservative component added (Gordon, 1996). This is covered in chapter 3 for nutrients.

Chapter 3

Spatial and temporal variability in nutrient fluxes and ecosystem metabolism

3.1 Introduction

The study of nutrient concentrations and dynamics in Lake Victoria has attracted increased attention from various researchers and research groups in the past 2 decades in response to the dramatic ecosystem changes that have occurred in the lake in the past half century (Ochumba & Kibaara, 1989; Kilham & Kilham, 1990; Hecky, 1993; Witte et al 2005). These changes include a 10-fold decrease in Si concentration in the lake water column compared to values reported by Talling (Talling, 1966) and increased sedimentation and burial of P and Si in response to increased phytoplankton productivity associated with increased eutrophication (Kilham & Kilham, 1990; Hecky, 1993; Hecky et al, 1996; Verschuren et al, 1998; Verschuren et al, 2001). The changes in nutrient status and cycling have taken place concurrently with biological changes associated with proliferation of exotic fish species and decimation of endemic species (Ogutu-Ohwayo, 1990), changes in phytoplankton productivity and species composition (Mugidde, 1993; Kling et al, 2001) and occurrence of more persistent hypolimnetic hypoxic conditions in the lake (Hecky, 1993). Several studies have explored the relationship between these changes (e.g. Hecky, 1993; Lehman & Branstrator, 1994; Hecky et al, 1996; Kling et al, 2001; Guildford et al 2003; Witte et al, 2005). The changes in nutrient concentration and cycles in the lake have been attributed to increased external nutrient loading associated with land degradation in the lake catchment (Hecky, 1994) and several studies have undertaken to characterize and quantify inputs from different sources (LVEMP, 2002; Mugidde, 2003; Tamatamah et al, 2005).

Although the studies done so far have helped to advance knowledge on nutrient status in Lake Victoria and identify the nature and magnitude of ecosystem changes that have occurred, much more is yet to be understood about this large and complex tropical lake. One

area that has not so far been investigated is the exchange and transport of nutrients between different lake zones and how it influences the lake ecosystem dynamics. Studies done in different lake zones have shown that inshore and offshore areas have different nutrient concentrations and biogeochemical cycles (Lehman & Branstrator, 1994; Mugidde, et al 2003; Gikuma-Njuru & Hecky, 2005) and even in the offshore areas variability may exist due to the large lake surface (LVEMP, 2002).

Different lake zones are normally linked by physical processes through mixing and exchange of water and associated chemical elements (MacIntyre & Melack, 1995; Talling, 2001). In Lake Tanganyika for example, nutrient inputs from upwelling in the Southern part are transported to the northern part of the lake through wind-generated surface currents, resulting in seasonal blooms in the northern part of the lake (Verburg, 2003). In marine environments nutrients transported from inshore areas through physical processes have been found to increase productivity in offshore areas (e.g. Sutcliffe, 1983). The purpose of this study is to characterize nutrient gradients along a transect between Nyanza Gulf and Lake Victoria proper and to quantify nutrient fluxes along the transect in order to establish the role of physical processes in influencing nutrient dynamics and ecosystem metabolism. Nyanza Gulf is a river-fed long and shallow embayment with different water quality characteristics compared to the main Lake Victoria (Gikuma-Njuru & Hecky, 2005). Nutrient fluxes through the Rusinga Channel, the exchange zone between the gulf and the main lake, and ecosystem metabolism along the transect will be calculated using a mixing multi-box model as described in Gordon et al (1996) and Smith & Hollibaugh (1997).

3.2 Methods

3.2.1 Field sampling

Between March 24, 2005, and March 21, 2006, 10 stations located along a transect between Nyanza Gulf and main Lake Victoria (Fig. 3.1) were sampled for nutrient concentrations in the water column. Water samples were collected near the surface (approximately 1 Secchi depth) using a 5-L Van dorn sampler and different portions treated

according to standard procedures (APHA 1995) before transport to the Kisumu laboratory, where analysis of different species was done. In the field, appropriate sample portions were immediately filtered through GFF filters (0.7 μm) for analysis of particulate phosphorus (PP), particulate nitrogen (PN) and particulate carbon (PC) and the filtrate was preserved on ice for analysis of soluble nutrient species: soluble reactive phosphorus (SRP; DIP), dissolved organic phosphorus (DOP), nitrate ($\text{NO}_3\text{-N}$), dissolved organic nitrogen (DON), ammonium ($\text{NH}_4\text{-N}$), nitrite ($\text{NO}_2\text{-N}$) and dissolved reactive silica ($\text{SiO}_2\text{-Si}$, DRSi). For the analysis of particulate biogenic silica (PBSi), an appropriate sample volume was passed through a cellulose nitrate filter (0.2 μm) and the filter with sample was preserved for analysis in the laboratory. A portion of the sample was preserved for the analysis of total phosphorus (TP) and total nitrogen (TN). All the water and filter samples were kept under ice during transportation to the lab, where they were analyzed immediately (soluble nutrients within 12 hours; total nutrients and PBSi within 48 hours). Filters for particulate fractions (PP, PC and PN) were oven dried (105 $^{\circ}\text{C}$) immediately on arrival in the laboratory and kept frozen during transportation to the University of Waterloo laboratories where analysis was done.

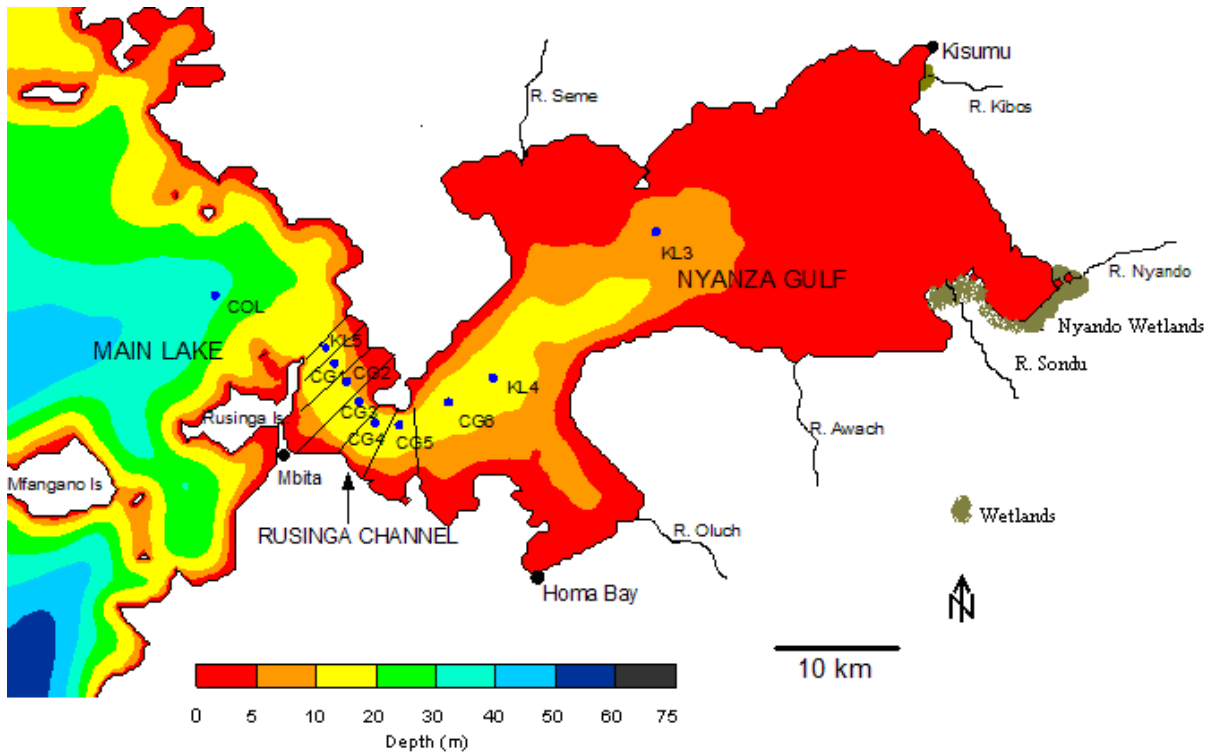


Figure 3.1 Map of the study area showing different study segments (Nyanza Gulf, Rusinga Channel and part of the main lake), sampling stations and delineation boundaries for the segments (systems) used in the budget model. The base map and the bathymetric data are from Silsbe (2003).

3.2.2 Laboratory analysis

Analysis of different nutrient species was done according to standard analytical methods as described in APHA (1995). TP and DOP were analyzed by first digesting 25ml of unfiltered and filtered sample respectively with ammonium persulfate for 30 min under pressure (137 kPa) in order to release the bound phosphorus, which was then analyzed as SRP. The PP samples were dried in an oven at 105 °C for 8 hours and after combustion at 550 °C for 30 minutes the samples were digested using ammonium persulfate for 30 min (137 kPa) to release the bound phosphorus, which was then analyzed as SRP. SRP in the filtered water and in the digested samples was analysed using ascorbic acid method.

TN and DON samples were digested with potassium persulfate solution in an autoclave at 200 kPa (121°C) for 30 minutes in order to release and oxidize the bound

nitrogen, which was then analysed as NO_3^- . NO_3^- -N in the filtered and digested samples was passed through a cadmium reduction column and then analyzed as NO_2 (APHA, 1995). Particulate organic carbon and nitrogen (PC and PN respectively) were analyzed using a Carbon-Nitrogen Analyzer, Model CE 440 Elemental Analyzer (Exeter Analytical, Inc.).

Ammonium nitrogen was analyzed using the fluorometric method described in Holmes et al (1999). In this method, 10 mL of working reagent (a mixture of orthophthaldialdehyde (OPA), sodium sulphite and sodium tetraborate) is added to 40 mL of the water sample and after incubating in the dark for 3 hours, fluorescence activity between ammonium and OPA is measured using a fluorometer (Turner Designs 10-AU).

3.2.3 Modeling nutrient fluxes and lake metabolism

In chapter 2 a mass budget model was used to calculate water fluxes across different sections of the gulf and the Rusinga Channel, using water conductance as a conservative tracer of the exchange process. Once validated with the conservative tracer, the model can be expanded to include a non-conservative element, which unlike water and conductivity can have net loss or gain during transit through the system due to factors other than water exchange processes. The expanded model is described in detail in the budgeting guidelines for the International Geosphere-Biosphere Program–Land-Ocean Interactions in the Coastal Zone (IGBP-LOICZ) (Gordon et al. 1996) and in Smith and Hollibaugh (1997). The model (Fig. 3.2) includes a residual flux term, ΔY , which is a measure of net internal fluxes within a segment of a modeled transect (that is, sources minus sinks) of the non-conservative material Y.

For a system at steady state, ΔY is related to other Y flux terms into and out of the modeled segment (Fig. 3.2) as follows:

$$\Delta Y = -V_O Y_O - V_R Y_R - V_E Y_E - V_P Y_P - V_X (Y_2 - Y_1) \quad (1)$$

The subscripts O, R, E, P and X denote fluxes associated with river inflows and groundwater, residual flow, evaporation, precipitation and mixing respectively. In the application here evaporation term is assumed to be negligible ($=0$) and groundwater is also assumed to be negligible and therefore O includes only flux from river inflows. Using this

equation, non-conservative fluxes of dissolved inorganic phosphorus (ΔDIP), dissolved organic phosphorus (ΔDOP), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON) and dissolved reactive silica ($\Delta DRSi$) have been determined for different segments of the Nyanza Gulf and the Rusinga Channel (Fig. 3.1) for 10 months (between March 2005 and March 2006; May, August and November 2005 were not included due to lack of sufficient data). The fluxes are normalized to the surface area of each modeled section and expressed per unit area for ease of comparison between the different sections and literature information. The flux terms that have been determined are the advective flux (also referred as residual or diffusive flux) which is associated with the residual flow (V_R), the mixing flux, associated with the mixing term (V_X) and the residual flux (ΔY) which is the net of all input sources minus sinks and is also referred to as production (or consumption when negative) within the segment.

Assuming that non-conservative reactions involving DIP and DIN are the result of production and consumption of organic matter, net ecosystem metabolism has been calculated using the stoichiometric relationship of particulate carbon, nitrogen and phosphorus (Gordon et al. 1996). The working assumption is that removal of DIP from a system results in net production of organic matter whereas release of DIP occurs in a system with net organic consumption (respiration of organic matter by bacteria or secondary producers; Smith & Hollibaugh, 2006). The net system metabolism (production, p , minus respiration, r) is therefore related to DIP residual flux and particulate carbon to phosphorus ratio as follows:

$$(p - r) = -(C : P)_{part} \cdot \Delta DIP \quad (2)$$

A system that is net autotrophic, $(p-r)>1$, has $\Delta DIP<0$ and is interpreted to be consuming DIC via net organic production, while a system that is net heterotrophic has $\Delta DIP>0$ and is interpreted to be producing DIC via net respiration (Gordon et al. 1996; Smith & Hollibaugh, 2006). The main assumption is that only aerobic conditions exist in the system's water column and at the sediment-water interface, since under anaerobic conditions redox mediated phosphorus desorption from organic (and inorganic) particles is likely to occur (Gordon et al. 1996) in which case P release may be in excess of P directly from

decomposition of organic matter. The water column oxygen concentration in the gulf and the channel are always above 3.5 mg/L (Chapter 2) and therefore this assumption is taken to be generally valid.

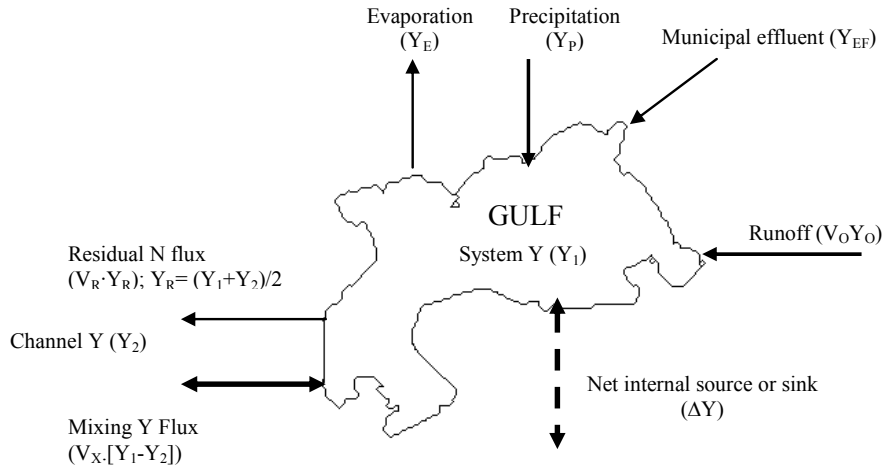


Figure 3.2 Conceptual budget model of a non-conservative material, Y, in the gulf up to the boundary with channel. V_R and V_X are respectively the residual (advective) and mixing water fluxes between the gulf and the channel (see chapter 2): $V_R=V_O+V_P-V_E$, where V_O is rivers' discharge, V_P is direct precipitation and V_E is evaporation; and $V_X = (V_O C_O + V_R C_R)/(C_1 - C_M)$, where C_O is conductivity of river inflows, C_1 is gulf conductivity, C_M is channel conductivity and C_R is $(C_1+C_M)/2$. The arrows indicate the direction of the flux in the system (Gulf). Adapted from Gordon et al. (1996)

The other metabolic rate that has been determined using the stoichiometric relationship is the net exchange between fixed nitrogen pool (DIN, DON, PN) and the gaseous nitrogen (N₂), through denitrification and nitrogen fixation processes (nfix – denit). Since from the stoichiometric relationships the dissolved nitrogen flux associated with production and decomposition is the dissolved phosphorus flux ($\Delta P = \Delta DIP + \Delta DOP$) multiplied by the particulate nitrogen to phosphorus ratio, (N:P)_{part}, (nfix – denit) is therefore the difference between the measured dissolved nitrogen flux ($\Delta N = \Delta DIN + \Delta DON$) and that expected from production and decomposition of the organic matter (Gordon et al. 1996):

$$(nfix - denit) = \Delta N - \Delta P(N : P)_{part} \quad (3)$$

3.2.4 Delineation of the study zones

The mass balance model was applied on different segments along the study transect. These included the gulf, represented by the sampling stations KL3, KL4 and CG6 and 5 segments along the Rusinga channel (Fig. 3.1). Delineation of the segments along the channel was arbitrary but each segment included a sampling station with the boundaries chosen to be approximately perpendicular to the general hydrographic flow. The morphometric and hydrographic data of each segment are presented in Table 3.1 and the segments are shown in Figure 3.1.

Table 3.1 Morphometric and hydrographic data for different zones (Fig. 3.1) used in the budget model. V_R and V_X are respectively, residual and mixing water fluxes between adjacent zones.

| | Gulf | CG5 | CG4 | CG3 | CG2 | CG1 | KL5 |
|---------------------------------|--------|--------|--------|-------|--------|--------|-------|
| Surface Area (km ²) | 1333.1 | 24.8 | 11.4 | 21.9 | 21.0 | 12.4 | 4.6 |
| Volume (km ³) | 6.07 | 0.23 | 0.19 | 0.24 | 0.24 | 0.18 | 0.10 |
| Depth (m) | 4.6 | 9.3 | 16.8 | 11.1 | 11.3 | 14.6 | 22.1 |
| V_R (m ³ /s) | -35.8 | -35.3 | -35.1 | -34.7 | -34.2 | -34.0 | -33.9 |
| V_X (m ³ /s) | 746.9 | 1596.8 | 1889.9 | 916.4 | 1688.3 | 1367.8 | 883.7 |

3.2.5 Data acquisition

Atmospheric DIN and DIP input to the gulf was estimated from TN and TP atmospheric loading values obtained from the Water Department in Kisumu (198 and 2300 t/yr respectively). DIP was estimated to be 32% of TP, as was reported by Tamatamah et al (2005) for southern Lake Victoria, and DIN was estimated to account for 50% of TN. The riverine input of DIN, DIP and SiO₂-Si (DRSi) into the gulf (43.7, 4.4 and 1449 kg/s respectively) was estimated from river water samples collected in October and December 2005 and January 2006 and were assumed to be fair estimates of the annual loadings since

the sampling dates coincided with both dry (October and December) and rainy (January 2006) periods.

Municipal effluent contribution to the DIN and DIP loadings (34.0 and 1.9 kg/s) to the gulf were calculated from data obtained from the Water Department in Kisumu. Dissolved organic nitrogen and phosphorus (DON and DOP) loading from the riverine and municipal sources into the gulf was not available and therefore an estimated value was used by assuming that DON and DOP accounted for 50% of TN and TP respectively. The water fluxes (V_O , V_R and V_X) calculated in Chapter 2 were used to calculate associated nutrient fluxes as shown in Figure 3.2 and the residual flow (V_R) was taken as the inflow (V_O) into the proceeding segment along the gulf-channel-lake transect (Fig. 3.1).

3.3 Results

3.3.1 Spatial variation of water column nutrient fractions

Figure 3.3 shows the spatial variation in concentration of different forms of phosphorus, nitrogen and silica and particulate carbon averaged over the study period (March 2005 to March 2006). TP and SRP concentrations were always high (mean 101.5; 31.7 $\mu\text{g/L}$) and showed little or no variation along the transect, except in the main lake where SRP was significantly higher than the inner-gulf (KL3, KL4). PP was high in the inner-gulf (KL3; mean 37 $\mu\text{g/L}$) and followed a decreasing trend to a minimum (21 $\mu\text{g/L}$) in mid-channel station, CG5, before increasing towards the main lake. DOP showed a wide intra-station variation (see the long error bars in Fig. 3.3) but little or no variation between stations. TN decreased continuously from the inner-gulf towards the main lake and $\text{NO}_3\text{-N}$ increased towards the channel to a maximum (mean 148 $\mu\text{g/L}$) in CG5 before decreasing to a minimum (mean 51 $\mu\text{g/L}$) in the main lake. In contrast to $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ and DON varied with a decreasing trend towards the channel followed by increase towards the main lake (DON only slight increase). PN and PC concentrations followed the same spatial trend as PP with a minimum in the mid-channel (CG4) and all the three (PP, PN, PC) were highly correlated (Table 3.2).

The percent contribution of dissolved inorganic and organic and particulate fractions to TP and TN varied differently along the study transect (Fig. 3.4). SRP accounted for between 19 and 46% of TP whereas DOP accounted for between 29 and 43% of TP and the two fractions (SRP and DOP) followed opposite spatial trends. DON was the most dominant TN fraction, accounting for over 42% of TN but in contrast, DIN had lowest contribution to TN (14-24%). Unlike DOP, whose % contribution to TP increased along the transect, the % contribution of DON to TN did not exhibit any defined spatial trend. The contribution of particulate fractions to TN and TP followed the same spatial trend, with relatively low % values occurring in the channel area between CG4 and CG6.

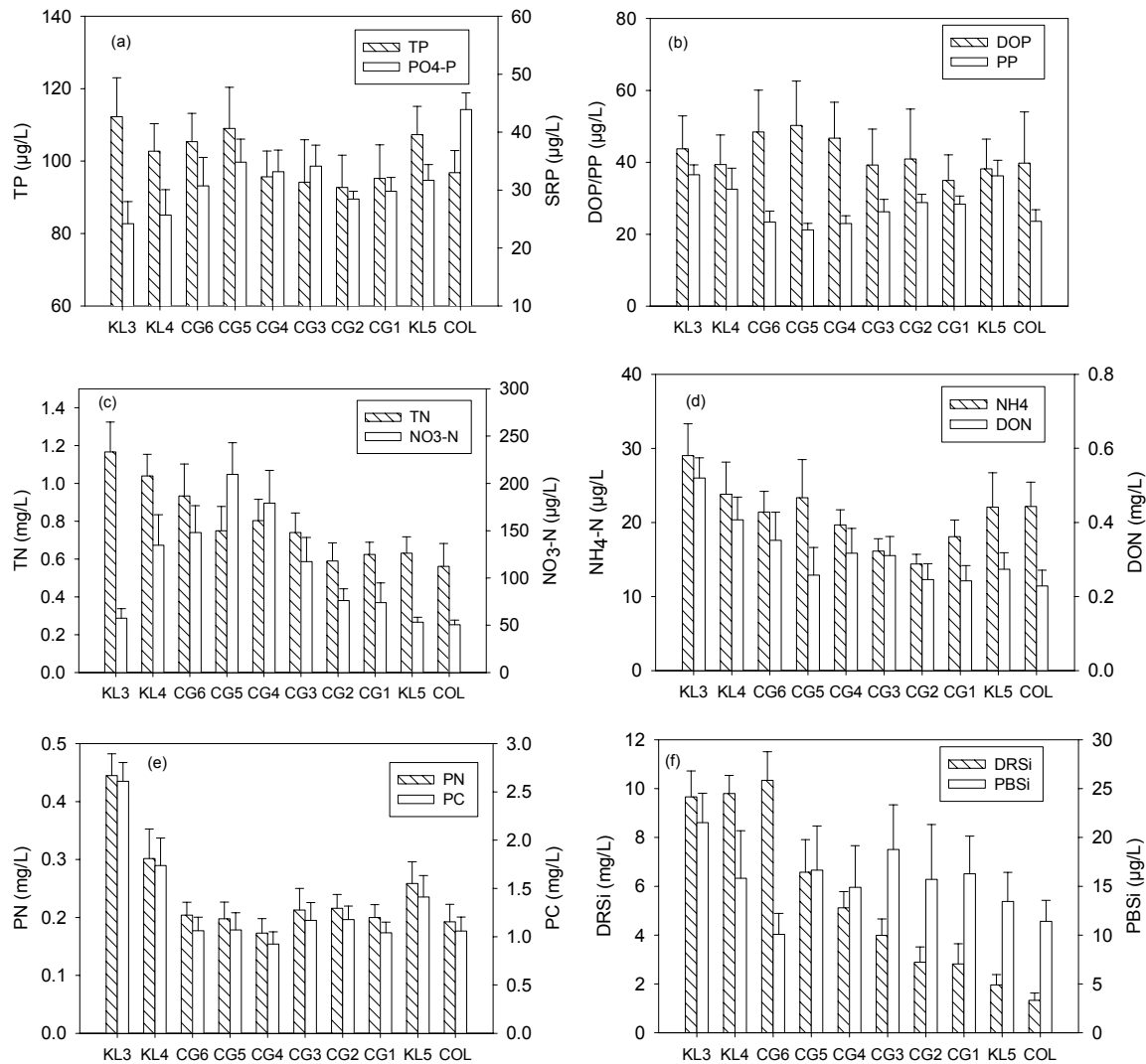


Figure 3.3 Spatial variation of dissolved and seston nutrient concentrations in the lake water column: (a) TP (total phosphorus) and SRP (soluble reactive phosphorus); (b) DOP (dissolved inorganic phosphorus) and PP (particulate phosphorus); (c) TN (total nitrogen) and NO₃-N (nitrate nitrogen); (d) NH₄-N (ammonium nitrogen) and DON (dissolved organic nitrogen); (e) PN (particulate nitrogen) and PC (particulate carbon) and (f) SiO₂-Si (dissolved reactive silica) and PBSi (particulate biogenic silica). Data is for surface samples (approximately 1 Secchi depth) collected monthly between 24 March 2005 and 21 March 2006. The error bars are standard errors.

Table 3.2 Pearson correlations between different nutrient fractions for all stations in the study (r -critical=0.381, 95% CI; $n=31$). Correlation was done after log-transformation. Highlighted values are those with significant correlation ($P < 0.05$).

| | TP | SRP | PP | TN | NO ₃ -N | NH ₄ -N | PN | PC | DRSi |
|--------------------|-------------|-------|-------------|-------------|--------------------|--------------------|-------------|------|-------------|
| SRP | -0.32 | | | | | | | | |
| PP | 0.27 | -0.22 | | | | | | | |
| TN | 0.49 | -0.13 | 0.28 | | | | | | |
| NO ₃ -N | 0.25 | 0.06 | -0.37 | 0.43 | | | | | |
| NH ₄ -N | 0.14 | -0.18 | 0.48 | 0.46 | -0.12 | | | | |
| PN | 0.46 | -0.15 | 0.77 | 0.29 | -0.38 | 0.44 | | | |
| PC | 0.35 | -0.09 | 0.75 | 0.27 | -0.40 | 0.45 | 0.98 | | |
| DRSi | 0.04 | 0.28 | 0.05 | 0.50 | 0.40 | 0.33 | 0.16 | 0.23 | |
| EC | 0.32 | -0.12 | -0.02 | 0.50 | 0.38 | 0.17 | 0.25 | 0.28 | 0.58 |

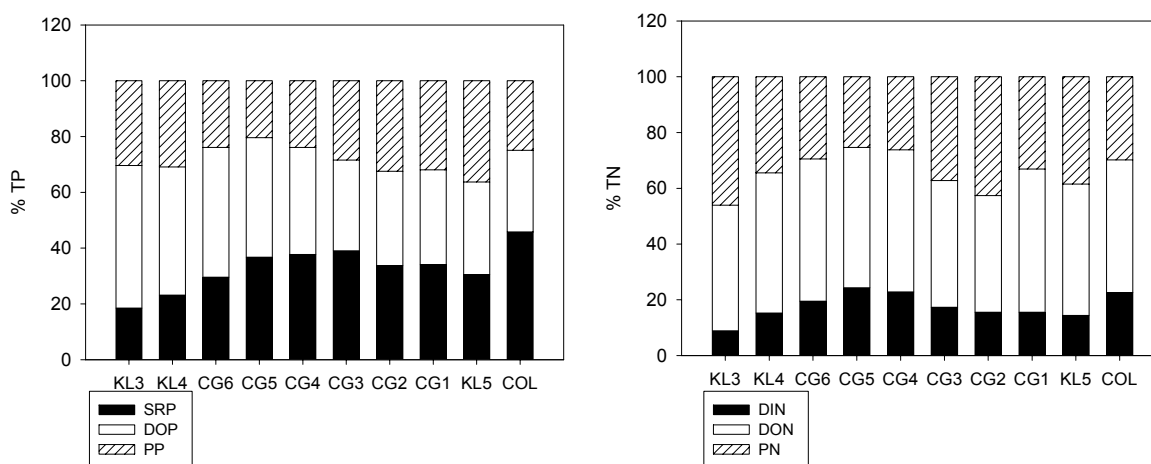


Figure 3.4 Percentage contributions of SRP, PP and DOP to TP and DIN, DON and PN to TN

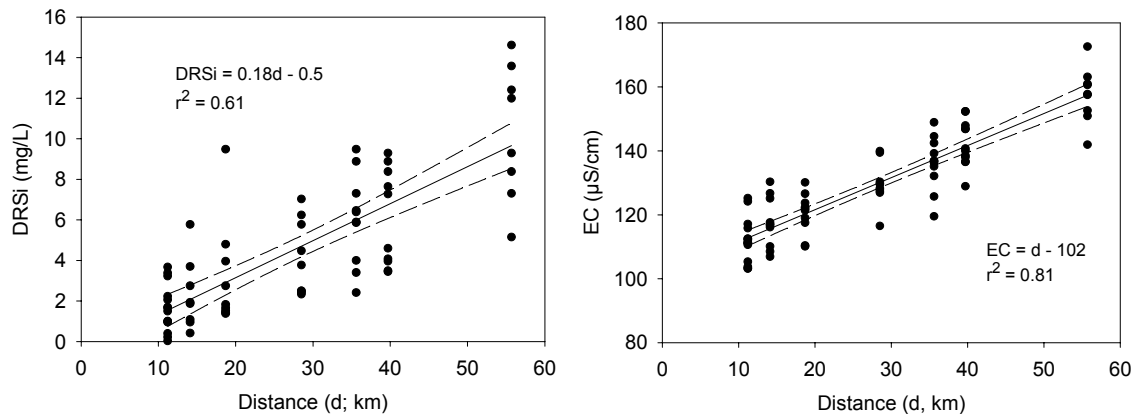


Figure 3.5 Variation in DRSi concentration (a) with distance from the main lake station (COL) and (b) with electrical conductance in the Rusinga Channel. The dotted lines are the 95% confidence interval.

DRSi concentration showed minimal variation between KL3 and CG6 but after CG6 it decreased monotonically towards the main lake. DRSi concentration along the channel was highly correlated with electrical conductance, EC, and distance from COL ($r^2=0.62, 0.61$; Fig. 3.5) and therefore behaved more like a conservative material along the channel. In contrast, PBSi varied widely (3.3 - 40 $\mu\text{g/L}$) over the study period, but without any defined spatial trend. Table 3.3 shows a matrix of statistical comparison (one-way ANOVA) between stations for the different nutrient fractions and electrical conductance (EC). The inner-gulf station, KL3 in the centre of the gulf, was the most different station compared to the other stations and had significantly higher PN, PC, DRSi and EC compared to the channel and main lake stations and significantly lower SRP and $\text{NO}_3\text{-N}$ ($P<0.05$) compared to the main lake and the mid-channel (CG6, CG5, CG4) respectively. The mid-channel (CG4, CG5) had significantly higher $\text{NO}_3\text{-N}$ ($P<0.05$) compared to the inner-gulf and the main lake (KL3, COL) and the area between CG2 and main lake (COL) had significantly lower DRSi compared to the rest of the study area.

Table 3.3 Statistical comparisons between stations for different nutrient fractions and electrical conductance (EC). The matrix shows the stations that have significantly lower nutrient concentration (ANOVA, $P < 0.05$) compared to the corresponding station on the top column. The dashes indicates no significant difference with any station

| | KL3 | KL4 | CG6 | CG5 | CG4 | CG3 | COL |
|--------------------|---------|---------|------------------|-----------------|-----------------|---------|----------|
| SRP | - | - | - | - | - | - | KL3, KL4 |
| PP | CG5 | - | - | - | - | - | - |
| TN | COL | COL | - | - | - | - | - |
| NO ₃ -N | - | - | KL3, KL5, COL | KL3, CG2-COL | KL3, CG1-COL | - | - |
| PN | CG6-COL | - | - | - | - | - | - |
| PC | KL4-COL | - | - | - | - | - | - |
| DRSi | CG2-COL | CG2-COL | CG2-COL | KL5, COL | KL5, COL | COL | - |
| EC | CG6-COL | CG5-COL | CG5-COL | CG3-COL | CG2-COL | CG1-COL | - |

The spatial variations of stoichiometric mass ratios of different nutrient fractions are presented in Figure 2.1. Particulate N:P, C:P and C:N were high in the gulf and varied with a decreasing trend towards the channel. In the channel the three ratios followed the same spatial pattern, increasing to a maximum value in CG3 and then decreasing to a minimum value in CG1 before increasing towards the main lake. Total nitrogen to phosphorus and total dissolved nitrogen to phosphorus ratios (TN:TP; TDN:TDP) varied with the same spatial trend and were higher in the gulf (9.3) compared to the channel and the main lake (6 to 9). Dissolved inorganic nitrogen to phosphorus ratios (DIN:DIP) were relatively low (2-5) compared to the ratios between other nitrogen and phosphorus fractions and followed a more pronounced reducing trend towards the main lake, especially after CG4. PBSi:PP decreased monotonically towards the main lake from a highest value of 0.39 in CG6 to a lowest value of 0.07 in KL5. PN:PBSi followed the same decreasing trend towards the channel as the other ratios, but in the channel the ratios varied with an initially increasing and then decreasing trend with lowest value at CG1 (13.5) and highest value at KL5 (27.2).

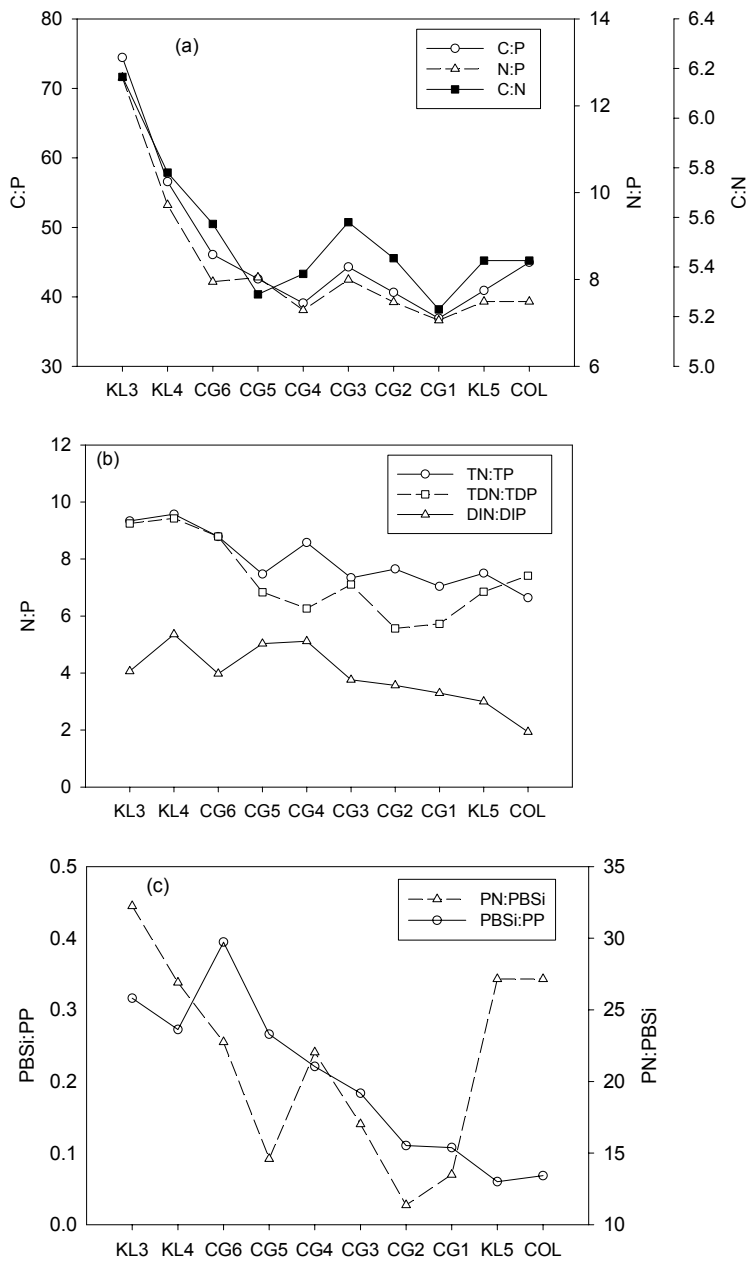


Figure 3.6 Spatial variation in mean stoichiometric (weight) ratios between different nutrient fractions: (a) particulate carbon and nitrogen to particulate phosphorus (C:P, N:P) and particulate carbon to particulate nitrogen (C:N); (b) total nitrogen to total phosphorus (TN:TP), total dissolved nitrogen to total dissolved phosphorus (TDN:TDP), and dissolved inorganic nitrogen to dissolved inorganic phosphorus (DIN:DIP), and (c) particulate biogenic silica to particulate nitrogen and phosphorus (PN:PBSi; PBSi:PP)

3.3.2 Seasonal variation

The seasonal variations in concentration of different nutrient fractions in the main lake station (COL) and the western gulf station (KL4) are shown in Figure 3.7. TP concentrations in the two zones were similar and followed the same general increasing temporal trend to a maximum value of 141 $\mu\text{g/L}$ in October. SRP in COL showed less temporal variation than in KL4 where there was a strong increasing trend up to October but after October both zones maintained similar concentrations. TN varied more widely at KL4 over time compared to COL where concentrations increased to maxima in January 2006 before declining towards March 2006. In April, DIN concentration in the gulf and in the main lake was similar (78 $\mu\text{g/L}$) but after that concentration gradient between the two stations progressively increased as the gulf concentration increased whereas concentration in COL decreased but with a less pronounced trend. The concentrations of particulate fractions (PN, PP and PC) varied with similar temporal trends and were relatively high between October 2005 and January 2006, in COL, compared to other sampling dates whereas in KL4 relatively high concentrations were observed in March 2006. DRSi concentration maintained a large gradient between KL4 and the main lake, with concentration in KL4 about 10-fold that in the main lake. The DRSi concentrations in the gulf maintained a high constant value (12 mg/L) between July and October but in the main lake relatively low values (<1 mg/L) were observed between June and September followed by a maxima (3 mg/L) in October. PBSi concentration in the gulf and the main lake varied but with no particular trend. Of all the nutrients DRSi maintained the most stable concentrations and concentration gradients over time suggesting that the greater variation and trends in other nutrients were the result of internal fluxes and not simply mixing of the two end member water masses in the gulf and the main lake.

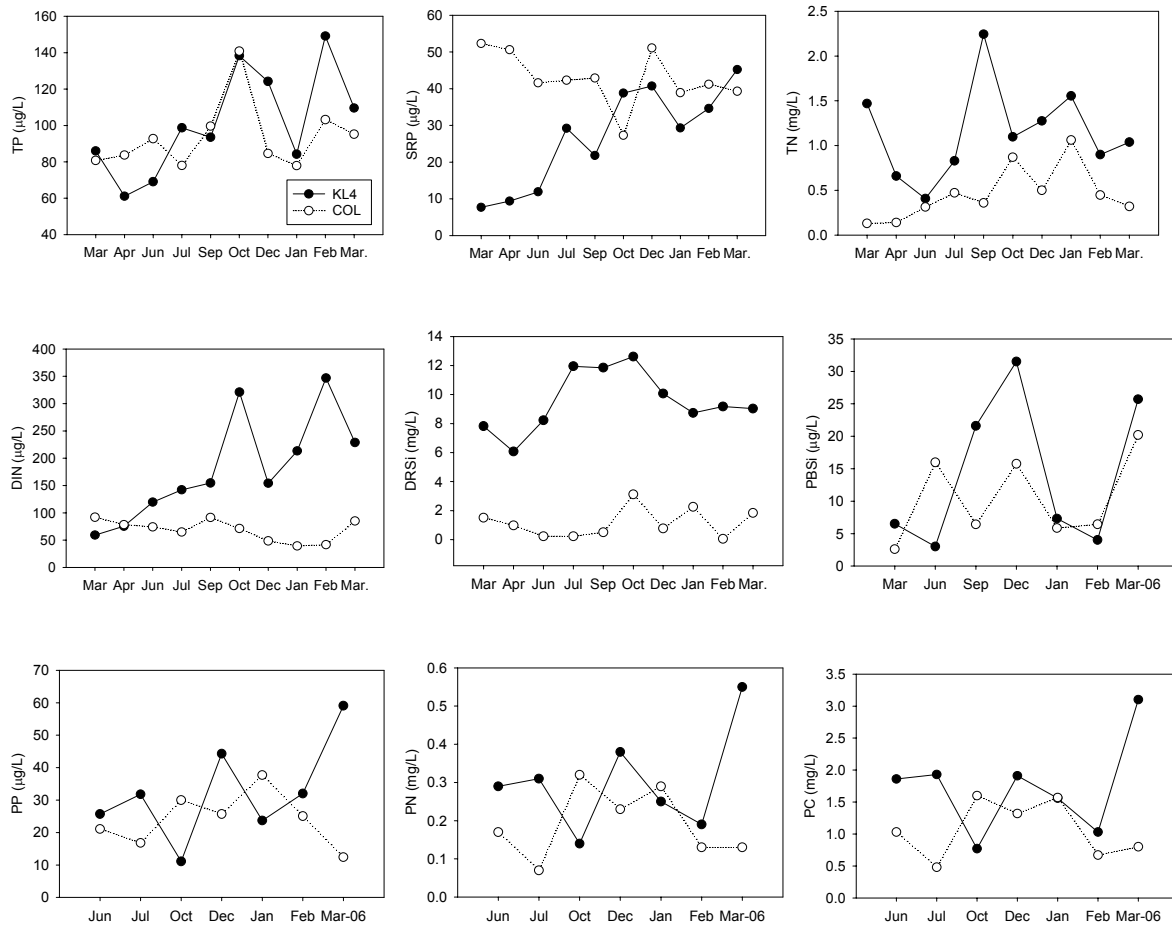


Figure 3.7 Seasonal variations in concentrations of TP, SRP, TN, DIN (dissolved inorganic nitrogen), PN, PP, PC, DRSi and PBSi in the gulf (KL4) and the Main Lake (COL).

3.3.3 Nutrient exchange between the Gulf, the Channel and the main lake

The horizontal advective fluxes for the different nutrient fractions were on average towards the main lake whereas the mixing flux always exported nutrients across the gradient from high concentration zone to the low concentration zone and was always higher than the advective flux (Fig. 3.8). The advective DIP flux in both the gulf and the channel (at KL5) was on average out of the systems (-42 and -76 kg/d) but the mixing flux brought in more than 8 times more DIP into the systems compared to the advective outflow, indicating a net export of DIP from the main lake into the channel and the gulf. DOP flux was on average out of the channel into the main lake, with average advective and mixing components of -63 and

-308 kg/d respectively. The DOP advective flux was out of the gulf (-96 kg/d) but was compensated more than 3 times by mixing flux (+354) into the gulf.

The total DIN flux (advective plus mixing) was into the gulf with advection removing 297 kg/d from the gulf and mixing bringing in 1903 kg/d from the channel. The channel was also a net source of DIN to the main lake since the mixing flux removed more than 3 times DIN from the channel compared to the advective flux into the channel (34.3 kg/d). The total DON flux (advection plus mixing) between the Gulf and the channel was negligible but the channel was a net source of DON to the main lake. There was a net export of DRSi to the main lake with a total flux of 82 t Si/d from the gulf to the channel, dominated by mixing flux of DRSi, and a total flux of 10 t Si/d from the channel into the main lake.

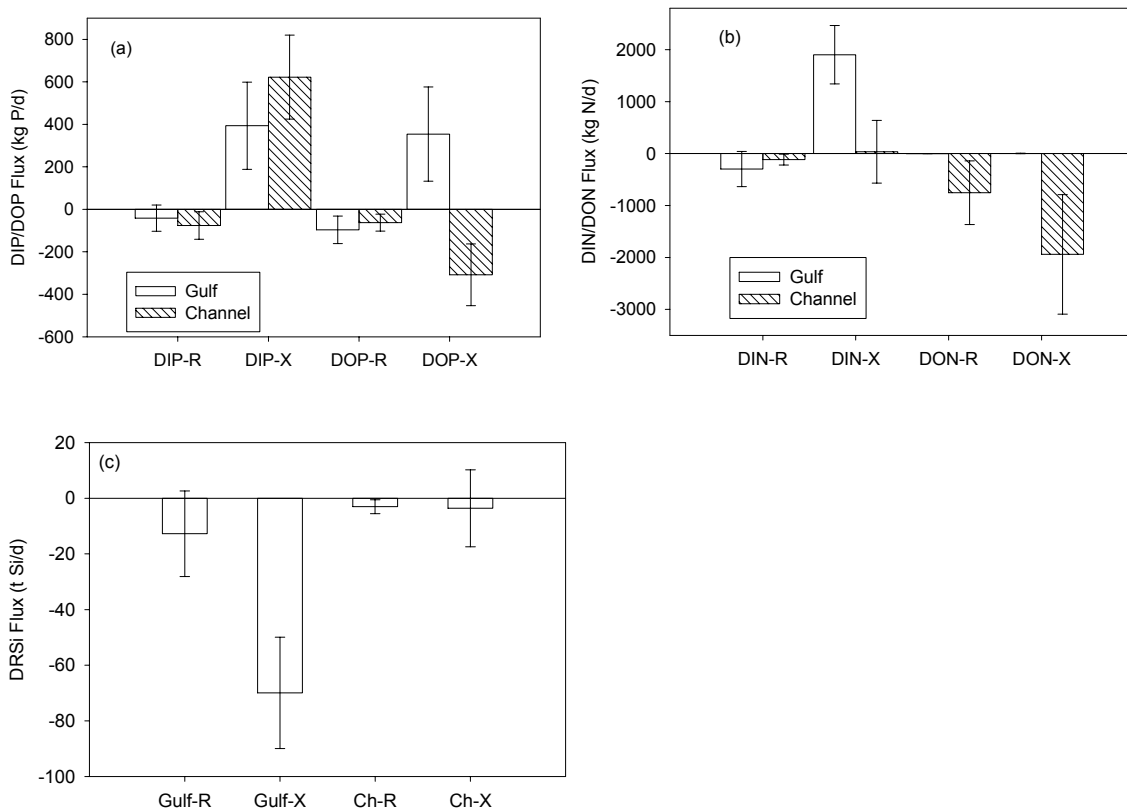


Figure 3.8 Mean and standard error of nutrient fluxes across the gulf-channel and the channel-main-lake interface. The letters R and X denote the advective and mixing fluxes respectively and Ch represents the channel (c).

3.3.4 Non-conservative nutrient fluxes

Figure 3.9 presents the spatial variation in non-conservative fluxes (production) of different nutrient fractions in the gulf and in different segments along the channel. There was net consumption of DIP ($-\Delta\text{DIP}$) in the gulf but in contrast, the channel (except CG5 and KL5) had net DIP production ($+\Delta\text{DIP}$). The gulf and the immediate two channel sections (CG5 and CG4) had net DOP consumption, although in CG4 and CG5 DOP production occurred during some months. In the rest of the channel, there was net DOP production with KL5 having a highest average value of $7 \text{ mg P/m}^2/\text{d}$. There was net consumption of DIN and DON in the gulf, but in contrast net DIN and DON production occurred in all the channel sections. All the study sections, except KL5, had net DRSi production ($+\Delta\text{DRSi}$), range $0.2 - 2 \text{ g Si/m}^2/\text{d}$. KL5 had net DRSi consumption, but the mean ($0.03 \text{ g Si/m}^2/\text{d}$) was not significantly different from zero ($t = -0.199$; $2Q=0.05$; $n=9$).

3.3.5 Ecosystem metabolism

The spatial variation of net ecosystem production (NEP; p-r) and nitrogen metabolism (nfix-denit) are presented in Figure 3.10. The gulf was always autotrophic with an average NEP of $566 \text{ mg C/m}^2/\text{d}$. In contrast, the channel NEP varied between autotrophy and heterotrophy over the study period but was on average heterotrophic (except CG5 and KL5); NEP range from -18 to $18 \text{ mg C/m}^2/\text{d}$. CG5 and KL5, located on both ends of the channel were always autotrophic with average NEP of 147 and $232 \text{ mg C/m}^2/\text{d}$ respectively. The nitrogen metabolism (nfix-denit) flux in the gulf indicated net nitrogen fixation (mean $+12 \text{ mg N/m}^2/\text{d}$) whereas in channel values varied between net nitrogen fixation and net denitrification as indicated by the error bars. However, the channel (except KL5) was on average nitrogen fixing ($3-15 \text{ mg N/m}^2/\text{d}$). KL5 is the only zone which had net denitrifying conditions over the study period ($-3 \text{ mg N/m}^2/\text{d}$).

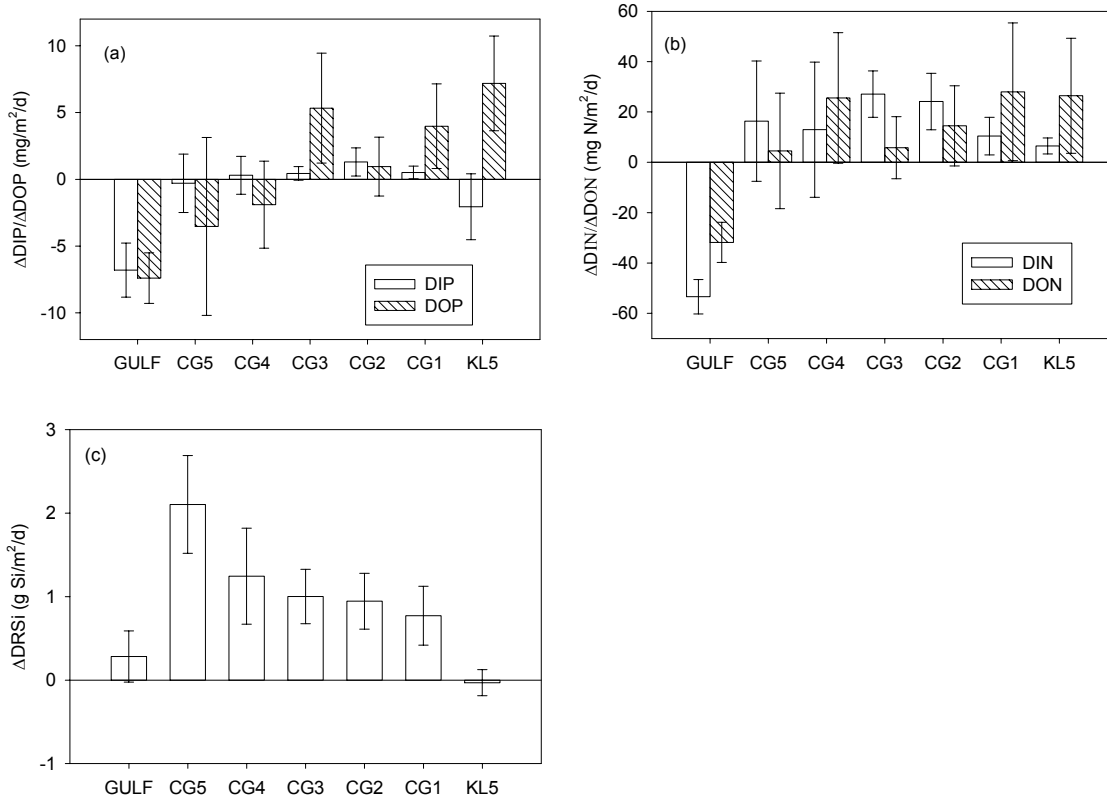


Figure 3.9 Mean and standard deviations of nonconservative fluxes of DIP, DOP, DIN, DON and DRSi in the gulf and in different channel sections, based on monthly budgets for the period between March 2005 to March 2006 (except May, August and November 2005)

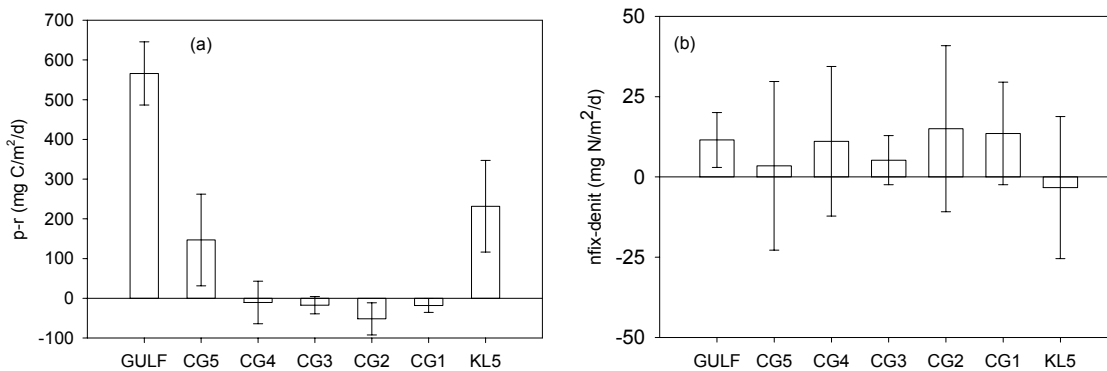


Figure 3.10 Mean and standard error of ecosystem metabolism, (a) net primary productivity ($p-r$), and (b) nitrogen metabolism ($n\text{fix-denit}$) in different study zone for the period between July 2005 and March 2006. Values >1 are for system which is (a) net autotrophic and (b) net N-fixing and values <1 represent system which is (a) net heterotrophic and (b) net denitrifying conditions

3.4 Discussion

3.4.1 Influence of lake morphometry on nutrient concentrations and availability

The observed spatial and seasonal variation along the study transect can partly be attributed to morphological differences between the wide and shallow inner-gulf, the narrow and deep channel and the deep main lake, which together with associated physical processes influence nutrient cycling and availability (Wallin & Hakanson, 1992; Kalff, 2002). The main lake is deep enough to undergo seasonal thermal stratification and develop hypolimnetic hypoxia (Talling, 1957; Talling, 1966; Chapter 2), which has direct influence on internal nutrient cycling. Hypolimnetic hypoxia enhances the release of SRP from the sediment (Kalff, 2002), which can partly account for the observed relatively high SRP in the main lake compared to the gulf and the channel (Fig. 3.3; Gikuma-Njuru & Hecky, 2005). Hypolimnetic hypoxia also enhances denitrification, which is a sink for combined nitrogen (Hecky et al. 1996) and the observed relatively low nitrate in the main lake can be attributed to increased denitrification in the hypoxic metalimnion (Hecky et al, 1996; Lehman et al, 1998). Increased metalimnetic denitrification associated with the now more extensive and prolonged hypolimnetic hypoxia in Lake Victoria (Hecky, 1993) has been blamed for the current dominance of nitrogen fixing blue-greens in Lake Victoria (Ochumba & Kibaara, 1989; Kling et al, 2001) compared to 4 decades ago when diatoms dominated the algal population in the lake (Talling, 1966).

The main lake, even when stratified, has a high mixing depth (>15m; Chapter 2) leading to light limitation of algal growth (Mugidde, 2001), which is reflected in relatively low algal biomass compared to the inshore areas (Mugidde et al 2003; Gikuma-Njuru & Hecky, 2005), despite (or resulting in) the relatively high SRP concentrations in the main lake. In the shallow gulf, relatively high net algal biomass result in high nutrient demand and may account for observed significantly low SRP in the gulf compared to the main lake. Nixdorf & Deneke (1997) studied lakes with wide ranging morphometry and mean depth in Berlin/Brandenburg region, Germany and found shallow lakes to be more efficient in converting the available phosphorus into phytoplankton biomass due to adequate underwater

light climate. SRP and PP concentrations followed similar but opposite spatial trends (i.e. increase of PP with decrease of SRP; Fig. 3.3), which reinforces the hypothesis of control of SRP control by the algal uptake. Hecky (1993) reported the same trend in Lake Victoria – high offshore SRP declining inshore as PP increased while TP is unchanged.

Unlike SRP, which was significantly higher in the main lake compared to the inner gulf, TP did not vary significantly between stations. Mugidde (2001) reported constant TP concentration in both inshore and offshore areas of northern Lake Victoria. However, Gikuma-Njuru & Hecky (2005), observed significantly higher TP in the main lake compared to the Nyanza Gulf (93, 57 $\mu\text{g/L}$). The average TP concentration in the main lake reported by Gikuma-Njuru & Hecky was similar to that observed during the current study (97 $\mu\text{g/L}$) but in the gulf average TP concentration measured during the current study (107 $\mu\text{g/L}$) is almost twice as high as that reported by Gikuma-Njuru & Hecky. It is important to note that the study by Gikuma-Njuru was carried out during the period of high water hyacinth (*Eichhornia crassipes*) infestation in Nyanza Gulf and other inshore areas of Lake Victoria (Mailu, 2001) and therefore the low TP observed may have been influenced by P uptake and retention by the water hyacinth mats (e.g. Reddy & DeBusk, 1985). The other likely explanation is seasonality of rainfall and influence on fluvial P loading into the gulf.

3.4.2 Fluvial input and spatial gradients

The gulf hydrology is dominated by input from the inflowing rivers (Calamari et al, 1995), and therefore fluvial nutrient input may play an important role in determining concentration and availability of different nutrients in the gulf. The observed relatively high TN, PN, PC, PP and DR_{Si} concentration in the gulf (KL3) compared to the channel and the main lake (Fig. 3.3) can partly be attributed to allochthonous inputs from the inflows. The high particulate N:P and C:P and TDN:TDP in the gulf (Fig. 3.6) indicate that fluvial input to the gulf is more enriched with particulate nitrogen and carbon and total dissolved nitrogen relative to phosphorus. The nutrient (PP, PN, TN) concentrations and elemental ratios (N:P, C:P and TDN:TDP) followed a decreasing trend towards the main lake in response decreasing influence of fluvial input, although in the channel the trend was different for

different nutrient fractions (Fig. 3.3) possibly due to influence of different biogeochemical processes. The observed concentration minima of particulate fractions (PP, PN and PC) correspond to similar minima in algal biomass (Chapter 5) and maybe as a result of light limitation due to vertical mixing observed in this zone (Chapter 2).

The observed relatively low nitrate concentration in the inner-gulf (KL3) may partly be associated with high algal uptake as earlier discussed in the case of SRP. However, since ammonium concentration in KL3 is relatively high (>25 µg/L; Fig. 3.3), algal uptake may not fully account for the observed low nitrate in this area. The other possible explanation for the low nitrate concentration in the inner-gulf is possible dilution by river inflows. The major rivers, Nyando and Sondu, enter the gulf after passing through an extensive wetland system where denitrification and uptake could be occurring (e.g. Saunders & Kalff, 2001; Kansiime & Saunders, 2007) as well as transforming inorganic N from rivers into DON, which is the dominant fraction at KL3. However the role of the fringing wetlands in nutrient recycling and retention is currently not well understood.

DRSi maintained relatively high but constant concentration between KL3 and CG6, possibly due to minimal uptake associated with low diatom population since the gulf is mainly dominated by cyanobacteria (Lungayia et al 2000; Gikuma-Njuru et al, 2005; Chapter 5 this study). In the channel, DRSi followed a well-defined reducing trend in response to mixing and was highly correlated with EC ($r^2 = 0.62$; Fig. 3.5), which can be interpreted to indicate low biological activity relative to transport across the channel (i.e. behaving like a conservative material). In the main lake DRSi concentration was relatively low and varied seasonally possibly in response to the diatom population (e.g. Sommer & Stabel, 1983). The observed low DRSi concentration in the main lake between June and September (Fig. 3.7) could be due to increased uptake associated with enhanced diatom growth, whereas the relatively high concentration in October may be associated with low diatom biomass during times of strong thermal stratification in the main lake (Chapter 2) as is also reflected in the low PBSi concentration (Fig. 3.7). Study of phytoplankton species succession in limnocorals and in-situ have shown that water column stability selects against diatoms in preference for the more buoyant algal species such as blue-greens (Reynolds, 1980; Trimbee & Harris,

1984). Conway et al (1977) observed 100% diatom dominated phytoplankton community in Lake Michigan, North America, prior to stratification in May but after stratification the community changed to approximately 12% diatoms. The observed depletion of DRSi in Lake Victoria in the past 4 decades has been associated with increased eutrophication and sedimentation (Hecky, 1993; Vershuren et al, 1998) and has resulted in change of algal population from that dominated by diatoms to the current dominance by cyanobacteria (Kilham & Kilham, 1988; Kling et al 2001). In the Laurentian Great Lakes Si depletion has been associated with P enrichment (Schelske & Stoermer, 1971).

3.4.3 Nitrification in the channel

The channel area between CG4 and CG6 had significantly higher average nitrate concentration compared to the gulf and the main lake (Fig. 3.3; Table 3.3) indicating existence of either external nitrate input or nitrate production through nitrification. The latter seems to be a more plausible source of nitrate as there are no inflows into this area, while rise in nitrate is accompanied by decline in DON (Fig. 3.3). Nitrification is a microbial-mediated process where ammonium is oxidized to nitrate by nitrifiers during mineralization of organic matter (Ward, 1996). This is a highly physically active area with strong horizontal currents (Njuru, 2001; Romero et al, 2005) and vertical mixing, resulting in resuspension and entrainment of bottom sediments (as reported in chapter 2, the area around CG5 has no fine bottom sediments but only pebbles on a rocky bottom). This zone had relatively low oxygen conditions compared to other study zones (although due to enhanced water column mixing DO concentration was never below 3.5 mg/L; Chapter 2), conditions that would favor nitrification (Hecky et al, 1996; Kalff, 2002). After CG5 nitrate concentration decreased monotonically (Fig. 3.3) in response to dilution with low nitrate water from the main lake.

3.4.4 Nutrient fluxes

Nutrient fluxes between different zones of a water body can play important role in influencing water chemistry and productivity and species composition of biotic community in the receiving zones (e.g., Sutcliffe et al 1983). The exchange process exported over 400 kg

of DIP per day from the main lake to the gulf, which is a significant amount since the total external DIP input to the gulf is about 900 kg P/d (LVEMP, 2002) and therefore the gulf-main-lake exchange plays an role important in the gulf phosphorus budget. The gulf was a net consumer of SRP (Fig. 3.9) and therefore the SRP flux into the gulf from the main lake helps to meet the high SRP demand and maintain the high net productivity (Fig. 3.10). The gulf was also a net recipient of DOP from the channel which helped to meet DOP demand in the gulf where there was net consumption. The DOP consumption in the gulf maybe through uptake by microbial biota (e.g. Berman, 1988; Stepanauskas et al, 2002) and possibly by phytoplankton (Rose & Axler, 1998). The gulf exported an average of 82 t/d of DRSi to the channel but in contrast, the channel (at KL5) exported only 10 t/d DRSi to the main lake. This low DRSi flux between the channel (at KL5) and the main lake is likely due to uptake by diatoms (e.g. Sommer & Stabel, 1983) or possibly a model artifact due high mixing at KL5 with low DRSi water from the main lake.

The gulf was a net sink of both dissolved phosphorus and nitrogen whereas the channel was net producer of nitrogen, phosphorus and silica (Fig. 3.9). The assumption made in the calculation of nonconservative nutrient fluxes was that production ($+\Delta Y$) is due to biological mineralization of particulate and dissolved organic matter and respiratory release by living organisms, and consumption ($-\Delta Y$) is through biological (mainly phytoplankton) uptake (Gordon et al. 1996). The consumption of nutrients in the gulf is through phytoplankton uptake, reflected in the relatively high net ecosystem metabolism (Fig. 3.10) and the relatively high algal biomass in the gulf (Chapter 5), whereas nutrient production in the channel is likely from microbial mineralization of the suspended particulate and dissolved organic matter (e.g. Wallin & Hakason, 1992). The biogeochemical differences in the two zones (Gulf and Channel) can be attributed to the unique morphological characteristics and physical processes in the two zones (Chapter 2).

In the channel, mixing and horizontal exchange processes (Chapter 2) result in resuspension and entrainment of particulate organic matter (Chapter 4) which are mineralized by heterotrophic bacteria in the water column, resulting in production of DOP and DON, which are subsequently mineralized to release SRP and NH_4 (Fig. 3.11). Part of the NH_4 is

oxidized to NO_3 by nitrifying bacteria as earlier discussed. The SRP that was released during microbial mineralization of the organic matter may have contributed to the observed relatively constant SRP concentration along the channel (Fig. 3.3) despite the significantly high concentration gradient between the gulf and the main lake; other nutrient fractions with relatively higher concentration in the gulf compared to the main lake followed a decreasing trend along the channel towards the main lake (e.g. TN, DON and DRSi; Fig. 3.3).

3.4.5 Ecosystem metabolism

The difference between the gulf and the channel is further reflected in the derived NEP (p-r; Fig. 3.10). The gulf showed net autotrophy with a high average net productivity of $566 \text{ mg C/m}^2/\text{d}$, whereas the channel (except in CG5 and KL5) showed net heterotrophy (NEP, -51 to $-11 \text{ mg C/m}^2/\text{d}$). The high autotrophy in the gulf implies high production over respiration and is reflected in the observed net consumption of inorganic nutrients in the gulf (Fig. 3.9). The channel is deeper than the gulf which, together with the observed high physical activity, makes it more light limited (Silsbe et al, 2006) leading to respiration dominating over production. Results of nitrogen metabolism (nfix-denit) showed that nitrogen fixation dominates over denitrification both in the gulf and in the channel (except KL5) (3 - $15 \text{ mg N/m}^2/\text{d}$; Fig. 3.10). This high nfix-denit in the gulf and the channel is in congruence with the reported high nitrogen fixation in the inshore areas of Lake Victoria (Mugidde et al 2003). Mugidde et al reported nitrogen fixation rates of between 30 and $56 \text{ mg N/m}^2/\text{d}$ in the inshore areas of northern Lake Victoria. Assuming Nyanza Gulf to have similar nitrogen fixation rates as those measured by Mugidde, denitrification rates in the gulf and the channel can be estimated to range between 15 and $53 \text{ mg N/m}^2/\text{d}$. Seitzinger (1988) reported denitrification rates of between 2.8 and $27 \text{ mg N/m}^3/\text{d}$ for low oxygen hypolimnia in lakes. Using these volumetric rates, areal rates for inner-gulf (mean depth, 4.6 m ; Table 2.1) can be estimated to range from 13 to $122 \text{ mg N/m}^2/\text{d}$ and therefore the box model appears to give reliable estimates of nfix-denit rates.

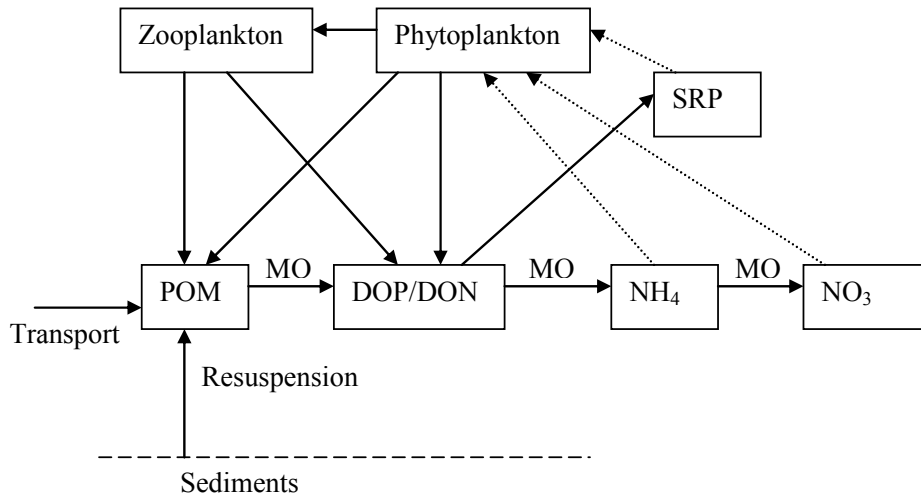


Figure 3.11 Major biogeochemical processes contributing to the net production of nutrients in the Rusinga channel. MO represents microorganisms. The solid arrows show the direction of net production while broken arrows represents uptake.

3.4.6 Predicting impact of phosphorus management on gulf environment

The gulf receives more than two-thirds of external N and P input from the river inflows and municipal effluent (LVEMP, 2001), both of which are related to human activities in the gulf catchment and can therefore be reduced through application of proper intervention measures. The box model was used to test the impact of phosphorus loading management on the gulf ecosystem metabolism. After applying a scenario where P loading from municipal effluent was reduced by 70% and P loading through river inflows was reduced by 50% to the box model, NEP (p-r) was found to reduce by at least 30% (Fig. 3.12). Assuming that this reduction in NEP will translate to proportional reduction in phytoplankton biomass, then the impact of P reduction on water transparency can be inferred from chlorophyll-water transparency relationship reported by Gikuma-Njuru & Hecky (2005):

$$\ln(SD) = -48.1Chll + 5.8 \quad (4)$$

Using a pre-management chlorophyll concentration of 31 $\mu\text{g/L}$ (Gikuma-Njuru & Hecky, 2005), then from Eq. 4, the gulf water transparency (Secchi depth) would increase from the 0.7m to 1.1m after reduction of P loading. The associated benefits from the improvement in water transparency will translate to improved water quality for domestic and recreational purposes, improved fish yield and species diversity and overall restoration of Lake Victoria ecosystem (Witte et al, 2005).

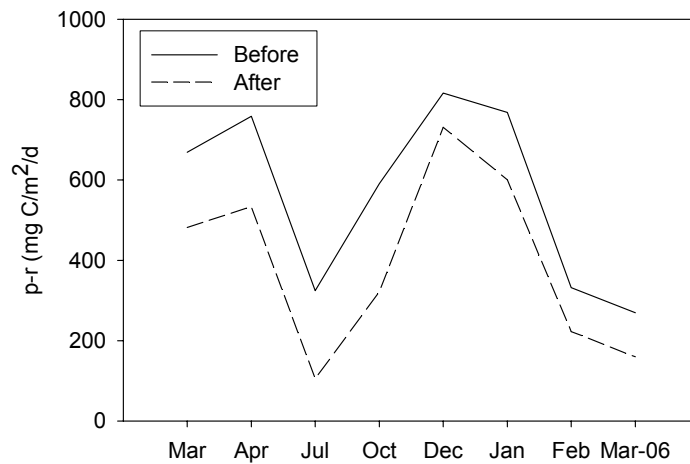


Figure 3.12 Net ecosystem metabolism (NEP, p-r) in the gulf before and after reduction of P loading. P loading from municipal effluent sources was reduced by 70% and input from river inflows was reduced by 50%.

The reduction of P loading from municipal effluent can be accomplished through rehabilitation and expansion of Kisumu City effluent treatment facility, which currently does not function, whereas that from river inflows can be accomplished through implementation of sustainable landuse practices and catchment reforestation; both of these management approaches are in various stages of implementation (LVEMP, 2005). Tertiary effluent treatment can reduce TP concentration by more than 90 % (Luederitz et al, 2001) and therefore the 70% reduction can easily be accomplished. Reduction of external phosphorus loading P loading has been a successful management tool in restoration of many previously eutrophic lakes with Lake Washington, USA, and North American Great Lakes being excellent examples (Wetzel, 2001).

Chapter 4

Spatial variation in surficial sediment phosphorus fractions and possible role in phosphorus recycling and internal loading

4.1 Introduction

Phosphorus entering aqueous environment is usually in different forms, including: crystalline, occluded, adsorbed, particulate organic, soluble organic and soluble inorganic phosphorus (Schaffer and Oglesby, 1978). The particulate form normally settles to the bottom or can be mobilized only through microbial activity and physical or chemical dissolution. In the sediments, phosphorus can be transformed and redistributed among the various chemical fractions according to biological activity, redox conditions, and pH (Holtan et al 1988). Its remobilization from sediments is dependent on the chemical fraction present and the other physical and chemical properties of the sediment (Kalf, 2002).

Study of phosphorus biogeochemistry in soils and in sediment of aquatic environments normally involves partition of the phosphorus pool into its labile and refractory components in order to determine its bioavailability (Bostrom et al., 1988; Levy and Schlesinger 1999). A number of sequential fractionation procedures have been developed (e.g. Williams et al, 1976; Hieltjes & Lijklema, 1980; Hedley et al, 1982; Ruttenburg, 1992 and Ruban et al, 2001) and used to characterize phosphorus in soil and sediment. The most widely used method (or its modification) is the Williams method (Williams et al., 1971, 1976), a modification of which has been developed and adopted by the European Union laboratories as a harmonized protocol for the determination of extractable contents of phosphorus in freshwater sediments (Ruban and Demare, 1998; Pardo et al 2001). This method, which has been used in this study, uses NaOH and HCl to sequentially extract different phosphorus fractions, namely: the apatite phosphorus (AP) fraction, which consists of orthophosphate present in crystal lattices of apatite grains and is normally considered unavailable; the non-apatite inorganic phosphorus (NAIP), which is associated with oxides

and oxyhydroxides of Al, Mn and Fe and is considered available; and the organic phosphorus which consists of all phosphorus associated with carbon atoms via C-O-P or C-P bonds, and is normally available to biological processing.

Most past studies in Lake Victoria have mainly focused on phosphorus concentration in the lake water column and possible relationship with external input (Talling, 1966; Kilham and Kilham; 1990; Lungayia et al, 2001; Guildford et al 2003; Gikuma-Njuru and Hecky, 2005; Tamatama et al., 2005). However, the dramatic ecosystem changes, including increased eutrophication, that have taken place in Lake Victoria in the past 5 decades have lead to increased interest in sedimentation processes and possible role of bottom sediments in nutrient recycling in the lake (Hecky, 1993; Hecky et al., 1996; Holtzman & Lehman, 1998; Vershuren et al., 1998, 2002). Analysis of phosphorus in sediment cores retrieved from an offshore station has shown evidence of increased phosphorus sedimentation in Lake Victoria in the past 4 decades (Hecky, 1993; Hecky, unpublished data). The reported high phosphorus concentration in the open waters of Lake Victoria (Hecky, 1993) has been associated with increased chemical weathering of eroded particulates due to land use changes in the lake catchment over the last century (Holtzman & Lehman, 1998).

The purpose of this study is to characterize different phosphorus fractions in the surficial sediments along a biogeochemical gradient between Nyanza (Winam) Gulf, a large shallow bay influenced by river input and the main lake in northeastern Lake Victoria, in order to assess the potential role of sediment phosphorus in contributing to the increasing P concentrations in Lake Victoria.

4.2 Methods and Materials

4.2.1 Study area

The study was carried out in the northeastern Lake Victoria between 34° 08.85' and 34° 55.30'E and between 0° 18.50' and 0° 20.81' S at 1143m asl (Fig. 4.1). The area has three morphologically distinctive areas, namely the main lake (mean depth 40m); the shallow, wide and elongated Nyanza gulf (surface area 1400 km², mean depth 10m,

maximum width 30km and length 50km); and the narrow and deep Rusinga Channel (minimum width 5km, depth between 12 and 39m), which connects the gulf and the main lake and is a zone of dynamic exchange between the gulf and the main lake. Several rivers drain into the Nyanza Gulf from the southeast, with an annual discharge of 2.4 km³ and carry with them high loads of suspended sediments and nutrients from their highly intensive agricultural catchments and industrial and municipal sources (Lungayia et al 2001, Calamari et al, 1995; LVEMP, 2005a). The hydrological and morphometric characteristics of Lake Victoria and Nyanza Gulf are presented in detail by Crul (1995); Bootsma & Hecky (1993) and Gikuma-Njuru and Hecky (2005).

Six stations, located along a transect between the Nyanza Gulf and the main Lake Victoria (Fig. 4.1), were sampled on three different occasions: June and September 2005 and February 2006. Sediment samples were collected using an Eckman Dredge sampler and the top (about 2cm) sediment was taken and transported to the laboratory, where it was dried in an air circulating oven at 80°C. The dried sediment was ground and preserved in airtight glass vials during transportation to the University of Waterloo laboratories for analysis. Sequential extraction of different phosphorus fractions was carried out using the method described by Ruban et al (2001) and Pardo et al (2003), which separates sedimentary associated phosphorus into four categories, namely the non-apatite inorganic phosphorus (NAIP), the apatite phosphorus (AP), inorganic phosphorus (IP), organic phosphorus (OP) and total phosphorus (TP). The method (hereinafter referred as the EU protocol) is derived from that used by Williams et al (1976), with the main difference being that only one extraction for NAIP is done whereas in Williams method the fraction is extracted in two different steps. The detailed description of the procedure is given in Ruban et al (2001) and Pardo et al (2003) and only a general outline will be described here. The extraction is done in three separate steps, each involving sequential extractions to separate different fractions from a 0.2 g sediment sample as follows:

To extract NAIP and AP fractions, the sample is extracted with 20 mL 1 molar NaOH with shaking for 16 hrs at room temperature. After centrifuging for 5 minutes at 1200 rps, the supernatant is separated from the residue and 4 mL of 3.5 molar HCl is added to 10 mL of

supernatant and allowed to settle for 16 hrs and after centrifuging NAIP is analyzed in the resultant supernatant. The residue from the first step is extracted using 20 ml 1 M HCl, shaking for 16hrs and after centrifuging AP is analyzed in the supernatant.

In the second extraction, the sample is extracted using 20 mL, 1 M HCl shaking for 16 hours and after centrifuging IP is analyzed in the supernatant. The residue is calcinated for 1 hour at 450 C and then extracted with 20 mL, 1 molar HCl shaking for 16 hours and after centrifuging OP is analyzed in the extract.

TP in the sample is extracted directly from the sample after calcination for 3 hours at 450 C using 20 mL, 3.5 M HCl, shaking for 16 hrs at room temperature.

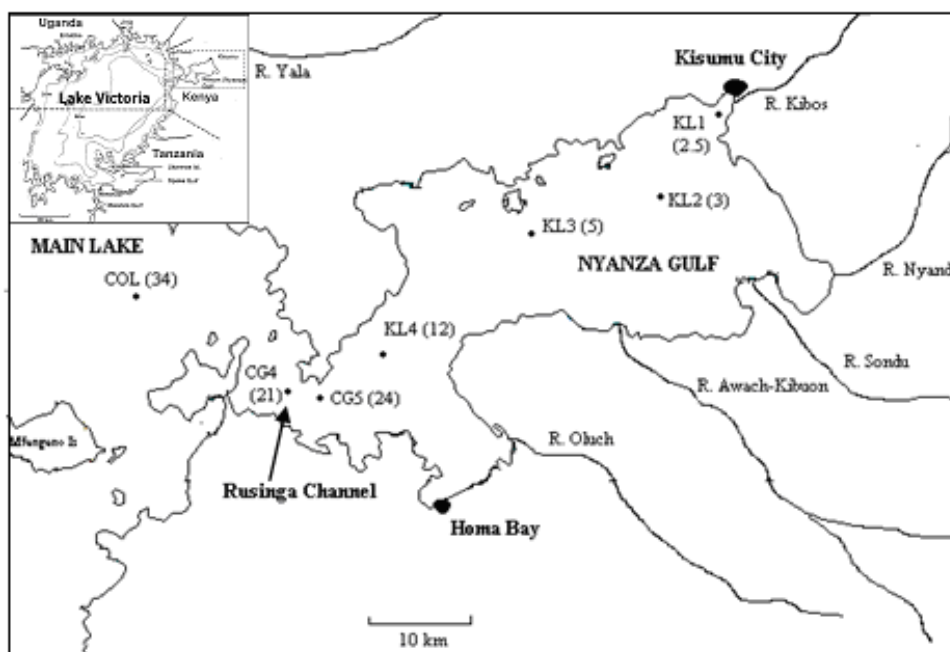


Figure 4.1 Map of Lake Victoria (inset) and the study area showing location of the sampling stations and depth (in parenthesis) in the Nyanza Gulf (KL1, KL2, KL3 and KL4), Rusinga Channel (CG4) and the main lake (COL), river tributaries and major towns. The station CG5 was not sampled because the bottom had no fine sediment but only a rocky surface and pebbles

Analysis of phosphate in the extracts was done according to APHA (1995) using the ascorbic acid method after necessary dilutions. All the samples required a 20 to 40 times

dilution and therefore pH adjustment was not necessary. Total organic carbon and nitrogen was analyzed using a Carbon-Nitrogen Analyzer, Model CE 440 Elemental Analyzer (Exeter Analytical, Inc.). Metal ions in the NAIP extract were analyzed using atomic absorption spectroscopy.

Elemental composition in the sediment was analyzed using ITRAX micro-X-ray fluorescence (XRF) core scanner (Cox Analytical System). Samples were packed in cuvettes and arranged on a piece of wood in a way to resemble a sediment core, since the scanner normally analyzes whole sediment cores, and the data for each sample was delineated using the X-ray scan characteristics of cuvette walls. The X-ray scanner gives relative element content.

Lake water samples were collected near the surface (approximately 1 Secchi depth) using a 5L van Dorn sampler and a known volume was immediately filtered through pre-combusted, pre-weighed GFF filters for the analysis of particulate phosphorus (PP) and the filtrate preserved at about 4 °C in cool boxes during transportation to Kisumu laboratory where soluble reactive phosphorus (PO₄-P) was immediately analyzed. The filters were dried in an air circulating oven at 105 °C for 24 hrs and after weighing to obtain a measure of Total Suspended Solids (TSS) the filters were combusted at 550 C and particulate phosphorus (PP) was extracted using the persulfate method (APHA 1995). For analysis of total phosphorus (TP), a known volume of the water sample was digested using ammonium persulfate in an autoclave for 30 min at 137 kPa. The concentration of phosphorus in all the fractions was analyzed using the ascorbic acid method as described in APHA (1995). During the February 2006 sampling, water samples were collected near the mouths of the inflowing rivers (Fig. 1) and TSS and PP in the river water was analyzed together with the lake water samples. Suspended particulate phosphorus concentration per unit dry weight (SP) in the lake and river water was calculated using PP and TSS values and was used to compare water column PP with the sediment P content.

Temperature, dissolved oxygen (DO) and pH in the water column were measured using a multiprobe, Hydrolab[®] Sonde with a Surveyor 2a[®] meter readout.

Five surficial sediment samples from four different North American Lakes were obtained from the National Laboratory for Environmental Testing (NLET), Burlington, Canada and analyzed together with the Lake Victoria samples. The samples had been pre-analyzed at NLET using the Williams extraction method and therefore it was possible to assess how this method compares with the EU harmonized protocol, used for Lake Victoria samples.

The station CG5 (Fig. 4.1) was not sampled, since the bottom had no fine sediment but only a rocky surface and pebbles and therefore no results will be reported but the station will be referred to in the discussion section.

4.3 Results

4.3.1 Comparison of extraction methods

The EU harmonized method was found to be highly reproducible in triplicate samples and also in samples collected from the same stations at different dates. The method was also found to be efficient in extracting different fractions, since the sum of different fractions agreed with the total (AP and NAIP with IP, and IP and OP with TP) within 0.1 to 5%. The concentration of phosphorus fractions in the North American lakes, extracted using the EU protocol and that of the Williams, showed that the two methods were comparable in extraction of TP and IP but differed to varying degrees in the extraction of AP, NAIP and OP (Table 4.1). NAIP extracted using the Williams protocol was higher than that extracted using EU protocol but AP extracted using the Williams method was lower than that obtained using the EU protocol. Observation of Table 4.1 shows that the two protocols vary in the ability to differentiate between AP, NAIP and OP fractions.

Table 4.1 Concentrations (mg/kg DW) of P fractions in surficial sediments from North American lakes as analyzed using the EU protocol. The samples had earlier been analyzed using the William’s method at NLET. The values in the parenthesis are the % deviations of EU values from the William’s values; a -ve % value indicates values lower than those obtained through Williams method whereas a +ve % value indicate higher values than those obtained through Williams method.

| | TP | AP | NAIP | OP | IP |
|-------------------|---------------|--------------|---------------|--------------|--------------|
| L. Ontario (E-30) | 1357.1 (18.6) | 494.3 (57.4) | 411.4 (-34.9) | 295.7 (40.8) | 920.0 (-1.5) |
| L. Ontario WB | 1342.9 (4.1) | 537.1 (47.2) | 448.3 (-24.9) | 388.6 (28.2) | 972.9 (-1.4) |
| Perch Lake | 1165.7 (0.3) | 470.0 (54.1) | 422.9 (-34.9) | 301.4 (42.9) | 980.0 (3.0) |
| L. Erie | 365.7 (-3.0) | 331.4 (1.0) | 8.6 (-72.3) | 28.6 (>100) | 365.7 (-2.5) |

4.3.2 Water quality properties

Lake water quality properties varied horizontally along the study transect and vertically in the water column (Fig. 4.2, Fig. 4.3). Temperature ranged from 24.40 to 28.21 °C with KL1 having the highest average temperature. Dissolved oxygen ranged from 0.71 to 10.98 mg/L and anoxic conditions were observed below the thermocline at COL in the main lake in September, when strong thermal stratification was occurring. Water column pH ranged from 7.79 to 10.27 and relatively lower values were observed at the Rusinga Channel station, CG4, compared to the other stations.

Total phosphorus (TP) concentration ranged from 86.3 to 242.7 µg/L and was higher in the river-influenced eastern gulf area (KL2) than the rest of the study area where it varied with an increasing trend between KL3 and COL. Orthophosphate (PO₄-P) concentration increased along the study transect, between KL2 and COL, from 15.3±6.0 to 41.9±0.9 µg/l but particulate phosphorus (PP) showed an opposite trend, decreasing from 43.2±20.9 to 23.2±6.1 µg/L (Fig. 4.3c). The contribution of PO₄-P to TP varied between 20 and 43 % with COL having the highest % contribution and KL2 having the lowest % contribution. PP accounted for between 24 and 34 % of TP with the eastern gulf stations (KL1-KL3) having

higher values (32 to 38 %) compared to the channel and main lake stations (CG4 and COL; 28 and 24 % respectively).

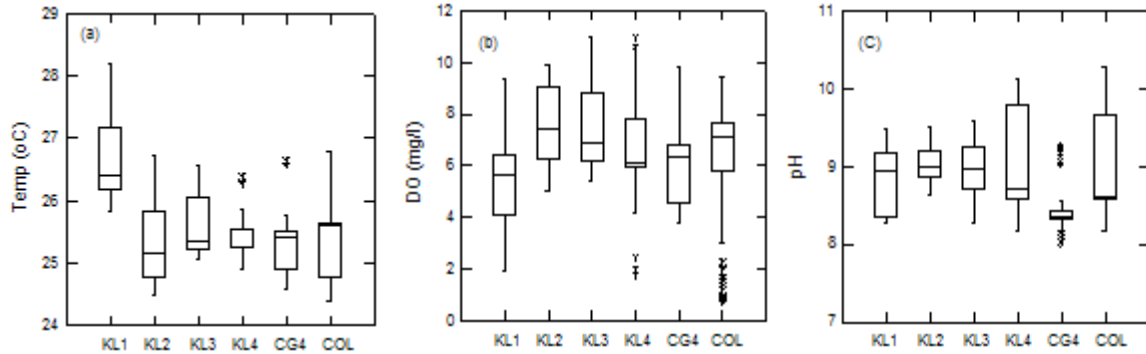


Figure 4.2 Box plots of (a) Temperature ($^{\circ}\text{C}$) (b) Dissolved oxygen (DO ; mg L^{-1}) and (c) pH for profiles taken in June and September 2005 and February 2006 in different stations along the study transect

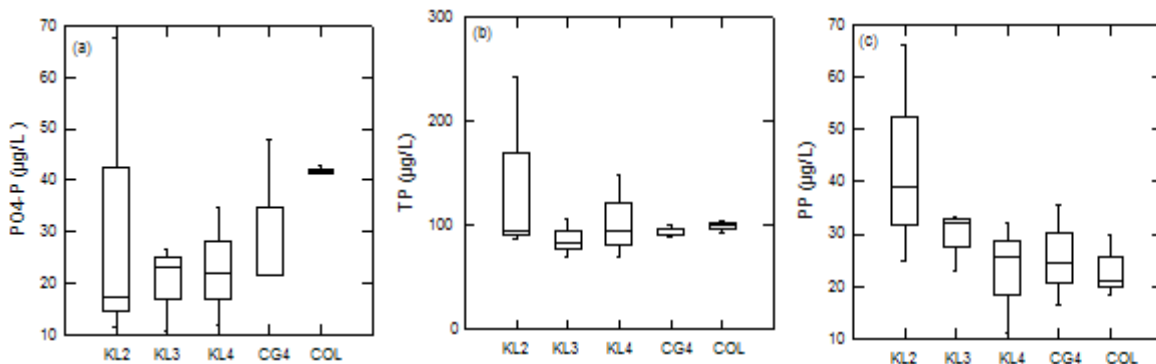


Figure 4.3 Box plots of phosphorus fraction concentration in the water column along the study transect: (a) Orthophosphate ($\text{PO}_4\text{-P}$; $\mu\text{g/L}$), (b) Total phosphorus (TP ; $\mu\text{g/L}$) and (c) Particulate phosphorus (PP ; $\mu\text{g/L}$). Data is based on samples collected in June and September 2005 and February 2006. KL1 is not included due to missing data for one of the dates.

The concentration of phosphorus in suspended sediment per dry weight (SP) increased along the gulf-main-lake transect from 1128.8 mg/kg DW in KL1 to 6800 mg/kg DW in COL (Fig. 4.4). In contrast, total suspended sediment (TSS) decreased along the transect, from 61.2 mg/L in KL1 to 3.3 mg/L in COL. The river tributaries had relatively lower SP concentration (689 mg/kg DW) compared to the lake water column (Fig. 4.4). Particulate carbon (PC) ranged from 1.1 ± 0.6 to 6.9 ± 0.5 mg/L and followed the same trend as

PP. KL1, located near Kisumu City and the Kibos River, had higher average TP, PP and PC concentrations than the other stations (222.5 $\mu\text{g/L}$, 79.5 $\mu\text{g/L}$ and 6.9 mg/l respectively).

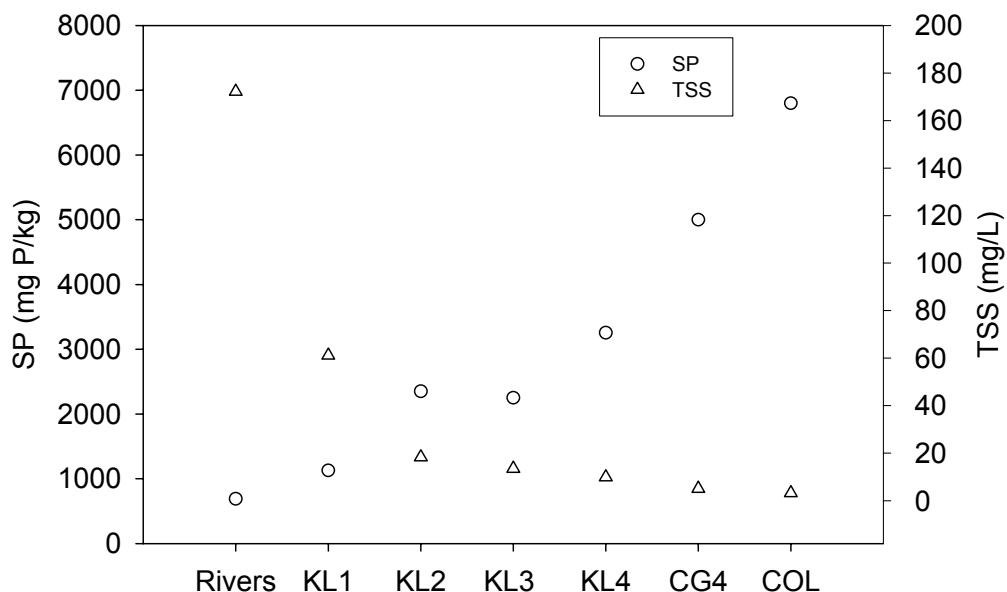


Figure 4.4 Average concentrations of suspended sediment phosphorus (SP) and Total suspended sediment (TSS) in the inflowing rivers and in the lake (KL1 to COL). The SP concentration was calculated from TSS and PP concentrations. Lake samples were collected in June and September 2005 and February 2006 and the samples for the rivers are for February 2006.

4.3.3 Surficial sediment fractions

The concentration of different phosphorus fractions in the surficial sediment varied differently along the study transect (Fig. 4.5). AP increased between KL1 and CG4, from 299.1 ± 19.8 to 947.6 ± 16.5 mg/kg DW, and then decreased to 593.3 ± 37.4 mg/kg in the main lake. TP followed the same trend, increasing approximately 2-fold between KL1 and CG4, from 812.7 ± 48.9 to 1738 ± 11.8 mg/kg, before declining to 1330.5 ± 10.6 mg/kg at the open lake station. NAIP followed the trend as TP and AP with the channel station CG4 having highest value of 306.0 ± 17.7 mg/kg. In contrast, OP and LOI increased continuously between the gulf and the main (Fig. 4.5e & f).

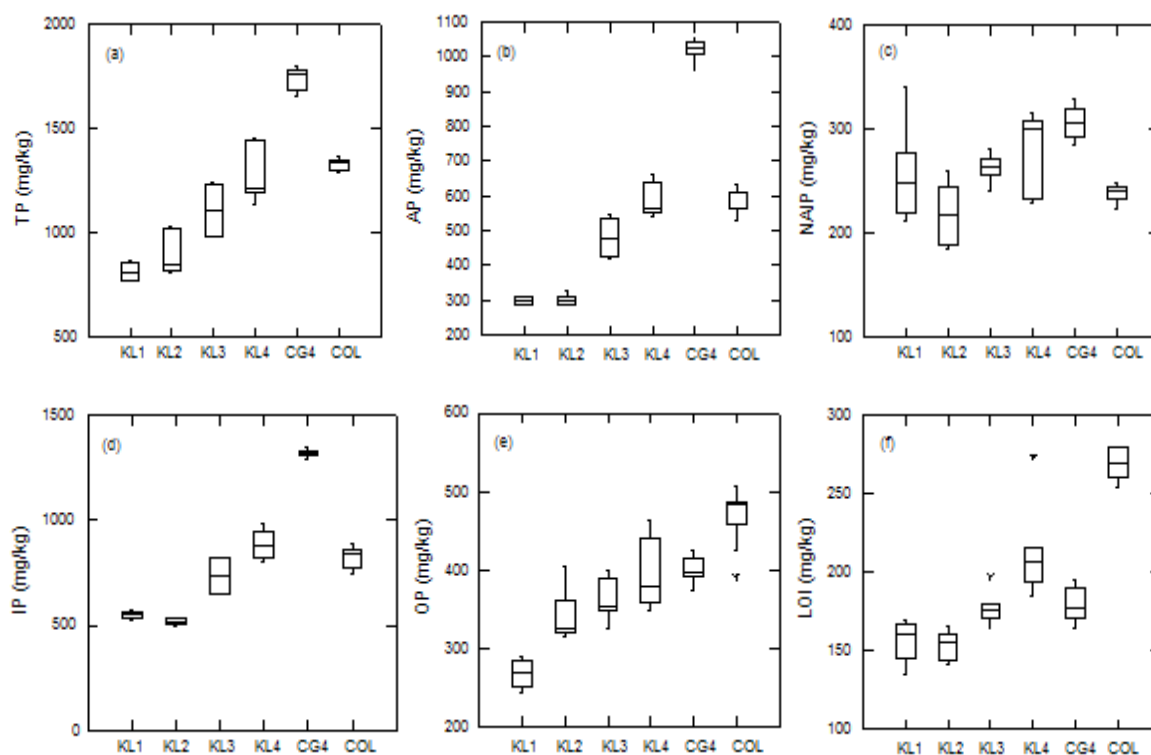


Figure 4.5 Box plots for different surficial sediment phosphorus fractions and loss on ignition (LOI) in the gulf (KL1 – KL4), channel (CG4 and KL5) and in the main lake (COL): (a) TP (total phosphorus); (b) AP (apatite phosphorus); (c) NAIP (non-apatite inorganic phosphorus); (d) IP (inorganic phosphorus); (e) OP (organic phosphorus); and (f) LOI

Trends were observed in the contribution of different P fractions (OP, AP and NAIP) to the TP in the sediment (Fig. 4.6). NAIP contributed between 18.2 and 31.2% of TP and AP contributed between 35.0 and 57.3% of TP and both fractions (NAIP and AP) varied with opposite trends along the study transect, with % of AP increasing towards the main lake and that of NAIP following a decreasing trend towards the main lake. The contribution of OP to TP varied between 24.2 and 39.6% but showed no monotonic trend. The channel station, CG4 had the lowest contribution of OP and highest contribution of AP to TP (24.2 and 57.3% respectively).

TP constituted between 0.08 and 0.18% of the sediment dry weight (DW), with a higher contribution observed in the channel compared to the gulf and main lake zones (0.08-0.13 and 0.13 % respectively). Organic carbon content constituted between 5 and 15% of the sediment DW and nitrogen contributed between 0.6 and 1.4%. The sediment carbon to

phosphorus molar ratios were higher than the Redfield value of 106 (Redfield, 1963), ranging from 122.5 ± 18.8 to 279 ± 10.0 , but the nitrogen to phosphorus ratios were close to the Redfield ratio (16) except in the main lake where a higher value of 23.7 ± 1.1 was recorded (Table 4.2). The channel station (CG4) had relatively lower C and N to P ratios (122.5 ± 1.1 and 11.9 ± 1.2 , respectively) compared to other stations indicating enhanced P enrichment of bottom sediment in this dynamic zone compared to other study zones.

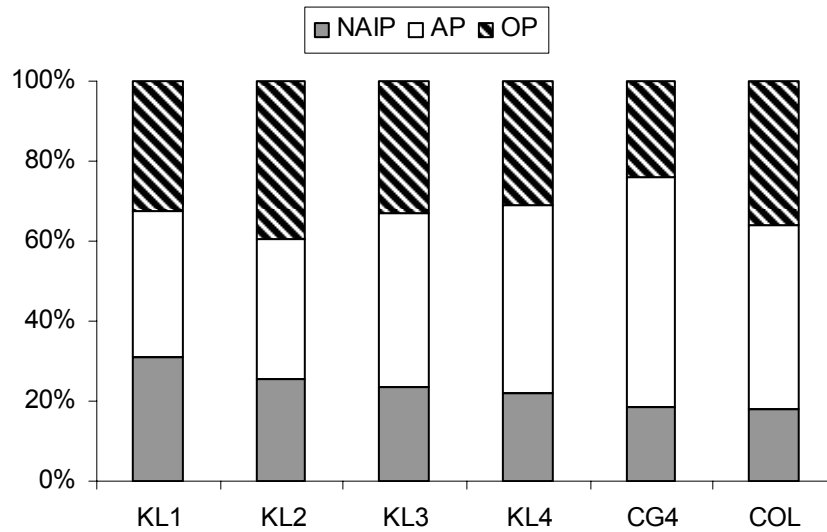


Figure 4.6 Distribution of forms of phosphorus (NAIP, non apatite inorganic phosphorus; AP, apatite phosphorus; OP, organic phosphorus) in sediment for different stations along the gulf-main-lake transect.

Table 4.2 Sedimentary carbon (C), nitrogen (N) and phosphorus (P) concentrations and molar ratios of P to N and C along the study transect. Values in the parenthesis are the standard deviations

| | KL1 | KL2 | KL3 | KL4 | CG4 | COL |
|-----------|-------|------------|-------------|-------------|-------------|-------------|
| C (g/kg) | 66.6 | 52.8(3.4) | 72.4(0.2) | 92.5(6.2) | 82.1(10.1) | 143.7(14.2) |
| N (g/kg) | 6.6 | 6.4(0.6) | 8.8(0.04) | 10.8(0.6) | 9.3(0.6) | 14.2(0.3) |
| P (mg/kg) | 813 | 896(102) | 1107(144) | 1275(136) | 1737(57) | 1331(31) |
| C:P | 212.3 | 152.9(9.1) | 171.4(28.0) | 189.9(32.9) | 122.5(18.8) | 279.3(10.0) |
| N:P | 18.0 | 16.0(0.5) | 17.8(2.8) | 18.9(3.1) | 11.9(1.2) | 23.7(1.1) |

The Pearson correlations between different sediment and water column fractions showed both positive and negative correlation between some P fractions (Table 4.3). AP was strongly correlated with IP, OP and TP in the sediment, indicating the importance of AP to these P fractions in the lake sediment (Fig. 4.6). Organic carbon content in the sediment was the most important characteristic accounting for over 36% of variability in TP, AP, and OP. Particulate phosphorus (PP) in the water column was negatively correlated with all the sediment fractions, and was positively correlated with the water column TP and PO₄-P. Station depth was significantly correlated with all sediment fractions except NAIP. There was no significant correlation between the TP and PO₄-P concentration in the water column and the sedimentary P fractions, except water column TP and sediment OP which were significantly correlated. Sedimentary nitrogen (N) was significantly correlated to the suspended sediment P (SP) and both N and SP were significantly correlated to all sediment fractions, except NAIP. SP had significant negative correlation with water column TP and PP but showed no correlation with PO₄-P.

Table 4.3 Pearson correlation coefficients (r-critical=0.576, 95% CI; n=12) between different phosphorus fractions in the water column and in the sediments and station depth. Correlation was done after log-transformation. Highlighted values are those with significant correlation ($P < 0.05$). Samples for June 2005 were excluded due to missing data on some stations.

| | Depth | PO ₄ * | TP* | PP* | SP* | NAIP | AP | TP | OP | IP | C |
|-------------------|--------------|-------------------|---------------|---------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| PO ₄ * | 0.411 | | | | | | | | | | |
| TP* | -0.313 | 0.532 | | | | | | | | | |
| TPP* | -0.478 | 0.355 | 0.677 | | | | | | | | |
| SP* | 0.844 | 0.051 | -0.660 | -0.628 | | | | | | | |
| NAIP | 0.096 | 0.206 | 0.119 | -0.144 | 0.021 | | | | | | |
| AP | 0.705 | 0.281 | -0.432 | -0.615 | 0.691 | 0.583 | | | | | |
| TP | 0.688 | 0.107 | -0.506 | -0.632 | 0.717 | 0.634 | 0.952 | | | | |
| OP | 0.758 | -0.099 | -0.663 | -0.716 | 0.815 | 0.238 | 0.672 | 0.746 | | | |
| IP | 0.588 | 0.223 | -0.350 | -0.549 | 0.579 | 0.676 | 0.959 | 0.952 | 0.531 | | |
| C | 0.930 | 0.524 | -0.119 | -0.390 | 0.705 | 0.175 | 0.680 | 0.602 | 0.693 | 0.530 | |
| N | 0.900 | 0.343 | -0.303 | -0.538 | 0.769 | 0.252 | 0.752 | 0.697 | 0.829 | 0.591 | 0.961 |

Legend: *Water column fractions; PO₄, orthophosphate; TP, total phosphorus; PP, particulate phosphorus in µg/L; SP, suspended sediment phosphorus in mg/kg; NAIP, non-apatite inorganic phosphorus; AP, apatite phosphorus; OP, organic phosphorus; IP, inorganic phosphorus; C, sedimentary organic carbon; N,

4.3.4 Elemental composition

Table 4.4 gives the concentration (mg/kg DW) of metal ions (Fe, Mn and Al) extracted together with NAIP fraction. Unlike NAIP concentration, which varied with defined trend along the study transect (Fig. 4.5c), concentration of metal ions varied between stations but with no defined pattern (except for Mn). Mn concentration increased from 2.07 mg/kg in KL1 to 4.72 mg/kg in COL. Fe concentration ranged from 38.5 to 53.8 mg/kg and Al concentration ranged from 215 to 295.0 mg/kg.

Table 4.4 Metal ion concentrations in the NAIP fraction extract

| | Al(mg/kg) | Fe(mg/kg) | Mn (mg/kg) |
|-----|-----------|-----------|------------|
| KL1 | 259.0 | 45.3 | 2.07 |
| KL2 | 257.0 | 38.5 | 2.87 |
| KL3 | 251.5 | 46.3 | 2.38 |
| KL4 | 275.0 | 52.4 | 3.14 |
| CG4 | 215.0 | 39.4 | 3.68 |
| COL | 295.5 | 53.8 | 4.72 |

Total phosphorus content, analyzed using the X-ray fluorescence scanning method, was highly correlated with calcium (Ca) content, with the latter accounting for >90% of TP variability in the sediment (Fig. 4.7) and over 98% of variability in the apatite phosphorus extracted using the EU protocol. Al and Fe showed strong negative correlation with TP, but Mn was not correlated with TP (Fig. 4.7 b to d). The Ca to P molar ratios in sediment samples (excluding COL) were between 1.5 and 1.8, which is close to that of apatite minerals ($\text{Ca}_5(\text{PO}_4)_3$). The main lake station, COL, had relatively low Ca to P ratio (0.95), indicating higher P enrichment relative to Ca and reduced association of apatite and phosphorus compared to other stations.

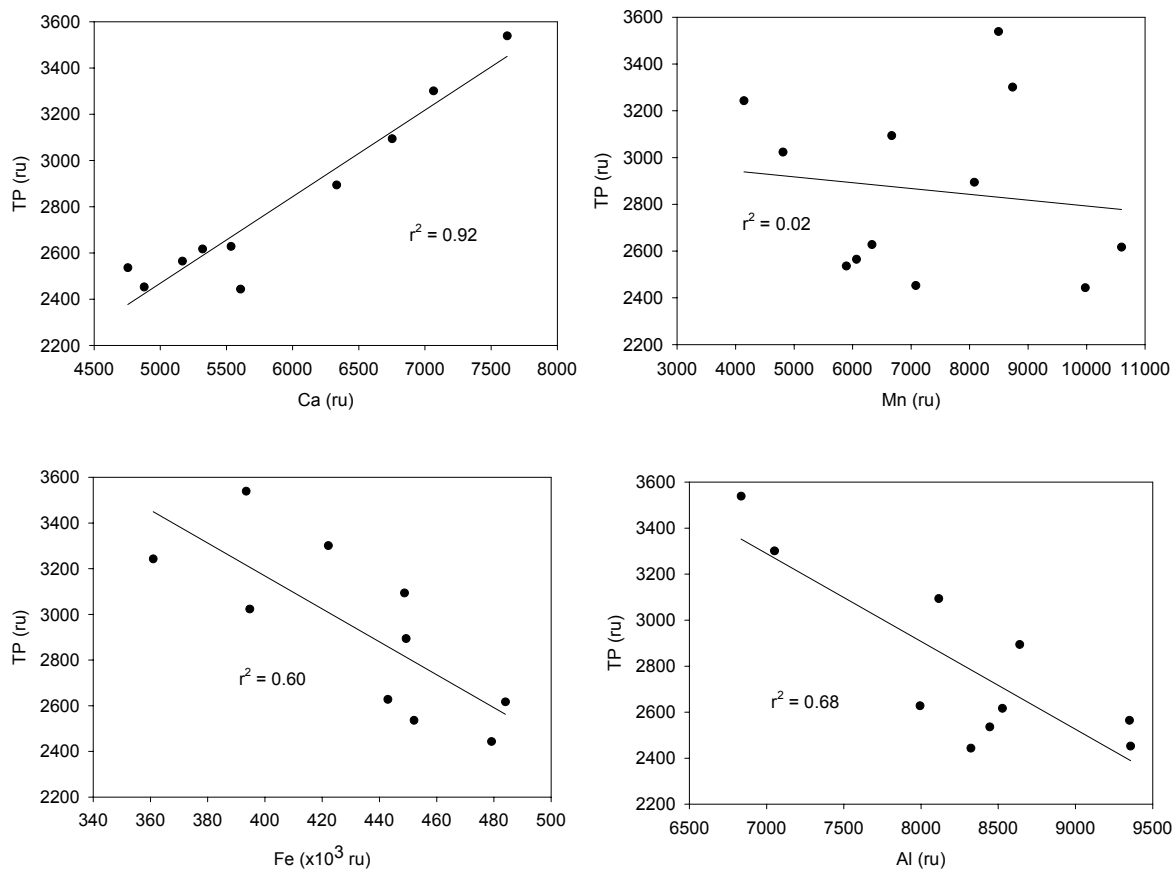


Figure 4.7 Relationship of total phosphorus (TP) as measured by X-ray fluorescence and different ions (Ca, Mn, Fe, Al) in the sediment. Main lake station (COL) is not included in Ca-P and Al-P relationships and KL1 is not included in Fe-P relationship as they were outliers

4.4 Discussion

Lake Victoria occupies a unique position among the African and world great lakes due to its high nutrient concentrations, relatively shallow depth and associated high algal productivity and biomass (Hecky & Bugenyi, 1992; Botsma & Hecky, 1993; Hecky, 2000). The relatively high algal productivity in Lake Victoria is reflected in the observed high seston phosphorus (PP) in the lake (Fig. 4.3c). This high PP concentration in Lake Victoria will result in high P sedimentation and consequent P enrichment of the bottom sediments (Hecky, 1993). The sedimented phosphorus may be permanently buried or may undergo biological and chemical mineralization to $\text{PO}_4\text{-P}$ which is recycled back into the water

column (Reynolds & Devies, 2001) and hence closing the loop between the water column and the bottom sediments.

4.4.1 Phosphorus in lake sediments

According to Holtan et al (1988), concentration of total phosphorus in natural lake sediments varies from approximately 10 mg/kg DW in sandy coastal sediment to about 10,000 mg/kg DW in iron and carbonate rich gyttja. The concentration range observed along the current study transect (770-1796 mg/kg DW) is in the lower range of Holtan but is within the range reported for other large lakes. Williams et al (1976) reported TP concentrations ranging from 188 to 2863 mg/kg in both offshore and highly impacted inshore stations in Lake Erie. The the two samples from Lake Ontario, which were analyzed together with the Lake Victoria samples, had a mean TP value of 1342 mg/kg DW (Table 4.1). OP concentration in Lake Victoria was higher than values by Williams (1976) reported for Lake Erie (0-286 mg/kg), consistent with higher phytoplankton biomass in Lake Victoria compared to Lake Erie (6.9-21.1 and 3.9-5.3 $\mu\text{g Chl}/\text{L}$ respectively; Gikuma-Njuru et al. 2005b; Smith et al. 2005).

4.4.2 Spatial gradients

Phosphorus in surficial sediments showed a well defined gradient along the study transect with TP, OP and AP concentrations increasing along the gulf into the main lake (Fig. 4.5). A similar increasing trend of TP was reported by LVEMP (2005b), from about 784 to 1407 mg/kg between KL1 and KL4. Higher TP values (2628-2773 mg/kg; Hecky et al, unpublished data) have been reported in a more offshore (about 60 km from nearest shoreline at depth of >65m) Lake Victoria station, V-96-5 (see Verschuren et al 2002 for location), an indication that the observed increasing trend may continue into the deep offshore areas.

The observed inshore to offshore increase of sedimentary phosphorus fractions and total concentration can most likely be associated with physical processes which act to resuspend and transport lighter colloidal and organic matter from shallow areas to deeper offshore areas. Norges and Kisand (1999) found twice as much TP in the depositional central and southern parts of Lake Vortsjarv, a shallow eutrophic lake in Estonia, compared to

northern erosional parts. Rusinga Channel, the exchange zone between the Nyanza Gulf and the main Lake Victoria is characterized with high water currents (Njuru, 2001; Romero et al, 2005), which act to transport bottom sediments and associated phosphorus from the gulf into the deeper areas in the channel and the main lake. The area around CG5 (Fig. 4.1) was found to have no bottom fine sediment, only bedrock, during sediment sampling and it is likely that the high TP and AP values observed in CG4 may be as a result of sediment focusing into this area from the eastern zones. The relatively high AP and low OP contribution to TP at the Rusinga Channel site (CG4; Fig. 4.6) may be associated with resuspension and transport of lighter organic sediments away from the higher energy narrow channel area, leaving behind heavier AP associated inorganic sediments. Sediment samples from CG4 also had lower C and N relative to P compared to other stations (Table 4.2). LVEMP (2005b) observed sediment sorting along the Nyanza Gulf, between KL1 and KL4, from a mixture of sand, silt and clay to dominance of silt and clay although with no discernible trends.

The trend of increasing P concentrations towards the deeper offshore areas may also be attributed to reduced mineralization of the settled organic sediments due to reduced biological activity associated with prolonged hypolimnetic anoxic conditions in the main lake (Hecky, 1993). Mineralization of organic matter in the sediment proceeds at a lower rate under anoxic conditions (Holtan et al. 1988; Moore et al, 1993), leading to accumulation of particulate organic matter and soluble organic substances in the sediment (Gale et al., 1992). Although anoxic conditions enhances release of phosphorus associated with metal oxides and oxyhydroxides (Wetzel, 2001; Kalff, 2002), release of organic matter bound P can reduce with decrease in oxygen conditions in the sediments (Gale et al, 1992).

4.4.3 Riverine influence

The low P concentrations in the eastern gulf area can be associated with the quality of the mineralogenic allochthonous sediment input from the rivers, which enter the gulf near this area (Fig. 4.1). The TP concentration in the riverine suspended sediments (689 mg/kg DW) is much lower than the concentrations of bottom sediments in KL1 and KL2 (1128.8 and 1352.0 mg/kg respectively), located in the gulf area directly influenced by the river

inflows, implying that the incoming riverine sediments have a diluting effect on the bottom sediments as has been observed elsewhere (Holtan et al, 1988). The riverine suspended sediments have coarser grain sizes and are mainly inorganic; and therefore, as they preferentially settle to the bottom finer more P rich fractions, including organic particles, remain in suspension. In addition, algal productivity will also produce relatively P rich particulate organic matter and consequently, along the gulf-main-lake transect, both TP and OP concentrations in deposited sediments would be expected to increase with distance from the riverine source areas. The observed high correlation between station depth and sediment P fractions (except NAIP) is consistent with the observed increasing trend of P concentration along the gulf-main-lake transect (Fig. 4.3) where depth increases from 2 to 34 m (Fig. 4.1).

4.4.4 Apatite-phosphorus association and P availability

Apatite phosphorus (AP) was the most important P fraction, contributing between 35 and 57.3% of TP (Fig. 4.6). Noges and Kisand (1999) found that AP contributed up to 85 % of TP in a shallow eutrophic Lake Vortsjarv, Estonia and Williams et al (1976) reported values between 20 and 100 % of AP in TP in Lake Erie. In the two lakes (Erie and Vortsjarv) the high % AP contribution to TP was in the near-shore areas where allochthonous input was high.

Apatite phosphorus (AP) consists of orthophosphate present in the crystal lattice of the mineral apatite, normally of detrital origin (Bostan et al, 2000), and therefore the concentration of AP in the eastern gulf area, near the river mouths, would have been expected to be higher than in other areas towards the main lake. However, AP in this part of the lake may be in the fine silt to clay-sized sediments which are susceptible to re-suspension and transport by physical processes that drive the gulf-main-lake exchange and therefore focusing AP towards the main lake. Williams et al (1976) observed both silt-sized and clay-sized apatite in Lake Erie together with the normal sand and other coarse fractions. However the source of apatite in Lake Erie was erosion of glacially formed clay and sand deposits while in Victoria the source would be highly weathered tropical soils. There is no literature

on apatite fractions in the soils of the gulf catchment and therefore the origin of apatite P in the lake sediment remains uncertain.

The observed strong relationship between TP and Ca in the sediment (Fig. 4.7) indicates that, in the Nyanza Gulf and Rusinga Channel, phosphorus is mainly in the apatite form and therefore not readily available for release to the water column. The TP in the main lake does not fit in this Ca-TP model and is mainly in autochthonous organic form, which can be remobilized through microbial mineralization and other biological processes (Montigny and Prairie, 1993).

4.4.5 Role of internal P loading

Bottom sediment can act both as a source or sink of phosphorus to the water column through release of phosphorus from the sediment or through permanent burial of sedimented particulate phosphorus (Holtan et al, 1988; Hecky et al 1996). If burial exceeds release there is a net loss of P from the water column whereas if release is higher than burial sediments act as net source of P to the water column (Katsev et al, 2007). There was no significant correlation ($P > 0.05$) between water column PO_4 -P and TP and sediment P fractions (Table 4.3), indicating that the lake sediment may not be an important source of P to the lake water column compared to external sources and P cycling in the water column. However, suspended sediment phosphorus (SP) in the water column showed significant correlation ($P < 0.05$) with all sediment P fractions (except NAIP). It is however important to note only one station was sampled in the main lake and therefore these relationships between water column and sediment P fractions maybe only valid for the gulf and the channel and especially given that the main lake has different water column oxygen conditions compared to the gulf and the channel (Chapter 2), which is important in determining P cycling (Hecky, 1996; Kalff, 2002; Gikuma-Njuru & Hecky, 2005): daily mixing keeps the gulf and the channel well oxygenated whereas in the main lake hypolimnetic hypoxia occurs most of the year (Chapter 2).

The available historical data for Lake Victoria show high P sedimentation rates compared to sediment P release rates: Kamp-Nielsen et al (1981) reported a TPP

sedimentation rate of 30 and 8 mg/m²/day in Nyanza Gulf and in a offshore station in northern Lake Victoria, respectively, and LVEMP (2005b) reported a P release rate of 1.73 mg/m²/day in the gulf, indicating that in the gulf sediments may be a net P sink. However, although no release data is available for the main lake it can be assumed the persistent hypolimnetic hypoxia in the main lake results in higher P release rates compared to the well oxygenated gulf and channel. Hypolimnetic P release in the main Lake Victoria has been invoked as one of the main causes of the observed relatively high PO₄-P concentration in the main lake compared to the inshore areas (Hecky et al, 1996; Gikuma-Njuru & Hecky, 2005). However, more studies are required in order to confirm this hypothesis.

The concentration of P in the suspended sediment (SP) was higher than that of the bottom sediment (Fig. 4.4 and Fig. 4.5), with higher differences (>60%) observed in the deeper stations (>10m). Diagenetic processes in the sediment produce more inorganic sediments, with less phosphorus per unit dry weight as phosphorus is released to upper sediment zones and then overlying water according to redox and physical conditions (Carignan and Fleet, 1981; Katsev et al 2007). The relatively high C:P ratios in the sediment (123 – 299; Table 2) may indicate differential mineralization of P from organic sediments during diagenesis (Holtzman & Lehman, 1998).

4.5 Conclusions

The river tributaries have a diluting effect on phosphorus associated with the lake bottom sediment, since they bring in suspended sediment with lower P concentrations compared to the surficial bottom sediments. Towards the main lake, the more inorganic allochthonous suspended matter is replaced by more organic and P rich autochthonous suspended particulate matter, which on sedimentation result in P enrichment of bottom sediments in the main lake. Resuspension and transport of the fine and light P rich sediments also contribute to the observed P gradient towards the main lake.

In the Nyanza Gulf and the Rusinga Channel, the less bioavailable apatite phosphorus dominate, whereas in the main lake the potentially available OP dominate, making internal P loading more important in the main lake compared to the gulf. Increased internal P loading

together with dominance of atmospheric input of readily available P into the main lake may account for the observed high P concentration in the main lake water column compared to the gulf (Mavuti & Litterick, 1991; Gikuma-Njuru & Hecky, 2005).

There are no documented studies on the geochemistry of the soils in the Nyanza Gulf catchment and therefore the source and form of apatite found in lake sediment is not known. It is therefore recommended that soil geochemical studies be carried out in order to understand the nature and mobility of phosphorus from the catchment and be able to predict the impact of changing land use on the phosphorus loading to the lake, in order to better inform decision makers and water quality managers.

This study confirms the EU protocol to be highly reproducible and able to differentiate between different P fractions. The AP fraction was highly correlated with Ca in the sediment and the sediment Ca to P ratio was close to that of the apatite mineral, indicating that the protocol accurately extracted and characterized the apatite phosphorus contrary to the conclusion by Pardo et al (2003) that the protocol underestimates NAIP and overestimates AP.

Chapter 5

Spatial variability in phytoplankton community composition, nutrient status and photosynthetic capacity in response to physical and nutrient conditions in Nyanza Gulf, Rusinga Channel and Lake Victoria (Kenya)

5.1 Introduction

The community structure and productivity of phytoplankton in aquatic systems is determined by several geochemical and environmental factors, the main ones being temperature, light and nutrients (P, N, C, Si and micronutrients). Light and temperature set the pace for photosynthesis (carbon fixing) since they determine the rate of photochemical and biochemical (enzymatic) processes (Kalff 2002). In tropical lakes where there is an 'endless summer' (Kilham and Kilham 1990), temperature, as an agent of biochemical processes, does not limit phytoplankton growth but plays an important role in lake hydrodynamics (stratification, mixing and movement of water masses), which determines the availability of light and nutrients for phytoplankton growth (Hecky, 1993; Hecky et al., 1996; Walsby et al 1997). Availability of light for phytoplankton growth is determined by water transparency, mixing depth and incident light intensity. Light limitation of phytoplankton growth occurs when the mixing depth becomes greater than the photic depth, as phytoplankton are forced to spend more time in the aphotic zone or can occur under high light attenuation conditions in the upper water column caused by mineral or biogenic turbidity (Sverdrup, 1953; Kalff 2002; Mugidde et al 2003). Some phytoplankton species have photophysiological adaptation to low light availability by adjusting their capacity to capture and use PAR while others have the ability to adjust their position in low turbulence water columns through production of gas vesicles or mobility, and therefore giving them an advantage over other species when light availability is low (Walsby et al 1997; Brookes et al 1999).

Nutrients are normally present in very variable quantities from one water body to another and even within the same system may vary in space (especially during stratification) or seasonally according to rainfall, temperature, wind and the nature of the phytoplankton community (Maitland 1990; Talling 1986). During prolonged thermal stratification, net primary production and sinking of autochthonous organic matter may deplete nutrients in the epilimnion, resulting in nutrient limitation of algal growth (Maitland 1990). Mixing, which occurs during the breakdown of stratification, helps in returning accumulated nutrients from the hypolimnion to the euphotic zone (Hecky et al 1996). Wind induced turbulent flow (and mixing) is important in nutrient cycling in the water column and is responsible for the dispersal of nutrients in the lake (Imboden & Wuest, 1995; Kalff 2002), especially between inshore (recipient of nutrient enrichment from the catchment) and offshore areas.

In order to attain optimum growth rates, phytoplankton require nutrients to be available within certain ranges of concentrations and proportions which are determined by their physiological needs (Hecky and Kilham, 1988). When the availability of a particular nutrient(s) is below the optimum concentration, phytoplankton productivity may be limited by that particular nutrient(s) and when the deficiency is critical, productivity for most species may stop altogether except for those species with physiological adaptation to cope with the deficiency (Evans et al 2000; Kalff 2002). For example, in cases where nitrogen is deficient but other nutrients and light are available, heterocystous blue green algal species normally dominate over the other less competitive species because they have the capacity to fix atmospheric nitrogen (Hecky et al 1996; Mugidde et al 2003; Tonno and Noges 2003).

In the past four decades Lake Victoria has experienced major ecological changes, including depletion in Si (required for diatom growth) (Hecky 1993), changes in phytoplankton assemblages with the bloom forming N-fixing cyanobacteria replacing the diatom *Aulacoseira* as the dominant phytoplankton (Kling et al 2001; Guildford et al 2003) and increased phytoplankton biomass and photosynthesis (Mugidde 1993). The suggested causes of these changes are: increased nutrient (mainly phosphorus) loading from surface runoff and atmospheric deposition resulting from increased human population and associated land degradation (Hecky 1993; Bootsma et al 1999; Mugidde et al 2003), increased water

column stability due to global warming, with consequent deoxygenation of deep waters, increased P release from the sediments and high levels of denitrification, which has favored proliferation nitrogen of fixing cyanobacterial species (Hecky 1993; Hecky et al. 1994, Hecky et al. 1996). The other suggested cause of these changes is the modified trophic status of the lake occasioned by the proliferation of the piscivorous Nile perch (*Lates niloticus*), which has led to decimation of endemic zooplanktivorous fish species (Ogutu-Ohwayo, 1990). However, the relative importance of the role of nutrient loading (bottom-up) and the trophic changes (top-down) in contributing to phytoplankton changes in the lake is yet to be fully understood (Verschuren et al. 2002; Witte et al. 2005).

The objective of this chapter is to study the role of spatially changing nutrient and physical conditions in influencing phytoplankton assemblage, biomass and productivity along a transect between the Nyanza Gulf and the main Lake Victoria which have quite different nutrient concentrations and stoichiometries. The findings of Chapters 2 (physical dynamics) and 3 (nutrient dynamics) will be used to examine hypotheses on the role of increased nutrient loading and water column stability in effecting the phytoplankton changes that have occurred in Lake Victoria. The physically active and continuously well-mixed shallow Nyanza Gulf and deep Rusinga Channel contrast with the seasonally stratifying main lake (Chapter 2) and the transition from well mixed deepening conditions from the Gulf through the channel can therefore be assumed to incorporate some of the trends in changing stratification and nutrient concentration historically observed in Lake Victoria (Hecky, 1993). For example, silica concentrations are also higher in the gulf and decline through the channel to the open lake (Chapter 3). Silica is an essential nutrient for diatoms but has decreased 10-fold in the pelagic waters of Lake Victoria in the past 50 years (Kilham & Kilham, 1990; Hecky, 1993; Verschuren et al, 1998) and Si concentrations along the transect similarly decline over the range of concentrations observed historically in Lake Victoria. The second objective is to determine adjustments in phytoplankton community composition, nutrient status and productivity along the study transect in order to determine the impact of increased nutrient loading and changing nutrient stoichiometry on the gulf environment and on the lake as a whole.

5.2 Methods and materials

Sampling for nutrients, phytoplankton biomass, photosynthesis, community structure and stable isotopes was done between March 2005 and March 2006 in 10 stations along a transect extending between well within the Nyanza Gulf (KL3) out to the main Lake Victoria (Fig. 5.1). Water samples were collected from near the surface (approximately 1 Secchi depth) using a 5-L Van Dorn sampler and immediately an appropriate amount was filtered through pre-ignited GFF filters for the analysis of chlorophyll *a*, particulate phosphorus (PP), particulate nitrogen (PN), and particulate carbon (PC). Additionally, a sample volume was passed through pre-ignited quartz glass-fiber filters for the analysis of ^{13}C and ^{15}N isotope fractions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in the particulate matter. The filters were then kept under ice during transportation to the lab, where chlorophyll *a* was analyzed immediately. The filters for particulate fractions (PP, PN and PC) and isotope composition were oven dried ($105\text{ }^{\circ}\text{C}$) and then kept frozen during transportation to the University of Waterloo laboratories where analysis was done. Chlorophyll *a* was extracted in the dark for 16 hrs using 90% ethanol and measured using a spectrophotometric method (Wetzel and Likens, 1991). The PP samples were combusted at $550\text{ }^{\circ}\text{C}$ for 30 minutes and then digested using ammonium persulfate to release the bound P, which was then analyzed as orthophosphate using the ascorbic acid method (APHA, 1995). Particulate carbon and nitrogen (PC, PN) were analyzed using a Carbon-Nitrogen Analyzer, Model CE 440 Elemental Analyzer (Exeter Analytical, Inc.). Suspended sediment (SS) concentration was estimated by filtering a known sample volume through a pre-weighed GFF filters and weighing after oven-drying (105) for 16 hrs. The stable isotope samples were analyzed at the Environmental Isotope Laboratory, University of Waterloo, using a Micromass VG-Isochrom Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS) and PeeDee belemnite and ambient air nitrogen gas as standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

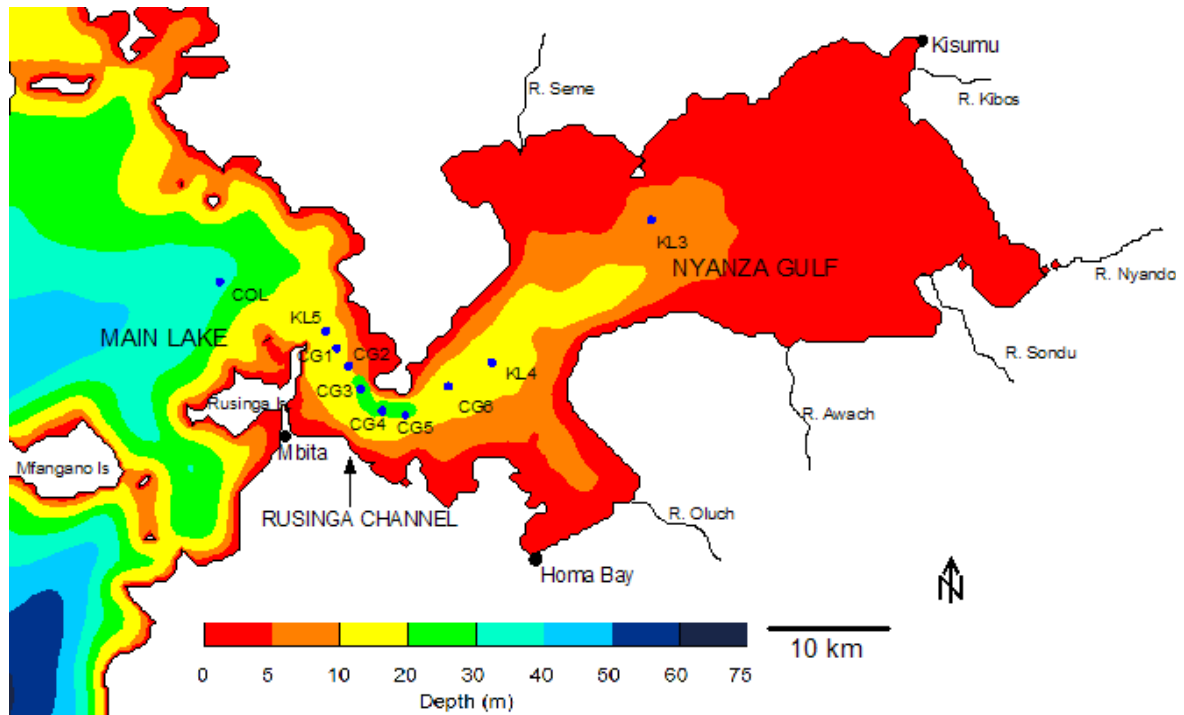


Figure 5.1 Map of the study area showing the location of sampling stations, river tributaries and major towns. The base map and the bathymetric data are from Silsbe (2003).

Underwater light climate and extinction were measured using a Li COR underwater quantum sensor and meter (Li-COR 1000), which measured photon flux density of PAR (400-700 nm). The vertical light attenuation coefficient (k_d , m^{-1}) was taken as the slope of the regression of $\ln(I_z)$ on depth (z), where I_z is the down-welling PAR at depth z . The daily mean water column irradiance (\bar{I}) was calculated as follows (Riley, 1967):

$$\bar{I} = I_o \frac{(1 - e^{-kz})}{kz}$$

Where k is the vertical light attention coefficient (k_d), z is the mixing depth and I_o is the daily mean (over 24 hours) solar flux at the lake surface. \bar{I} is the daily (24 h) mean irradiance which a free circulating algal cell would receive within the mixed layer (Guildford et al, 2000).

Samples for analysis of phytoplankton biomass and composition were preserved by adding Lugol's iodine solution and a few drops of formaldehyde before analysis using microscopic method. Phytoplankton productivity was measured using light-dark oxygen-

change after incubating lake water in a series of 150 mL bottles along a light gradient in an insulated incubator. Dissolved oxygen concentration in the initial and incubated samples was measured using modified Winkler titration (Wetzel and Likens, 1990). Light gradient in the incubator was measured using a Li COR spherical probe and the values used to calculate photosynthetic parameters (α_B , P_{BM} and E_K). Areal daily phytoplankton productivity was estimated from photosynthetic parameters (α and P_{BM}), phytoplankton biomass (chlorophyll *a*) and light attenuation coefficient (k_d) using a modified Fee Model (Silsbe 2004). Appropriate sample volume was filtered, in triplicate, through GFF filters and after dark adapting the filters for 30 minutes the photosynthetic capacity of PSII (F_v/F_m) was measured using a Diving PAM[®] fluorometer.

Metabolic nutrient status assays (P-debt, N-debt and alkaline phosphatase activity, APA) were done in the field immediately after sampling. The N-debt and P-debt were calculated as the amount of N and P respectively, removed per unit of chlorophyll *a* after incubating an enriched sample (Healey 1977; Guildford et al 2003) and is based on the principal that an algal population growing under a nutrient (N, P) limited environment takes up more of the limiting nutrient than when the nutrient is sufficient (Healey, 1978; Healey and Hendzel 1980). Alkaline phosphatase is normally produced when algae are P deficient and acts to hydrolyze P bound in soluble organic matter, making it available to the phytoplankton and therefore APA content is higher in P deficient cells (Rose and Axler 1998). P debt assay was done in triplicate by adding potassium dihydrogen phosphate (KH_2PO_4) solution into a 100 mL water sample to a final concentration of about 150 $\mu\text{g/L}$ and then incubating in dark for 24 hrs. Orthophosphate concentration, before and after incubation, was determined and P debt was taken as the amount of P uptake per unit chlorophyll *a* over a 24-hr period. N debt was determined following the same procedure as P debt except that ammonium chloride (NH_4Cl) solution was added (final concentration about 120 $\mu\text{g/L}$). APA was measured fluorometrically using o-methyl-fluorescein-phosphate (OPA) as the substrate following method of Healey and Hendzel, (1979). Total APA in the unfiltered sample and soluble APA in the filtered sampled (0.2 μm) were determined separately and the difference between them was taken as the particulate APA. In addition to

metabolic nutrient status indicators, seston atomic ratios (C:P, N:P and C:N) and carbon to chlorophyll *a* ratio (C:Chl) were calculated and used as indicators of nutrient status (Healey and Hendzel 1979).

5.3 Results

On average, chlorophyll *a* concentration varied with a defined trend along the study transect decreasing from a highest average value of 21.6 $\mu\text{g/L}$ at KL3 to a lowest value of 11 $\mu\text{g/L}$ in the mid-channel station CG4 before increasing to a high average value of 20.5 $\mu\text{g/L}$ in KL5 (Fig. 5.2). The main lake station (COL) had similar average chlorophyll to that of CG4. Chlorophyll varied widely over time with a 3 to 10-fold variation between months within stations (Fig. 5.2). In the gulf (KL3) chlorophyll followed a general increasing trend to a maximum in November and then decreased monotonically towards March 2006, whereas in the main lake an increasing and decreasing trend was observed with maximum values in September and January and minimum value in April (Fig. 5.3). Over this range of variability, KL3 had consistently higher chlorophyll concentrations than COL. Between year variation was also substantial depending on the station. The gulf station KL3 had a 2-fold higher chlorophyll in March 2006 compared to the same time in March 2005 but in the main lake the two years had similar chlorophyll concentration.

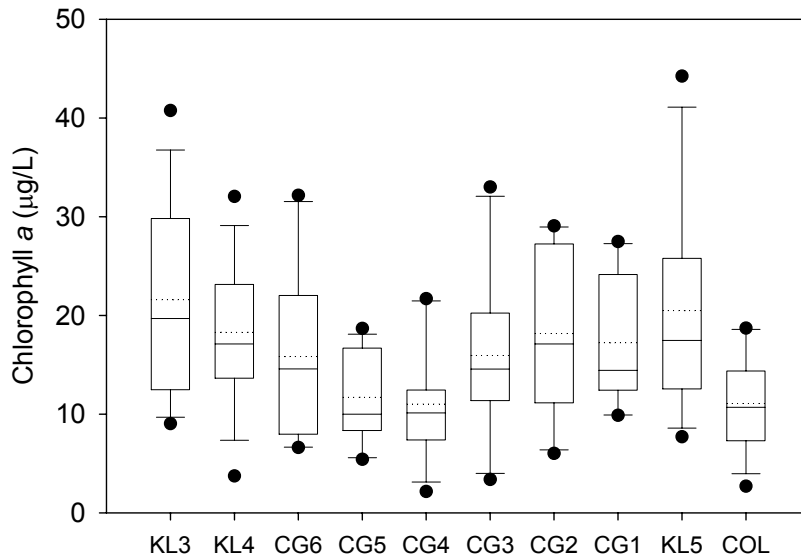


Figure 5.2 Mean (broken line), median and percentiles of chlorophyll *a* along the study transect from samples collected monthly between March 2005 and March 2006. The solid diamonds above and below the whiskers (90th and 10th percentiles) represents outliers.

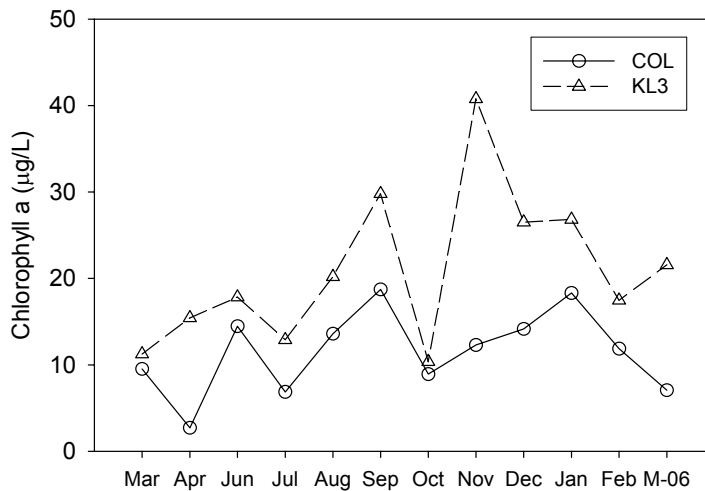


Figure 5.3 Temporal variation of chlorophyll *a* in the gulf (KL3) and the main lake (COL)

Phytoplankton biomass (wet weight), based on samples taken between December 2005 and March 2006, showed similar spatial trend as chlorophyll with the gulf having highest biomass and the channel station, CG5, having the lowest biomass (Fig. 5.4). In the channel diatoms (Bacillariophyceae) accounted for about 60% of biomass whereas in the

main lake they accounted for 43% of the biomass. Cyanobacteria accounted for 72 % of biomass in the gulf and about 54% biomass in the main lake but 15% or less in the channel. Chlorophytes were relatively low in the main lake but accounted for between 20 and 30% biomass in the channel and about 15% in the gulf. Profiles of accessory pigment fluorescence signals taken in December 2005 and January 2006 using a FluoroProbe[®] showed the contribution of diatoms to total algal biomass to increase along the channel with a maxima observed in the area between CG1 and CG3 (Fig. 5.5). The FluoroProbe profiles showed high biomass of cryptophytes in the main lake and the channel stations but this signal was assumed to be from phycoerethrin pigments in the cyanobacterial species since microscopic analysis of samples taken at the same time showed little or no cryptophytes.

Diatoms in both the main lake and the channel were dominated (counts/volume) by *Nitzschia* sp. (mainly *N. acicularis*) but in the gulf *Cyclostephanos* sp. were more common during the sampled dates. *Aphanocapsa* sp. (*A. delicatissima*, *A. holisatica*) were the dominant cyanobacterial species in the main lake and in the gulf *Cyanodictyon* sp and *Aphanocapsa* sp contributed the highest biomass. *Anabaena* was the main heterocystous cyanobacteria in all three stations although *Cylindrospermopsis* and *Aphanizomenon* also occurred in the channel and main lake stations (CG5, COL). The ratio of heterocysts to the heterocystous cyanobacterial cells was high in the main lake (7.8%) compared to the gulf and the channel (1.8, 0.9%) indicating differences in the importance of atmospheric nitrogen fixation as a nitrogen source between the three lake zones.

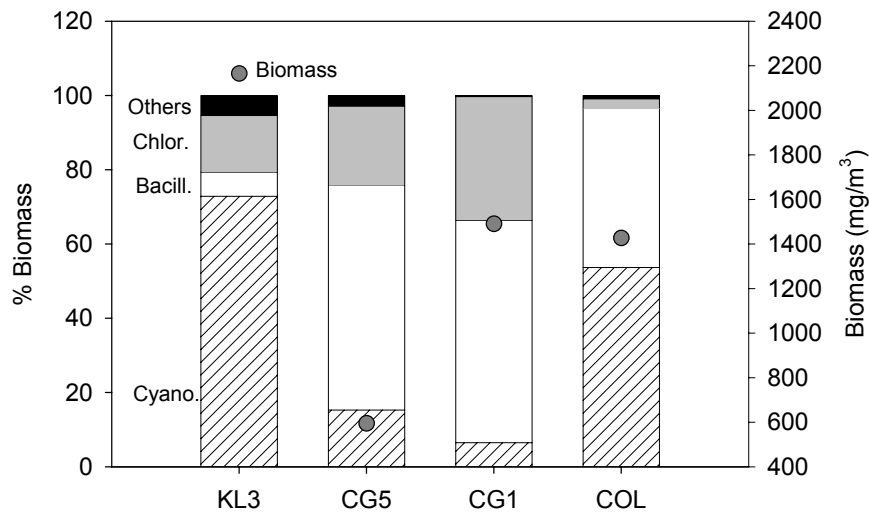


Figure 5.4 Total phytoplankton biomass and percentage contribution of different groups (Cyano., cyanophytes; Bacill., bacillariophytes; Chlor., chlorophytes; Others, dinoflagellates, cryptophytes) in the main lake (COL), channel (CG1, CG5) and gulf (KL3) stations for samples collected in December 2005 and February and March 2006 (CG1, data for Feb 2006 only).

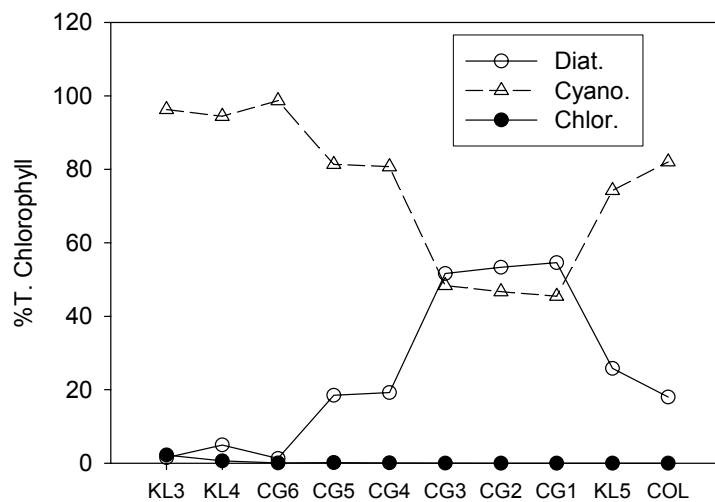


Figure 5.5 Percentage fractions of total chlorophyll for different algal groups (Diat., diatoms; Cyano., cyanobacteria plus cryptophytes; Chlor., chlorophytes) based on fluoroprobe profiles taken in December 2005 and January 2006.

The means and standard errors of phytoplankton photosynthetic parameters (P_{BM} , α_B , and E_K) in the gulf, channel and main lake stations (KL3, CG5 and COL) are presented in Figure 5.6. P_{BM} was higher in the channel compared to the gulf and the main lake, which had similar values. α_B the initial slope of the light response curve, showed the same spatial trend as P_{BM} although KL3 had higher temporal variability (note long error bars). E_K the quotient of P_{BM} and α_B was slightly lower in the main lake (mean 148) compared to the gulf and the channel (mean 167, 176). The mean integral photosynthesis was twice as high in the main lake compared to the gulf (11.7, 5.4 g O₂/m²/d) and the channel stations CG5 had an intermediate mean value of 6.0 g O₂/m²/d.

Photosynthetic efficiency (F_v/F_m) varied with a well defined spatial trend, increasing monotonically between the gulf station, KL3, to the channel station CG1 and then decreasing towards the main lake (Fig. 5.7). The highest value was in CG4 and was similar to the theoretical maximum value of 0.65 (Falkowski & Raven, 1997). KL3 had significantly lower F_v/F_m (ANOVA, $P < 0.05$) than the channel stations CG4 to KL5 and the main lake. The channel stations occasionally had low fluorescence signals, but there was always good reproducibility between the triplicates.

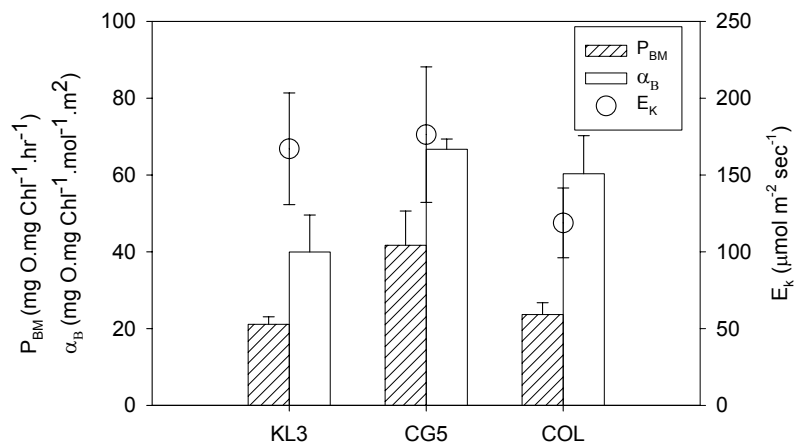


Figure 5.6 Mean (n=4) and standard error of photosynthetic irradiance (P-E) curve derived parameters in the gulf (KL3), channel (CG5) and main lake stations (COL) measured between December 2005 and March 2006: P_{BM} , light saturation photosynthetic rate per unit chlorophyll a ; α , light limited slope of P-E curve; and E_K , index of onset of light saturation photosynthesis ($E_K = P_{BM}/\alpha$).

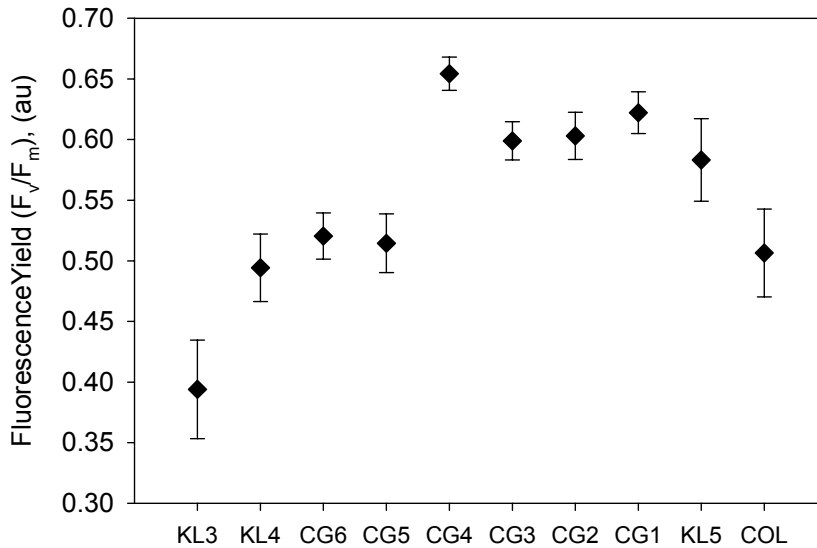


Figure 5.7 Means (n=4) and standard errors of fluorescence yield (F_v/F_m) measured between November 2005 and March 2006.

5.3.1 Light climate

The concentration of suspended sediments (SS) was high in the gulf and varied with similar spatial trend as that of chlorophyll (Fig. 5.8a). In the channel, SS showed a general increasing trend towards KL5 before decreasing to minima in COL. The high SS in the gulf is both from algal biomass and inorganic sediments from the river inflows. The ratio of particulate carbon to suspended sediments (PC:SS) increased along the channel (Fig. 5.8a), an indication of gradual settling out of inorganic sediments and increase of biogenic suspended matter towards the main lake. Light attenuation (k_d) was high in the gulf (mean 2.4 m^{-1}) but decreased monotonically towards the main lake to a low mean value of 0.6 m^{-1} (Fig. 5.8b). The mean irradiance (\bar{I}) followed a similar decreasing trend as k_d up to CG3 and then increased 2-fold to $52 \mu\text{mol photons/m}^2/\text{s}$ in CG2, similar to KL3 (Fig. 5.8b). The ratio of the euphotic depth to mixing depth (Z_{eu}/Z_{mix}) was always less than 1 and was lowest in the deep channel area between CG3 and CG5 (Table 5.1). k_d was highly correlated with SS ($r^2=0.66$, $n=71$) but had no correlation with chlorophyll *a* (Fig. 5.9a, b). However, in the main lake and the adjacent channel station (KL5) there was strong correlation between k_d and

Chlorophyll ($r^2=0.84$, $n=19$; Fig. 5.9c) indicating reduced influence of vertical light attenuation by the mineral suspended sediments towards the main lake.

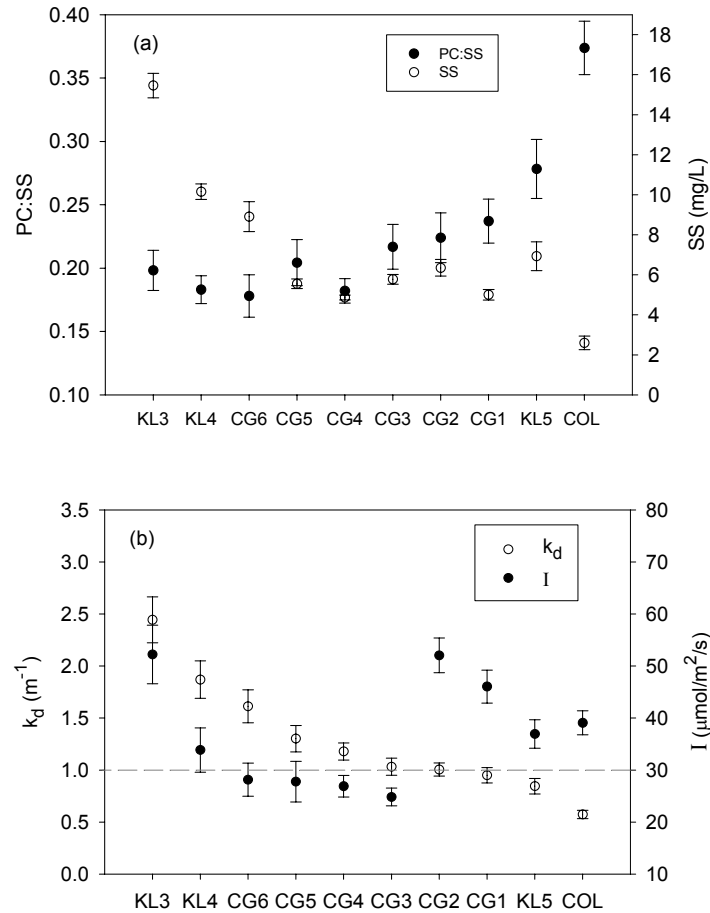


Figure 5.8 Means ($n=12$) and standard errors of (a) suspended sediments and ratio of particulate carbon to suspended sediments (PC:SS) and (b) light extinction coefficient (k_d) and mean irradiance over 24 hour period \bar{I} along the study transect, from measurements made between March 2005 and March 2006. The dashed line in (b) is the light level below which Guildford and Hecky (1984) found phytoplankton to be light limited in Indian Lake, Canada.

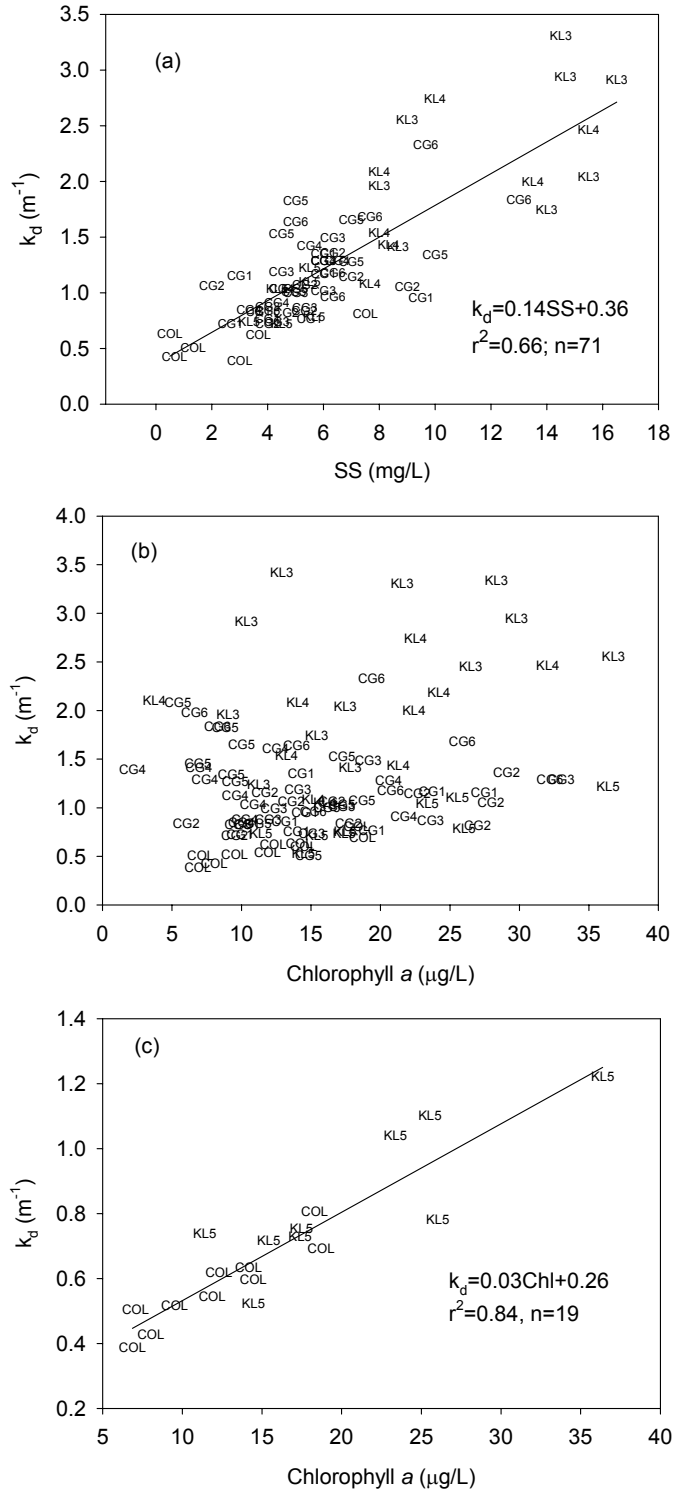


Figure 5.9 Relationship of extinction coefficient (k_d) to (a) Suspended sediments (SS) (b) chlorophyll for all stations and (c) chlorophyll a for stations COL and KL5

Table 5.1 Morphometric details (Z_{\max} , maximum depth; Z_{mix} , mixing depth; and Z_{eu} , euphotic depth) of the sampling stations and mean Secchi depth and turbidity. Values are averages (n=12) of measurements made between March 2005 and March 2006

| | KL3 | KL4 | CG6 | CG5 | CG4 | CG3 | CG2 | CG1 | KL5 | COL |
|--------------------------------|------|------|------|------|------|------|------|------|------|------|
| Z_{\max} (m) | 5.3 | 12.1 | 14.0 | 23.5 | 20.8 | 27.1 | 12.1 | 14.9 | 21.8 | 34.1 |
| Z_{mix} (m) | 5.0 | 12.1 | 14.0 | 23.5 | 20.8 | 27.1 | 12.1 | 14.9 | 21.8 | 27.0 |
| Z_{eu} (m) | 2.08 | 2.72 | 2.94 | 4.19 | 4.24 | 4.76 | 5.18 | 5.30 | 5.73 | 8.20 |
| $Z_{\text{ue}}/Z_{\text{mix}}$ | 0.43 | 0.25 | 0.21 | 0.21 | 0.20 | 0.19 | 0.41 | 0.35 | 0.25 | 0.28 |
| Turbidity (NTU) | 16.3 | 12.2 | 10.3 | 6.6 | 6.4 | 5.4 | 4.6 | 4.5 | 4.4 | 2.9 |
| Secchi (m) | 0.60 | 0.98 | 0.91 | 1.15 | 1.26 | 1.24 | 1.35 | 1.56 | 1.45 | 1.86 |

5.3.2 Phytoplankton nutrient status

Figure 5.10 shows the mean and standard errors of total and dissolved inorganic nutrient concentrations (TP, SRP, DIN and DRSi) along the study transect. The spatial variability in nutrient concentration and underlying physical and biogeochemical processes were discussed in detail in chapter 3. TN and DRSi concentrations were significantly higher (ANOVA; $P < 0.05$; Table 3.3) in the gulf and followed a decreasing trend along the channel to minimum values in the main lake. In contrast SRP was significantly higher in the main lake compared to the gulf whereas DIN was significantly higher in the channel compared to the gulf and the main lake.

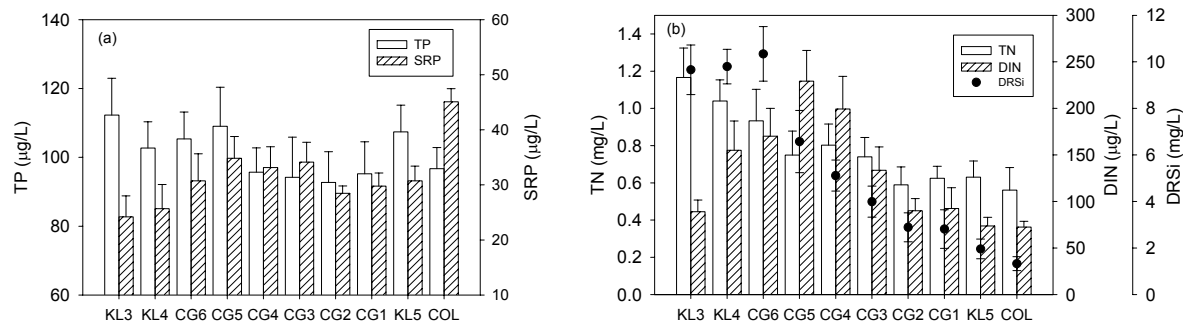


Figure 5.10 Spatial variation in concentration of (a) TP (total phosphorus) and SRP (soluble reactive phosphorus) and (b) TN (total nitrogen), DIN (dissolved inorganic nitrogen) and DRSi (dissolved reactive silica). The error bars are standard errors

The levels of limitation of phytoplankton growth by phosphorus or/and nitrogen are indicated by the dotted horizontal lines and the embedded text in Figure 5.11, based on Healey and Hendzel (1979). The ratio of carbon to phosphorus (C:P) showed that phytoplankton in the gulf stations KL3 and KL4 was moderately P limited, while N:P, and the P-debt and APA assays showed P deficiency in the two Gulf stations. C:N showed no nitrogen deficiency of phytoplankton growth in all the stations but the N-debt assay showed nitrogen deficiency in phytoplankton in all the stations measured, except CG5. The ratio of particulate carbon to chlorophyll (C:Chl) can indicate either N or P deficiency in phytoplankton (Healey & Hendzel, 1980). C:Chl ratio showed N or/and P deficiency in the gulf (KL3, KL4) and occasional deficiency in the main lake (COL). C:Chl values indicating N or P deficiency in the main lake were observed in October 2005 when strong thermal stratification occurred (Chapter 2).

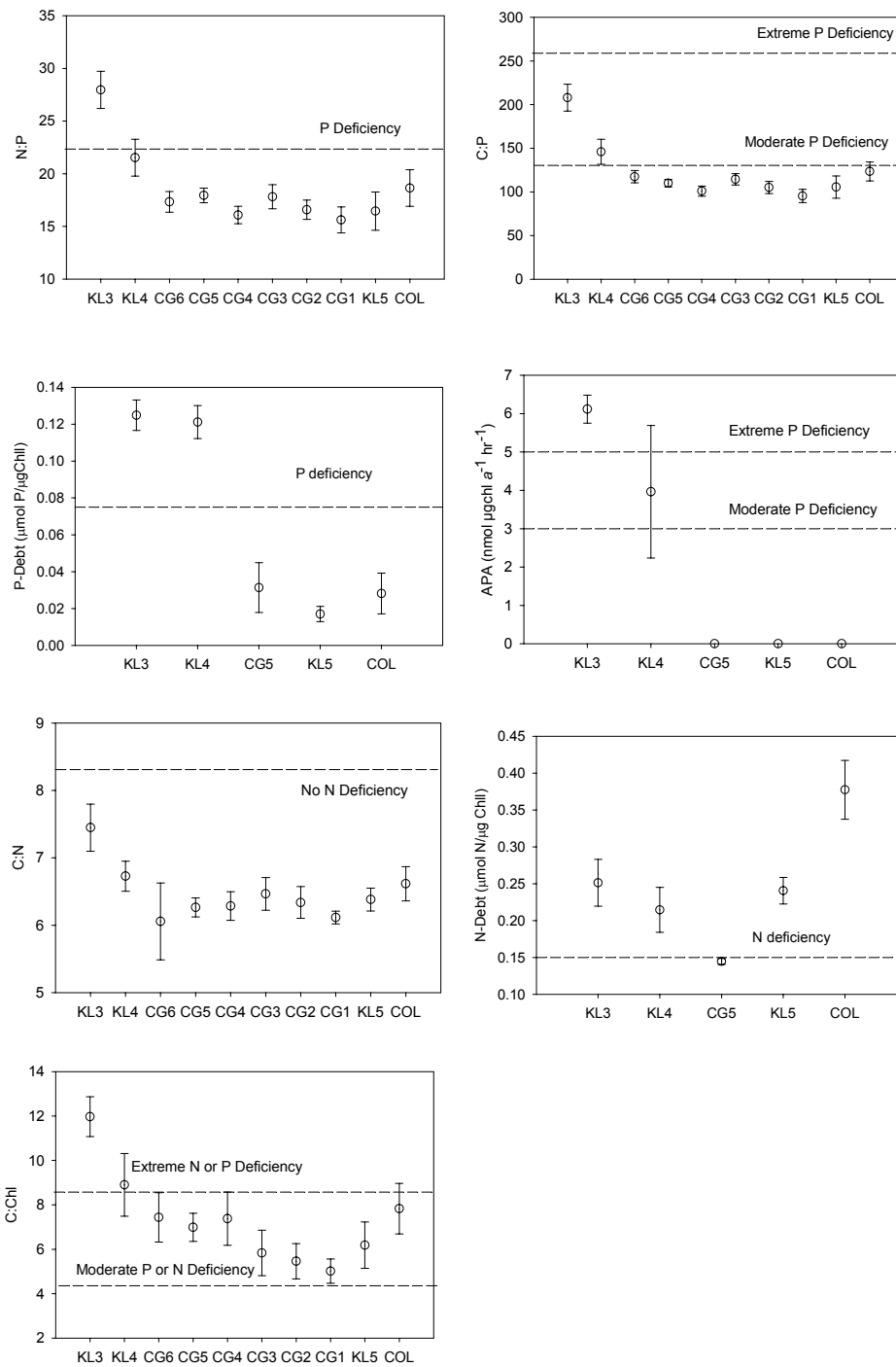


Figure 5.11 Means and standard errors of nutrient status indicators measured between March 2005 and March 2006 (C:P, N:P, C:P, C:Chl; n=12) and between April and July 2005 (N and P-debt, APA; n=3). The horizontal dotted lines indicate limits of levels of nutrient(s) deficiency as indicated in the embedded text

The ^{13}C and ^{15}N stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) varied with defined but opposite trends along the gulf-main-lake transect (Fig. 5.12). $\delta^{13}\text{C}$ increased monotonically towards the main lake, from mean value of -24.1‰ in KL3 to -20.7‰ in COL. $\delta^{15}\text{N}$ did not vary much between KL3 and CG4 but after CG4 it followed a decreasing trend towards the main lake. The highest $\delta^{15}\text{N}$ ratio was 7.42‰ in CG4 and the lowest mean value was in COL, 1.84‰.

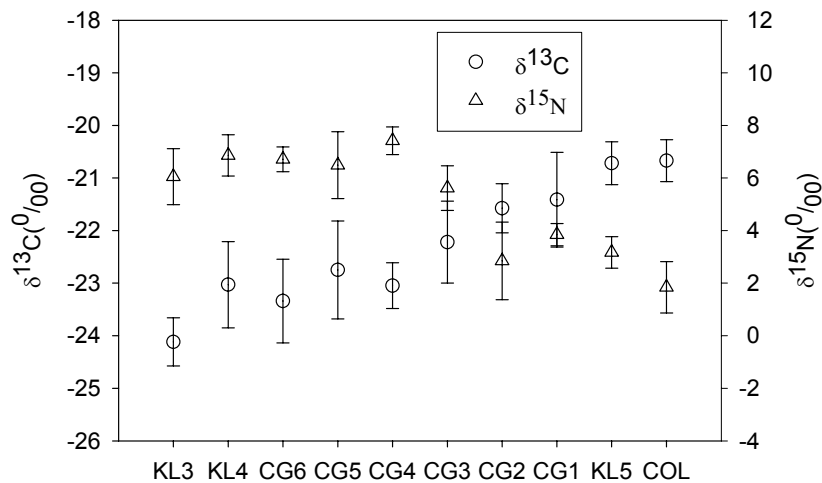


Figure 5.12 Means (n=5) and standard errors of ^{13}C and ^{15}N isotopic fractions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) measured between June 2005 and January 2006.

5.4 Discussion

5.4.1 Historical changes in phytoplankton biomass, productivity and composition

Phytoplankton changes that have occurred in the Lake Victoria in the past half century include increased phytoplankton biomass and productivity, decreased photosynthetic capacity and a modified composition (Kilham & Kilham, 1988; Mugidde, 1992; Hecky, 1993; Kling et al, 2001). These changes have been confirmed in the current study for the main lake. Phytoplankton biomass (as indicated by chlorophyll) measured during this study in the main lake (Fig. 5.2) was up to 3 times that reported by Talling (1965), 1.2-5.5 $\mu\text{g/L}$, for

Bugaia, northern part of the lake. Compared to the values reported by Talling (1965), integral phytoplankton productivity in the main lake was almost double and similar to what Mugidde (1992) reported ($13.9 \text{ g O}_2/\text{m}^2/\text{d}$). Mugidde (1992) reported a decrease in maximum photosynthetic capacity (P_{BM}) compared to what Talling reported (from 25 to $19.6 \text{ mg O}_2/\text{m}^3/\text{h}$). Similarly, the average P_{BM} measured in the current study was lower than Talling although slightly higher than Mugidde's (Fig. 5.6).

The earliest available measurements of phytoplankton biomass and productivity in the Nyanza Gulf were done in 1973 by Melack (1979) in the eastern part of the gulf, west of KL3. Melack reported chlorophyll concentration of $17 \mu\text{g}/\text{L}$, which is lower than the current average value for KL3 (Fig. 5.2), indicating an increase in phytoplankton biomass in the gulf in the past 2 decades consistent with increased nutrient input into the gulf from the catchment (Calamari et al, 1995; Lungayia et al, 2001). The average integral phytoplankton productivity reported by Melack (1979a, b) in the gulf was similar to that measured in the current study ($5.9, 5.6 \text{ g O}_2/\text{m}^2/\text{d}$), indicating little or no change in phytoplankton productivity in the gulf in the past 2 decades. Mugidde (1992) reported a 2 to 4-fold increase in chlorophyll and a 2-fold increase in productivity in the Pilkington Bay, northern Lake Victoria compared to the Talling (1965) values. It is however important to note that the stations sampled by Melack are east of KL3, near the river mouths and Kisumu City and therefore comparison with the current study (in KL3) may not fully reflect historical changes in the gulf.

Phytoplankton composition in the gulf and the main lake was dominated by cyanobacteria (Fig. 5.4), consistent with the reported historical changes from diatom dominated phytoplankton population in early 1960s (Talling, 1966) to that dominated by cyanobacteria (Kilham & Kilham, 1988, Ochumba & Kibaara, 1989; Kling, 2001). In contrast, diatoms dominated in the Rusinga channel in this study, indicating existence of different limnological conditions in this exchange zone. The channel is a physically active zone (Chapter 2), where the exchange (mixing) between the silica and nitrogen rich gulf water and the main lake water with relatively high soluble reactive phosphorus (SRP) occur (Chapter 3), resulting in changing stoichiometry in nutrient availability conditions which can influence the phytoplankton community (Levasseur, et al 1984; Kilham & Kilham, 1986).

5.4.2 Co-dependence of light climate and phytoplankton biomass

Light attenuation (k_d) showed a strong covariance with suspended sediments (Fig. 5.9a) consistent with the absorption and scattering of incident light by suspended sediments in the water column (Kalff, 2001). The wide data scatter for the gulf stations in Figure 5.9a indicate existence of dissolved light absorbers in the gulf possibly consisting of allochthonous chromophoric dissolved organic matter (CDOM; e.g. Bracchini et al, 2006) and may account for the k_d variability unexplained by SS (e.g. Silsbe et al, 2006). In contrast, k_d did not show any covariance with chlorophyll, except in stations KL5 and COL (Fig. 5.9b, c), indicating the dominant role of terrigenous sediments in controlling optical properties in the river-influenced gulf (Gikuma-Njuru & Hecky, 2005). With transport along the channel towards COL, the terrigenous sediment settle out and are replaced by biogenic (phytoplankton) matter (see increasing PC:SS in Fig. 5.8a) and in the main lake the dominant phytoplankton biomass directly influences optical properties (Fig. 5.9c) and may result in self-shading (Kling et al. 2001) controlling the maximum biomass achieved under light limitation (Mugidde 1993).

Chlorophyll followed similar spatial trend as mean irradiance (\bar{I}) and the two parameters were lowest in the channel area between CG4 and CG5 (Fig. 5.2 & Fig. 5.8). This is a physically active area characterized with upwelling and downwelling processes (Chapter 2), which generally maintain whole water column mixing in this relatively deep area and therefore imposing light limiting conditions on algal growth (e.g. Mugidde, et al 2003; Silsbe et al 2006). The \bar{I} in this area was always below the light level below which Guildford and Hecky (1984) found phytoplankton to become light limited (Fig. 5.8). After CG4, towards the main lake, light climate improved, in response to reduced mixing depth and lowered inorganic turbidity, and therefore higher biomass was achieved.

The channel station KL5 had relatively high chlorophyll (similar to KL3) compared to other channel stations despite the low \bar{I} value. The \bar{I} value is a function of the mixing depth, which in KL5 was taken to be same as the station depth (Table 5.1) since the station mixes daily (Chapter 2). However, this area is sheltered and warm stable water is normally maintained over underflow of cooler water from eastern part of the channel with whole

column mixing only occurring overnight, conditions which create a microclimate favoring development of high biomass of positively buoyant cyanobacteria, which normally form surface blooms between morning and mid-afternoon hours (Personal observation). Algal growth in this area may also be enhanced by improved light conditions, associated with reduced mineral turbidity and enrichment of orthophosphate from the main lake.

The relatively low chlorophyll in the main lake (Fig. 5.2) may be due to light limitation of algal growth associated with deeper mixing depth (Mugidde, 2003; North, 2008). Low chlorophyll concentration was observed during deep mixing season between March and July (Fig. 5.3). However, during strong stratification (thermocline at 16m) in October biomass was depressed possibly as a result of nutrient depletion in the mixed layer (mainly P; Chapter 3, Fig. 3.7). The October depression was followed by gradual biomass increase, to a maxima in January, as the thermocline deepened and metalimnetic water was entrained replenishing nutrients (e.g. Hecky et al. 1996).

5.4.3 Physical control of phytoplankton composition and productivity

Phytoplankton composition varied between the gulf, channel and the main lake with cyanobacteria (variously, *Cyanodictyon imperfectum*, *Aphanocapsa* sp. and *Anabaena* sp.) dominating (counts/volume) in the gulf, diatoms (mainly *Nitzschia* sp.) dominating in the channel while in the main lake both cyanobacteria (*Aphanocapsa* sp., *Cyanodictyon imperfectum*) and diatoms (*Nitzschia* sp.) were co-dominant (Fig. 5.4; Fig. 5.5). The high mineral turbidity in the gulf reduces light penetration and may induce light limitation for many phytoplankton taxa (Gikuma-Njuru & Hecky, 2005) but favor growth of cyanobacterial species with the capacity to control buoyancy. The shallow depths at KL3 and KL4 allow the mean water column irradiance (\bar{I}) to exceed the critical level (Fig. 5.8) and allow for development of high algal biomass (Fig. 5.2 & Fig. 5.4), development of P deficiency (Fig. 5.11), reduced fluorescent yield (Fig. 5.7) and reduced P_B^m compared to deep gulf stations farther west and into Rusinga Channel. Heavy algal blooms frequently normally occur in the gulf (personal observation; Plate 5.1), especially after rains and the associated influx of mineral turbidity and nutrients from the river inflows. These heavy blooms mainly consist of

the colony forming *Microcystis* species (Lungayia, et al 2000; Gikuma-Njuru, et al. 2006), which has the ability to control buoyancy (Reynolds, 1973; Bormans et al. 1999) thereby overcoming possible light limitation.



Plate 5.1 Heavy algal blooms in the Nyanza Gulf. Note the high mineral turbidity in water.

The dominance of diatoms in the channel can be attributed to physical processes which maintain daily mixing of the water column in this exchange zone (Chapter 2). Studies in limnocorals and in the field have shown unstable water column to selectively favor diatoms while cyanobacterias are favored under stable (stratified) conditions (Levasseur, et al 1984; Trimbee, 1984; Reynolds, 1994). Water column mixing helps to keep the diatom cells suspended in the water column while allowing for nutrient recycling, whereas stratified conditions result in increased sedimentation of algal cells from the photic zone and leads to ultimate depletion of nutrients in the mixed zone (Levasseur, et al 1984; Guildford et al. 1994).

Diatoms have a high photosynthetic efficiency relative to maintenance respiration and are therefore able to dominate under the low mean light conditions imposed by deep water column mixing (Harris & Piccinin, 1980; Cushing, 1989). The maximum specific

photosynthetic rate (P_{BM}) and the photosynthetic capacity of PSII (F_v/F_m) were higher in the channel compared to the gulf and the main lake (Fig. 5.6 & Fig. 5.7) consistent with dominance of diatoms in this region. Similarly α_B was higher in the channel than in the gulf and the main lake, indicating the high light harvesting efficiency of diatoms which allows them to maintain high photosynthetic rates under low light conditions as found in the channel (Haffner et al 1980).

In the main lake, seasonal stratification favors growth of cyanobacteria throughout most of the stratified period (Mugidde, et al. 2003) while greater mixing depth allows for development of diatoms. Increased water column stability in Lake Victoria, associated with climate warming has been suggested as a contributing factor in the change of phytoplankton assemblage from that dominated by diatoms in the early 1960s to that currently dominated by cyanobacteria (Hecky, 1993; Kling et al, 2001). However, despite the increased thermal stability, seasonally deep mixing depth allows for the development of diatoms, which have been observed to have maximum but low total algal biomass during deep mixing season (Kling et al, 2001).

5.4.4 Phytoplankton nutrient status

All the indicators of phosphorus limitation of phytoplankton growth showed the gulf to be moderately to extremely P limited at KL3 and KL4 whereas in the channel and the main lake there was no P limitation of phytoplankton growth (Fig. 5.11). In contrast, recent measurements in the northern part of the lake involving seston ratios and metabolic indicators have reported occasional evidence of N limitation in phytoplankton in the nearshore areas (Guildford et al, 2003; North, 2008) although light limitation is generally limiting algal biomass of nitrogen fixing cyanobacteria (Mugidde et al 2003). The dissolved inorganic nitrogen (DIN) in the Nyanza Gulf is more than two and half times higher than that of Napoleon Gulf, where Guildford and North made their measurements, whereas SRP concentration in the two gulfs is similar (Table 5.2), which can account for the difference in nutrient status between the two gulfs. Pilkington Bay is also more similar to nearby Napoleon Gulf in having lower DIN to SRP concentration ratios compared to Nyanza Gulf (Table 5.2),

but variability in actual nutrient concentrations in inshore areas (Table 5.2) will be a complex function of local mixing depth and water column stability. Napoleon Gulf and adjacent Pilkington Bay are near the Nile River outflow at Jinja and consequently the open Lake Victoria is the ultimate source of water to those locations. In contrast Nyanza Gulf exchange with the open lake is restricted by Rusinga Channel and its dominant source of water are the inflowing rivers. This dominance by riverine inflow contrasts with the open lake where the water input is dominated by direct precipitation on the lake surface. In addition the larger open lake has a long residence time for water, on the order of 100 years (Hecky & Bugenyi, 1992), while the gulf has a much shorter residence time (<5 years; Chapter 1). The presence of persistent hypoxic and anoxic conditions in the open lake, in contrast to the well ventilated gulf, results in intensive internal processing favoring regeneration of P and loss of N to denitrification (Hecky et al 1996). This results in very low TN:TP ratios in Lake Victoria as opposed to the much higher ratios in the Gulf.

Table 5.2 Nutrient concentrations ($\mu\text{g/L}$) in three Lake Victoria inshore areas. Pilkington Bay and Napoleon Gulf after Mugidde (2001). DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; TP, total phosphorus; and TN, total nitrogen.

| | DIN ($\mu\text{g/L}$) | SRP ($\mu\text{g/L}$) | TP ($\mu\text{g/L}$) | TN ($\mu\text{g/L}$) |
|----------------|-------------------------|-------------------------|------------------------|------------------------|
| Pilkington Bay | 65.8 | 43.4 | 71.3 | 1400 |
| Napoleon Gulf | 33.6 | 24.8 | 89.9 | 1484 |
| Nyanza Gulf | 86.4 | 24.2 | 112.2 | 1166 |

The seston ratio between carbon and nitrogen showed lack of nitrogen limitation in the study area whereas the N-debt assay showed evidence of N limitation of phytoplankton growth in all the stations except the channel station, CG5. N limiting conditions favor the growth of heterocystous algal species, which are capable of fixing atmospheric nitrogen (Mugidde 2003). The observed presence of heterocysts in phytoplankton is evidence of existence of transient nitrogen limitation as measured by N-debt assay, which measures short-term nitrogen limiting conditions. In contrast, C:N integrates long-term nitrogen status.

Over the long-term, nitrogen fixation by heterocysts is able to alleviate the short-term nitrogen limitation, which may explain why C:N did not show any nitrogen limitation. The lack of nitrogen limitation in the channel area, CG5, may be due to high nitrate concentration possibly from nitrification (Chapter 3, Fig. 3.3c) and reduced nitrogen demand due to the low phytoplankton biomass (Fig. 5.2) caused by deep mixing and light limitation.

The higher percentage ratio of heterocysts to heterocystous cyanobacterial cells in the main lake compared to the gulf (7.8, 1.8%) indicate that nitrogen fixation may be a more important source of inorganic nitrogen in the main lake compared to the gulf. In the channel (CG5) the percentage ratio was relatively small, which is consistent with the dominance of diatoms in this area (Fig. 5.4 & Fig. 5.5). In contrast to the observations in the current study, Mugidde et al (2003) measured higher N-fixation rates nearshore compared to offshore in northern part of the lake, indicating marked biogeochemical differences between Nyanza Gulf and other inshore areas, as was pointed earlier. Nyanza Gulf is unique among the other inshore areas of Lake Victoria due to its hydrology, which is dominated by river inflows and associated influence on nutrient and sediment loading, The rivers appear to provide more nitrogen relative to phosphorus and therefore making the main gulf area to be P limited while DIN remains in excess to algal demand. The outer channel area between CG3 and KL5 did not show strong nutrient limitation, as was observed in KL3 and KL4, despite apparently having adequate light, possibly due existence of optimal nutrient conditions due to the mixing of two water types from gulf and the main lake. Additionally, rapid flashing could be occurring in this area and therefore not allowing for development of steady state with ambient conditions.

5.4.5 Spatial variability in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope ratios and relationship to nutrient status and phytoplankton productivity

The $\delta^{13}\text{C}$ of particulate matter increased between the gulf and the main lake from -24.1 to -20.7‰ (Fig. 5.12). This change in $\delta^{13}\text{C}$ (3.4‰) followed a well defined trend signifying existence of biogeochemical gradient along the transect. $\delta^{13}\text{C}$ values in phytoplankton are normally related to the form of inorganic carbon assimilated during

photosynthesis. Atmospheric carbon has $\delta^{13}\text{C}$ of about -7 but when in water solution, it fractionates among the dissolved inorganic carbon (DIC) forms, which are dissolved CO_2 ($\text{CO}_{2\text{diss}}$), HCO_3^- and CO_3^{2-} with $\delta^{13}\text{C}$ of -8, +1 and -1‰ respectively (Hecky & Hesslen, 1995). During photosynthesis, phytoplankton preferentially uptake the lighter CO_2 since it requires no energy expenditure for uptake or charge balance (Sharkey & Perry, 1985; In Hecky & Hesslen, 1995), but under low $\text{CO}_{2\text{diss}}$ conditions, as happens during high rates of phytoplankton production, DIC uptake becomes less discriminative as $\text{CO}_{2\text{diss}}$ diminishes and resulting in heavier $\delta^{13}\text{C}$ in phytoplankton. The observed $\delta^{13}\text{C}$ increase along the study transect may therefore be in response to increasing phytoplankton productivity along transect between the gulf and the main lake. The other possible explanation is the relative availability of DIC for phytoplankton uptake along the study transect as indicated by the observed alkalinity gradient between the gulf and the main lake (Chapter 2, Fig. 2.10), which followed similar but opposite trend as $\delta^{13}\text{C}$ (Fig. 5.12). Alkalinity is a measure of the total quantity of base (mainly HCO_3^- and CO_3^{2-}) present in water and therefore the high alkalinity in the gulf indicate relatively excess $\text{CO}_{2\text{diss}}$. In this case the gradient may simply reflect a mixing gradient along Nyanza Gulf through the channel to the open lake where DIC concentrations are lower.

Similar to $\delta^{13}\text{C}$, which is related to the form of inorganic carbon assimilated during photosynthesis, $\delta^{15}\text{N}$ can give an indication of the source or form of nitrogen used by phytoplankton during phytoplankton photosynthesis. Atmospheric nitrogen has $\delta^{15}\text{N}$ of 0‰ and therefore nitrogen fixation by phytoplankton produces particulate matter with $\delta^{15}\text{N}$ close to 0‰, whereas inorganic nitrogen produced through internal recycling through microbial action is heavier and produces more positive particulate matter (Peterson & Fry, 1985; Kendall et al, 2001). $\delta^{15}\text{N}$ in the gulf and the channel area between CG6 and CG3 was more positive (+6.1 - +7.4‰) compared to the rest of the channel and the main lake (Fig. 5.12), indicating increased importance of nitrogen-fixation as inorganic nitrogen source towards the main lake. As earlier discussed, the importance of atmospheric nitrogen fixation in the main lake is confirmed by the higher ratio of heterocysts to heterocystous cyanobacterial cells in the main lake compared to the gulf and the channel.

5.5 Conclusions

The results from this study have demonstrated the important role of physical conditions in influencing phytoplankton productivity and assemblage in the lake. The phytoplankton community in the deep and physically active channel was dominated by diatoms and had relatively high photosynthetic capacity compared to the gulf and the main lake, similar to conditions observed in Lake Victoria in the early 1960s (Talling, 1965; Kling, 2001). Hecky (1993) reported on the increased water column stability in Lake Victoria and the possible effects of higher TP concentrations and greatly reduced dissolved Si concentrations on phytoplankton community and productivity. Increasing hypolimnetic hypoxia and anoxia (Hecky et al 1994) has increased hypolimnetic denitrification and phosphorus release. These changes in internal cycling together with higher phosphorus input from the catchment and atmospheric sources have led to lower N availability, and increased P availability. Increased algal productivity led to increased Si demand and depletion of Si similar to that observed in other great lakes (Schelske and Stoermer, 1971) eventually leading to Si limitation of many formerly dominant diatom species (Hecky 1993). Increasing P concentrations and Si limitation of diatoms has favored the growth of nitrogen fixing cyanobacteria in the Lake Victoria (Kling, 2001; Mugidde, 2003) and higher primary productivity (Mugidde 1993). The mixing of SRP-rich open lake water and DIN and silica-rich gulf water together with high nutrient regeneration in the channel (Chapter 3) create a transition in nutrient conditions along Rusinga channel that mimics historical time trends that occurred in Lake Victoria. However, strong mixing induces light limitation along the channel (Fig. 5.8; Table 5.1) that constrains biomass development and nutrient limitation, as indicated by the nutrient status measurements (Fig. 5.11).

In the shallow river-influenced gulf area, mineral turbidity determines the optical conditions and therefore influencing phytoplankton assemblage and biomass. The colonial *Microcystis*, with their capacity to control buoyancy, dominate phytoplankton assemblages in the gulf. Both seston ratios and metabolic nutrient assays have shown the gulf to be phosphorus limited resulting in lower P_B^m and variable fluorescence yields in the central gulf stations and indicating that the maximum phytoplankton biomass and productivity in the gulf

is determined by phosphorus availability. This finding is important for the management of the gulf water quality since an increase in P loading will translate to high algal biomass, mainly of the bloom forming and potentially toxic blue greens such as *Microcystis* (Plate 5.1; Aline, 2007). Reduction of P loading into the gulf should be a management priority in order to protect the gulf environment from further deterioration.

Chapter 6

Summary and Conclusions

The results from this thesis have clearly demonstrated the influence of hydrological and physical factors on nutrient recycling and availability and on the light climate and consequently on phytoplankton community and productivity. The inputs from the river tributaries to the southeastern gulf area together with varying morphology along the gulf-main-lake transect are the main factors accounting for the observed physical and biogeochemical spatial variability along the transect. Inputs from the river tributaries maintain high levels of turbidity, electrical conductivity, TN and DRSi in the inner gulf but their levels progressively reduce along the Rusinga Channel in response to exchange and mixing with the main lake water and therefore creating well defined spatial gradients. The river inflows have a diluting effect on the lake surficial sediment P as they bring in suspended sediment less rich in P compared to the lake bottom sediment. The high inorganic (and organic) turbidity in the gulf resulted in high light attenuation and increased albedo in the water column with consequent reduction in absorption of solar energy and therefore resulting in differential heating along the study transect. The water column temperature in the inner gulf was on average lower than in the main lake possibly as a result of influence by the cooler water from the river inflows together with reduced absorption of solar energy associated with high inorganic (organic) turbidity in the gulf area. Morphology varied along the study transect from the wide and shallow inner gulf to the deep and narrow Rusinga Channel and the deep and open waters of main lake, with consequent influence on the physical and biogeochemical processes. Wind turbulence in the shallow, wide and well exposed inner gulf maintains daily water column mixing resulting in a well-oxygenated water column while enhancing evaporative cooling. In the narrow, deep and wind exposed mid channel area evaporative cooling and possible flow of cooler water from shallow areas maintain cooler water leading to density driven flow of water into the lower depths of the main lake and a compensational overflow of warm water from the main lake and from the more sheltered and relatively warm channel area near the Rusinga Island. Upwelling and

downwelling and horizontal flow processes in the Rusinga channel maintain whole water column mixing conditions and consequently influencing nutrient recycling and phytoplankton community composition and productivity. In the main lake, seasonal stratification and deep mixing depth act in concert to influence nutrient availability and light conditions and therefore influencing phytoplankton community composition and photosynthesis.

The exchange between the gulf and the main lake, across the Rusinga Channel, was through advective (residual) flow and mixing flux and resulted a in gulf exchange time of 1981 days. The advective flow was on average out of the gulf ($35 \text{ m}^3/\text{s}$), although in months with low precipitation and associated low river discharges reverse flow occurred. The mixing flux accounted for the tidal exchange between the gulf and the main lake, associated with water level changes due to wind action and density driven exchange, and was the dominant exchange process. The exchange processes across the Rusinga Channel resulted in transport of 10 t/d of DRSi from the gulf into the main lake and transport of 400 kg/d of DIP from the main lake into the gulf. The channel was a net source of DIN to the gulf and the main lake (1600, 70 kg/d). Mixing processes in the channel resulted in resuspension and entrainment of bottom sediment leading to physical sorting of sediment and associated phosphorus fractions. Resuspension and entrainment of bottom sediment enhanced mineralization of particulate and dissolved organic matter and hence increased nutrient regeneration as reflected in the dominance of heterotrophy over autotrophy in the channel. In the gulf there was net nutrient uptake and associated net autotrophy as reflected in the relatively high NEP ($566 \text{ mg C/m}^2/\text{d}$). This high NEP in the gulf was reflected in the relatively high phytoplankton biomass in the gulf compared to the channel and the main lake (Chapter 5). The high NEP in the gulf and the associated high nutrient demand coupled with possibly low SRP to DIN supply ratio lead a to P limitation of phytoplankton in the gulf as indicated by all indicators of nutrient status.

The spatial variability in physical and nutrient conditions had direct influence on phytoplankton community assemblage and photosynthesis along the gulf-main lake transect. In the shallow and turbid inner gulf the colony forming cyanobacterial species dominated

whereas in the deep and physically active channel diatoms dominated and in the main lake seasonal stratification and deep mixing depth equally favored cyanobacteria and diatoms (Chapter 5). Deep mixing depth in the channel and the main lake created low light environment and consequently light limiting conditions of phytoplankton growth, leading to low phytoplankton biomass compared to the shallow inner gulf. Physical and nutrient variability along the study transect resulted in phytoplankton photosynthetic gradient along the transect as indicated by the Fv/Fm and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values, which varied with a defined trend along the transect.

Nyanza Gulf is unique among the inshore areas of Lake Victoria due to the dominance of its hydrology by the river inflows. This makes the gulf sensitive to the changes in river flow regimes in response to changes in climate and land use in the catchment. As demonstrated in Chapter 2 increased river discharge resulted increased advective flow from the gulf into the main lake and therefore enhancing flushing of the gulf but in contrast, reduced river discharge associated with low precipitation decreased advective flow or resulted in reverse flow into the gulf. Consequently, any change in gulf hydrology will have direct biogeochemical implications as it will affect the exchange of nutrient and suspended matter between the gulf and the main lake and therefore effecting ecological and water quality changes in the gulf and in the main lake. Increased sediment and nutrient input into the gulf, resulting from increased industrial and municipal waste and agricultural and urban runoff in the gulf catchment, will have direct impact on the gulf water quality through increased algal blooms and turbidity, which in recent years have become more prevalent. Since the gulf is P limited, any increase in P loading will translate to increase in algal biomass, mainly the bloom-forming and potentially toxic species and increased proliferation of the exotic water hyacinth mats, and hence presenting management and ecological challenges. Additionally flushing of these nutrients through the exchange with the main lake will contribute to the nutrient enrichment of the main lake and therefore exacerbating the eutrophication problem in the lake.

The enhanced physical processes and the varying light and nutrient conditions along the Rusinga Channel and in the main lake present a prototype for testing the hypotheses on

the factors that have contributed to the changes that have occurred in Lake Victoria over the past century, viz. increased nutrient enrichment and increased stability of the water column associated with climate change (Hecky, 1993):

1. The mixing processes in the channel can be compared to conditions in Lake Victoria 50 years ago when the water column was less stable and whole water column mixing occurred more frequently in contrast to the current more thermally stable conditions.
2. Mixing in the channel enhances nitrogen production through nitrification (Chapter 3), which contrasts with the more thermally stable main lake water column where high denitrification occurs and has resulted in nitrogen limitation and associated increased dominance by the heterocystous nitrogen fixing cyanobacterial algal species (Hecky, 1993; Hecky et al 1996).
3. The channel is a net recipient of DRSi from the gulf (82 t Si/d), which supports and possibly favors the dominance of the siliceous diatoms as was observed in this study. In contrast, silica concentrations have reduced 10-fold in the past 5 decades and which may have contributed to the decline in the relative biomass of diatoms in the lake. The phytoplankton community in Lake Victoria was dominated by diatoms 5 decades ago, which is similar to the current finding for the channel.

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