AN ANALYSIS OF PRIMARY AND SECONDARY PRODUCTION IN LAKE KARIBA IN A CHANGING CLIMATE

MZIME R. NDEBELE-MURISA

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Supervisor: Prof. Charles Musil
Co-Supervisor: Prof. Lincoln Raitt

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An analysis of primary and secondary production in Lake Kariba in a changing climate

Mzime Regina Ndebele-Murisa

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Abstract

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M.R. Ndebele-Murisa PhD, Biodiversity and Conservation Biology Department, University of the Western Cape

Analysis of temperature, rainfall and evaporation records over a 44-year period spanning the years 1964 to 2008 indicates changes in the climate around Lake Kariba. Mean annual temperatures have increased by approximately 1.5^{o}C, and pan evaporation rates by about 25%, with rainfall having declined by an average of 27.1 mm since 1964 at an average rate of 6.3 mm per decade. At the same time, lake water temperatures, evaporation rates, and water loss from the lake have increased, which have adversely affected lake water levels, nutrient and thermal dynamics. The most prominent influence of the changing climate on Lake Kariba has been a reduction in the lake water levels, averaging 9.5 m over the past two decades. These are associated with increased warming, reduced rainfall and diminished water and therefore nutrient inflow into the lake. The warmer climate has increased temperatures in the upper layers of lake water, the epilimnion, by an overall average of 1.9°C between 1965 and 2009. The warmer epilimnion has led to a more stable thermocline in the lake, and its upward migration from a previously reported 20 m depth to the current 2 to 5 m depth reported in the lake's Sanyati Basin. A consequence of the more stable thermocline has been the trapping of greater amounts of nutrients in the deep, cold bottom waters of the lake, the hypolimnion, and this coupled with a shorter mixing (turnover) period is leading to reduced nutrient availability within the epilimnion. This is evident from a measured 50% reduction in nitrogen levels within the epilimnion, with phosphorus levels displaying a much smaller net decline due to localised sources of pollution inflows into the lake. These changes in lake thermal dynamics and density stratification have reduced the volume of the lake epilimnion by ~50%, which includes the well mixed, oxygenated euphotic zone leading to more acidic waters (lower pH) and increased water ionic concentrations (conductivity), and decreased dissolved oxygen levels, which have resulted in a 95% reduction in phytoplankton biomass and a 57% decline in primary production rates since the 1980s. The reduced nitrogen levels especially have contributed to a proliferation of nitrogen-fixing Cyanophyceae, the dominant *Cylindrospermopsis raciborskii* comprising up to 66% of the total phytoplankton biomass and 45.6% of the measured total phytoplankton cellular concentrations. Also, shifts in seasonal dominance of different phytoplankton groups have been observed in the lake during turnover, the Cyanophyceae having increased in dominance from 60% of the total phytoplankton biomass in the early 1980's to the current 75%. In contrast, the Bacillariophyceae have declined substantially, from 18% of the total phytoplankton biomass in the early 1980's to the current 1.7%. The diminished phytoplankton biomass of more palatable phytoplankton, and the proliferation of smaller, less palatable phytoplankton taxa, has resulted in reduced zooplankton biomass and species richness and altered zooplankton species composition. Concentrations of large Cladocera and Copepoda especially have declined substantially in the lake by up to 93.3% since the mid 1970s, with small Rotifera currently comprising 64% of the total zooplankton biomass. The reductions in zooplankton biomass correspond with recorded decreases in catches per unit effort for the sardine *Limnothrissa miodon (*Kapenta), which have been steadily declining in the lake since 1986.

May 2011

Declaration:

I declare that ‘An analysis of primary and secondary production in Lake Kariba under a changing climate’, is my own work, that it has not been submitted for any degree or examination to any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Full Name…… Mzime R. Ndebele-Murisa…… Date…May 2011…..

Signed…Ndebele- Murisa.

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CONTENTS **Page**

Keywords ... i

Abstract ... ii
Declaration ... iv

Acknowledgements ... v

Contents ... vi
List of Figures ... viii
List of Appendices ... xii
Chapter 1 A review of phytoplankton dynamics in tropical African lakes ... 1
Abstract ... 1
1.1. Introduction ... 1
1.2. Primary production ... 2
1.3. Stratification ... 4
1.4. Seasonality ... 5
1.5. The influence of nutrients ... 7
1.6. Climate warming ... 8
1.7. Human livelihoods ... 12
1.8. References ... 13

Chapter 2 Lake description, study hypothesis and rationale, research objectives, and thesis structure ... 19
2.1. Lake description ... 19
2.1.1. General features and location ... 19
2.1.2. Geology and vegetation ... 20
2.1.3. Physiognomy and hydrology ... 22
2.1.4. Water levels ... 22
2.1.5. General climatic characteristics ... 23
2.1.6. Climatic trends ... 25
2.1.7. Lake water physical and chemical characteristics ... 25
2.1.8. Phytoplankton ... 28
2.1.9. Zooplankton ... 30
2.1.10. Ichtyofauna ... 31
2.2. Study hypothesis ... 32
2.3. Study rationale ... 32
2.4. Study objectives ... 34
2.5. Thesis structure ... 34
2.6. References ... 34

Chapter 3 The physical and chemical dynamics of Lake Kariba water ... 41
Abstract ... 41
3.1. Introduction ... 41
3.2. Methods and materials ... 43
3.2.1. Study area ... 43
3.2.2. Experimental design and sampling stations ... 43
3.2.3. Physical and chemical properties of lake water ... 44
3.2.4. Statistical analysis ... 44
3.3. Results ... 46
3.3.1. Lake basin physical and chemical properties ... 46
3.3.2. Sanyati Basin water properties ... 46
3.3.2.1 Physical properties ... 46
3.3.2.2. Chemical properties ... 47
3.4. Discussion ... 55
3.5. References ... 61

Chapter 4 Phytoplankton biomass and primary production dynamics in Lake Kariba.........66
Abstract.........66
4.1. Introduction.........66
4.2. Methods and materials.........69
4.2.1. Study area.........69
4.2.2. Experimental design and sampling stations.........69
4.2.3. Phytoplankton biomass and photosynthetic quantum yield.........69
4.2.4. Primary production.........71
4.2.5. Statistical analysis.........71
4.3. Results.........72
4.3.1. Lake basin phytoplankton biomass.........72
4.3.2. Lake basin net primary production.........72
4.3.3. Sanyati Basin phytoplankton biomass.........73
4.3.4. Sanyati Basin net primary production.........73
4.4. Discussion.........81
4.5. References.........86

Chapter 5 Phytoplankton species richness and abundance in Lake Kariba's Sanyati Basin 94
Abstract.........94
5.1. Introduction.........95
5.2. Methods and materials.........96
5.2.1. Study area.........96
5.2.2. Experimental design and sampling stations.........97
5.2.3. Phytoplankton species richness and cellular concentrations.........97
5.2.4. Statistical analysis.........98
5.3. Results.........98
5.3.1. Species richness in different phytoplankton classes.........98
5.3.2. Cellular concentrations and species composition of different phytoplankton classes.99
5.4. Discussion.........109
5.5. References.........112

Chapter 6 Zooplankton species richness and concentrations in Lake Kariba.........126
Abstract.........126
6.1. Introduction.........127
6.2. Methods and materials.........128
6.2.1. Study area.........128
6.2.2. Experimental design and sampling stations.........128
6.2.3. Zooplankton species richness and concentration.........128
6.2.4. Statistical analysis.........130
6.3. Results.........131
6.3.1. Whole lake zooplankton species richness.........131
6.3.2. Whole lake zooplankton concentrations.........131
6.3.3. Sanyati Basin zooplankton species richness.........138
6.3.4. Sanyati Basin zooplankton concentrations and bio-volumes.........138
6.4. Discussion.........144
6.5. References.........150

Chapter 7 Associations between climate, water environment, plankton, and fish production 163
7.1. General Discussion.........163
7.2. Conclusion.........174
7.3. References.........175

List of Figures Page

Figure 1.1. The location of some major lakes in tropical Africa **2**

Figure 1.2. The shrinking of Lake Chad from 1963 to 2007 ....**10**

Figure 2.1. The location of Lake Kariba in Zimbabwe showing some major tributaries **21**

Figure 2.2. The basins of Lake Kariba, basin delineation modified from the original description by Balon and Coche (1974). B1- Mlibizi, B2- Binga, B3- Sengwa, B4- Ume and B5- Sanyati......**23**

Figure 2.3. Average annual water levels in Lake Kariba over the period 1964 to 2008 ....**24**

Figure 2.4. Mean monthly air temperatures and rainfall at Lake Kariba (1964- 2008) **25**

Figure 2.5. Observed trends (solid lines) in A. mean annual temperature, B. rainfall, and C. pan evaporation at Lake Kariba, spanning the years 1964 to 2008; dashed line = linear regression **27**

Figure 2.6. Trophic levels (green arrows) associated with different size (*Aulacoseira* = large-sized, *Cylindrospermopsis* = small-sized) phytoplankton; red arrow represents an additional trophic level **33**

Figure 3.1. Location of sampling stations in Lake Kariba's five basins (B1 to B5), with those located in the centre of the lake designated lacustrine, and those located along the lake margin in proximity to river inflows designated riverine **44**

Figure 3.2. Seasonal variation in A. water temperature, B. photosynthetic active radiation (PAR), C. conductivity and D. pH across Lake Kariba's five basins. Average standard error of differences shown by bars **49**

Figure 3.3. Seasonal variation in dissolved oxygen (DO), B. dissolved organic carbon (DOC) and C. total nitrogen (total N) across Lake Kariba's five basins. Average standard error of differences shown by bars...**50**

Figure 3.4. Variation in A. water transmission of PAR and B. dissolved oxygen at different water depths in different seasons in Lake Kariba across all basins. Average standard error of differences shown by bars...**51**

Figure 3.5. Monthly variation in A. temperature, B. transmission of PAR, C. conductivity and D. pH in lacustrine and riverine habitats in the Sanyati Basin of Lake Kariba. LC= lacustrine and RV= riverine habitats. Average standard error of differences shown by bars.................................**53**

Figure 3.6. Monthly variation in A. temperature, B. transmission of PAR and C. pH at different depths in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars..**54**

Figure 3.7. Monthly variations in A. dissolved oxygen and B. dissolved organic carbon in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars **55**

Figure 3.8. Monthly thermocline depths in the Sanyati Basin (B5) of Lake Kariba **57**

Figure 4.1. Distribution of sampling stations in Lake Kariba's five basins, with those located in the centre of the lake designated lacustrine and those located along the lake margin in proximity to river inflows designated riverine **70**

Figure 4.2. Seasonal variations in A. total phytoplankton biomass and that of B. Cyanophyceae, C. Chlorophyceae and D. Bacillariophyceae in different basins of Lake Kariba. Average standard error of differences shown by bars **75**

Figure 4.3. Seasonal variations in net primary production in A. different basins and B. water depths of Lake Kariba. Average standard error of differences shown by bars **76**

Figure 4.4. Monthly variations in A. total phytoplankton biomass and those of B. Cyanophyceae, C. Bacillariophyceae, and D. Chlorophyceae in lacustrine and riverine habitats in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars **78**

Figure 4.5. Monthly variations in Cyanophyceae biomass with water depth in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars.......................................**79**

Figure 4.6. Monthly variations in primary production in A. lacustrine and riverine habitats and B. different water depths in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars...**80**

Figure 4.7. A plot of primary production against dissolved oxygen in Lake Kariba's Sanyati Basin. Z_c is the compensation depth at which oxygen evolution during photosynthetic carbon assimilation balances respiratory oxygen uptake..**84**

Figure 5.1. Distribution of 5 sampling stations in Lake Kariba's Sanyati Basin, with those located in the centre of the lake designated lacustrine and those located along the lake margin in proximity to river inflows designated riverine **97**
Figure 5.2. Monthly variation in species richness of A. Cyanophyceae and Chlorophyceae, B. Bacillariophyceae and Dinophyceae and C. Euglenophyceae, Xanthophyceae and Chrysophyceae. Standard error of differences shown by bars..**104**
Figure 5.3. Monthly variation in cellular concentrations of A. Cyanophyceae and Chlorophyceae, and cellular concentrations of most common species of B. Cyanophyceae and C. Chlorophyceae. Standard error of differences shown by bars **105**
Figure 5.4. Monthly variation in cellular concentrations of A. Dinophyceae and Bacillariophyceae, and cellular concentrations of most common species of B. Dinophyceae and C. Bacillariophyceae. Standard error of differences shown by bars...**106**
Figure 5.5. Monthly variation in cellular concentrations of A. Euglenophyceae, Xanthophyceae and Chrysophyceae, and cellular concentrations of most common species of B. Euglenophyceae, C. Xanthophyceae and D. Chrysophyceae. Standard error of differences shown by bars **107**
Figure 5.6. Monthly changes in species richness and cellular concentrations of Bacillariophyceae (A and B) and Cyanophyceae (C) at different water depths...**108**
Figure 6.1. Distribution of 17 sampling stations for zooplankton assays in Lake Kariba's five basins **129**
Figure 6.2. Seasonal and seasonal versus depth variations in A & B Cladocera and C and D Copepoda species richness in different lake basins. Standard error of differences shown by bars...**133**
Figure 6.3. Seasonal variations in Rotifera species richness in different lake basins. Standard error of differences shown by bars...**134**
Figure 6.4. Seasonal and seasonal versus depth variations in A & B Cladocera and C and D Copepoda concentrations in different lake basins. Standard error of differences shown by bars **135**
Figure 6.5. Seasonal variations in A. Rotifera species concentrations and B. seasonal versus depth variations in Rotifera species concentrations in different lake basins. Standard error of differences shown by bars...**136**
Figure 6.6. Seasonal variation in concentrations of the most common A Cladocera, B. Copepoda and C. Rotifera species in different lake basins **137**
Figure 6.7. Monthly variations versus habitat in A. Cladocera and B. Copepoda with water depth in the Sanyati Basin. Standard error of differences shown by bars...**140**
Figure 6.8. Monthly variations versus habitat in Rotifera A. species richness and B. individual concentrations with water depth in the Sanyati Basin. Standard error of differences shown by bars...**141**
Figure 6.9. Monthly variations in A. Cladocera and B. monthly variations and habitat in Copepoda with water depth in the Sanyati Basin. Standard error of differences shown by bars **142**
Figure 6.10. Monthly variation in concentrations of the most common A. Cladocera, B. Copepoda and C. Rotifera species in the Sanyati Basin **143**
Figure 6.11. Variation in the concentration of two major zooplankton groups in Lake Kariba (1975-2009). CLA= Cladocera; COP= Copepoda. Source of data: Cochrane (1978), Marshall (1980), Masundire (1989) and Harding and Rayner (2001) and present study.................................**146**
Figure 6.12. A comparison of the species richness of three major zooplankton groups in ten tropical water bodies: Lakes Albert, Chivero, Cleveland Dam (Elenbaas and Grundel, 1994), Kainji, Kariba (this study), Kivu (Isumbisho *et al*., 2006), Naivasha (Uku and Mavuti, 1987), Nasser (Mageed and Heikal, 2006), Turkana (Green, 1985) and Victoria (Mutune *et al*., 2007) **149**
Figure 7.1. Monthly variation in A. phytoplankton cellular, zooplankton individuals' concentration and Kapenta catch (CPUE kg d^{-1}) in the Sanyati Basin coincident with this study, and Kapenta CPUE from B. 1992 to 1995, C. 1996 to 1999 and D. 2000 to 2003 in the whole lake..........**170**
Figure 7.2. Annual variation in Kapenta catch (CPUE kg d^{-1}) in A. different basins of Lake Kariba from 1974 to 2003, and from B. 1986 to 2003 in the whole lake, C. in different seasons in the Sanyati Basin, and D. from June to August in the Sanyati Basin **173**

List of Tables **Page**

Table 1.1. Phytoplankton primary production in some tropical African lakes **3**
Table 2.1. General properties and morphometry of Lake Kariba **20**
Table 2.2. Physical and chemical characteristics of Lake Kariba (adapted from Balon and Coche, 1974) **28**
Table 3.1. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of season, basin, water depth and their interactions on various lake water physical and chemical properties. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ **48**
Table 3.2. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth, and their interactions on various physical and chemical properties of lake water in the Sanyati Basin of Lake Kariba. Values presented in bold significant at $*P <0.05$, $**P <0.01$, $***P <0.001$ **52**
Table 3.3. Changes in the physical and chemical properties of Lake Kariba over a 44-year period (1965-2009). Temperature averages computed from integrated epilimnion depth temperatures; all values presented as averages **58**
Table 4.1. Wald χ² statistics derived from REML (repeated measures model), which tested the effects of season, lake basin and water depth and their interactions on the biomass of different phytoplankton groups and net primary production in Lake Kariba. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ **74**
Table 4.2. Wald χ² statistics derived from REML (repeated measures model), which tested the effects of month, habitat (riverine versus lacustrine) and water depth, and their interactions on the biomasses of different phytoplankton groups and net primary production in the Sanyati Basin of Lake Kariba. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ **77**
Table 4.3. Comparison of average biomass (chlorophyll a) and primary production levels in some major African lakes **85**
Table 5.1. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth and their interactions on phytoplankton species richness in different taxonomic classes in Lake Kariba's Sanyati Basin. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ **101**
Table 5.2. Relative concentrations in decreasing order of the 20 most common phytoplankton species **102**
Table 5.3. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth and their interactions on phytoplankton cellular concentrations in different taxonomic classes in Lake Kariba's Sanyati Basin. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$ **103**
Table 5.4. A comparison of the total numbers of phytoplankton species present in different algal classes and orders recorded in Lake Kariba at different intervals between 1959 and 2009 ....**110**
Table 6.1. Formulae applied for calculation of bio-volumes of six dominant zooplankton species in Lake Kariba (l= length μm^{-1}, w= width μm^{-1} and d= diameter μm^{-1}) **130**
Table 6.2. Wald χ² statistics derived from REML (repeated measures mixed model), which tested the effects of season, lake basin and water depth and their interactions on zooplankton species richness in different taxonomic classes in Lake Kariba. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P <0.001$ **132**
Table 6.3. Wald χ² statistics derived from REML (repeated measures mixed model), which tested the effects of season, lake basin and water depth and their interactions on the concentration of zooplankton individuals in different taxonomic classes in Lake Kariba. Values presented in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P <0.001$ **132**
Table 6.4. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth, and their interactions on zooplankton

species richness in different taxonomic classes in the Sanyati Basin of Lake Kariba. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001 ....**139**

Table 6.5. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth, and their interactions on zooplankton concentrations in different taxonomic classes in the Sanyati Basin of Lake Kariba. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001 ....**139**

Table 7.1. t-statistics for Pearson correlations between measured biomasses and concentrations of different phytoplankton and zooplankton taxa and lake water physical and chemical properties. Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001 ....**165**

Table 7.2. t-statistics for Pearson correlations between measured concentrations of different phytoplankton and zooplankton taxa. Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001 ....**171**

Table 7.3. t-statistics for Pearson correlations between measured Kapenta catch (CPUE kg month-1) and temperature, rainfall and lake level. Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001. The Kapenta catch statistics returned by commercial fishing companies between 1974 and 2003 to the Lake Kariba Fisheries Research Station and expressed as kg wet weight of Kapenta caught per standard unit net panel 45.7 m in length...**172**

Table 7.4. t-statistics for slopes and intercepts of least squares regressions of Kapenta catch (CPUE kg month^{-1}) against year for the period 1986 to 2004. Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001 ....**172**

List of Appendices **Page**

Appendix 5.1. A list of Chlorophyceae species and their average concentrations in the Sanyati Basin of Lake Kariba (2007-2009) **120**
Appendix 5.2. A list of Cyanophyceae species and their average concentrations in the Sanyati Basin of Lake Kariba (2007-2009) **121**
Appendix 5.3. A list of Bacillariophyceae, Dinophyceae, Euglenophyceae, Chrysophyceae and Xanthophyceae species and their average concentrations in the Sanyati Basin of Lake Kariba (2007-2009) **122**
Appendix 5.4. Scanning Electron Microgram (SEM) images of Dinophyceae species; A. *Peridionipsis* sp., B. *Peridinium gatunense,* C. *Ceratium furcoides and* D. *C. hirundinella* (short horns on the apotheca) sampled in the Sanyati Basin of Lake Kariba **123**
Appendix 5.5. Scanning Electron Microgram (SEM) images of Chlorophyceae species of A. *Staurastrum johnsonii*, B. *S. gracile*, C. *S. limnetica* and D. *Pediastrum simplex* sampled in the Sanyati Basin of Lake Kariba **124**
Appendix 5.6. Scanning Electron Microgram (SEM) images of Bacillariophyceae species of A. *Alacuseira granulata*, B. *Navicula digitoradiata*, C. *Cyclotella stelligera* and D. *Alacuseira* sp. sampled in the Sanyati Basin of Lake Kariba **125**
Appendix 6.1. A list of Rotifera species in Lake Kariba (2007-2009). Species with an asterisk (*) denote species found in lake basins other than the Sanyati (Basin 5) **157**
Appendix 6.2. A list of Cladocera, Copepoda in the Sanyati Basin of Lake Kariba (2007-2009). Species with an asterisk (*) denote species found in lake basins other than the Sanyati (Basin 5) **158**
Appendix 6.3. A comparison of Cladocera and Copepoda species complements in the Sanyati Basin between 1976 and 2009. ‘+g’ = organism identified to genus level, ‘+’ = organism present, ‘_’ = absent and ‘o. i. a. c.o.’ = organism identified as copepods only **159**
Appendix 6.4. SEM image of *Thermocyclops* sp. captured from Sampling Station 38 (Zambezi River Mouth) of Basin 1 in February 2009 .... **160**
Appendix 6.5. Photograph of *Keratella quadrata* (centre) sampled from Station 1 (Charara River Mouth) in October 2008; Magnification = X 400 with *Cylindrospermopsis* sp. (rods) in the background and *Microcystis* sp. colony (bottom right corner) **161**
Appendix 6.6. SEM image of *Mesocyclops* sp. sampled from Sampling Station 7 (Sanyati River Mouth) in December 2008 .... **162**

Chapter 1

A review of phytoplankton dynamics in tropical African lakes

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Abstract

This review provides a synthesis of current knowledge on phytoplankton production, seasonality, and stratification in tropical African lakes, and considers the effects of nutrient enrichment and the potential impacts of air and water climate warming on phytoplankton production and composition. Tropical African lakes are especially sensitive to climate warming, as they experience wide fluctuations in the thermocline over a narrow range of high water temperatures. Recent climate warming has reduced phytoplankton biomass and production in the lakes; negatively impacting on the production of palatable Chlorophyceae and increasing Cyanophyceae, which leads to reduced zooplankton production and a consequent decline in fish stocks, all of which can be associated with elevated water temperatures. This could mean that even moderate climate warming may destabilise phytoplankton dynamics in tropical African lakes, thereby reducing water quality and food resources for planktivorous fish, with consequent negative impacts on human livelihoods.

1.1. Introduction

In this review both the natural and man-made reservoirs are combined as Tropical African lakes, and the location of the major lakes, which are herein referred to, are shown in Figure 1.1. These lakes are havens for diverse endemic fish fauna of immense ecological and scientific importance that are dependent on sustained phytoplankton seasonality as well as stratification. Furthermore, many provide an important source of dietary protein to rural communities, potable water for humans, livestock and agriculture, a means of transportation of goods and generation of hydro-electric power, and a source of revenue from fishing and eco-tourism. Previous reports on phytoplankton in tropical African lakes have predominantly had a taxonomic focus, with some considering phytoplankton composition and production in specific lakes as these reflect their overall health (Talling and Talling, 1965). However, with the exception of Talling and Lemoalle (1998) and Talling (2001) who focused on ecological dynamics of tropical inland waters and African shallow lakes, a comprehensive review of phytoplankton production, seasonality and stratification in all tropical African lakes, as well as phytoplankton responses to eutrophication and climate warming and consequent impacts on fish stocks and human livelihoods, has not been undertaken and is the focus of this paper. Such information is especially pertinent, since many tropical African lakes have experienced recent deterioration in water quality and declines in fish abundance and diversity which are likely to be exacerbated by climate change, and increased anthropogenic pressures (Magadza, 1994).

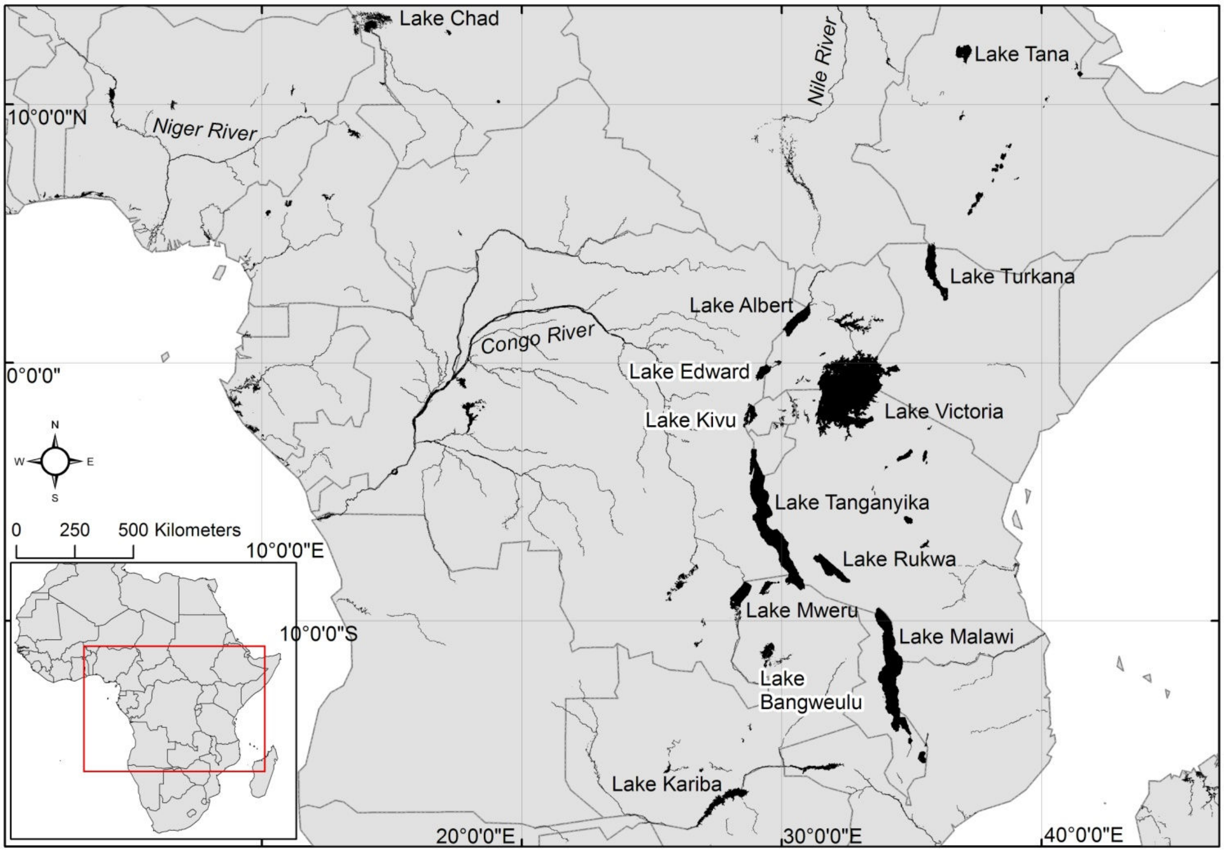

Figure 1.1. The location of some major lakes in tropical Africa

1.2. Primary production

Tropical African lakes display a considerable range in phytoplankton production (Table 1.1), which reflects their trophic state. Lake Kainji is a typical example of a nutrient-poor (oligotrophic) African lake with a low phytoplankton production of 0.3 g C m^{-2} h^{-1} (Karlman, 1982). Towards the middle of the production scale is the nutrient-rich (eutrophic) Lake Nasser, whose phytoplankton production has been reported to average 4.48 g C m^{-2} h^{-1} (Samaan, 1972) and Lake Chivero and Hartbeespoort Dam are at the upper end of this scale. Increased nutrient inflows, resulting from expanding urbanisation and agriculture, have elevated primary production levels in many African lakes. A good example is Lake Chivero, whose primary production levels have increased by over ten-fold from its previously reported range of 1.64- 6.03 g C m^{-2} h^{-1} in 1979 to its current range of

18.5- 140 g C m^{-2} h^{-1} (Robarts, 1982; Ndebele, 2003). Similarly, in the physiognomically similar Hartbeespoort Dam, primary production levels which normally range between 0.40 and 30.90 g C m^{-2} h^{-1} were recorded to be as high as 185 g C m^{-2} h^{-1} in the 1980s (Robarts, 1984).

Table 1.1. Phytoplankton primary production in some tropical African lakes

Country where study was conducted	Lake	Primary production (g C m^{-2} h^{-1})	Source
Chad	Chad	0.70- 2.69	Carmouze *et al.*, 1983
Egypt	Nasser	4.48	Saaman, 1972
Ghana	Volta	0.12- 0.48	John, 1986
Kenya	Baringo	0.22- 0.70	Talling and Talling,
Kenya	Crescent Island	1.13- 3.15	Melack, 1979
Kenya	Naivasha	1.39- 2.33	Melack, 1979
Kenya	Oloiden	1.58- 4.54	Melack, 1979
Kenya	Winam Gulf	1.61- 3.68	Melack, 1979
Malawi	Malawi	0.24- 1.14	Hecky and Kling, 1987
Nigeria	Kainji	0.30	Karlman, 1982
South Africa	Sibaya	0.23- 1.85	Allanson, 1979
South Africa	Hartbeespoort	0.40- 30.90	Robarts, 1984
Tanzania	Tanganyika	0.16- 4.30	Hecky and Kling, 1987
Tanzania	Edward	0.78	Hecky and Kling, 1987
Tanzania	Kivu	0.85- 2.20	Hecky and Kling, 1987
Uganda	Albert	0.18	Hecky and Kling, 1987
Uganda	George	1.95- 5.80	Ganf, 1975
Uganda	Victoria	3.30- 13.50	Hecky and Kling, 1987
Zimbabwe	Kariba	0.10- 1.70	Cronberg, 1997
Zimbabwe	Chivero	1.64- 6.03	Ndebele, 2003
Zimbabwe	Cleveland	0.07-0.87	Ndebele, 2009

These elevated primary production levels correspond with algal blooms, and are a direct consequence of high nutrient inflows which overburden the lake's natural purification systems (Robarts, 1984; Mhlanga *et al.*, 2006). In deeper African lakes, nutrient inflows also exert prominent effects on primary production. Examples include Lake Malawi, where primary production levels of 0.24 to 1.14 g C m^{-2} h^{-1} have risen to range between 14.04- 26.20 g C m^{-2} h^{-1} in recent years (Guildford *et al.*, 2007), and Lake Victoria where primary production of 3.30- 13.50 g C m^{-2} h^{-1} have risen to as high as 234 g C m^{-2} h^{-1} (Mugidde, 1993). Primary production in tropical African lakes is often low at or near the water surface due to photo-inhibition. The optimal habitat for phytoplankton is in the first few meters of the water column. Production tends to decrease with depth, until light becomes the limiting factor after the euphotic depth. Light is the primary limiting factor to the growth of phytoplankton in Lake Chivero, whereas conductivity and trophic status (measured as chlorophyll a) are the most important environmental variables influencing the distribution of phytoplankton species in this and other African lakes (Robarts and Southall, 1977; Yasindi and Taylor, 2003). This is compliant with a classification of 17 East African lakes on the basis of water conductivity and associated phytoplankton species (Talling and Talling, 1965).

1.3. Stratification

Environmental factors such as water pH, conductivity, dissolved oxygen, nutrient concentration, and light intensity influence primary production, and these in turn are affected by thermal stratification, which is a common feature of tropical African lakes. Stratification is a result of thermal differences in the upper warm layer of water, the epilimnion, and the lower cold layer, the hypolimnion, separated by a zone of steep temperature gradient, the thermocline, and is usually created during periods of high summer temperatures. Stratification is characterised by vertical profiles of water temperature, conductivity, dissolved oxygen concentration, and pH. In Lake Tanganyika a fairly stable stratification is established during the wet season, which is generated by increased water temperatures and diminished wind intensities (O'Reilly *et al*., 2003). However, currents and internal waves, as well as coastal jets and return flows, do cause localised up-welling, which may partly disrupt this stratification (Chale, 2004). Stratification is also prevalent in many deep tropical African lakes, such as Albert, Cabora Bassa, Chad, Kariba, Malawi, Niger and Turkana, often influencing the seasonality and abundance of phytoplankton.

The general annual cycle of thermal stratification in these lakes includes a short phase of partial vertical mixing, which is often accompanied, or immediately followed, by a peak of algal abundance, to which Bacillariophyceae make a major contribution (Reynolds, 1984; Chale, 2004). A second peak dominated by Cyanophyceae often develops after stratification (Chale, 2004). In Lake Ogelube in Nigeria, phytoplankton biomass during the rainy season (April-October) is much higher than during the dry season (November-March). Chlorophyceae (mostly desmids) are most abundant during the rainy season, followed in decreasing order of abundance by Cyanophyceae, Bacillariophyceae, Euglenophyceae, Dinophyceae, Cryptophyceae, Chrysophyceae, and Xanthophyceae (Nweze, 2006). This order changes in the dry season, when the relative abundance of Bacillariophyceae is greater than that of Cyanophyceae, and Dinophyceae greater than that of Euglenophyceae. A similar seasonal pattern is found in other African lakes, such as Kariba, Malawi, Tanganyika and Victoria, where Cyanophyceae bacteria dominate during summer stratification, with Bacillariophyceae tending to dominate in winter at turn-over when stratification breaks down (Hecky and Kling, 1987; Cronberg, 1997).

Density stratification is also a natural feature of many shallow, naturally saline African lakes such as George (Ganf, 1975; Wood *et al*., 1976), Naivasha (Hubble and Harper, 2002), and Nakuru (Vareschi, 1982). However, this stratification can be disrupted by strong winds, which influence water circulation, thereby preventing the development of a consistent thermocline (Langenberg *et al.,* 2002). This feature has been observed in the four Kenyan lakes, Naivasha, Crescent Island Crater, Oloiden Lake and Winam Gulf, which display complete vertical mixing and well-oxygenated water throughout the water profile during periods of strong winds (Melack, 1979). Stratification in some shallow African lakes traps nutrients from riverine inflows contaminated by effluent discharges. This is apparent in Lake Chivero during hot summer months (Ndebele, 2003), with stratification break-down during winter months, resulting in the temporary upwelling of nutrients and localised algal blooms (Mhlanga *et al*., 2006).

In general, stratification has a negative impact on primary production, as it confines nutrients to deeper waters of greater density beyond the euphotic zone (Spigel and Coulter, 1996). Therefore, phytoplankton species diversity and total biomass is elevated only in nutrient-rich waters at river inflows (Vuorio *et al*., 2003). As a result, the highest primary production normally occurs in the first few metres of the water column, is often inversely correlated with water transparency, and is usually depressed at the water surface, particularly where temperatures exceed 30°C (Robarts, 1979). In most African lakes, strong thermal gradients often develop from daytime warming in the zero to five-metre layer. These gradients frequently trap photosynthetic oxygen to form well-defined maxima, which demarcate deeper, oxygen-poor layers (Talling *et al*., 1973). In some lakes, the de-oxygenation layer is so deep that oxygen disappears from the hypolimnion and hydrogen sulphide is produced. The epilimnion maintains a high oxygen concentration throughout the year, except during partial stratification which may develop during the day, causing a gradient of decreasing oxygen concentration with depth. Some features of stratification in artificial African lakes are also influenced by the positioning of turbines. For instance, Lake Kainji's rapid deepening of the epilimnion during stratification has been attributed to discharges from the lake, as the levels of the spillways and turbine intakes are situated below the thermocline (Henderson, 1973), whilst a substantive level of nutrients is drawn from Lake Kariba, whose turbines are situated below the thermocline (Chifamba, 2000).

1.4. Seasonality

Most African lakes have a well-established seasonality in phytoplankton abundance, governed mainly by climate. The community of larger phytoplankton in Lake Tanganyika is mainly composed of Chlorophyceae and Bacillariophyceae (*Nitzschia* spp.), with large blooms of diastrophic[1] filamentous Cyanophyceae periodically observed during September to November at the onset of the rainy season (Salonen *et al*., 1999; Cocquyt and Vyverman, 2005). However, more recently these Cyanophyceae have not been observed as a major constituent of the phytoplankton

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[1] Diastrophic meaning 'twisted' and referring to the filamentous Cyanophyceae

biomass (Descy *et al*., 2005; De Wever *et al*., 2008), with contrasting pico-Cyanophyceae and Bacillariophyceae concentrations due to changes in water column stability at the southern and northern ends of the lake (Hecky and Kling, 1981; Vuorio *et al*., 2003). A seasonal succession of major algal groups, similar to that in Lake Tanganyika, is found in the naturally oligotrophic Lakes Edward, Kivu and Malawi, which have a low phytoplankton biomass and species diversity (Hecky and Kling, 1987), as well as in the artificial, oligotrophic Lake Kariba, where Cyanophyceae (*Cylindrospermopsis, Anabaena, Pseudoanabaena*) dominate, and Chlorophyceae co-dominate when the phytoplankton biomass reaches its peak (up to 1.52 mg l^{-1} chlorophyll) during the rainy season, with Bacillariophyceae dominating at turnover during the dry season (Ramberg, 1987). Similarly, Bacillariophyceae are the dominant group in Lake Kivu during episodes of deep mixing in the dry season, with filamentous, diastrophic Cyanophyceae and pico-Cyanophyceae forming a substantial fraction of the autotrophic biomass under conditions of reduced nutrient availability in the stratified water column during the rainy season (Sarmento *et al*., 2006). Lake Kivu's phytoplankton species assemblage is somewhat intermediate in composition between the oligotrophic Lakes Malawi and Tanganyika and the more eutrophic Lake Victoria, though the dominant Bacillariophyceae of Lake Kivu (*Urosolenia* sp., *Nitzschia bacata, Fragilaria danica*) are normally associated with oligotrophic, phosphorus-deficient African lakes (Sarmento *et al*., 2006).

The concept of stable phytoplankton communities in some African lakes has been questioned. Observations of primary production and phytoplankton densities at regular (weekly and fortnightly) intervals in Lake Kinneret (Israel) over 35 years (1969- 2004) have led to a repudiation of the concept of a stable phytoplankton seasonality (Zohary, 2004). These observations demonstrated remarkable stability in algal species composition and abundance in summer and spring algal blooms in the lake during the first 24 years of monitoring. After 1994, however, deviations from the previously predictable annual pattern of algal blooms were apparent. They were characterised by the absence of prevailing spring *Peridinium gatunense* blooms, intensification of winter *Aulacoseira granulata (=Melosira)* blooms, and increased variability in the magnitude of blooms in other species. Also, nanoplanktonic palatable forms in the high summer phytoplankton biomass were replaced by less palatable forms, and there was a new appearance and increase in absolute biomass of toxin-producing, nitrogen-fixing Cyanophyceae, as well as an increased incidence of fungi attacking the Dinophyta *Peridinium gatunense* (Zohary, 2004). In Lake Tanganyika, shifts in phytoplankton seasonality have been detected through the application of Empirical Orthogonal Function Analysis to a seven-year satellite observation record (Bergamino *et al*., 2007). Similarly, a comparison of the phytoplankton composition in Lake Kariba between 1959 and 1964 with that between 1986 and 1990 has shown a change from a riverine-dominated species component rich in desmid flora and large algal species, to that dominated by small-celled chlorococcal Chlorophyceae, mainly due to the apparent stabilisation of the lake over time (Cronberg, 1997).

1.5. The influence of nutrients

In the tropics and at mid-latitudes, phytoplankton are typically nutrient-limited, and reduced biological productivity, phytoplankton biomass and growth have been linked to increased water temperatures and reduced nutrient supply (Bergamino *et al*., 2007). Nitrogen (N) and phosphorus (P) have been identified as the major nutrients governing primary production and phytoplankton biomass in tropical African lakes (Talling and Talling, 1965; Viner, 1977). Indeed, in many African lakes nitrogen-fixing taxa such as *Anabaena* and *Cylindrospermum* proliferate due to the limiting concentrations of this nutrient for other taxa in their waters (Talling and Talling, 1965; Ganf, 1975; Hubble and Harper, 2002; Chale, 2004; De Wever *et al*., 2008). The low phytoplankton biomass variability of Lake George in Uganda has been attributed to both N and P limitation and the extreme predominance of inedible Cyanophyceae over that of other biota (Ganf, 1975). Similarly, in Lake Kariba it has been demonstrated that the waters are principally P-limited for most of the year, with a possibility of N co-limiting at other times (Moyo, 1991; Magadza, 1992). In this case the ability to fix nitrogen becomes an added advantage, and may explain the dominance of nitrogen-fixing taxa in this lake. In Lake Naivasha, N is more limiting than P, with an algal preference for ammonium over nitrate (Hubble and Harper, 2002). In Lake Tanganyika, the addition of N, P and Iron (Fe) stimulates total phytoplankton production, based on both High Performance Liquid Chromatography (HPLC) pigment analysis and cellular counts using epifluorescence microscopy (De Wever *et al*., 2008). Iron enhances production of mainly prokaryotic pico-phytoplankton; N and P increase Chlorophyceae, and in some cases Bacillariophyceae production and Fe, in combination with N and P, improves pico-Cyanophyceae production (De Wever *et al*., 2008). Silica (Si) is known to increase Bacillariophyceae production because of their siliceous shells, and this has been demonstrated in mesocosmic experiments (De Wever *et al*., 2008). Guildford *et al*. (2003) concluded that N was the major limiting nutrient in Lakes Malawi and Victoria, whilst the combination of N and P with Fe resulted in the highest increase in chlorophyll a, suggesting that, after N and P, Fe is the next most likely nutrient to limit phytoplankton growth in these lakes.

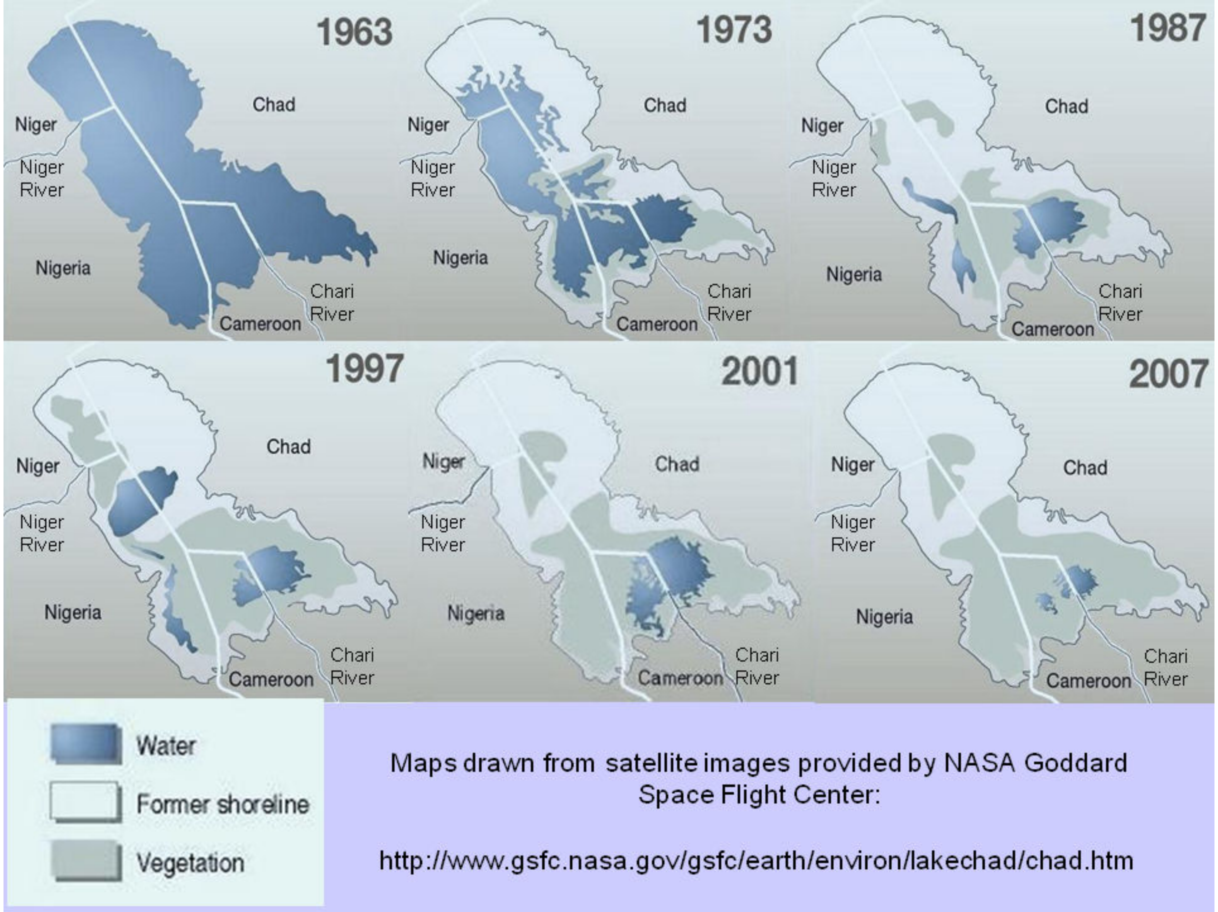
The composition and abundance of phytoplankton often reflect the nutrient status of African lakes with, for example, the low Euglenophyceae biomass in Lake Ogelube proposed as indicative of low organic pollution, and the predominance of desmids indicative of oligotrophic conditions (Nweze, 2006). Low nutrient contents have also been observed in the normally oligotrophic Lakes Kariba, Kivu and Malawi, yet, despite this, many African lakes are now prone to nutrient enrichment from anthropogenic activities, and this has led to eutrophication and associated problems. Classical examples of eutrophic African water bodies are Lakes Chivero and Victoria and the Hartbeespoort Dam, with recorded N concentrations of over 50 mg l^{-1}. Elevated nutrient levels in Lake Chivero, caused by discharge of partially treated sewage and industrial effluent into the lake, has resulted in an increase in phytoplankton biomass by a factor of more than ten, and corresponding reductions in water transparency (Mhlanga *et al*., 2006). Associated with these changes is a progressive decrease in phytoplankton species diversity, with the Cyanobacterial species *Microcystis aeruginosa* dominating and *Aulacoseira* spp. (=*Melosira)* co-dominating the phytoplankton community (Ndebele, 2003; Mhlanga *et al*., 2006). Cyanobacterial blooms have also been reported in nutrient-enriched South African impoundments, namely the Hartbeespoort Dam (Robarts and Zohary, 1986, Van Ginkel *et al*., 2001) and the Erfenis and Allemanskraal Dams (Van Ginkel and Hohls, 1999), as well as the Orange River (Janse van Vuuren and Kriel, 2008). Similarly, nutrient-rich inflows into a shallow tropical lake in the Cameroon (Yaoundé Municipal Lake) have resulted in a massively increased phytoplankton dry biomass of 225 µg ml^{-1} and chlorophyll-a concentration of 566 mg $m^{-3,}$ dominated by Euglenophyceae and Chlorophyceae (Kemka *et al*., 2006).

Eutrophication tends to impact shallow lake systems more than deeper tropical lakes such as Lakes Malawi and Victoria, with incidences of localised pollution only occasionally reported in the deeper lakes such as Kariba (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996). In fact, in Lake Kariba the water has changed from an initial nutrient-rich (eutrophic) state to that of its current nutrient-poor (oligotrophic) state, with P limiting primary production (Moyo, 1991). However, the high concentrations of faecal coliform bacteria recorded along the northern shoreline of Lake Kariba indicate that the lake waters are moving towards mesotrophy (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996). The initial eutrophic state in the lake has led in the past to the proliferation of the noxious aquatic weed *Salvinia molesta* (Kariba weed), and more recently to the propagation of another aquatic weed, *Eichhornia crassipes* (water hyacinth). This weed is currently prevalent in Lakes Chivero and Victoria as well as in Lakes Baringo, Chad, Malawi, Naivasha, Nakuru, Tanganyika and Victoria, where it is adversely affecting fishing industries (Ogutu-Ohwayo and Balirwa, 2006).

1.6. Climate warming

The impact of global warming projected by climate change models (Hulme, 1996; Hulme *et al*., 2001; IPCC, 2007) on the function of African aquatic ecosystems is uncertain, though some likely impacts have been reported (Magadza, 1994). Inter-annual variations in phytoplankton composition and biomass in temperate regions are known to reflect changes in climate (Lehman *et al*., 1998). Reduced depths of light transparent epilimnions, due to upward shifts in thermoclines in response to elevated temperatures, could potentially adversely affect primary production in deep African lakes such as Kariba, Malawi, Tanganyika and Victoria. However, relatively few data exist on the influence of climate variability on phytoplankton biomass and composition in tropical African lakes. Only a few phytoplankton studies, which do not specifically address climate-driven changes, have been undertaken in Africa, such as in Lake Volta (John, 1986), and in Lakes Malawi, Tanganyika and Victoria (Cocquyt and Vyverman, 1994). However, some trends have been noted (Magadza, 1994; O'Reilly *et al*., 2003). East African lakes, for example, are known to be potentially highly sensitive to climate change (Johnson and Odada, 1996), as small variations in climate cause wide fluctuations in the thermocline over a narrow range of high water temperature (O'Reilly *et al*. 2003; Stenuite *et al*., 2007). Indeed, thermal stratification, which isolates nutrients from the euphotic zone, is strongly linked to hydrodynamic and climatic conditions in Lake Tanganyika (Plisnier *et al*., 1999). Also, an analysis of climatic data for the middle Zambezi Valley shows that warming around Lake Kariba is proceeding at a faster rate than regional models predict, which points to future shifts in phytoplankton species richness and production (Magadza, 2010). In Lake Tanganyika, it was reported that regional climate change over the past 80 years has reduced productivity, and more specifically primary production (O'Reilly *et al*., 2003). However, other climatic factors such as the South-East trade winds impact the primary production in this lake by increasing wave action and upwelling, which bring nutrients from deeper regions of the lake to the surface. Conversely, during less windy El Niño years the lake water column is more stable, resulting in enhanced nutrient depletion in surface waters and diminished phytoplankton production (O'Reilly *et al*., 2003; Stenuite *et al*., 2007). These findings, corroborated by a modeling study, demonstrated a close correspondence between phytoplankton biomass and climate in Lake Tanganyika (Bergamino *et al*., 2007). This seven-year study revealed that shifts in phytoplankton dominance were due to the lake's high sensitivity to climate change, as variations in wind and air temperatures favoured the release or entrapment of nutrients present in deeper waters (Bergamino *et al*., 2007).

Much of what is happening to lakes across Africa is attributable to years of drought that reduce river inflows, and rising temperatures that cause increased evaporative water loss (Arnell, 1999). The extreme example is Lake Chad, once the world's sixth-largest lake, which has decreased to 5% of its original size of approximately 25 000 km^2 in 1963 to 1 350 km^2 in 2001 (Figure 1.2). This is attributed to large and unsustainable irrigation projects built by Niger, Nigeria, Cameroon and Chad which have diverted water from the lake as well as from the Chari, Logone and Niger Rivers, major overgrazing in the region resulting in a loss of vegetation, and serious deforestation contributing to a drier climate (Carmouze *et al*., 1983; Coe and Foley, 2001). Other examples of African lakes that may be responding to increasing temperatures driven by climate change are Lake Turkana, which is the largest, most northerly and most saline of Africa's Rift Valley lakes, whose level has dropped 10 m between 1975 and 1992 due to reduced inflow (McGinley, 2008), and Lake Victoria, whose level has dropped over 1.5 m in five years (Phoon *et al*., 2004; Awange *et al*., 2008).



Maps drawn from satellite images provided by NASA Goddard Space Flight Center:

http://www.gsfc.nasa.gov/gsfc/earth/environ/lakechad/chad.htm

Figure 1.2. The shrinking of Lake Chad from 1963 to 2007

For the Zambezi Basin, simulated run-off under climate change is projected to decrease by about 40% or more, which would greatly reduce the size and depth of Lakes Cabora Bassa, Kafue and Kariba (DeSanker and Magadza, 2001). In the deep, meromictic Lake Tanganyika, warming has increased water column stability and decreased vertical mixing, thereby reducing nutrient loading to the upper mixed layer (O'Reilly *et al*., 2003). Observations since 1974 in this lake document decreases in phytoplankton abundance and increases in dissolved silica, both indicative of declining primary production, with negative implications for the pelagic fishery which accounts for more than 90% of all landings (O'Reilly *et al*., 2003; Stenuite *et al*., 2007). However, fishing effort continues to rise and technologies have improved so that landings have increased during the warming period, making it difficult to decipher any impact on fish productivity in response to warming. In Lake Victoria, climate warming has been implicated in the eutrophication of the world's largest lake fishery (Fryer, 1997). However, increased phosphorus loading is more likely the direct cause, with climate probably playing a smaller role by increasing stability of seasonal stratification and accelerating the onset of hypolimnetic de-oxygenation (Fryer, 1997). Consequences of lake-warming for the hundreds of endemic cichlid fishes, especially those occurring in littoral areas of the lake, are speculative (Phoon *et al*., 2004).

Increased water temperatures associated with climate warming are likely to cause a shift in phytoplankton species composition from Chlorophyceae to Cyanophyceae, which are competitively superior at higher temperatures. Microcosm studies have demonstrated that elevated temperatures suppress total zooplankton biomass by altering phytoplankton community composition towards high temperature-tolerant species, though total phytoplankton biomass is not usually altered (Doney, 2006). For the phytoplankton community of Lake Chivero, it was found that the water temperature at which the Cyanophyceae-dominated cultures was between 25ºC and 26ºC, whereas for Chlorophyceae it was between 21ºC and 23ºC (Sibanda, 2003). These findings may explain the low biomass of the previously dominant Chlorophyceae in Lake Kariba, where 73% of the temperatures recorded at 5 m depth exceed 24ºC (Magadza, 2008). Since its creation, Lake Kariba has exhibited distinct changes in water chemistry and thermal properties, the latter seemingly due to global warming, as the rate of warming in the Zambezi valley has nearly doubled the IPCC global average of 0.2°C per decade (Magadza, 2010). This change in the lake's thermal properties is reflected in an upward migration of the thermocline, apparent from the smaller metalimnion temperature gradient and an upward movement of the low (<2 mg l^{-1} DO) oxygen layer. These changes in thermal properties ostensibly correspond with declines in *Limnothrissa* fish populations (Magadza, 1994).

As water temperatures increase, algal succession follows a progression from Bacillariophyceae through to Chlorophyceae to Cyanophyceae (Pliński and Jóźwiak, 1999). In Lake Victoria, the phytoplankton blooms observed during February and August comprise over 90% *Microcystis* sp., at concentrations of 34 000 colonies ml^{-1} (77.6 mg l^{-1}). The blooms corresponded with high temperatures, discharge of nutrients from river inflows, nutrient upwelling, and nutrient release from sediments (Ochumba and Kibaara, 1989). The preponderance of Cyanophyceae at higher water temperatures (> 25ºC) has led to concerns that increased water temperatures due to global warming could result in a decline in the production of palatable Chlorophyceae, leading to decreased zooplankton production and a consequent decline in fish stocks. Indeed, fisheries data from Lake Tanganyika show significant correlations with climatic (ENSO) data over the last 40 years (Stenuite *et al*., 2007). This suggests that moderate warming could destabilise plankton dynamics, thereby potentially reducing water quality and food resources for higher trophic levels such as planktivorous fish as seen in shallow cold-water ecosystems (Strecker *et al*., 2004).

Also, oxygen depletion and release of toxins caused by algal bloom die-off may lead to massive fish mortalities, as reported in Lake Chivero (Moyo, 1997; Mhlanga *et al*., 2006). In this lake, the dissolved oxygen concentrations occurred after an algal bloom die-off that ranged from 2 mg l^{-1} at 5 m depth to 3.9 mg l^{-1} at the lake surface. These oxygen concentrations were lower than those (3.2- 4.8 mg l^{-1}) measured in the Nyanza Gulf of Lake Victoria, following the collapse of a phytoplankton bloom and associated with high mortalities of Nile tilapia (*Oreochromis niloticus*) (Ochumba and Kibaara, 1989). Algal toxins caused by algal bloom die-off have also been previously detected in Lake Chivero and in tap water emanating from the lake (Johansson and Olsson, 1998; Mhlanga *et al*., 2006; Ndebele and Magadza, 2006), and though toxic to fish, it has not been established whether these are toxic to humans and other fauna (Moyo, 1997). However, toxic strains of *Microcystis* have been identified in other African fresh-water bodies as well as in fresh-water systems (Robarts, 1984) elsewhere in the world (Chen *et al.*, 2009).

1.7. Human livelihoods

The fate of tropical African lakes in a changing climate seems uncertain, and this poses several challenges, the most important of which is an understanding of how changes in climate will affect aquatic ecosystems and human livelihoods, which need to be overcome (Magadza, 1994; Hulme, 1996; IPCC, 2007). The consequences of climate warming on lake hydrology through destabilisation of stratification, and on lake temperature, could affect phytoplankton production by reducing both abundance and composition in many tropical African lakes. The consequent cascade through a longer trophic chain, due to the dominance of smaller phytoplankton, could potentially affect zooplankton and fish production, and ultimately threatens the viable fishery industries that sustain the livelihoods of riparian communities. Unfortunately, the poor are most at risk, as they depend on the natural resources provided by many African lakes; yet policies around these resources do not benefit them to a large extent. For instance, at Lake Kariba's creation, 57 000 people were resettled to make way for the lake, but suitable land was not sufficiently available in the immediate vicinity (Scudder, 1966). These same people should presently be reaping the benefits of the artificial lake; however, there is a disparity in the allocation of resources and policies that govern the use of the lake (Magadza, 1994). The value of African lakes is without question, for they contribute significantly to poverty reduction and food security. They are a source of cheap dietary proteins, with lakes such as Chilwa, Kariba, Malawi, Tanganyika and Victoria contributing approximately 60% of the dietary protein to bordering rural communities. The lakes provide potable water for human and livestock use, irrigation water for agriculture, are a means of transportation of goods, generate hydro-electric power; and are a source of revenue from fishing and eco-tourism. Lakes Malawi, Tanganyika and Victoria particularly are a haven of diverse endemic fish fauna of immense ecological and scientific importance. Generating deep concern are the declines in fish abundance and diversity and the deterioration in water quality experienced by many tropical African lakes. Although policies have been implemented to mitigate these threats, there remains an urgent need to consistently monitor the health of tropical African lakes to circumvent adverse effects caused by anthropogenic pressures and a changing climate.

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Chapter 2

Lake description, study hypothesis and rationale, research objectives, and thesis structure

2.1. Lake description

2.1.1. General features and location

Lake Kariba is an artificial dam that was created on the Zambezi River by the impoundment of the Zambezi River at the Kariba Gorge. Dam wall construction began in 1955, with construction completed in December 1958. The lake filled to capacity in 1963 when it reached its maximum extent (approximately 5 580 km^2). Currently, Lake Kariba is the third largest man-made lake in the world, and the largest volumetrically (approximately 185 km^3). The primary function of the lake was to provide hydro-electricity for Zambia and Zimbabwe (then known as Northern and Southern Rhodesia) that jointly owned the lake (Magadza, 2006). The major features of the lake are highlighted in Table 2.1.

Lake Kariba's precise location (Figure 2.1) is some 365 km north-west of Harare in Zimbabwe, and lies within the Matusadonha National Park, a protected, wildlife area. It stretches from the confluence of the Deka and Zambezi Rivers in the south-west (18´ 04˝S, 26´ 42˝E) to the Kariba Gorge (16´ 31˝S, 28´ 45˝ E) in the north-east, and is approximately 277 km long and 40 km at its widest point. It has a catchment area of 663 848 km^2 extending over parts of Angola, Zambia, Namibia, Botswana and Zimbabwe. The lake is bordered by Zambia in the north and Zimbabwe in the south, and exhibits a general SW-NE orientation.

The Zambezi is Southern Africa's fourth largest river after the Nile, Congo and Niger, and it stretches for 2 500 km to the Indian Ocean in central Mozambique. The river rises in north-western Zambia, flows through Angola, and re-enters Zambia, where it flows southwards through the marshy Barotse plains (FAO, 1997). It forms the border between Zambia and the eastern Caprivi Strip of Namibia and farther east between Zambia and Zimbabwe, where it plunges over the Victoria Falls. It finally enters Mozambique, where it splits into a wide delta ending its 2 500 km course (FAO, 2005). The Zambezi Basin comprises three sub-catchments, subdivided into the Upper, Middle and Lower catchments. Besides various smaller lakes, two large man-made lakes, Lake Kariba on the border between Zambia and Zimbabwe and Lake Cabora Bassa in Mozambique, lie within the basin (FAO, 1997). The Zambezi River has a vast catchment basin of 1 193 500 km^2 which includes the states of Mozambique and Malawi.

The topography of the basin varies in altitude, from the mountain areas lying over 2 000 m above sea level to the delta in Mozambique. A plateau, deeply dissected by river valleys with altitudes ranging from 1 000 to 1 500 m above sea level, covers a large proportion of the basin

(Madamombe, 2004). The hydrology of the basin is largely dependent on the rainfall pattern, with maximum discharge occurring between January and March, and minimal dry season flows from October to November (Beilfuss and dos Santos, 2001). The main Zambezi River is perennial, reaching peak flows around May and lowest in October. Several tributaries feed the Zambezi, the major ones being the Chobe River, the Shire River that drains the freshwater Lake Malawi (Lake Nyasa), and the Kafue, and the Luangwa Rivers. The major rivers that drain directly into Lake Kariba are the Sanyati, Charara, Gache-gache, Nyaodza, Ume and Sengwa on the Zimbabwean side (Figure 2.1), and Lufua, Luizilukulu and Sengwe on the Zambian side.

Table 2.1. General properties and morphometry of Lake Kariba

Properties	Statistics
Impoundment type	Double curvature concrete arch
Height (m)	128.0
Crest Length (m)	617.0
Flood Gates	6 gates 8.8 m width * 9.0 m height
Discharge Capacity of flood gates ($m^3 s^{-1}$)	9 500.0
Minimum Retention Level (m)	488.5
Minimum Operating Level (m)	475.5
Total Storage (km^3)	180.6
Live Storage (km^3)	64.8
Depth of Stilling Pool (m)	78.0
Volume of Stilling Pool (m^3)	410 x 106
Generation Capacity (MW)	Total capacity of 1 320
Area at Full Capacity (km^2)	5 580.0
Catchment Area (km^2)	663 848.0
Islands	293.0
Length (km)	277.0
Maximum Depth (m)	97.0
Mean Breadth (km)	19.4
Mean Depth (m)	29.2
Shoreline Length (km)	953.8
Surface Area (km^2)	5 364.0
Volume (km^3)	185.0
Volume Development	2.1
Water Retention (years)	3.3

2.1.2. Geology and vegetation

Geologically the middle Zambezi Valley is divisible into two zones, namely the valley floor composed of Triassic karoo system grits, sands and silts, and the highlands comprised of gneisses of varying ages. The Zambezi River originates in Kalahari-swept sands, and thus the lake lies over infertile bedrock (Moreau, 1997). Before the impoundment of the Zambezi River, the Gwembe Valley was described as woodland and, in the driest part, thicket vegetation (Child, 1968). The vegetation surrounding Kariba can be described as open, savannah woodland (Mapaure and

Mhlanga, 2001). The valley floor contains a mosaic of vegetation types based around *Colophospermum mopane*, although pure stands are not common. Grasses include *Heteropogen; Loudetia*, *Andropogen*, *Eragrostis*, *Sporobolus* and *Aristida* spp. Highland and escarpment areas consist of typical miombo woodland on shallow gravelly soils dominated by *Brachystegia boehmii* and *Julbernardia globiflora*. The vegetation has been extensively modified through fire and elephant damage (Mapaure and Mhlanga, 2001). Dunham (1989) identified seven vegetation types, which could be separated on the basis of their topsoil texture and flooding frequency. These include sandbanks, young *Acacia albida* woodland, *A. albida* woodland, *A. albida*-dominated mixed woodland, mixed riverine woodland with understory, mixed riverine woodland, and grassland on clay soils.

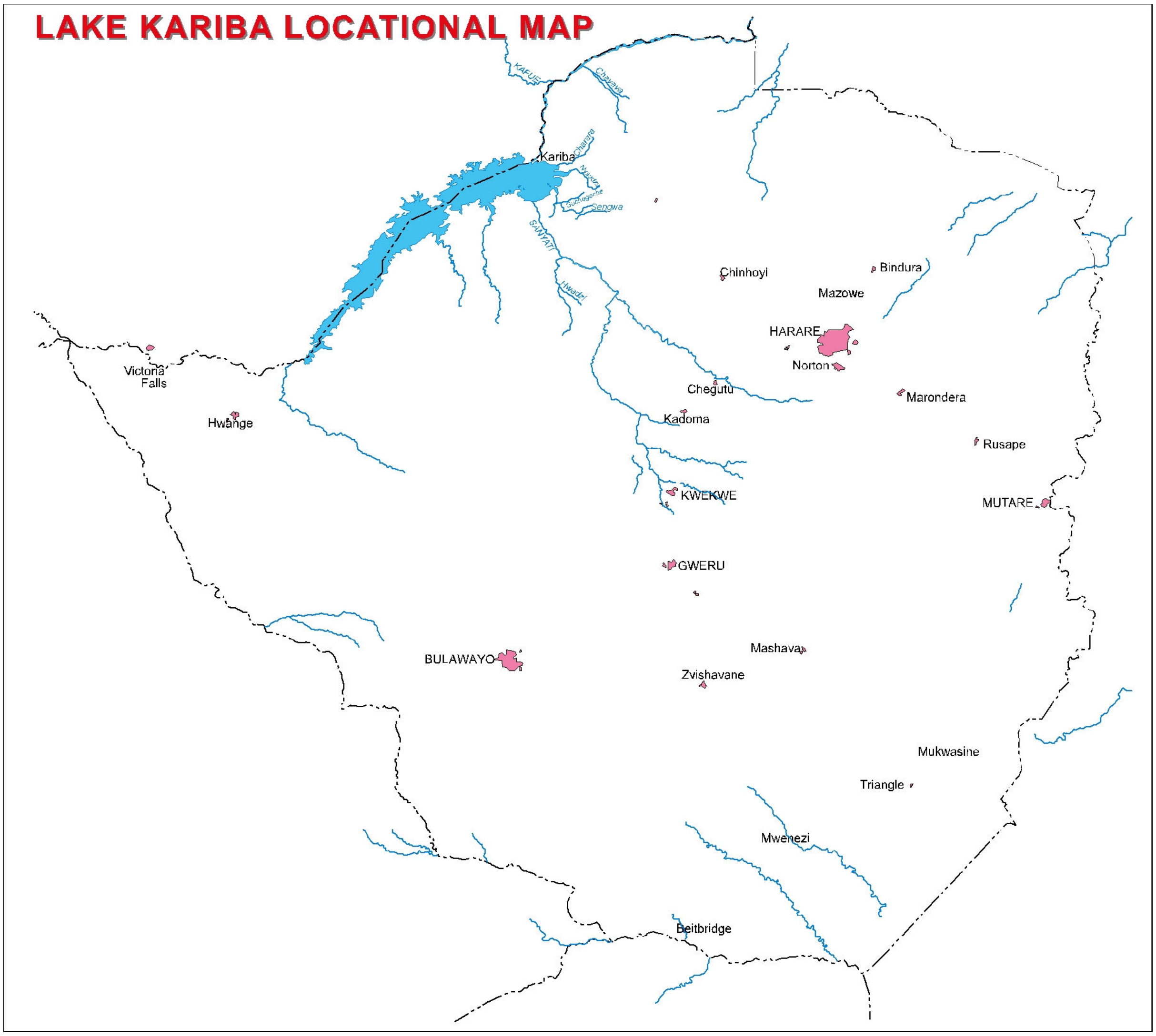


Figure 2.1. The location of Lake Kariba in Zimbabwe showing some major tributaries

2.1.3. Physiognomy and hydrology

The Zambezi River contributes 80% of the total water inflow into Lake Kariba, with the Sanyati and Gwaai Rivers contributing 10% (Balon and Coche, 1974). The remaining 10% of the water inflow is from direct rainfall onto the lake surface as well as other tributaries (Marshall, 1982). The Sanyati River delivers highly mineralised water from upland farms, and receives sewage and mining drainage effluent from Kwekwe via the Sebakwe River (Magadza, 1980). The Charara River has a smaller catchment than the Sanyati River, and mining as well as farming form part of the land-use activities, whilst the Gache-gache River drains primarily wilderness areas (Magadza, 1980).

Coche (1968) initially described four basins in Lake Kariba, but the last basin has been split into two, constituting the Ume and Sanyati. The lake therefore is divided into five basins, namely Mlibizi (B1), Binga (B2), Sengwa (B3), Ume (B4) and Sanyati (B5), separated naturally by topographical features of promontories or by chains of islands. The Sanyati Basin is at the northern end of the lake followed by the Ume Basin, whilst the Sengwa Basin occupies the centre of the lake, with the Mlibizi and Binga basins at the southern end of the lake (Figure 2.2). The productivity of these basins varies significantly due to variations in the water inflow from river tributaries and adjacent land use. Mlibizi and Binga Basins are predominantly riverine, and highly productive due to the influence of the Zambezi River which is the major source of nutrients and water (Marshall, 1982). The Sanyati Basin is also relatively productive, due to a high nutrient inflow from four major rivers, namely the Charara, Nyaodza, Gache-gache and Sanyati Rivers, the last contributing 8% of total water inflow into the lake (Marshall, 1982). The central Sengwa Basin is the longest and most turbulent, as its shores are open to strong winds that promote wave action.

The lake physiognomy, together with the influence of the Zambezi River, creates a hydrological gradient in the lake, with light penetration increasing (Begg, 1974) and phytoplankton production decreasing along its longitudinal axis (Masundire, 1997). For six months of the year (November - May), the period in which the Zambezi is at peak flow, Basins 1 and 2 have riverine characteristics (Coche, 1968). By July, with the recession of the floods, the influence of the river decreases and both basins assume lake-like characteristics (Moreau, 1997). The Zambezi River has a large influence over these two basins which are turbid from floodwater (Coche, 1968), whereas the Sengwa, Ume and Sanyati Basins are lacustrine all year round.

2.1.4. Water levels

A 49-year (1959 to 2008) record of lake water levels shows distinct seasonal fluctuations, with the average lake water levels of 485 m varying between 458 and 487 m. The lake levels rise from January, reaching a peak in September due to river inflows during the rainy season, with the lowest lake levels occurring between October and November, which coincides with the hot, dry season.

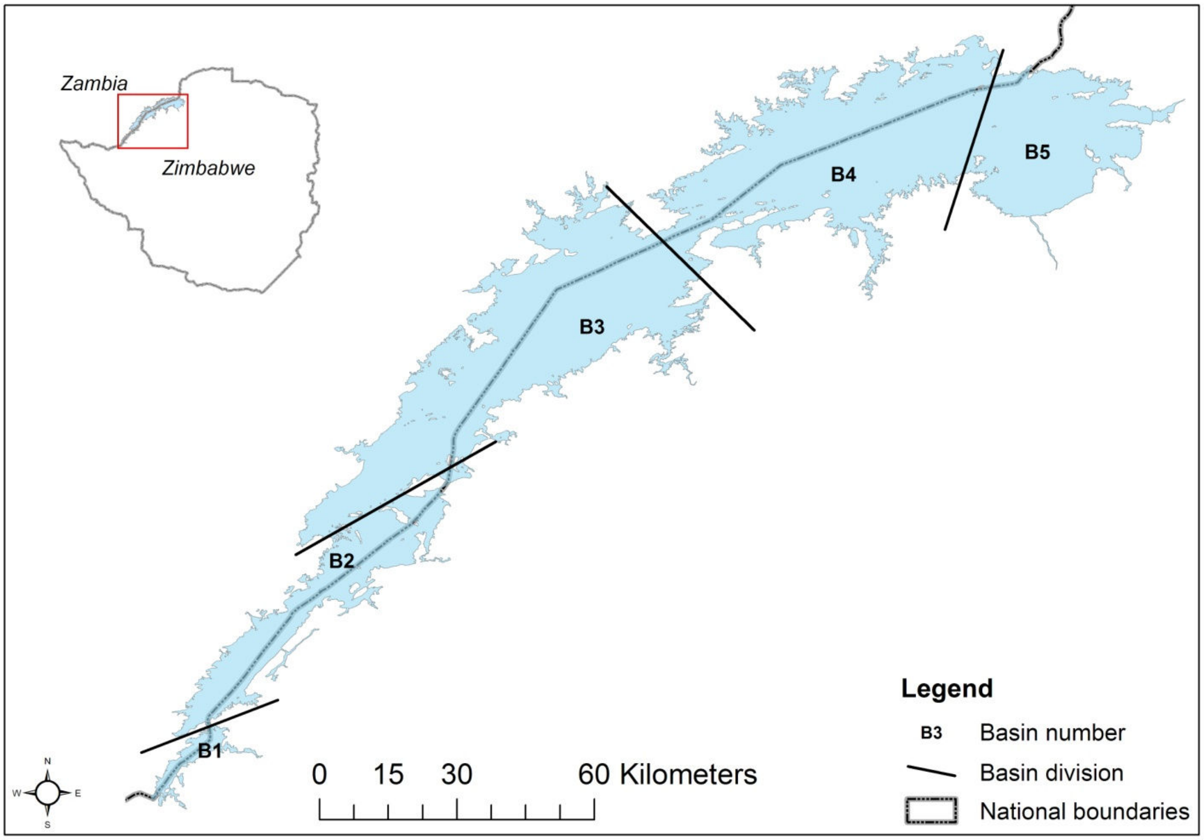


Figure 2.2. The basins of Lake Kariba, basin delineation modified from the original description by Balon and Coche (1974). B1- Mlibizi, B2- Binga, B3- Sengwa, B4- Ume and B5- Sanyati

Variation in lake water levels (Figure 2.3) have been as much as 23 m between 1959 and 1964, with 9.5 m amplitude recorded between 1996 and 1998 when water levels ebbed between 477.1 and 486.6 m. The lake experienced its lowest water levels over the 12-year period between 1984 and 1996, which coincided with low annual rainfalls and exceptionally high temperatures. In this period severe droughts were experienced, with the lake falling between 7 and 12 m, and river flows 40% less than normal.

2.1.5. General climatic characteristics

The climate of Kariba is typically tropical and semi-arid (Coche, 1968), with four distinct seasons in the Gwembe Valley where the lake is located (Howe, 1953). These seasons are described as rainy (November-February), post-rainy (March-May), dry-cool winter (June-July) and dry-hot (August-October). According to Coche (1974), air temperatures are consistently high with a mean annual temperature range of 24.4- 24.7ºC. A 44-year rainfall and temperature record from 1964 to 2008 revealed that maximum monthly air temperatures occurred during the dry-hot October month, averaging 30.7ºC, with those during the cold July winter month averaging 21.7ºC (Figure 2.4). Between December and March relative humidity can exceed 70%.

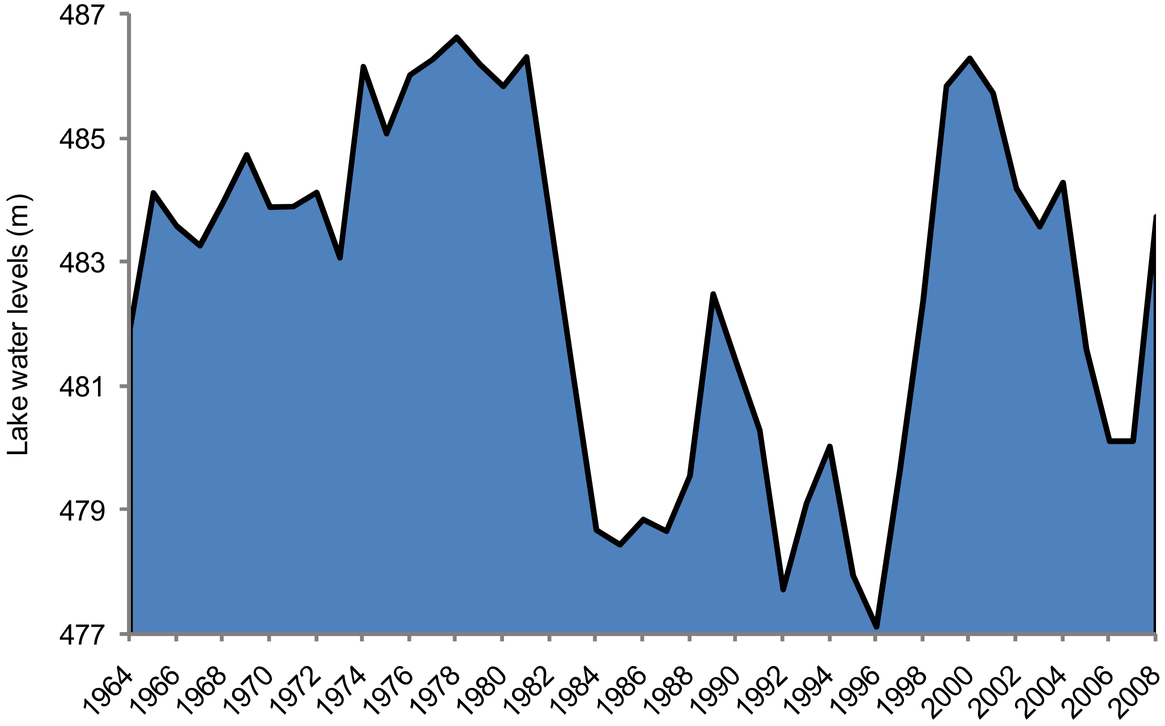
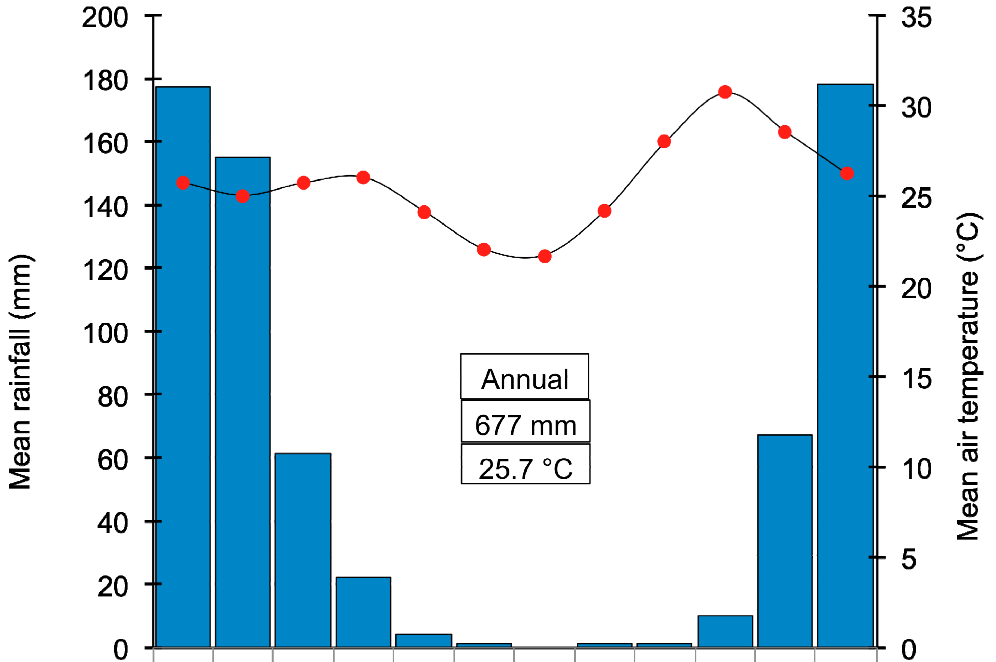


Figure 2.3. Average annual water levels in Lake Kariba over the period 1964 to 2008

Total precipitation averages above 610 mm a year, but varies widely, ranging from 350 to 1 015 mm a year^{-1} (Zimbabwe Meteorological Services, 2007), with a mean annual rainfall of 766 mm in the 1980s (Sayce, 1987) and 677 mm for the period 1964 to 2008, and a rainfall coefficient of variability of about 30%. Droughts and floods of varying magnitude and amplitude do occur (Ifejika Speranza, 2010). The El Niño/Southern Oscillation and the Inter-Tropical Convergence Zone (ITCZ) are the major factors that influence rainfall in the Zambezi Basin (Hulme *et al*., 2001; Fauchereau *et al*., 2003). Other major rain-bearing systems in the basin are the Indian Ocean tropical cyclones (FAO Aquasat, 2005). Rainfall in most of the basin is uni-modal, with rains occurring from November to March/April (Figure 2.4) in response to the movements of the ITCZ. Annual rainfall in the basin decreases from above 1 000 mm in the north to approximately 750 mm in the south (FAO Aquasat, 2005). Evaporation is high, ranging between 1 500- 3 600 mm annually, (Coche, 1974) with an annual average of 1 700 mm (Sayce, 1987). Estimated water loss by evaporation from the lake is 4 190 million cubic metres per annum (Shand, 1960) There are four main categories of wind on the lake, namely land and sea breezes, katabatic winds, local winds, and gales that usually blow from west to southwest (Law, 1965). The windy period is characterised by warm, gusty, strong winds that occur between September and October (Ward, 1979). Wind speeds are generally low with a mean velocity of 7.2 km hr$^{-1,}$ but do not exceed 16 km hr^{-1} (Ward, 1979).



	J	F	M	A	M	J	J	A	S	O	N	D
▬ Rainfall (mm)	177	155	61	22	4	1	0	1	1	10	67	178
● Mean temperature (°C)	25.7	25	25.7	26	24.1	22	21.7	24.2	28	30.7	28.5	26.2

Figure 2.4. Mean monthly air temperatures and rainfall at Lake Kariba (1964- 2008)

2.1.6. Climatic trends

Historical trends, based on records supplied by the Zimbabwe Meteorological Services (2007), in mean annual temperature, rainfall and pan evaporation rates spanning the years 1964 to 2008, are presented in Figures 2.5 A, B & C. Mean annual temperatures have increased by approximately 1.5ºC over the 44-year period, pan evaporation rates by about 25%, with rainfall having declined by an average of 27.1 mm since 1964 at an average rate of 6.3 mm per decade. Years 1987 to 1995 with above average temperatures coincide with those with above average pan evaporation rates and below average rainfall.

2.1.7. Lake water physical and chemical characteristics

Detailed accounts of the physical and chemical characteristics of Lake Kariba water between 1965 and 1989 are presented by Coche (1974) and Lindmark (1997), with supplementary reports provided by Harding (1961), Bowmaker (1976), Begg (1970) and Magadza *et al*. (1987, 1988, 1989). These are summarized in Table 2.2.

Water temperatures are generally high, with 73% of the first 5 m of the water in the lake above 24ºC (Magadza, 2010). The lake is characterised as warm and monomictic with homothermy exhibited from June to July at 20-22ºC, whilst thermal stratification occurs between October and June (Coche, 1968). The most important influence of temperature is stratification resulting in a chemocline, which follows the profile of the thermocline.

Secchi disc water transparencies normally range up to 6 m in depth and currently lie between 0.5 to 1.6 m, though earlier studies reported transparencies ranging up to 10.6 m in depth (Begg, 1967; Coche, 1968; Balon and Coche, 1974; Burne, 1981). The general trend in transparency is an increase from Basins 1 to 5 (Begg, 1970). The depth of the euphotic zone is approximately 12 m, though previously it ranged up to 16 m in the 1960s (Begg, 1967) and as much as 24 m in the 1970s (Coche, 1974). Surface waters are normally alkaline, the pH varying between 7.5 and 8.5, with pH values up to 9.0 measured when phytoplankton biomass is particularly high (Magadza *et al*., 1987, 1988, 1989). Dissolved oxygen (DO) in open water ranges from 6 to 10 mg l^{-1}. It varies with depth with a clear oxycline formed during stratification. High oxygen concentrations occur in the hypolimnion, at the time of turnover reaching a maximum of 6 mg l^{-1} (Begg, 1970), with a steady decline evident during stratification to a minimum of 2 mg l^{-1} just before turnover.

Complete de-oxygenation in the hypolimnion was observed during the early formative years of the lake (Begg, 1970). This was due to decomposing organic matter from the inundation of large forested areas, and associated with large algal blooms and the proliferation of the floating fern (*Salvinia molesta*). As a consequence, thermal discontinuities formed at 30 m, below which de-oxygenation occurred as the result of the decomposition of vegetation on the lake bottom, with the oxygen replaced by high concentrations of hydrogen sulphide (World Commission on Dams, 2000). In the 1960s, the degree of de-oxygenation declined, though high concentrations of hydrogen sulphide were still found in the deeper, bottom valleys towards the end of the annual stratification period (Coulter, 1967).

Total dissolved solids (TDS) ranged between 40 and 70 mg l^{-1} in the late 1980s (Magadza *et al*., 1988), from earlier values of 55 mg l^{-1} in the Zambezi River and 65 mg l^{-1} in the lake during the 1960s (Begg, 1970). The conductivity of Zambezi floodwaters varies between 40 and 50 µS cm^{-1} (Balon and Coche 1974), but has risen to as much as 100 µS cm^{-1} (Magadza *et al*., 1989) during an extreme low flow in the 1980s. In the early formative stages of the lake, conductivity ranged between 40 µS cm^{-1} (upstream) to 80 µS cm^{-1} at the dam site. Since then, water conductivity has stabilised at 75 µS cm^{-1} from an original value, before inundation, of less than 30 µS cm^{-1}. The higher conductivities of between 50 and 115 µS cm^{-1} recorded downstream are attributed to greater evaporative water loss (Machena, 1989). The physical and chemical characteristics of the lake are summarised in Table 2.2.

The lake water has evolved from an initial eutrophic state in the 1960s to a mesotrophic state in the early 1970s to its current oligotrophic state, which Balon and Coche (1974) predicted would persist. However, reports of increased fecal coliform concentrations along the Zambezi and lake shoreline close to the town of Kariba point to localised eutrophication (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996).

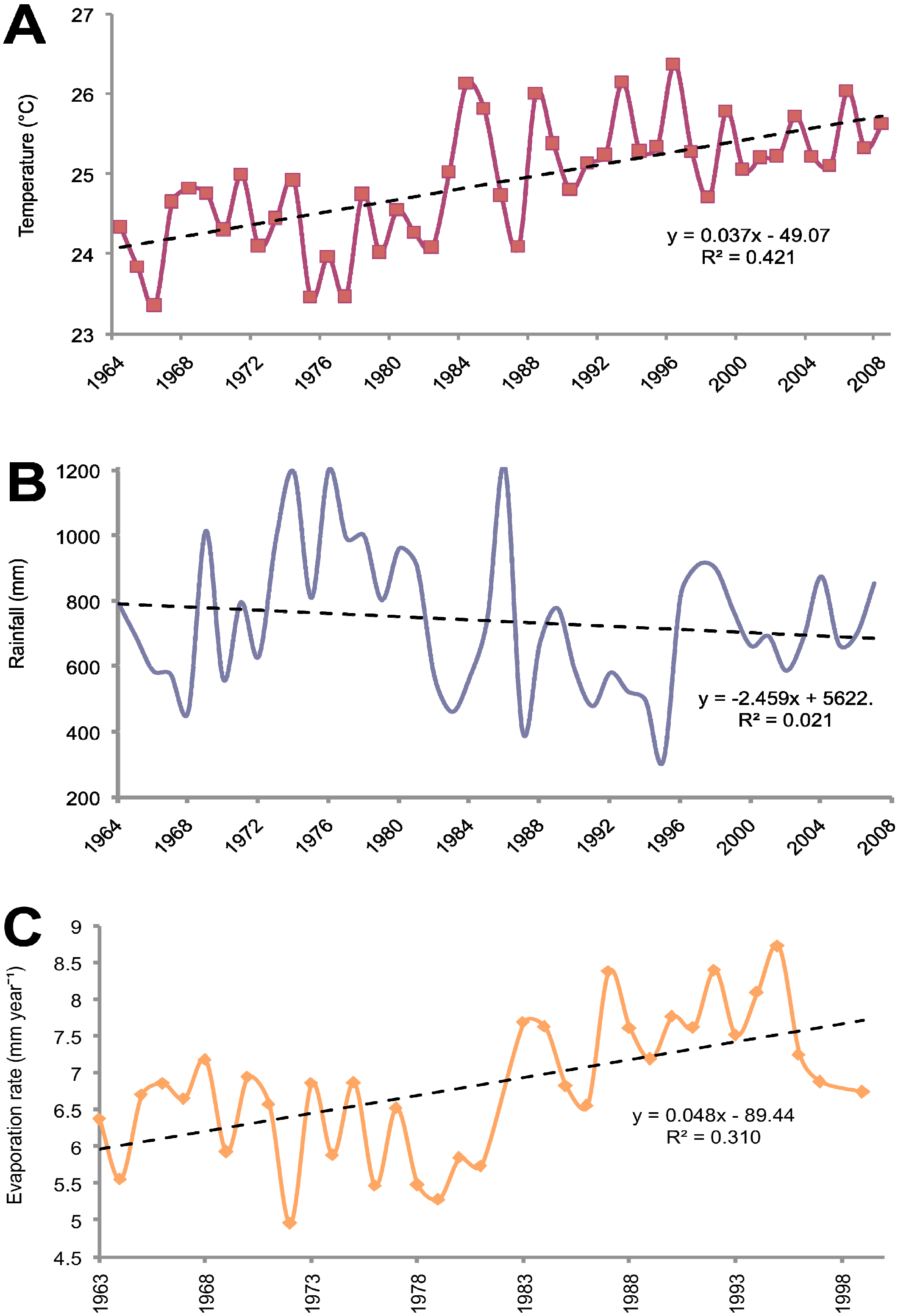


Figure 2.5. Observed trends (solid lines) in A. mean annual temperature, B. rainfall, and C. pan evaporation at Lake Kariba, spanning the years 1964 to 2008; dashed line = linear regression

Table 2.2. Physical and chemical characteristics of Lake Kariba (adapted from Balon and Coche, 1974)

Characteristics	Parameter	Value
Physical	Temperature range	17-32˚C
	Thermal cycle	Warm monomictic
	Temperature homothermy	20-22˚C (June- July)
	Thermal stratification period	October- June
	Depth of mixed layer	15- 25 m
	Transparency (Secchi disc)	0.50- 1.06 m
	Depth of euphotic zone	2- 24 m
	pH	6.8- 8.9 units
	Conductivity k20	50- 115 µS cm^{-1}
	Total solids	40- 70 mg l^{-1}
	Dissolved oxygen surface	6- 10 mg l^{-1}
	Oxygen stratification	October- June
Chemical	Na+	1.8- 4.7 mg l^{-1}
	K+	0.6- 1.8 mg l^{-1}
	Ca++	1.3- 2.0 mg l^{-1}
	Mg++	0.5- 3.0 mg l^{-1}
	Cl	1.0- 3.0 mg l^{-1}
	Nitrite	Trace
	Nitrate	0.01- 0.05 mg l^{-1}
	Phosphate	0.01- 0.05 mg l^{-1}

Water discharge through the turbines and harvesting of the sardine, *Limnothrissa miodon*, which removes 50 tons of phosphorus from the lake annually, are considered the primary causes of nutrient loss from the lake (Magadza, 2002). Phosphorus appears to be the primary nutrient limiting biological productivity, while nitrogen fixation by Cyanophyceae has become particularly important in the dry season (Moyo, 1991; 1997). Both nitrogen and phosphorus levels increase following overturn in winter, indicating a release of nutrients from deeper waters and in the rainy season (April).

2.1.8. Phytoplankton

Initial, predominantly qualitative studies, described the phytoplankton of the lake as evolving from a riverine-dominated to a lacustrine-adapted species complement (Thomasson, 1965; Mitchell, 1969; Bowmaker, 1973; Hancock, 1979; Thomasson, 1980; Ramberg, 1984, 1987; Cronberg, 1997). Following construction of the dam wall in 1958, blooms of the Cyanophyceae, *Microcystis* were observed, with Cronberg (1997) listing 69 species of Chlorophyceae in samples collected by Douglas from the lake between 1959 and 1964. Thomasson (1965) reported that the lake's phytoplankton community initially comprised riverine species, with a species richness of 171 for the whole lake. Bacillariophyceae, Cyanophyceae, Chlorophyceae, Chrysophyceae, Dinophyceae and Euglenophyceae represented the greatest proportion (75%) of the species. The number of phytoplankton species increased as the lake formed, with new species being identified and riverine ones such as the desmids occurring less frequently. *Volvox* and *Microcystis* were the most abundant species in 1967-68, as they are relatively large and were less susceptible to grazing by Cladocera and Diaptomids (Bowmaker, 1973).

Long-term studies of the Bacillariophyceae associations in the lake between 1958 and 1972 demonstrated that *Melosira granulata* var. *anguistima* (=*Aulacoseira granulata*) dominated with *Cyclotella, Fragilaria* and *Synedra* species during the turn-over period, and were abundant in the first two lake basins, which are essentially riverine in nature (Hancock, 1979). In his analysis of the phytoplankton population in the lake between 1968 and 1970, Thomasson (1980) recorded a total of 156 species, which was slightly less than the numbers recorded in his 1965 study. These findings pointed to a more lacustrine-adapted plankton community as these increased in abundance.

The first quantitative study of the phytoplankton in the lake was conducted by Ramberg (1984) in the Ume and Sanyati basins between November 1982 and April 1983. A mean phytoplankton biomass of 0.29 chlorophyll a mg l^{-1} was observed, with 80% of the phytoplankton biomass occurring in the rainy season (December- January), and 60% comprised of Cyanophyceae genera and dominated by *Cylindrospermopsis* and *Anabaena*. In a later study conducted between 1982 and 1984, Ramberg (1987) reported a mean phytoplankton biomass of 0.31 mg chlorophyll a l^{-1} in an integrated surface to 10 m deep sample. He also observed that during the rainy season when the phytoplankton biomass was highest, Cyanophyceae comprised 80% and Dinophyceae 13% of the total phytoplankton biomass, whereas Bacillariophyceae, which dominated at turnover, comprised 18% of the total phytoplankton biomass in the turn-over period. Chlorophyceae and Chrysophyceae contributed a low proportion to total phytoplankton biomass. Ramberg (1987) concluded that a regularity or stability has been established within its phytoplankton. A total of 82 algal species were recorded by Ramberg (1987) from the Sanyati Basin, these numbers concurring with those reported by Moyo (1991) in whose study the dominant algae were *Cylindrospermopsis*, *Anabaena* and *Pseudoanabaena* spp.

More recently Cronberg (1997) examined the lake phytoplankton composition between 1986 and 1990. She recorded a total of 155 algal species in the lake, and observed that the Cyanophyceae *Cylindrospermopsis* and *Anabaena* dominated in the Binga, Sengwa and Ume Basins during March. In contrast, the monads (collective group for small, round cells that cannot be identified to genus or species level) and the Bacillariophyceae were most dominant in the Sanyati Basin while the Mlibizi Basin had a bloom of *Anabaena* sp. However, at turnover (June and July), an even phytoplankton distribution was observed in the lake, with the Bacillariophyceae *Cyclotella* and *Aulacoseira* dominating throughout. During the October to November sampling period, the Bacillariophyceae *Aulacoseira* (=*Melosira*) *granulata* was dominant in the Mlibizi Basin while the Cyanophyceae species *Anabaena recta* and *Cylindrospermopsis raciborskii,* and the Chlorophyceae *Monoraphidium consortium* occurred throughout the rest of the lake and in the Ume and Sanyati Basins. From these observations Cronberg (1997) concluded that the phytoplankton population in the lake had stabilised from an original riverine type rich in desmids and large algal species to a lacustrine type dominated by small-celled chlorococcal Chlorophyceae with a typical seasonality, where the Cyanophyceae dominate in summer and the Bacillariophyceae dominate at turn-over in winter.

2.1.9. Zooplankton

Initial investigations conducted by Fryer (1957) in May 1956 involved the collection of free-living micro-Crustacea from the flooded backwaters of the Zambezi River. Seven species of Cladocera were recorded, dominated by *Diaphanosoma excisum* and *Moina micrura,* five species of cyclopoids, dominated by *Mesocyclops major*, the Calanoid *Tropodiaptomus* cf. *kraepelini* and the Decapod shrimp *Caridina nilotica* (JFRO Annual Report, 1959). Between May 1959 and September 1963, Harding (1961) collected zooplankton samples from both open water and from under submerged water plants in the lake. The samples were analysed by Thomasson (1965), who showed that the collections comprised four Protozoa, 34 Rotifera, the most common of which were *Branchionus falcatus*, *Keratella tropica*, *Lecane bulla*, *Filinia opoliensis* and *Hexarthra mira*, 13 Cladocera, the most common of which were *Diaphanosoma excisum*, *Chydorus sphaericus*, *Daphnia lumholtzi* and *Bosmina longirostris*, one Calanoid (*Tropodiaptomus* cf. *kraepelini*), one cyclopoid (*Mesocyclops major*), and one *Chaoborus* sp.

Harding and Rayner (2001) examined samples collected by Harding from the Kariba Gorge outflow and all inflowing rivers in the lake. Species of *Ceriodaphnia* were recorded in 51 of the 54 stations, of which *C. quadrangula* was the most common species, followed by *Bosmina longirostris* and *Diaphanosoma excisum,* which occurred in 43 and 48 respectively of the 54 stations. Among the copepods, *Thermodiaptomus mixtus* was the most common species, occurring in 34 of the 54 stations. These findings concluded that the zooplankton composition of the lake was typical of warm water impoundments similar to those found in sub-Saharan artificial tropical lakes (Fryer, 1957; Harding and Rayner, 2001).

Marshall (1984) and Paulsen (1994) show that the zooplankton abundance in Lake Kariba varies in response to phytoplankton biomass, and its production is determined more by food availability than fishing pressure and predation. Consequently, there is also a clear correlation between zooplankton and river flows (Begg, 1974; Magadza, 1980; Masundire, 1992; Chifamba, 2000). The overall standing crop of zooplankton in Sanyati Bay has been reported as ranging from 0.26 to 15.9 mg m^3 (Magadza, 1980). The mean abundance of Cladocera has declined since the introduction of the Tanganyika sardine, *Limnothrissa miodon,* whilst that of Copepoda has remained relatively stable (Cochrane, 1978; Masundire, 1989; Marshall, 1991). The highest zooplankton densities occur during the post-rainy season between January and March, and during the turnover and thermal mixing period between June and September (Masundire, 1994).

2.1.10. Ichtyofauna

In the pre-impounded river, the Zambezi was poor in fish species, with a listing of only 28 species due to a short breeding season and predation by the tiger fish (*Hydrocynus vittatus*) (Jackson, 1961). A much more favourable environment prevailed during the years immediately after impoundment, as the predators were dispersed and blooms of phytoplankton boosted the zooplankton and fish production. To date, the lake supports a total of 40 fish species and yields an average of 30-57 kg ha^{-1} $year^{-1}$ for pelagic fishes, and up to 60 kg ha^{-1} $year^{-1}$ when inshore fisheries are included (Machena, 1988). The artisanal fishery catches total 9 000 to 10 000 metric tons annually (Moyo, 1990).

The Tanganyika sardine, *Limnothrissa miodon* (Boulenger) commonly known as 'Kapenta', was introduced into Lake Kariba in 1958 from Sinazongwe (Zambia) to 'fill the hitherto empty pelagic niche that was created with the impoundment, then thought to be teeming with zooplankton' (Begg, 1976: Pp 530). Kapenta feeds predominantly on Cladocera, with *Daphnia* spp., *Bosminopsis deitersi* and *Bosmina longistrosis* occurring most frequently in its stomach constituents (Bell-Cross and Bell-Cross, 1971; Begg, 1976; Cochrane, 1978, 1984; Marshall, 1984, 1985, 1988; Machena, 1988; Moyo, 1994; Sanyanga, 1996; Mandima, 1999; Chifamba, 2000; Moyo and Fernando, 2000; Zengeya and Marshall, 2008). By 1964, Kapenta had successfully occupied the empty pelagic zone, and a viable commercial industry was formed. With its introduction, the fish yield in Lake Kariba rose from 5.6 kg ha^{-1} in 1968-1969 to 31.7- 342 kg ha^{-1} in 1986, and has developed to over 30 metric tons $year^{-1}$ (Fernando and Holick, 1991).

Though the lake has a potential total yield of over 100 000 tons of fish per year (Chenge and Johnsons, 1996), only 26 060 tons of Kapenta production were recorded in 1991 (Sanyanga *et al*., 1992). In fact, Kapenta fish production has been declining in Lake Kariba since the late 1980s (Moyo, 1990; Machena 1995; Magadza, 1995). Magadza (2008) suggested that the fisheries decline occurred around 1987, which coincided with one of the severest droughts ever experienced in the Kariba area and the Gwembe Valley. Relationships between Kapenta catches and the environment have been noted as Kapenta catches per unit effort decline during drought periods (Magadza, 1980), are negatively correlated with the degree of thermal stratification (Mtada, 1987) and closely linked to water temperature (Chifamba, 2000). Also, positive correlations between Kapenta catches and lake water level have been noted (Marshall, 1982). Both inshore artisanal and offshore pelagic fish production estimates fluctuate synchronously, and exhibit a remarkably high correlation with different time-lagged indices of water level changes, particularly water level rises in the lake (Karange and Kolding, 1995).

2.2. Study hypothesis

The main hypothesis examined was that climate warming will result in a more stable, shallower thermocline in Lake Kariba, leading to a diminished phytoplankton biomass, especially that of palatable species, due to lower nutrient concentrations in the epilimnion, and consequent decreased zooplankton biomass and fish stocks.

2.3. Study rationale

Despite the importance of Lake Kariba, little research has been conducted on the phytoplankton community and primary production. Only two detailed long-term studies of the phytoplankton community have been conducted, namely by Ramberg between 1982 and 1983 and Cronberg between 1986 and 1990. Phytoplankton forms the base of the food web in the lake, and therefore variations in phytoplankton biomass and primary production can influence fish production. Fish stocks, as evident from records of catches per unit effort of the sardine *Limnothrissa miodon*, have been decreasing since about 1990, and this affects the livelihoods of the local people and the commercial fishing industry. These changes in fish stocks may be related to changes in phytoplankton biomass and species composition, especially the sizes of the individual species, which in turn alter the structure of the food web as illustrated in Figure 2.6. For example, a predominance of smaller phytoplankton species under low lake water nutrient concentrations provides a less efficient food chain, since smaller phytoplankton are grazed exclusively by micro-zooplankton, which in turn are grazed by macro-zooplankton that are directly consumed by fish. Consequently, there is need to ascertain whether changes in climate are reflected in the lake water’s physical and chemical properties, phytoplankton and zooplankton species composition and biomass, and, ultimately, the Kapenta production.

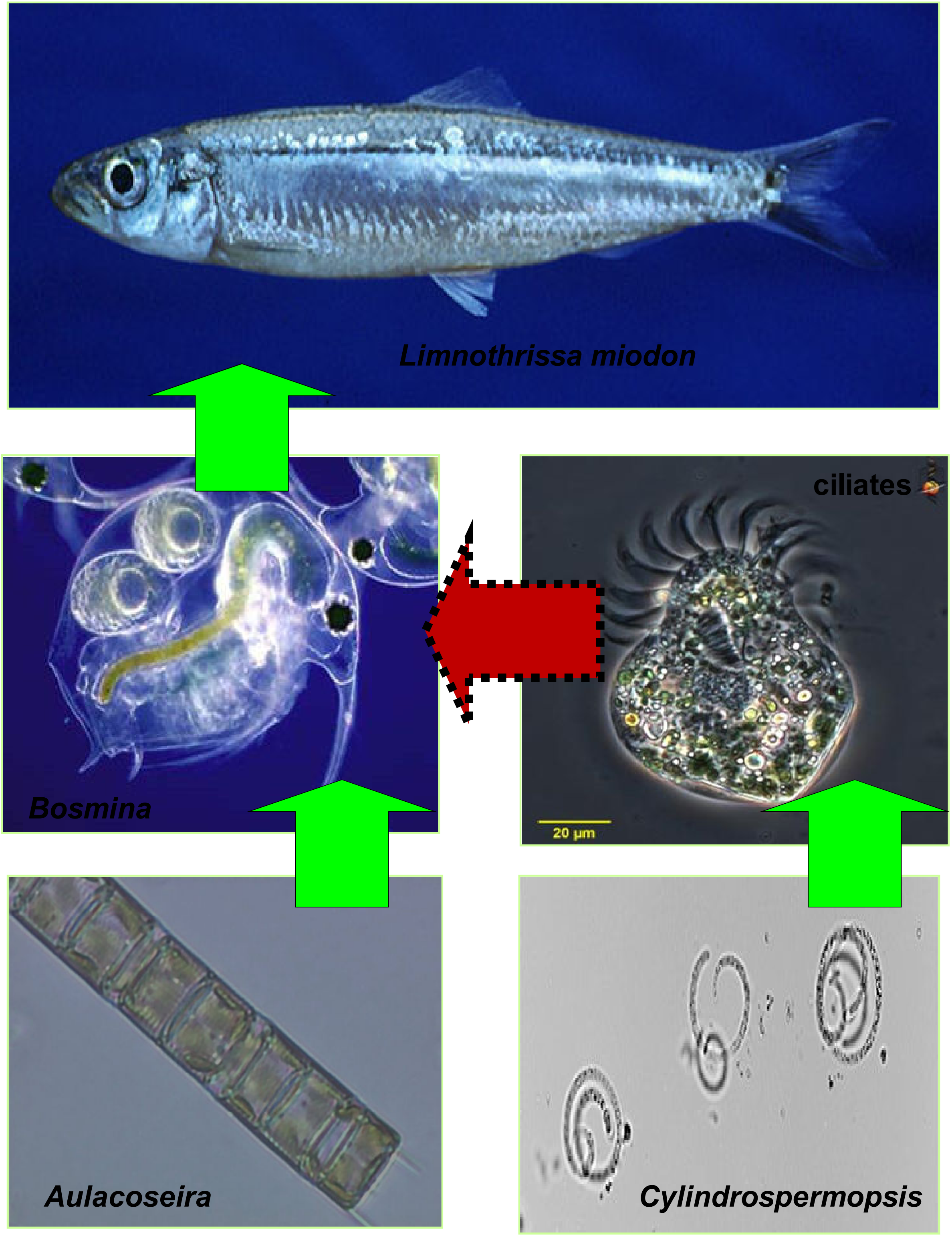


Figure 2.6. Trophic levels (green arrows) associated with different size (*Aulacoseira* = large-sized, *Cylindrospermopsis* = small-sized) phytoplankton; red arrow represents an additional trophic level

2.4. Study objectives

1. To determine whether there have been any changes in the physical and chemical properties of Lake Kariba water that may be linked to climate warming from 1965 to 2009;
2. To determine whether changes in the physical and chemical properties of Lake Kariba are refelected in altered primary production, phytoplankton biomass, and species composition from 1982 to 2009;
3. To determine whether changes in phytoplankton biomass and species composition in Lake Kariba are reflected in corresponding changes in zooplankton biomass, species composition, and Kapenta fish stocks from 1974 to 2009;
4. To ascertain the associations among the climate, water environment, phytoplankton, zooplankton and Kapenta fish production in Lake Kariba from 1964 to 2008

2.5. Thesis structure

The thesis comprises seven chapters. Chapter 1 comprises a detailed review of phytoplankton dynamics in tropical African lakes based on 84 sources of reference. Chapter 2 presents a general description of Lake Kariba and its location, research hypothesis, and objectives and study rationale. This chapter also comprises a detailed review of Lake Kariba's climate covering the period 1964 to 2008, its physical and chemical properties, primary production, phytoplankton and zooplankton. Chapter 3 examines current spatial, seasonal and depth changes in the physical and chemical properties of Lake Kariba's water, and compares these with historical records and those reported in other African tropical lakes and therefore examines objective 1.

Chapter 4 examines current spatial, seasonal, and depth changes in primary production and phytoplankton biomass of three major phytoplankton groups (Bacillariophyceae, Chlorophyceae, Cyanophyceae) in Lake Kariba, and compares these with historical records and those reported in other African tropical lakes. Chapter 5 examines current seasonal and depth changes in phytoplankton species composition and abundance in the Sanyati (B5) - Lake Kariba's main basin - and compares these with historical records and those reported in other African tropical lakes. Chapters 4 and 5 therefore examine objective 2. Chapter 6 examines current seasonal and depth changes in zooplankton species composition and abundance in the lake, and compares these with historical records and those reported in other African tropical lakes. Chapter 7 integrates the climate, lake water physical and chemical properties with those of the phytoplankton, zooplankton measurements and fisheries records and draws conclusions on the causes of the changes in the primary and secondary levels of production in Lake Kariba. Chapters 6 and 7 examine objectives 3 and 4.

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Chapter 3

The physical and chemical dynamics of Lake Kariba water

Abstract

This study examined spatial, seasonal and depth variations in the physical and chemical properties of Lake Kariba water, compared these with those in other tropical African lakes, and ascertained whether the measured changes in water properties might be linked to climate warming. Measurements of water temperature, conductivity, pH, transmission of photosynthetically active radiation (PAR), dissolved oxygen (DO), dissolved organic carbon (DOC), total nitrogen (total N), and orthophosphate (PO_4^{-3}-P) were conducted in midwinter and midsummer, at six different depths, at 35 sampling stations distributed across Lake Kariba's five basins. In the fifth (Sanyati) basin, a more rigorous sampling regime was followed, with the above-mentioned physical and chemical properties measured every second month over a 24- month period, at six different depths at ten sampling stations located in riverine and lacustrine waters. All measured physical and chemical water properties differed significantly between the lake basins and between winter and summer seasons, with the exception of DO and DOC, and with increasing water depth, with the exception of conductivity, DOC, total N and PO_4^{-3}-P. In the fifth basin all physical and chemical properties differed significantly monthly between lacustrine and riverine waters, with the exception of total N and PO_4^{-3}-P, and with increasing water depth, with the exception of DOC and Total N. Comparison of the lake water physical and chemical properties in the fifth basin with previously published records revealed increased water temperatures, conductivity and PO_4^{-3}-P levels, and decreased DO, pH and total N levels. The average 1.9°C increase in water temperature observed in the fifth basin corresponded with an upward migration of the thermocline from its previously recorded 20 m depth to its present depth of between 2 m and 5 m. This has resulted in a reduction of the total volume of epilimnion, as well as a diminished mixed layer and decreased water transparencies in the euphotic zone.

3.1. Introduction

African lakes are havens for diverse endemic flora and fauna of immense ecological and scientific importance. Their productivity and health are dependent on good water quality, which is influenced by several factors inclusive of inputs into the lakes and seasonal effects of climate and stratification. Furthermore, many provide an important source of dietary protein to rural communities in the form of fish and prawns, potable water for humans, livestock and agriculture, a means of transportation of goods and generation of hydro-electric power, and a source of revenue from fishing and eco-tourism (Ogutu-Ohwayo and Balirwa, 2006). However, many of these lakes are under threat, as they are experiencing deteriorations in water quality and consequent declines in biotic abundance and diversity, which are likely to be exacerbated by climate change and increased anthropogenic pressures from increased land use in the lakes' catchments (Bootsma and Hecky, 1993; Magadza, 1994, 2003, 2006; Hecky *et al*., 1999; Kling *et al*., 2001; Hecky *et al*., 2010).

African tropical lakes are classified in three trophic classes based on their total ionic concentrations and conductivity levels (Talling and Talling, 1965). Class I lakes have low total concentrations of ions (alkalinity of less than 6 mg l^{-1}) and conductivities of less than 600 µS cm^{-1}, and derive their water from direct surface runoff or rivers with little salt. Examples of Class I lakes include Cleveland Dam, Lakes George, Kariba, Malawi, Malombe and Victoria (Ndebele, 2009; Lindmark, 1997; Guildford *et al*., 2007; Haande *et al*., 2010). Class II lakes have higher total ion concentrations (alkalinity of about 6 to 60 mg l^{-1}), and conductivities of between 600 and 6 000 µS cm^{-1} caused by inflows rich in solutes, particularly sodium carbonate and bicarbonate, drainage from alkaline lavas, and high evaporation in their closed basins (Talling and Talling, 1965). They include Lakes Albert, Edward, Kivu, Tana, Tanganyika and Turkana (Chale, 2004; Lorke *et al*., 2004; De Wever *et al*., 2008). Class III lakes are highly saline, with alkalinities mostly above 60 mg l^{-1} and conductivities above 6 000 µS cm^{-1}, and often contain solid mineral deposits such as trona. They include Lakes Eyasi, Katwe, Magadi, Manyara, Nakuru, Natron and Naivasha, which are mostly shallow, endorheic, and exhibit significant density stratification despite their shallowness (Melack, 1979; Hubble and Harper, 2002; Okoth *et al*., 2009).

However, despite these classifications, the trophic status of many tropical African lakes and impoundments is changing, due to rising global temperatures, reduced river inflows, fertiliser runoff, and effluent discharges resulting from increased anthropogenic activity in lake catchments (Ogutu-Ohwayo and Balirwa, 2006). These factors have contributed to increased lake eutrophication, with consequent negative effects on phytoplankton and fish production (Ndebele-Murisa *et al*., 2010). Lake Kariba is a typical Class I African lake, which has exhibited distinct changes in its physical, chemical and thermal properties since its creation between 1953 and 1958 (Harding, 1961; Begg, 1970; Coche, 1974; Bowmaker, 1976; Magadza *et al*., 1987; 1988, 1989; Lindmark, 1997). Initially, when the lake was formed, large forested areas were inundated, and nutrients leached from the soil and decomposing organic matter increased the fertility of the lake's water. The lake's initial eutrophic status was characterised by continuous blooms of algae, the proliferation of the aquatic fern (*Salvinia molesta*), and the de-oxygenation of the hypolimnion. However, the lake's initial eutrophic state in the 1960s has subsequently declined to its current oligotrophic state, which coincides with a concomitant decline in *S. molesta* (Kariba weed) populations. The degree of de-oxygenation in the lake hypolimnion has also declined since the 1960s, with high concentrations of hydrogen sulphide now restricted to deep waters towards the end of the annual stratification period.

Balon and Coche (1974) predicted that the lake would retain its oligotrophic status. This assertion was disputed by Magadza (2002), who argued that increased incidences of localised pollution in the lake, evident from elevated concentrations of faecal coliform bacteria (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996), would shift the lake water back towards a mesotrophic state. This study resolved this impasse by comparing the current physical and chemical properties of the lake water at different localities, depths and times of the year, with previously published records on this and other tropical African lakes. The aims of this investigation were 1. to test whether the physical and chemical properties of the lake water vary spatially and temporarily across Lake Kariba, its five basins, between the riverine and lacustrine habitats, as well as among the depth zones in the mixed layer, and 2. to determine whether there have been any changes in the physical and chemical properties of Lake Kariba water that may be linked to climate warming.

3.2. Methods and materials

3.2.1. Study area

The study area was Lake Kariba, which stretches from the confluence of the Deka and Zambezi Rivers in the south-west (18´ 04˝S, 26´ 42˝E) to the Kariba Gorge (16´ 31˝S, 28´ 45˝ E) in the north-east. The lake is divided arbitrarily into five basins arranged in a south-west to north-east direction (Figure 3.1). A detailed description of the lake and its surrounds is presented in Balon and Coche (1974) and Moreau (1997), and summarised in Chapter 2.

3.2.2. Experimental design and sampling stations

Two separate studies measured lake water physical and chemical properties at six different depths (0, 2, 5, 10, 15, 20 m) at 35 sampling stations in total, distributed across the entire length of the lake from Basin 1 in the south-west to Basin 5 in the north-east. Based on preliminary sampling and past studies, the thermocline depth below which there is negligible primary production rarely exceeded 20 m and this formed the rationale for the maximum depth sampled. In the first study, physicochemical measurements were conducted twice annually, namely during lake turnover in midwinter (July) and again during lake stratification in midsummer (February), at four sampling stations located in Basin 1, seven in Basin 2, six in Basin 3, eight in Basin 4, and ten in Basin 5.

In the second study, physicochemical measurements were conducted at 2-monthly intervals over a 24-month period, extending from March 2007 through to February 2009 at ten sampling stations in Basin 5, where the majority of previous long-term phytoplankton studies have been conducted (Coche, 1974; Magadza *et al*. 1987, 1988, 1989; Lindmark, 1997). Four of these sampling stations were located at the margins of the lake basin in close proximity to the Charara, Gache-Gache and Sanyati River inflows and designated riverine habitats. The other six sampling stations traversed the centre of the basin and were designated lacustrine habitats. The same depth profiling described for the whole lake sampling (0, 2, 5, 10, 15, 20 m) was also used at each of the sampling stations in the Sanyati Basin. Figure 3.1 shows the sampling stations.

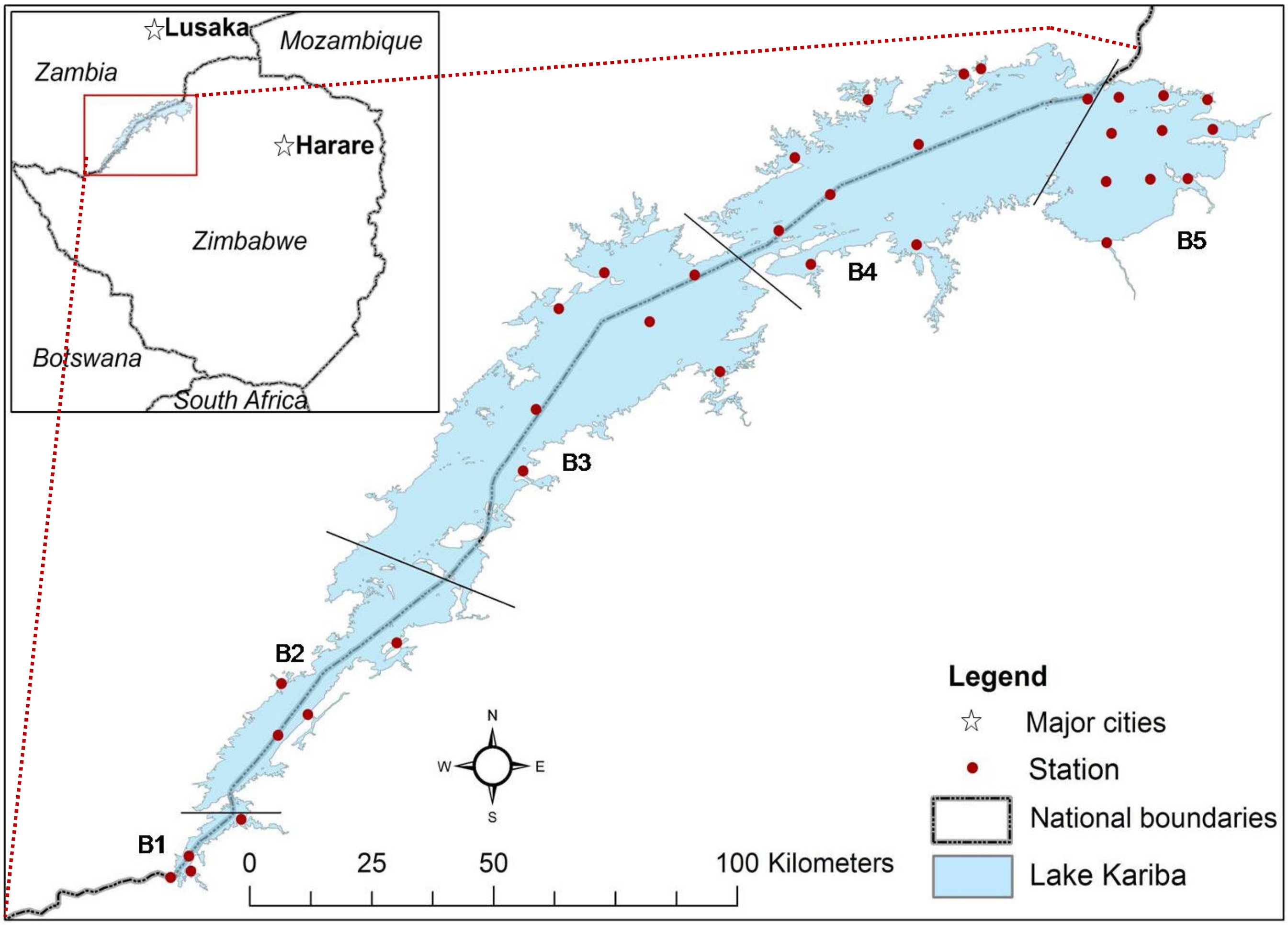

Figure 3.1. Location of sampling stations in Lake Kariba's five basins (B1 to B5), with those located in the centre of the lake designated lacustrine, and those located along the lake margin in proximity to river inflows designated riverine

3.2.3. Physical and chemical properties of lake water

At each sampling station and in each depth zone, water temperature, pH, conductivity, dissolved oxygen (DO), and water transparency to photosynthetic active radiation (PAR), were measured in situ under clear sky conditions two hours on either side of midday (1000 to 1400 hours), with sensors interfaced with portable meters (DO and Conductivity meters, Hach Co., Germany; PAR meter, LiCor Lincoln, NE, USA). For chemical assays, twenty-litre (20 l) water samples were collected from each depth zone with a Ruttner sampler, and filtered through 0.5 µm GF/F filters (Whatman, Germany). The filtered water samples were transferred into 500 ml polyethylene bottles, frozen, and transported to the laboratory. Total nitrogen concentrations in the defrosted water samples were determined by the micro-Kjeldahl distillation method (Volleinweider, 1969; Bartram and Ballance, 1995). Devardas alloy was added to catalyse the reduction of NO_3-N and NO_2-N to NH_4^+-N. The total N concentrations as NH_4^+-N were determined colorimetrically at 425 nm with a Hach spectrophotometer (DR010 Hach Co., Loveland, Colorado, USA), after the addition of potassium sodium tartrate and Nesslers reagent, suitable for the detection of low levels of nitrogen.

Orthophosphate (PO_4^{-3}-P) concentrations in the defrosted water samples were determined colorimetrically by the molybdate colour reaction method (Volleinweider, 1969; Bartram and Ballance, 1995). Antimony potassium tartrate and ammonium molybdate were added to the water samples, followed by the addition of ascorbic acid. Ammonium molybdate and antimony potassium tartrate react in an acidic medium with dilute solutions of phosphate to form an antimony-phospho-molybdate complex. This complex is reduced to an intensely blue-coloured complex by ascorbic acid, whose absorbance is proportional to the phosphate concentration present in the water sample (Zimmerman and Keefe, 1997), this measured at 880 nm with a Hach spectrophotometer (DR010 Hach Co., Loveland, Colorado, USA) in this study. Water standards of known PO_4^{-3}-P concentration were used to construct the calibration curve.

Organic matter was extracted from the water samples, with inert glass fibre filters and their dissolved organic carbon (DOC) concentrations determined from their measured reductions in mass, following high temperature catalytic combustion (Dafner and Wangersky, 2002).

3.2.4. Statistical analysis

The experimental design was not fully balanced, due to unequal numbers of measurements. Consequently, a REML (residual maximum likelihood) variance component analysis (repeated measures mixed model) was applied to test for significant differences in measured lake water physical and chemical properties between seasons, months, lake basins, water depth and their interactions, using the Wald X^2 statistic generated by REML (GENSTAT Discovery Edition 3, VSL Lty, UK). In the first REML analysis of all 35 sampling stations, lake basins and water depth were fitted in the fixed model, and replicated winter and summer seasons in the random model. In the second REML analysis of the 10 sampling stations in the Sanyati Basin, the lacustrine and riverine habitats and water depth were fitted in the fixed model, and replicated months in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is equal to two.

3.3. Results

3.3.1. Lake basin physical and chemical properties

All measured lake water physical and chemical properties displayed significant ($P \leq 0.001$) differences between seasons, apart from DO and DOC, and significant differences ($P \leq 0.05$) in all variables were evident between lake basins (Table 3.1). Higher water temperatures and conductivities but lower water transmission of PAR and pH were more evident during summer than winter months (Figures 3.2A, B, C & D). Higher levels of DO, DOC, total N and PO_4^{-3}-P were more evident in summer than winter seasons in all basins, with exceptions of DO and DOC in Basins 1 and 2 and total N in Basin 5, where the converse was apparent (Figures 3.3A, B & C). Only water temperature, PAR, pH and DO declined significantly ($P \leq 0.001$) with increasing water depth (Table 3.1). The vertical decline in PAR and to a lesser extent in DO, was more prominent during the summer than winter season (Figure 3.4A & B). This was apparent from the significant ($P \leq 0.001$) interaction between season and water depth for PAR and DO (Table 3.1). Also, there were significant ($P \leq 0.001$) interactions between season and lake basin for all measured water physical and chemical properties, except PO_4^{-3}-P (Table 3.1). The horizontal gradients in water temperature, conductivity, pH, PAR, DO, DOC and total N between lake basins were more prominent during winter turnover than during summer stratification.

3.3.2. Sanyati Basin water properties

3.3.2.1 Physical properties

Water temperature, its PAR transparency, conductivity and pH all differed significantly ($P \leq 0.05$) monthly and with increasing water depth, and also differed significantly ($P \leq 0.05$) between lacustrine and riverine habitats (Table 3.2). The highest water temperatures were recorded in late summer (February) and the lowest in mid-winter (July) while December riverine temperatures were also notably low. The highest water transmissions of PAR were recorded in April and the lowest in August. The highest water conductivities were measured in April and May and the lowest in August. Water pH displayed no distinct seasonal peaks or troughs (Figures 3.5A, B, C &D). However, all measured lake water physical water properties, displayed significant ($P \leq 0.001$) interactions between month and habitat (Table 3.2). Higher ($P \leq 0.05$) water temperatures were evident in lacustrine than riverine waters only in July and December, with the converse apparent in April (Figure 3.5A). Higher ($P \leq 0.05$) water transmissions of PAR were apparent in lacustrine than riverine waters only in April, July, September and November (Figure 3.5B). Similarly, higher ($P \geq 0.05$) water conductivities were observed in lacustrine than riverine waters only in July, with the converse evident in February and March (Figure 3.5 C). Also, higher ($P \leq 0.05$) water pH's were recorded in lacustrine than riverine waters only in October, November and December, with the converse evident in January and April (Figure 3.5D). There were significant ($P \leq 0.01$) interactions between month and water depth for water temperature, PAR, and pH. The steepest vertical declines in water temperature and pH, were evident during spring in September, October and November (Figures 3.6 A, B & C), and in March for pH. The steepest declines in PAR, with increasing water depth, were apparent during summer, between September and March (Figure 3.6B).

3.3.2.2. Chemical properties

All lake water chemical properties (DO, DOC, total N, PO_4^{-3}-P) differed significantly ($P \leq 0.001$) monthly, between lacustrine and riverine waters, and with increasing water depth with the exception of DOC and total N (Table 3.2). The lowest DO concentrations occurred in April and the highest in June. The lowest DOC concentrations occurred in February and the highest in December. The lowest total N concentrations were measured in February and the highest in August, and the lowest PO_4^{-3}-P concentrations recorded in October and the highest in June. However, there were significant interactions ($P \leq 0.001$) between month and habitat for DO and DOC (Table 3.2). Significantly ($P \leq 0.05$) higher DO concentrations were recorded in lacustrine than riverine waters in January and in April, and between September and December, with the converse evident in July. Significantly ($P \leq 0.05$) lower DOC concentrations were recorded in lacustrine than riverine waters in September and October only (Figures 3.7A & B). DO concentrations declined and PO_4^{-3}-P concentrations increased with increasing water depth, but all other interactions between month and water depth for these and all other measured lake water chemical properties were insignificant ($P \geq 0.05$) (Table 3.2).

Table 3.1. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of season, basin, water depth and their interactions on various lake water physical and chemical properties. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001

REML		Wald χ² statistic							
		Physical properties				Chemical properties			
	df	Temp	PAR	Conductivity	pH	DO	DOC	Total N	PO_4^{-3}-P
__Main effects__									
Season	1	__2 534.48***__	__156.70***__	__27.15***__	__16.12***__	1.11	0.01	__8.51*__	__32.16***__
Basin	4	__14.56***__	__55.19***__	__244.13***__	__41.24***__	__11.20*__	__14.79**__	__10.60*__	__15.82*__
Depth	5	__22.41***__	__2 647.67***__	0.82	__21.26***__	__24.50***__	3.27	1.55	1.60
__2-way interactions__									
Season x Basin	4	__8.17***__	__19.95***__	__89.65***__	__37.58***__	__39.92***__	__29.97***__	__23.94***__	4.73
Season x Depth	5	0.32	__37.61***__	7.58	0.64	__21.42***__	1.78	7.65	1.33
Basin x Depth	20	0.61	__43.73*__	10.39	14.68	10.10	12.17	15.45	10.86
__3-way interactions__									
Season x Basin x Depth	20	0.65	27.39	13.73	12.95	18.31	13.38	13.13	15.17

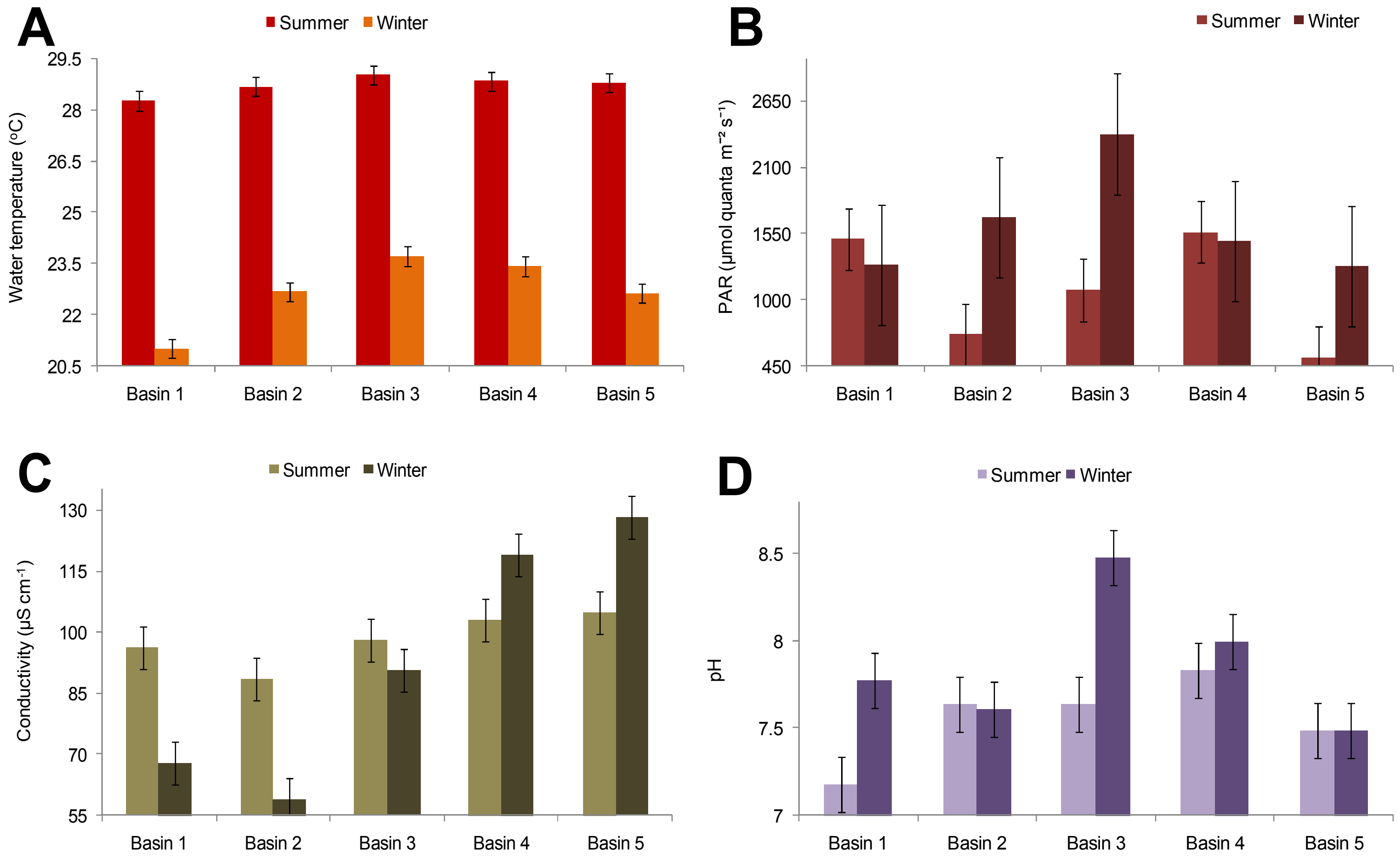

Figure 3.2. Seasonal variation in A. water temperature, B. photosynthetic active radiation (PAR), C. conductivity and D. pH across Lake Kariba's five basins. Average standard error of differences shown by bars

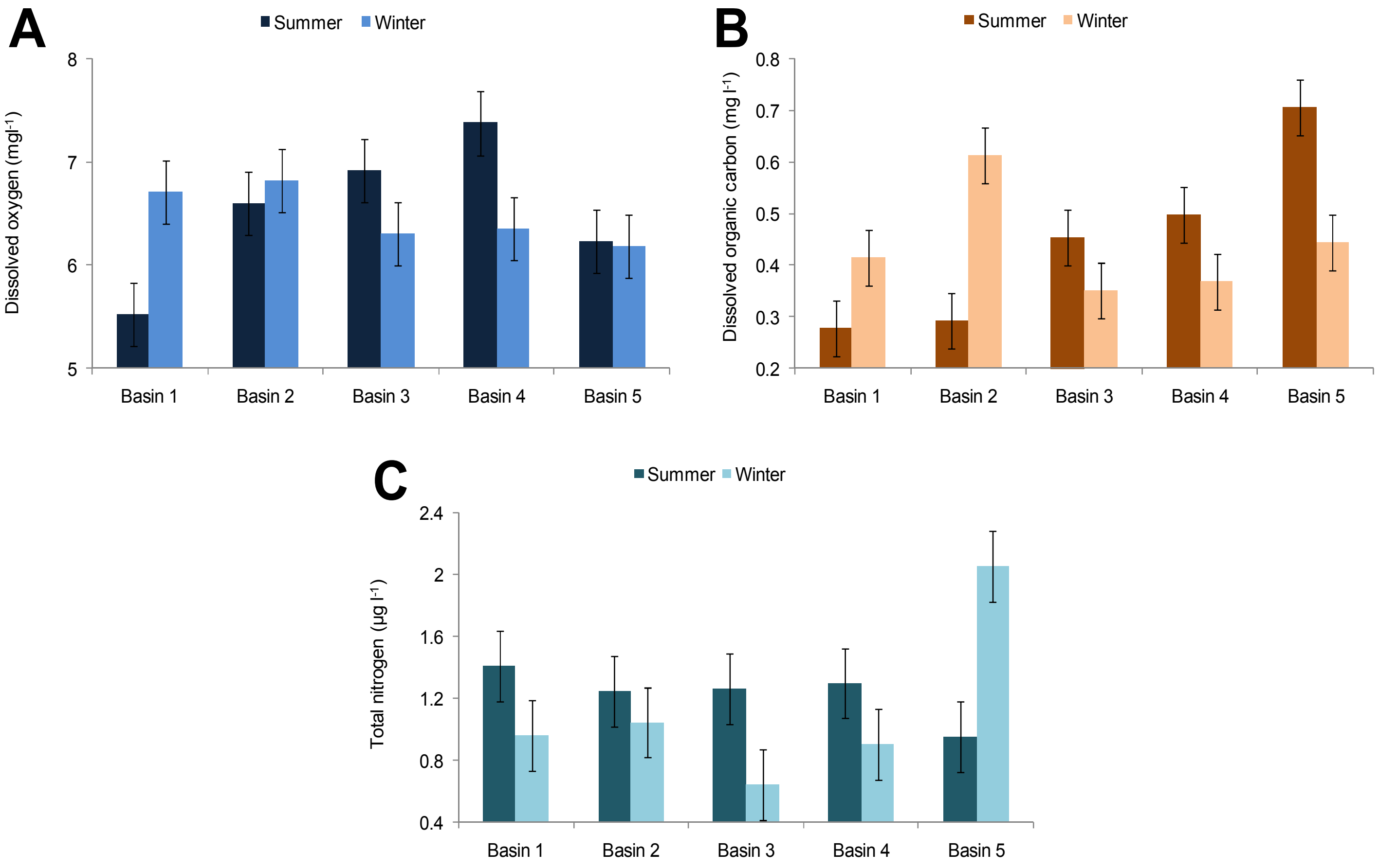

Figure 3.3. Seasonal variation in dissolved oxygen (DO), B. dissolved organic carbon (DOC) and C. total nitrogen (total N) across Lake Kariba's five basins. Average standard error of differences shown by bars

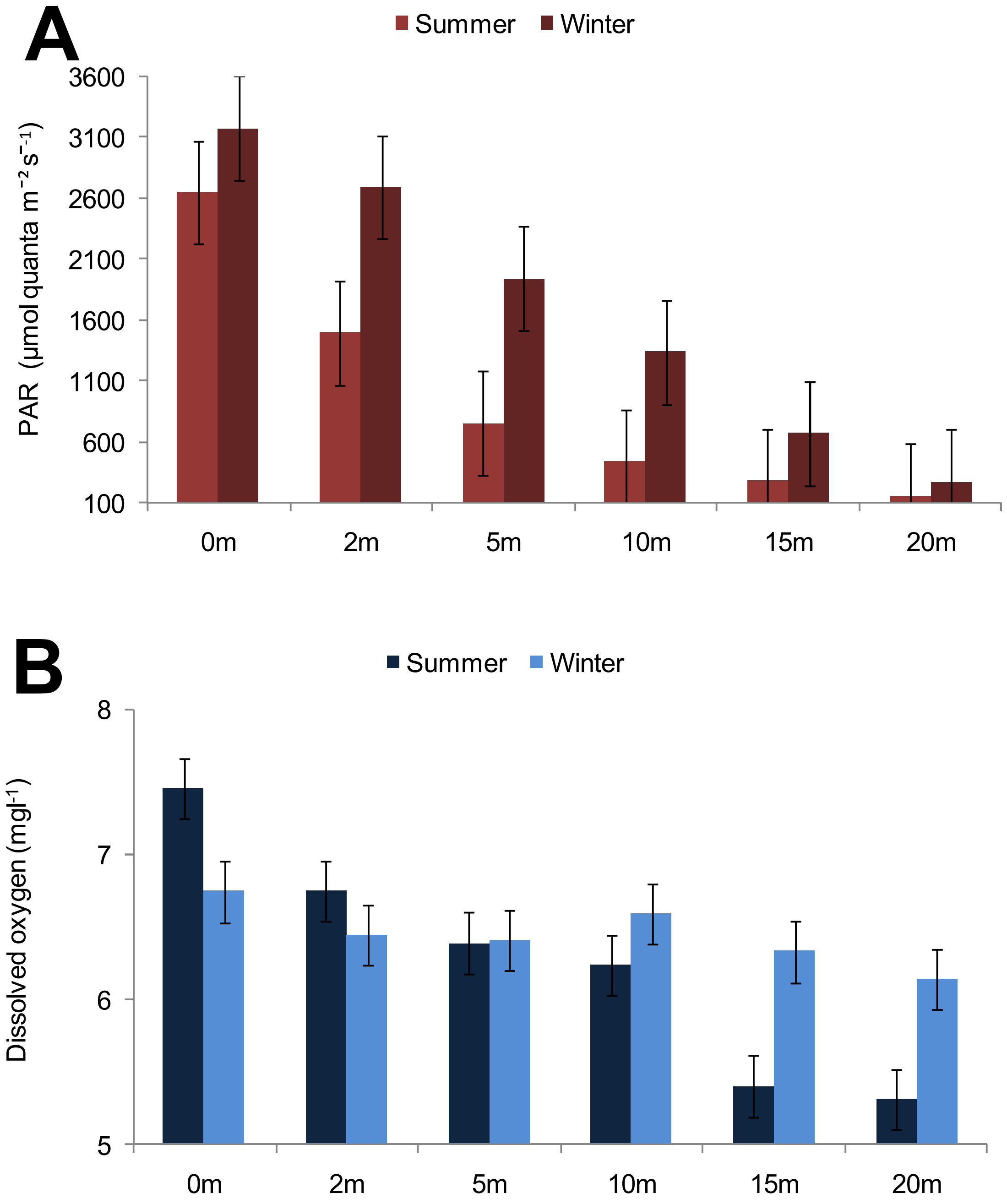

Figure 3.4. Variation in A. water transmission of PAR and B. dissolved oxygen at different water depths in different seasons in Lake Kariba across all basins. Average standard error of differences shown by bars

Table 3.2. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth, and their interactions on various physical and chemical properties of lake water in the Sanyati Basin of Lake Kariba. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001

REML		Wald χ² statistic							
		Physical properties				Chemical properties			
	df	Temp	PAR	Conductivity	pH	DO	DOC	Total N	PO_4^{-3}-P
Main effects									
Month	11	**11 615.86*** **	**869.24*** **	**17 764.91*** **	**466.11*** **	**4 356.23*** **	**423.64*** **	**1 337.81*** **	**888.65*** **
Habitat	1	**15.77*** **	**4.57* **	**60.15*** **	**7.33** **	**45.5*** **	**12.09*** **	0.08	0.42
Depth	5	**566.28*** **	**2 372.98*** **	**21.86*** **	**106.16*** **	**40.28*** **	1.05	5.13	**22.65*** **
2-way interactions									
Month x Habitat	11	**146.86*** **	**72.06*** **	**72.53*** **	**139.68*** **	**203.38*** **	**50.19*** **	12.65	13.23
Month x Depth	55	**241.66*** **	**634.32*** **	29.66	**112.69*** **	50.27	42.77	41.76	61.94
Habitat x Depth	5	0.42	6.67	4.36	1.65	0.75	2.88	0.7	6.09
3-way interactions									
Month x Habitat x Depth	55	46.51	42.16	33.76	30.75	25.85	52.99	56.25	44.53

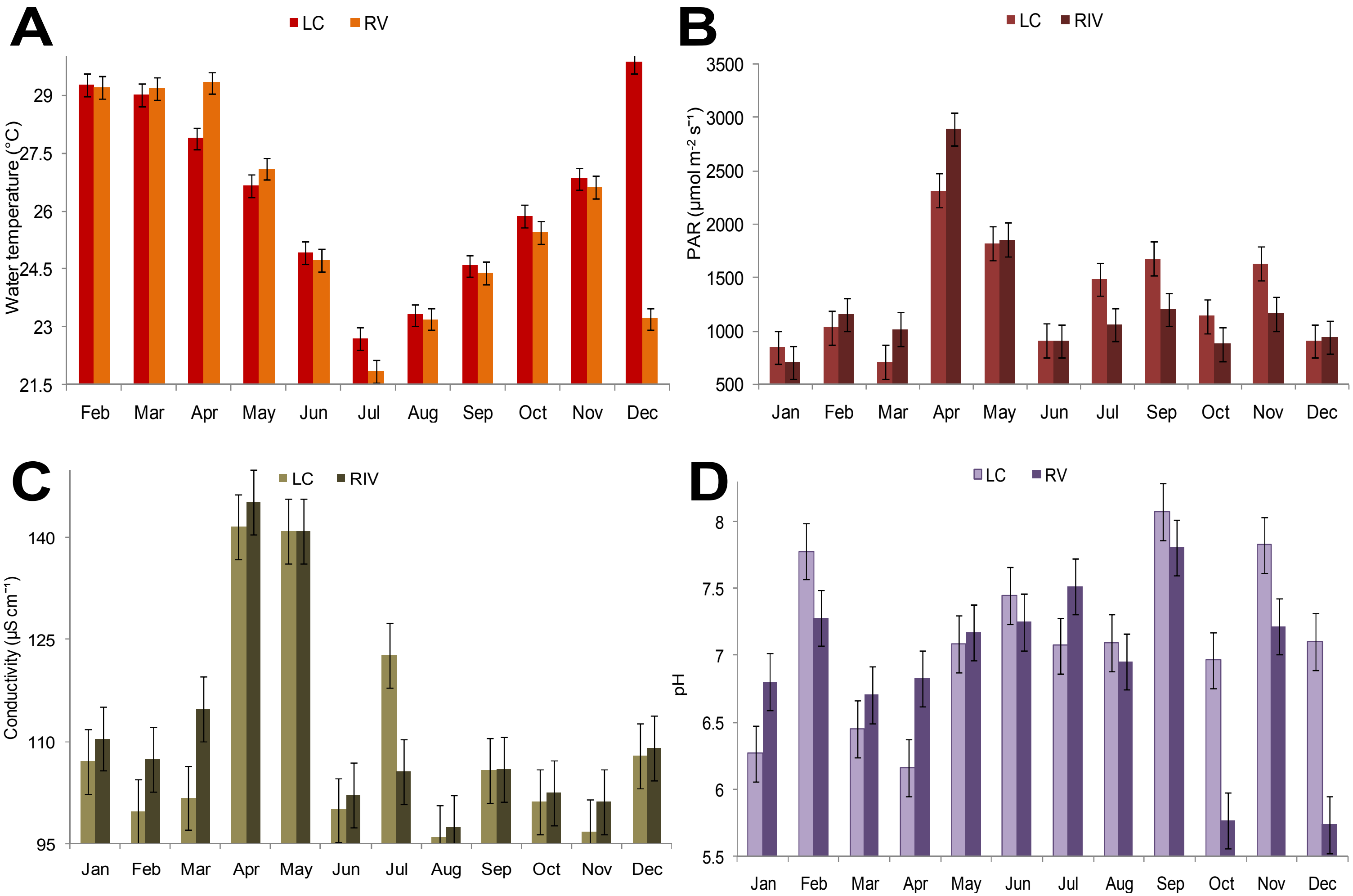

Figure 3.5. Monthly variation in A. temperature, B. transmission of PAR, C. conductivity and D. pH in lacustrine and riverine habitats in the Sanyati Basin of Lake Kariba. LC= lacustrine and RV= riverine habitats. Average standard error of differences shown by bars

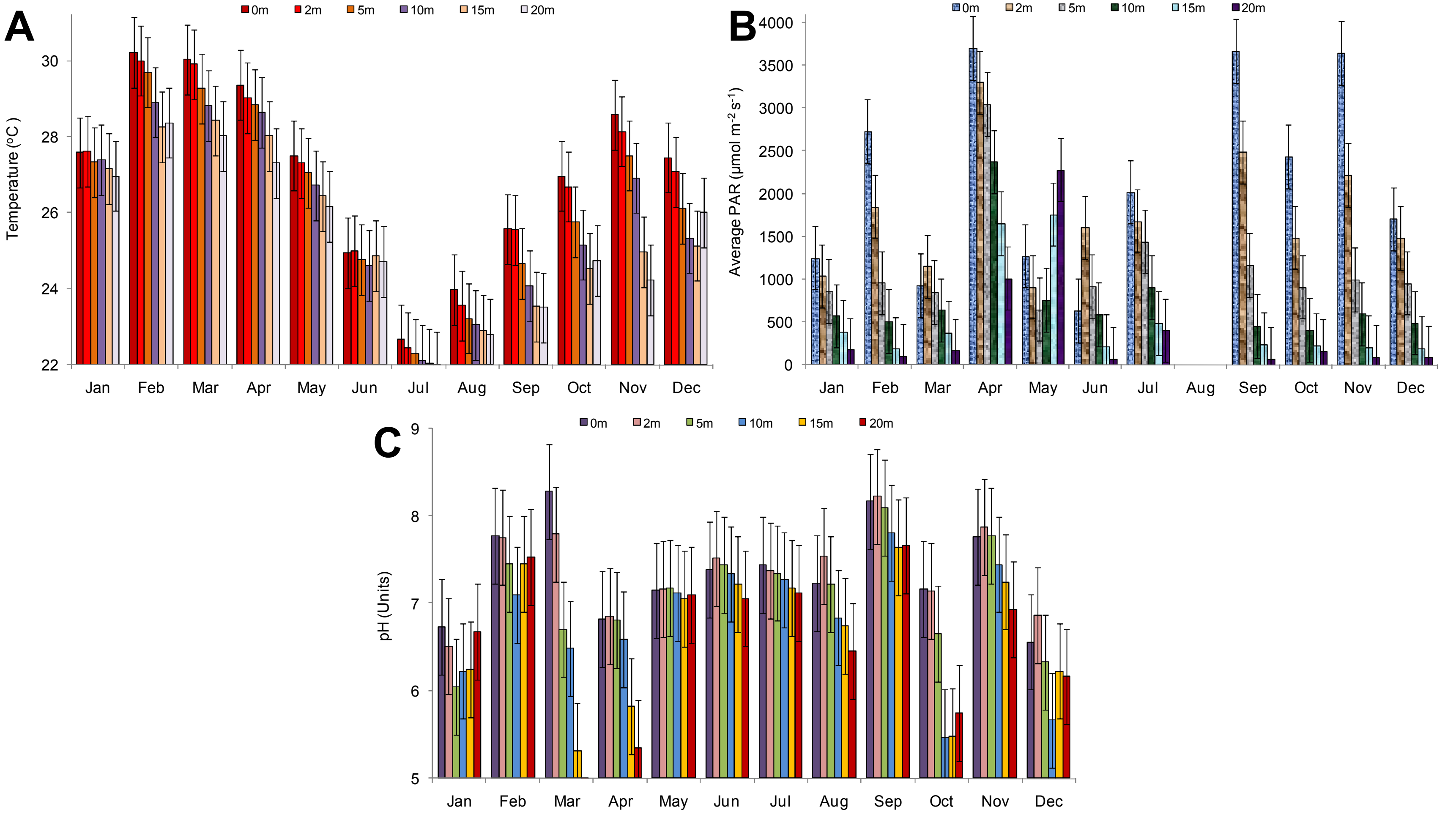

Figure 3.6. Monthly variation in A. temperature, B. transmission of PAR and C. pH at different depths in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars

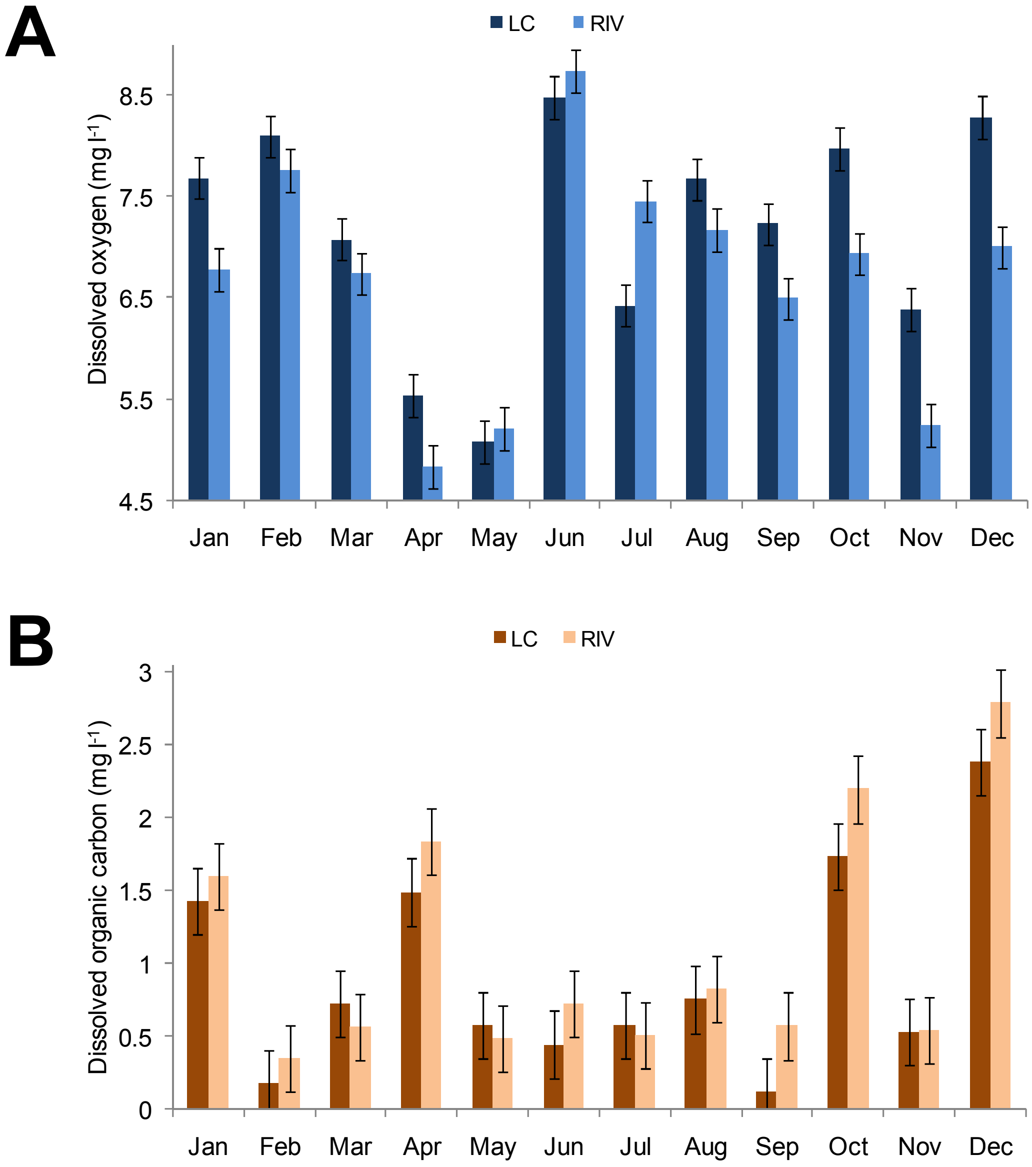

Figure 3.7. Monthly variations in A. dissolved oxygen and B. dissolved organic carbon in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars

3.4. Discussion

Lake Kariba is typically monomictic with one turnover event per annum, and this was reflected in the present study, as mixing occurred once between June and July in the annual cycle. This contrasts with deeper tropical African lakes such as Albert, Kivu, Malawi, Niger, Tanganyika, Turkana and Victoria, which are typically meromictic with infrequent turnover events, the incidence of complete mixing varying with the depth and shape of the lake basin (Baxter *et al.*, 1965). In addition, it contrasts with many shallower, naturally saline African lakes such as Naivasha (Hubble and Harper, 2002), Nakuru (Raini, 2007; Okoth *et al.*, 2009), Crescent Island Crater, Oloiden and

Winam Gulf (Melack, 1979; Osumo, 2001), which are typically polymictic with several turnover events per annum. In meromictic Lake Tanganyika, a fairly stable stratification is established during summer, which is generated by increased water temperatures and diminished wind intensities (O'Reilly *et al*., 2003). However, currents and internal waves, as well as coastal jets and return flows, do cause localised upwelling, which may partly disrupt this stratification (Chale, 2004). In the polymictic African lakes, density stratification is a natural feature, which is disrupted by strong winds that influence water circulation, thereby preventing the development of a consistent thermocline (Langenberg *et al.,* 2002).

The physical and chemical properties of lake waters are not only governed by stratification but also by hydrological dynamics. Coche (1968) reported that Lake Kariba is homothermic in June and July (range: 20ºC - 22ºC), with thermal stratification prevalent between October and May. This is corroborated by the contrasting physical and chemical properties measured in the lake water during winter turnover and summer stratification. Indeed, the physical and chemical water properties of Lake Kariba are closely related to thermal stratification as well as to the hydrological gradient along the lake from Basins 1 to 5, due to the influence of the Zambezi River, which contributes 80% of the total inflow in the lake (Marshall, 1982). The observed vertical gradients in lake water properties between basins are more distinct during summer stratification than winter turnover. This feature is reflected as steeper gradients in pH, conductivity, DO and DOC between basins in summer than winter, and in steeper summer than winter depth gradients in water temperature, transmission of PAR, pH and DO.

In the Sanyati Basin, water temperatures during the 2-year period of this study displayed an average annual range of 8.3°C (22.9°C to 31.2°C), and declined at an average rate of 0.11°C per m of water depth. This pattern was observed throughout most of the year, indicating that the lake was consistently stratified except at turnover in June and July, when the smallest decline in water temperatures averaging 0.02ºC m^{-1} of water depth was observed, a consequence of vertical water mixing and stratification disruption. These findings are consistent with those reported previously (Coche, 1974; Magadza *et al*., 1987, 1988, 1989). Coche (1974) demonstrated that the thermocline was established at a depth of up to 30 m in Lake Kariba between 1965 and 1968, whilst Magadza *et al*. (1987) reported the thermocline at a depth of 25 m depth in 1986 and 17 m in 1987. In this study, sectors of the water depth profile displaying the largest temperature gradient (rate of decrease) defined the thermocline and these sectors pointed to a thermocline depth ranging predominantly between 2 m and 5 m, with a deeper thermocline of 10 to 15 m apparent only in February (Figure 3.8).

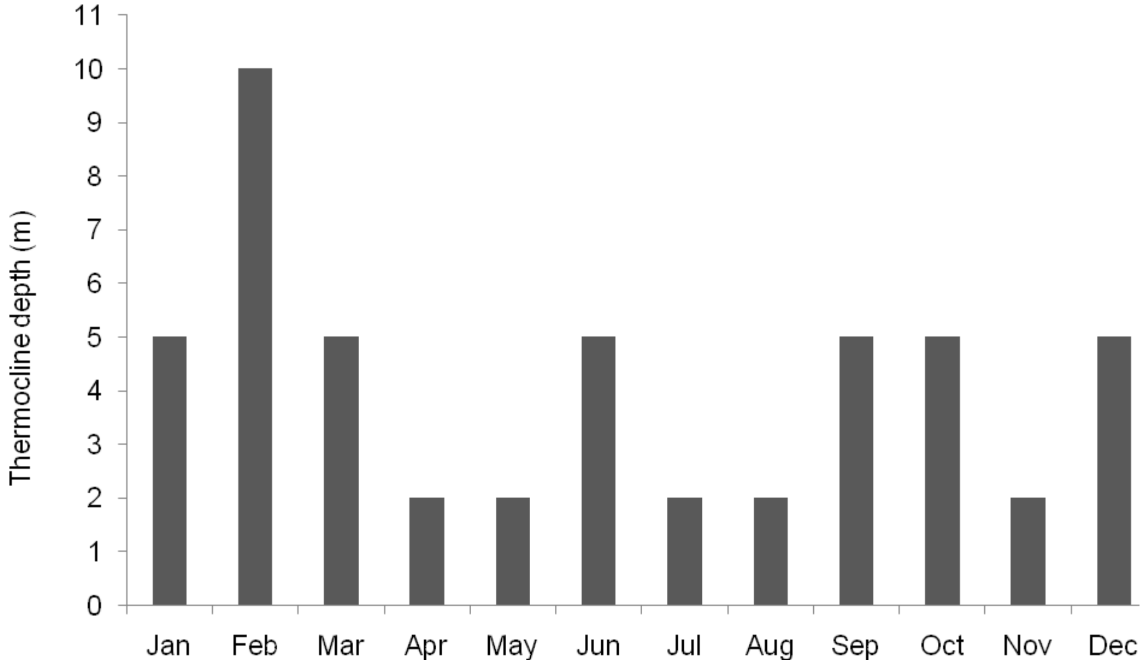

Figure 3.8. Monthly thermocline depths in the Sanyati Basin (B5) of Lake Kariba

These findings indicate that in the Sanyati Basin the thermocline has migrated upward by over 80% from the maximum thermocline depth of 30 m reported during the late 1960s by Coche (1974), and by over 60% from the maximum thermocline depth of 20 m reported during the late 1980s by Magadza *et al.* (1989). This upward shift in the depth of the thermocline corresponds with elevated, integrated water temperatures, which have increased by an average of 1.9ºC since the 1960s (Table 3.3). The largest temperature increases apparent in the minimum daily water temperatures, which have risen from an annual average of 17.0ºC in the 1960s to the present 19.1ºC (Table 3.3), correspond with reported increases in minimum daily air temperatures in Lake Kariba's Gwembe Valley, which have increased at a faster rate than IPCC Climate Model Intercomparison Project Version 3 (CMIP3) models predict (Magadza, 2008). Conversely, increases in the lake's maximum daily water temperatures have been minute, ranging from an annual average of 32.0ºC in the 1960s to the present 32.3ºC (Table 3.3). A consequence of the increased water temperatures and upward shift in the thermocline depth has been an approximate 50% reduction in the depth of the euphotic zone, from its original depth of 16.0 m to its current depth of 8.4 m (Table 3.3), this resulting in a smaller volume of lake water for phytoplankton primary production, with potential adverse effects on fish stocks. Consequently, the depth of the mixed layer (Zm), estimated from the depth of the top of the thermocline as shown by the temperature and oxygen vertical profiles, has also declined by approximately 50% since the mid-1960s, from 25 m to 12 m from 1965 to 2009 (Table 3.3).

Table 3.3. Changes in the physical and chemical properties of Lake Kariba over a 44-year period (1965-2009). Temperature averages computed from integrated epilimnion depth temperatures; all values presented as averages

Period	1965 – 1969	1986 - 1989	2007- 2009
Source	Coche (1974)	Magadza *et al*. (1987, 1988, 1989)	Present study
Physical			
Minimum temperature (˚C)	17.0	18.5	19.1
Maximum temperature (˚C)	32.0	32.5	32.3
Mean temperature (˚C)	24.5	23.9	26.4
Thermal stratification period	Oct- June	Aug- May	Aug- May
Depth of mixed layer (m)	25.0	17.9	12.0
Transparency (m)	4.1	4.6	2.8
Depth of euphotic zone (m)	16.0	13.8	8.4
pH	8.0	7.6	7.0
Conductivity (µS cm^{-1})	73.0	126.9	111.1
Total dissolved solids (mg l^{-1})	50.0	75.0	72.1
Dissolved oxygen (mg l^{-1})	8.0	4.3	7.0
Oxygen stratification period	Oct- June	Aug- May	Aug- May
Chemical			
Total N (µg l^{-1})	7.7	12.8	4.2
PO_4^{-3}-P (µg l^{-1})	1.1	3.5	4.1

Elevated water temperatures have also been reported in other tropical African lakes. The upper (above 250 m) water layers of Lake Kivu, for example, have warmed up by 0.5°C between 1937 and 2002 in response to increased air temperatures (Halbwachs *et al*., 2002), resulting in a sharper water-density gradient at depths below 250 m. Similarly, the upper (below 100 m) waters in Lake Tanganyika have warmed by an average of 0.34°C between 1946 and 1994, with evidence of warming of deeper (up to 300 m) water layers (Plisnier, 2000). This has led to a reduction in the thermocline depth from 68 m to 55 m, diminished water transparency, and a reduction in the depth of the oxygenated layer from 80-100 m to 60 m (Plisnier, 2000). These changes concur with altered ENSO oscillations around the lake that have reduced wind forces, which prolong stratification. In turn, this has resulted in the persistence of the shallower oxygenated layer (O'Reilly *et al*., 2003; Plisnier, 2004), a diminished nutrient supply, and reduced phytoplankton production dependent on vertical water mixing (Plisnier, 2004). Also, in Lake Malawi a 60-year (1930 to 2000) temperature record shows that the temperature of deep water below 300 m has increased by 0.78°C, due to reduced cold-water intrusions associated with milder winters (Vollmer *et al*., 2002, 2005), since rainfall and cold river inflow are critical factors in controlling thermal structure and the rate of deep-water recharge in this tropical lake. In Lake Kariba, the mixing of the waters is also mainly governed by thermal dynamics, stratification, the hydrodynamic state of the lake, and by the overturn event, and in Tanganyika upwelling by winds plays a major role in water mixing, with the reduced winds exposing the phytoplankton to low light conditions in deeper waters (O'Reilly *et al*., 2003; Naithani *et al*., 2007).

The elevated conductivities measured in the Sanyati Basin during April and May were attributed to increased rainfall run-off into the lake from its catchment, and those during July to vertical mixing of nutrient poor waters in the epilimnion with nutrient rich waters in the hypolimnion, following thermocline disruption. The measured average conductivity of 111.1 μS cm^{-1} (annual range 96.5 to 145.3 μS cm^{-1}) concurred with records from 1986-89 (Table 3.3), but was substantially higher than the average lake water conductivities of 40 to 80 μS cm^{-1} reported during the 1960s and 1970s (Coche, 1974), and 50 to 115 μS cm^{-1} reported in the early 1980's (Machena, 1988). Magadza (2008) postulated a 0.48 μS cm^{-1} per decade increase in the lake water conductivity due to increased evaporative water loss associated with elevated temperatures in the Zambezi Valley. However, a substantially higher rate of conductivity increase of 0.76 μS cm^{-1} per decade was computed from the difference between the 1965-1969 average record of 73 μS cm^{-1} (Coche, 1974) and the average record of 111.1 μS cm^{-1} in this study. This pointed to factors other than increased evaporation, such as sewage and fertiliser runoff, due to increased anthropogenic activity in the lake catchment area contributing to increased, localised lake eutrophication. Localised pollution has been documented along the Zambezi River and the Sanyati Basin (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996), with *Tilapia* sp. fish cage cultures (Troell and Berg, 1997) and the discharge of partially treated sewage effluent averaging 3.6 metric tons per day into the lake (Mulendema, 2000), as the main sources of contamination (Ndebele-Murisa and Phiri, 2008). In addition localised pollution from activities such as crocodile farming along the shoreline in Binga and Charara (Basin 4 and 5) has been noted, with the notorious weed *Eichhornia crassipes* proliferating at these enriched sites (Tumbare, 2008).

The average pH of the lake water was generally below the expected alkaline range of 7.5 to 8.5, and has decreased from an average of 8.0 in the 1960s to the current 7.0 (Table 3.3). DO levels have also declined from an average of 8.0 mg l^{-1} in the 1960s to the current 7.0 mg l^{-1}. Low DO levels of 4.3 mg l^{-1} were reported during March at 15 m depth in the 1980s, with even lower DO levels of less than 3 mg l^{-1} measured at the same depth and month in this study. This pointed to increased de-oxygenation of the hypolimnion towards the end of the annual stratification period, which corresponded with the observed upward shift in the thermocline depth. PO_4^{-3}-P levels in the principally P-limited lake water (Moyo, 1991; Magadza, 1992; Lindmark, 1997) displayed an approximate three-fold increase from an average of 1.1 μg l^{-1} PO_4^{-3}-P reported in the 1960s to the current average of 3.3 μg l^{-1} PO_4^{-3}-P (Table 3.3). The elevated PO_4^{-3}-P concentrations, a possible consequence of localised pollution from *Tilapia* fish cage cultures (Troell and Berg, 1997), discharge of partially treated sewage effluent (Mulendema, 2000) as well as diminished phosphorus removal from the Clupeid sardine (*L. miodon*) harvesting, estimated at 50 tons per annum, which has steadily declined in the lake since 1987 (Magadza, 2008). In contrast, total N concentrations in the lake water exhibited an almost 50% reduction from an average of 7.7 μg l^{-1} N reported in the 1960s to the current average of 4.1 μg l^{-1} N (Table 3.3). This reduced total N content is a possible consequence of an upward shift in the thermocline depth, resulting in a larger sink for nitrogen by an expanded anoxic hypolimnion as measured by Ndebele-Murisa and Phiri (2008). The nitrogen trapped as ammonia in the anoxic hypolimnion only oxidised to nitrate when mixed with the oxic epilimnion during turnover (Lindmark, 1997).

Several workers (Magadza, 1980; Marshall, 1982; Lindmark, 1997) have reported that nutrients are replenished in Lake Kariba by silt and organic matter transported in inflowing rivers. Clearly apparent during the summer rainy season (November-May) were distinct hydrological gradients of decreasing PO_4^{-3}-P and total N concentrations from Basin 1 (1.34 μg l^{-1} PO_4^{-3}-P, 2.36 μg l^{-1} N) to Basin 5 (1.29 μg l^{-1} PO_4^{-3}-P, 1.95 μg l^{-1} N), this attributed to nutrient-rich silt particles borne by the highly turbid Zambezi River flood waters. These hydrological gradients in PO_4^{-3}-P and total N are less distinct under reduced Zambezi River flow rates during winter. Lindmark (1997) concluded that only river beds, estuaries and sheltered bays and trees hold sufficient organic matter and fine silt material rich in N and P, but once the water reaches the main lake the nutrient levels are depleted due to efficient utilisation. Consequently, Basins 1 and 2 display typically riverine characteristics under high Zambezi River inflows during summer (Coche, 1968), after which the influence of the Zambezi River decreases, and both basins assume lake-like characteristics during winter (Moreau, 1997).

Many oligotrophic African lakes like Lake Kariba, which derive their water from direct surface runoff or rivers with little salt, are exhibiting deteriorations in water quality caused by mismanagement, pollution and climate change that may potentially alter their trophic status (Bootsma and Hecky, 1993; Ogutu-Ohwayo and Balirwa, 2006; Ndebele-Murisa *et al*., 2010). For instance, in Lake Malawi, increased population growth and land cultivation in its catchment have led to an increased input of sediment and nutrients, and a consequent decline in lake water quality. These factors, together with intensive fishing, have resulted in a loss of endemic fish species and the proliferation of alien aquatic plants (Bootsma and Hecky, 1993; Hecky *et al*., 1999; Hecky *et al*., 2010). Magadza (1980) predicted that the oligotrophic Lake Kariba would shift towards a mesotrophic state, this assertion supported by Cronberg (1997), who measured greater increases in phytoplankton biomass and primary production levels in the lake between 1986 and 1990 than reported in Lakes Malawi, Tanganyika and Victoria. In fact, phosphorus loading and localised pollution has recently been documented in Lake Kariba (Feresu and van Sickle, 1989; Magadza and Dhlomo, 1996; Mulendema, 2000; Magadza, 2002; Ndebele-Murisa and Phiri, 2008). These changes emphasise the need to consistently manage sources of pollution, and to monitor Lake Kariba's water quality (Tumbare, 2008) and that of other relatively pristine oligotrophic impoundments in Zimbabwe, such as the Cleveland Dam, currently under threat from increased land use in their catchments (Ndebele, 2009). This is especially pertinent since several African lakes and impoundments, such as Lake Chivero and the Hartbeespoort and Yaoundé Municipal Dams, have already surpassed their threshold levels and are currently hyper-eutrophic (Van Ginkel *et al*., 2001; Magadza, 2003; Kemka *et al*., 2006; Njine *et al*., 2007).

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Chapter 4

Phytoplankton biomass and primary production dynamics in Lake Kariba

Abstract

The study examined spatial, seasonal and depth variations in phytoplankton biomass and primary production, compared these with those in other tropical African lakes, and established whether measured phytoplankton changes might be linked to climate warming. Biomasses of three major phytoplankton classes (Cyanophyceae, Chlorophyceae and Bacillariophyceae) and net primary production were measured in midwinter and midsummer, at six different depths, at 35 sampling stations distributed across the lake's five basins. In the fifth basin, a more rigorous sampling regime was followed, with phytoplankton biomasses and primary production rates measured every second month over a 24-month period, at six different depths, at ten sampling stations located in riverine and lacustrine waters. Cyanophyceae, which displayed a gradient of decreasing biomass from Basins 2 to 5, contributed 69% of the total phytoplankton biomass in the lake's five basins during summer, which was approximately four times greater than that contributed by the Bacillariophyceae and about 10 times greater than that contributed by the Chlorophyceae. During winter, Bacillariophyceae biomasses were equivalent to those of the Cyanophyceae, but displayed an opposing gradient of increasing biomass from Basins 1 to 3, with a subsequent biomass decline from Basins 3 to 5. Chlorophyceae exhibited no distinct biomass gradient across the five lake basins and were undetectable during winter. Biomasses of all three phytoplankton classes and net primary production varied in magnitude and direction monthly between lacustrine and riverine waters and with increasing water depth, with no distinct seasonal patterns evident. These monthly variations in biomass related to the thermal stratification cycle, hydrological gradients and extent of mixing of the waters, and were similar to those reported in other tropical African lakes. Noteworthy was that total phytoplankton biomass and primary production in Lake Kariba have declined by about 95% and 57% respectively since the 1980s. These declines correspond with an upward shift in the depth of the thermocline, associated with an average temperature increase of 1.9ºC and a 50% reduction in the depth of the euphotic zone since the 1960s.

4.1. Introduction

Tropical African lakes have a well-established seasonality in phytoplankton abundance and biomass (Ndebele-Murisa *et al*., 2010). Naturally oligotrophic lakes such as Edward, Kariba, Kivu and Malawi have a low phytoplankton biomass and species diversity, and display a seasonal succession of major phytoplankton classes similar to that in Lake Tanganyika, where Cyanophyceae and Chlorophyceae co-dominate when the phytoplankton biomass reaches its peak during the rainy season, with Bacillariophyceae dominating at turnover during the dry season (Cronberg, 1997; Evans, 1997; Descy *et al*., 2005; Sarmento *et al*., 2006; Guildford *et al*., 2007).

The composition and abundance of phytoplankton often reflect the nutrient status of African lakes with, for example, the low Euglenophyceae biomass in Lake Ogelube proposed as indicative of low organic pollution, and the predominance of desmids indicative of oligotrophic conditions (Nweze, 2006). Low nutrient concentrations have been observed in the normally oligotrophic Lakes Kariba, Kivu and Malawi, yet, despite this, many African lakes are now prone to eutrophication resulting from increased nutrient inflows from anthropogenic activities in their catchments. This is apparent from the substantial increases in primary production observed in several tropical African lakes such as Chivero, Malawi and Victoria, and the Hartbeespoort Dam, where levels of primary production have risen by several orders of magnitude from previously reported ranges, as a direct consequence of high nutrient inflows which overburden these lakes' natural purification systems (Robarts, 1979, 1984; Mugidde, 1993; Ndebele, 2003; Mhlanga *et al*., 2006; Haande *et al*., 2010).

Cyanophyceae blooms have also been reported in several nutrient-enriched water bodies such as the Hartbeespoort Dam (Robarts and Zohary, 1986, Van Ginkel *et al*., 2001), the Erfenis and Allemanskraal Dams (Van Ginkel and Hohls, 1999), the Orange River (Janse van Vuuren and Kriel, 2008) and in the shallow tropical Yaoundé Municipal Lake in the Cameroon, where nutrient-rich inflows have resulted in a massively increased phytoplankton biomass dominated by Euglenophyceae and Chlorophyceae (Kemka *et al*., 2006). Eutrophication tends to impact shallow lake systems more than deeper tropical lakes such as Lakes Malawi, Victoria and Kariba, with incidences of localised pollution only occasionally reported in Lakes Malawi and Victoria as well as in Lake Kariba (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996; Verschuren *et al.* 1998; Hecky *et al.* 1999). In Lake Kariba the water has changed from an initial eutrophied state to that of its current oligotrophic state, with phosphorus limiting primary production (Moyo, 1991; Ndebele, 2007). However, the high concentrations of faecal coliform bacteria recorded in Zambezi waters above the Victoria Falls and along the northern shoreline of Lake Kariba infer that the lake waters are moving towards mesotrophy (Feresu and Van Sickle, 1989; Magadza and Dhlomo, 1996).

Inter-annual variations in phytoplankton composition and biomass are known to reflect changes in climate (Lehman *et al*., 1998), yet the impact of global warming projected by climate change models (Hulme, 1996; Hulme *et al*., 2001; IPCC, 2007) on phytoplankton production in tropical African lakes has not been studied extensively (Magadza, 1994). Most of the phytoplankton studies that have been conducted in the past did not specifically address climate-driven changes, such as in Lake Volta (John, 1986) and in Lakes Malawi, Tanganyika and Victoria (Talling, 1966; Hecky and Kling, 1981, 1987; Cocquyt and Vyverman, 1994; 2005), and in several other African lakes (Talling *et al*., 1973; Robarts and Southall, 1977; Melack, 1979; Girma and Ahlgren, 2009). East African lakes are potentially highly sensitive to climate change (Johnson and

Odada, 1996). In Lake Tanganyika, thermal stratification is strongly linked to hydrodynamic and climatic conditions (Plisnier *et al*., 1999), with small climatic variations causing wide fluctuations in the thermocline which isolate nutrients from the euphotic zone, thereby affecting phytoplankton biomass and primary production (Lewis, 1974; O'Reilly *et al*., 2003). Indeed, regional climatic changes around Lake Tanganyika over the past 80 years have already resulted in reduced primary production (O'Reilly *et al*., 2003, Stenuite *et al*., 2007; Verburg and Hecky, 2009; Tierney *et al*., 2010). These findings are corroborated by another study which has demonstrated a close correspondence between phytoplankton biomass and climate in Lake Tanganyika (Plisnier, 2000; Bergamino *et al*., 2007, 2010).

Increased water temperatures associated with climate warming are likely to cause a shift in phytoplankton species composition from Chlorophyceae to Cyanophyceae, which are competitively superior at higher temperatures. Microcosm studies have demonstrated that elevated temperatures suppress total zooplankton biomass by altering phytoplankton community composition towards high temperature-tolerant species, though total phytoplankton biomass is not usually altered (Doney, 2006). These findings are corroborated by observed changes in phytoplankton composition in Lake Chivero, where it was found that the water temperatures at which Cyanophyceae dominated were several degrees higher than those at which Chlorophyceae were dominant (Sibanda, 2003). As water temperatures increase, algal succession follows a progression from Bacillariophyceae through to Chlorophyceae to Cyanophyceae (Pliński and Jóźwiak, 1999). The preponderance of Cyanophyceae at higher water temperatures has led to concerns that increased water temperatures due to global warming could result in a decline in the production of palatable Chlorophyceae, leading to decreased zooplankton production and a consequent decline in fish stocks. Indeed, fisheries catches data from Lake Tanganyika show significant negative correlations with climatic (ENSO) data over the last 40 years (Plisnier, 2000; Plisnier, 2004; Stenuite *et al*., 2007). This suggests that moderate warming could destabilise plankton dynamics, thereby potentially reducing water quality and food resources for higher trophic levels such as planktivorous fish, as observed in shallow cold-water ecosystems (Strecker *et al*., 2004).

Analyses of climatic data for the middle Zambezi valley show that warming around Lake Kariba is proceeding at a faster rate than regional models predict (Magadza, 2010). These changes in the lake's thermal properties are already reflected in an upward migration of the thermocline, which points to future shifts in phytoplankton species richness and production with potential negative impacts on fish stocks and human livelihoods. In view of all these findings, this study's aims were 1. to examine season and depth variations in phytoplankton biomass and primary production across the lake and the influence of riverine inflows on these and 2. to determine whether there have been any changes in phytoplankton biomass and primary production that may be linked to climate warming, and how these compare with those in other tropical African lakes.

4.2. Methods and materials

4.2.1. Study area

The study area was Lake Kariba (16-18°S, 27-29°E), the third largest man-made lake in the world and the largest volumetrically. The lake was formed by the impoundment of the Zambezi River in 1955 at the Kariba Gorge (Balon and Coche, 1974), and is located in the lower Zambezi Basin, being bordered by Zambia in the north and Zimbabwe in the south.

4.2.2. Experimental design and sampling stations

Two separate studies measured phytoplankton biomass and primary production at six different depths (0, 2, 5, 10, 15, 20 m) at 35 sampling stations in total, distributed across the entire length of the lake from Basin 1 in the south west to Basin 5 in the north east. Based on preliminary sampling and past studies, the thermocline depth below which there is negligible primary production rarely exceeded 20 m and this formed the rationale for the maximum depth sampled. In the first study, phytoplankton measurements were conducted twice annually, namely during lake turnover in midwinter (July) and again during lake stratification in midsummer (February), at four sampling stations located in Basin 1, seven in Basin 2, six in Basin 3, eight in Basin 4, and ten in Basin 5. In the second study, phytoplankton measurements were conducted at 2-monthly intervals over a 24-month period extending from March 2007 through to February 2009 along the vertical profile described above at ten sampling stations in Basin 5, where the majority of previous long-term phytoplankton studies have been conducted (Ramberg, 1984, 1987; Cronberg, 1997). Four of these sampling stations were located at the margins of the lake basin, in close proximity to the Charara, Gache-gache and Sanyati River inflows and designated riverine habitats. The six other sampling stations traversed the centre of the basin and were designated lacustrine habitats. Figure 4.1 shows all the sampling stations in the lake.

4.2.3. Phytoplankton biomass and photosynthetic quantum yield

Chlorophyll fluorescence provides a very sensitive technique for assessment of phytoplankton biomass as chlorophyll content, and in distinguishing between different phytoplankton classes such as the Bacillariophyceae, Chlorophyceae and Cyanophyceae, on the basis of the specific fluorescence excitation properties of these differently pigmented phytoplankton classes (Schreiber, 1998). In this study, chlorophyll fluorescence measurements were performed with a Pulse Amplified Modulated Phytoplankton (Phyto-PAM) Analyzer (Heinz Walz GMBH, Effeltrich, Germany), which has been successfully applied in accurately measuring chlorophyll content in several tropical lakes such as Kivu and Tanganyika (Salonen *et al.,* 1999; Sarmento *et* *al*., 2006; Stenuite *et al*., 2007; De Wever *et al*., 2008). Samples of water were collected from each depth zone at each sampling station with a Ruttner sampler. Concurrently, photosynthetically active radiation (PAR) was measured in situ under clear sky conditions two hours on either side of midday (1000 to 1400 hours), with sensors at each depth zone using a Licor light meter (LiCor Lincoln, NE, USA). The light meter was connected to the phyto-PAM and fed the PAR measurements, which were then used to calculate primary production as described in detail in the next section.

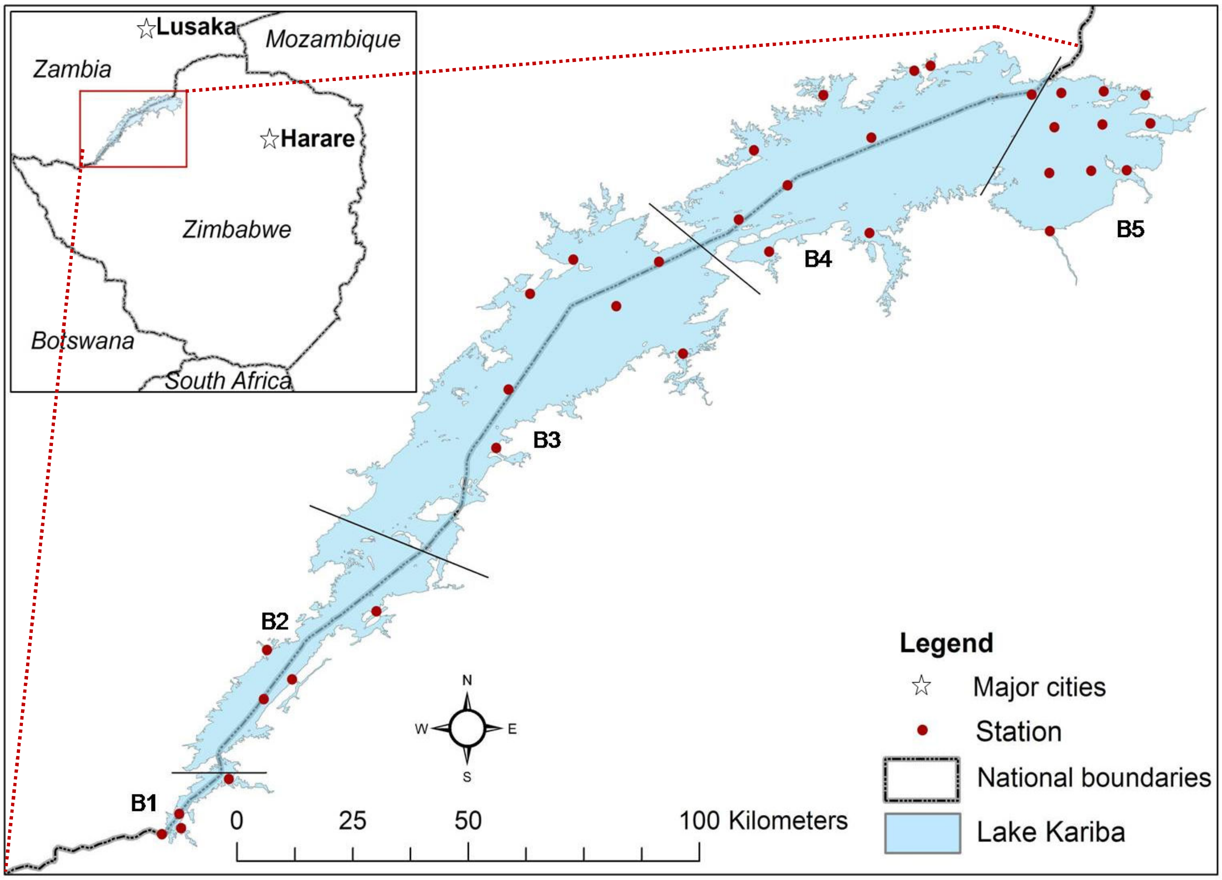

Figure 4.1. Distribution of sampling stations in Lake Kariba's five basins, with those located in the centre of the lake designated lacustrine and those located along the lake margin in proximity to river inflows designated riverine

Fresh, unfiltered 2 to 3 ml sub-samples were placed into special 15 mm Ø quartz cuvettes, optimised for a low background signal corresponding to 0.2 µg chlorophyll litre^{-1}, with background signals determined on filtered water samples. Chlorophyll fluorescence in the unfiltered water samples was excited by the Phyto-PAM light-emitting-diodes (LED), which emit alternating 10 µs light pulses at four different wavelengths (470, 520, 645 and 665 nm). The fluorescence pulses that are detected by a photomultiplier and amplified under microprocessor-control result in four separate continuous signals (four channels). Chlorophyll biomass determination was on the basis of chlorophyll fluorescence yield in the quasi-dark state (Fo), and the quantum yield of Photosystem II (PSII) under a brief pulse of saturating light. The momentary fluorescence yield (Ft) obtained when a saturation pulse was triggered allowed the determination of the increase in fluorescence, (Fm-Ft) with the quantum yield (QY) PSII of corresponding with (Fm-Ft)/Fm. Blue-green (Cyanophyceae), green (Chlorophyceae) and brown (Bacillariophyceae) phytoplankton biomasses were calculated from the original 4-channel fluorescence data by an on-line de-convolution routine, based on previously stored "reference excitation spectra" determined from pure cultures of Bacillariophyceae (diatoms), Chlorophyceae, and Cyanophyceae sourced from Lake Kariba.

4.2.4. Primary production

Phytoplankton primary production (PP) was computed for the water column at each sampling station for each of the six sampling depths, using the equation of Gilbert *et al*. (2000):

$PP = \varphi \times PAR \times 0.156 \times 3\,600$ ....1.
PP = primary production [$\mu g\ O_2\ m^{-2}\ h^{-1}$]
φ = quantum yield
PAR = photosynthetic active radiation [$\mu mol\ m^{-2}\ s^{-1}$]
0.156 = conversion factor, which considers the absorption cross-section of photosystem II in natural phytoplankton populations and the number of electrons required to produce one molecule of oxygen (Estevez-Blanco *et al*. 2006; Kromkamp *et al*. 2008)
3 600 = factor converting seconds to hours

Values were converted to mg C $m^{-2}\ d^{-1,}$ assuming a molecular photosynthetic quotient of 1 (Ganf and Horne, 1975; Goto *et al*., 2008) and a 12-h daily photoperiod.

4.2.5. Statistical analysis

The experimental design was not fully balanced, due to unequal numbers of measurements. Consequently, a REML (residual maximum likelihood) variance component analysis (repeated measures mixed model) was applied to test for significant differences in measured phytoplankton biomasses and primary production between seasons, months, lake basins, water depth, and interactions, using the Wald X^2 statistic generated by REML (GENSTAT Discovery Edition 3, VSL Lty, UK). In the first REML analysis of all 35 sampling stations, lake basins and water depth were fitted in the fixed model, and replicated winter and summer seasons in the random model. In the second REML analysis of the 10 sampling stations in the Sanyati Basin, the lacustrine and riverine habitats and water depth were fitted in the fixed model, and replicated months in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

4.3. Results

4.3.1. Lake basin phytoplankton biomass

Total phytoplankton biomasses and those of Cyanophyceae, Chlorophyceae and Bacillariophyceae differed significantly ($P < 0.001$) between winter and summer seasons and between lake basins (Table 4.1). The lowest total phytoplankton biomasses and those of all three phytoplankton groups were observed in Basin 5 (Figure 4.2A, B, C & D). Overall, Cyanophyceae and Chlorophyceae biomasses were significantly ($P \leq 0.05$) higher in summer than winter and the converse is true in the total phytoplankton biomass and the Bacillariophyceae (Figure 4.2A, B, C & D). However, there were significant ($P \leq 0.05$) interactions between season and lake basin for total phytoplankton biomasses and those of all three phytoplankton groups (Table 4.1). Significantly ($P \leq 0.05$) higher total phytoplankton and Bacillariophyceae biomasses were observed during winter than summer, but these were confined to the first three and four lake basins respectively (Figure 4.2A & D). In contrast, significantly ($P \leq 0.05$) smaller winter than summer Cyanophyceae biomasses were observed in all lake basins, these biomasses displaying a gradient of decreasing concentrations from Basins 2 to 5, with undetectable Chlorophyceae biomasses in all lake basins during winter (Figure 4.2B & C).

4.3.2. Lake basin net primary production

Net primary production differed significantly ($P \leq 0.001$) between the winter and summer seasons, between lake basins, and with water depth (Table 4.1). Overall, net primary production was significantly ($P \leq 0.05$) higher in winter than in summer, with the highest net primary production apparent in Basin 3 and the lowest in Basin 5 (Figure 4.3A). However, there was a significant ($P \leq 0.001$) interaction between season and lake basin for net primary production (Table 4.1). Significantly ($P \leq 0.05$) higher winter than summer net primary production rates were confined to Basins 2, 3 and 5 (Figure 4.3A). In addition, there was a significant ($P \leq 0.05$) interaction between season and water depth on net primary production (Table 4.1). A steeper decline in net primary production, with increasing water depth, was observed during summer than winter, with significantly ($P \leq 0.05$) higher winter than summer net primary production rates apparent at 2, 5 and 10 m water depths, but not at the water surface or at depths of 15 m and greater (Figure 4.3B).

4.3.3. Sanyati Basin phytoplankton biomass

Total phytoplankton biomasses and those of Cyanophyceae, Chlorophyceae and Bacillariophyceae differed significantly ($P \leq 0.001$) monthly, and in the Cyanophyceae they also differed significantly ($P < 0.05$) between lacustrine and riverine waters and along the water depth profile (Table 4.2). Overall, the highest total phytoplankton, Cyanophyceae, Bacillariophyceae biomasses occurred in July, the lowest in June and October. The highest Chlorophyceae biomasses occurred in January and March, with Chlorophyceae undetectable (<0.1 $\mu g\ l^{-1}$) between May and August and between November and December (Figure 4.4A, B, C & D). Overall, Cyanophyceae biomasses increased with increasing water depth, with peak biomasses observed at 10m water depths with a subsequent decline at greater water depths (Figure 4.5). However, there were significant ($P \leq 0.05$) interactions between month and habitat for total phytoplankton, Cyanophyceae and Bacillariophyceae biomasses (Table 4.2), which were significantly ($P \leq 0.05$) higher in July and November, with the converse evident in January (Figures 4.4A, B, & C). Chlorophyceae biomasses were significantly ($P \leq 0.05$) higher in riverine than lacustrine waters in March, with the converse evident in January as well (Figure 4.4D). In addition, there was a significant ($P \leq 0.001$) interaction between month and water depth for Cyanophyceae biomass, which varied monthly with increasing water depth. Peak Cyanophyceae biomasses, for example, were observed at 20 m depth in July, at 10 m depth in September, and between 0 and 5 m in November (Figure 4.5).

4.3.4. Sanyati Basin net primary production

Net primary production differed significantly ($P \leq 0.01$) monthly and with water depth (Table 4.2), with the highest values overall observed in February and April and in surface waters (Figure 4.6A & B). However, there were significant ($P < 0.05$) interactions between month and habitat, and between month and water depth for net primary production (Table 4.2). Significantly ($P \leq 0.05$) higher net primary production rates were observed in riverine than lacustrine waters in February (Figure 4.6A). Declines in net primary production, with increasing water depth, were observed in all months except January, March, June and October, when values did not differ significantly ($P \geq 0.05$) along the depth profile (Figure 4.6B). The steepest declines in net primary production, with increasing water depth, were observed in February and November, April and December, with significantly ($P \leq 0.05$) higher values evident in surface waters during these months than at all other water depths (Figure 4.6B).

Table 4.1. Wald χ^2 statistics derived from REML (repeated measures model), which tested the effects of season, lake basin and water depth and their interactions on the biomass of different phytoplankton groups and net primary production in Lake Kariba. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤0.001

REML	df	Wald χ^2 statistic				
		Total phytoplankton	Cyanophyceae	Chlorophyceae	Bacillariophyceae	Net primary production
Main effects						
Season	1	**9.61*** **	**100.03*** **	**173.31*** **	**60.41*** **	**22.11*** **
Basin	4	**48.17*** **	**49.49*** **	**17.91** **	**37.30*** **	**24.20*** **
Depth	5	2.75	2.19	5.59	5.57	**355.93*** **
2-way interactions						
Season x Basin	4	**36.17*** **	**11.79* **	**18.98*** **	**32.59*** **	**34.50*** **
Season x Depth	5	2.56	1.61	8.16	3.83	**14.77* **
Basin x Depth	20	8.12	15.12	10.88	11.11	23.76
3-way interactions						
Season x Basin x Depth	20	15.12	24.69	17.41	8.51	21.47

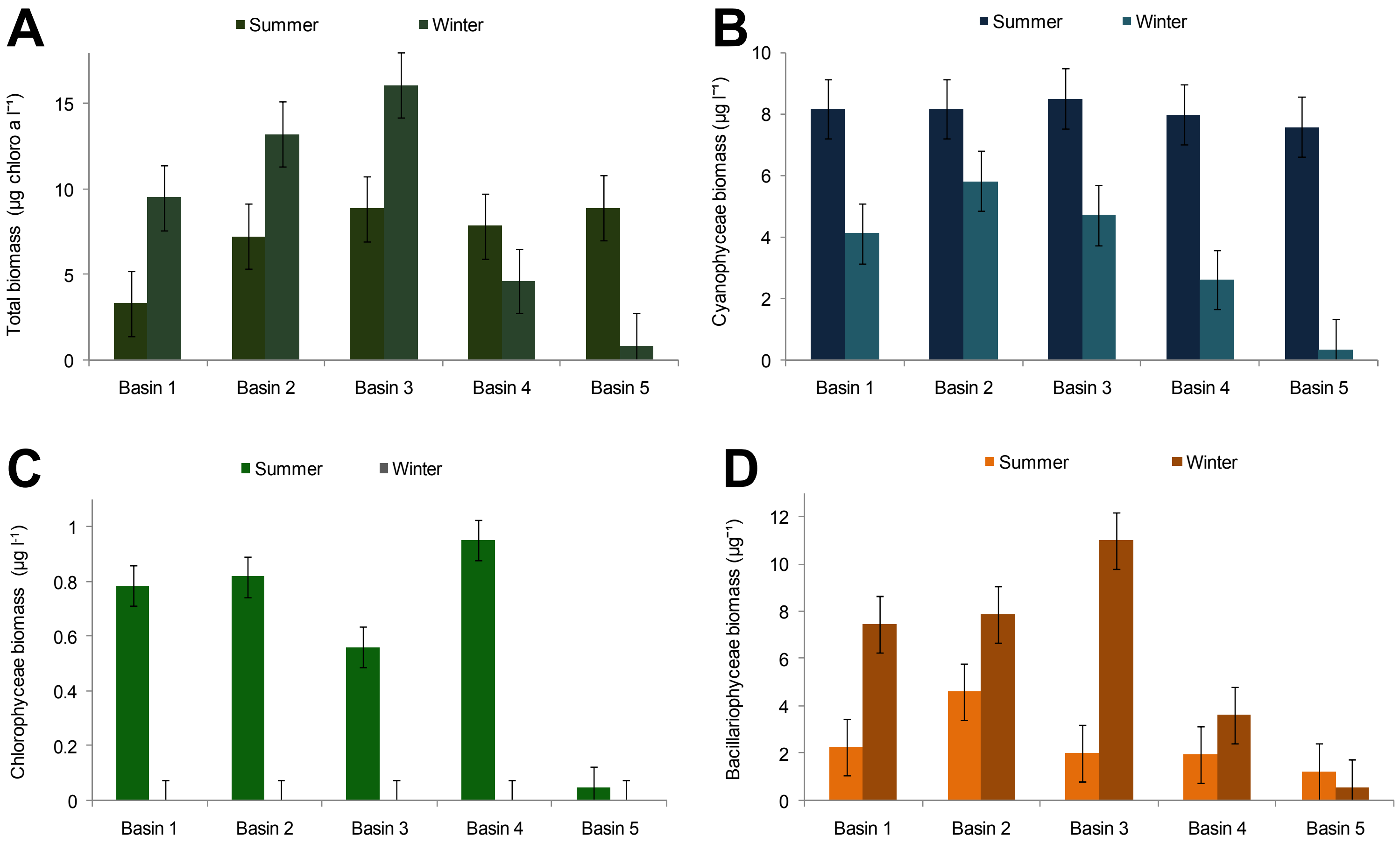

Figure 4.2. Seasonal variations in A. total phytoplankton biomass and that of B. Cyanophyceae, C. Chlorophyceae and D. Bacillariophyceae in different basins of Lake Kariba. Average standard error of differences shown by bars

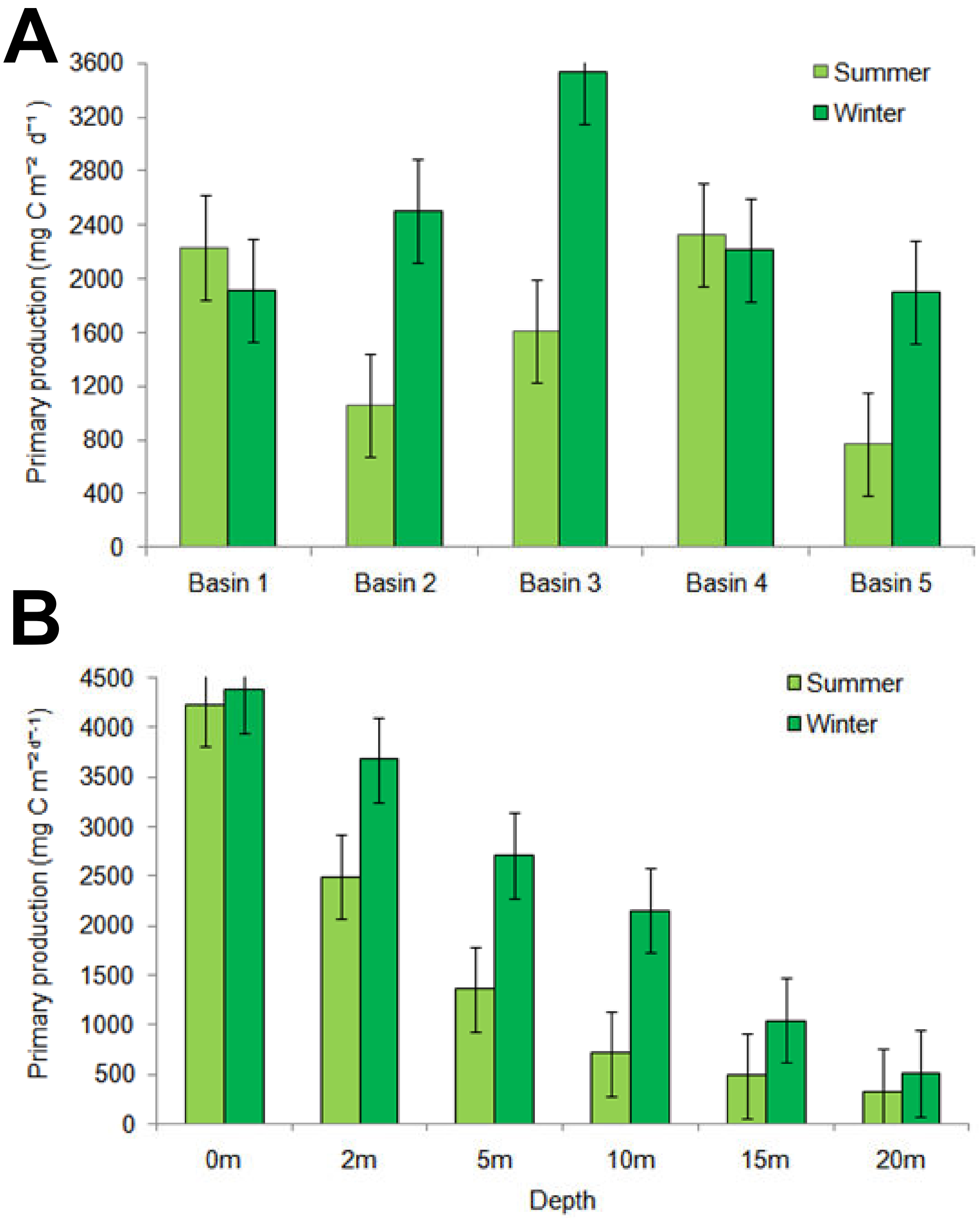

Figure 4.3. Seasonal variations in net primary production in A. different basins and B. water depths of Lake Kariba. Average standard error of differences shown by bars

Table 4.2. Wald χ^2 statistics derived from REML (repeated measures model), which tested the effects of month, habitat (riverine versus lacustrine) and water depth, and their interactions on the biomasses of different phytoplankton groups and net primary production in the Sanyati Basin of Lake Kariba. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001

REML	df	Wald χ^2 statistic				
		Total phytoplankton	Cyanophyceae	Chlorophyceae	Bacillariophyceae	Net primary production
Main effects						
Month	3	**1 552.46*** **	**17.65*** **	**116.29*** **	**30.79*** **	**44.57** **
Habitat	1	0.01	**7.02* **	1.60	0.18	0.49
Depth	55	5.88	**7.02* **	9.44	6.14	**227.14*** **
2-way interactions						
Month x Habitat	11	**94.89*** **	**15.03* **	3.08	**14.58** **	**7.64* **
Month x Depth	55	76.55	6.87	6.3	11.43	**63.97*** **
Habitat x Depth	5	3.89	6.13	6.09	3.56	1.89
3-way interactions						
Month x Habitat x Depth	55	53.19	7.97	6.68	9.53	9.19

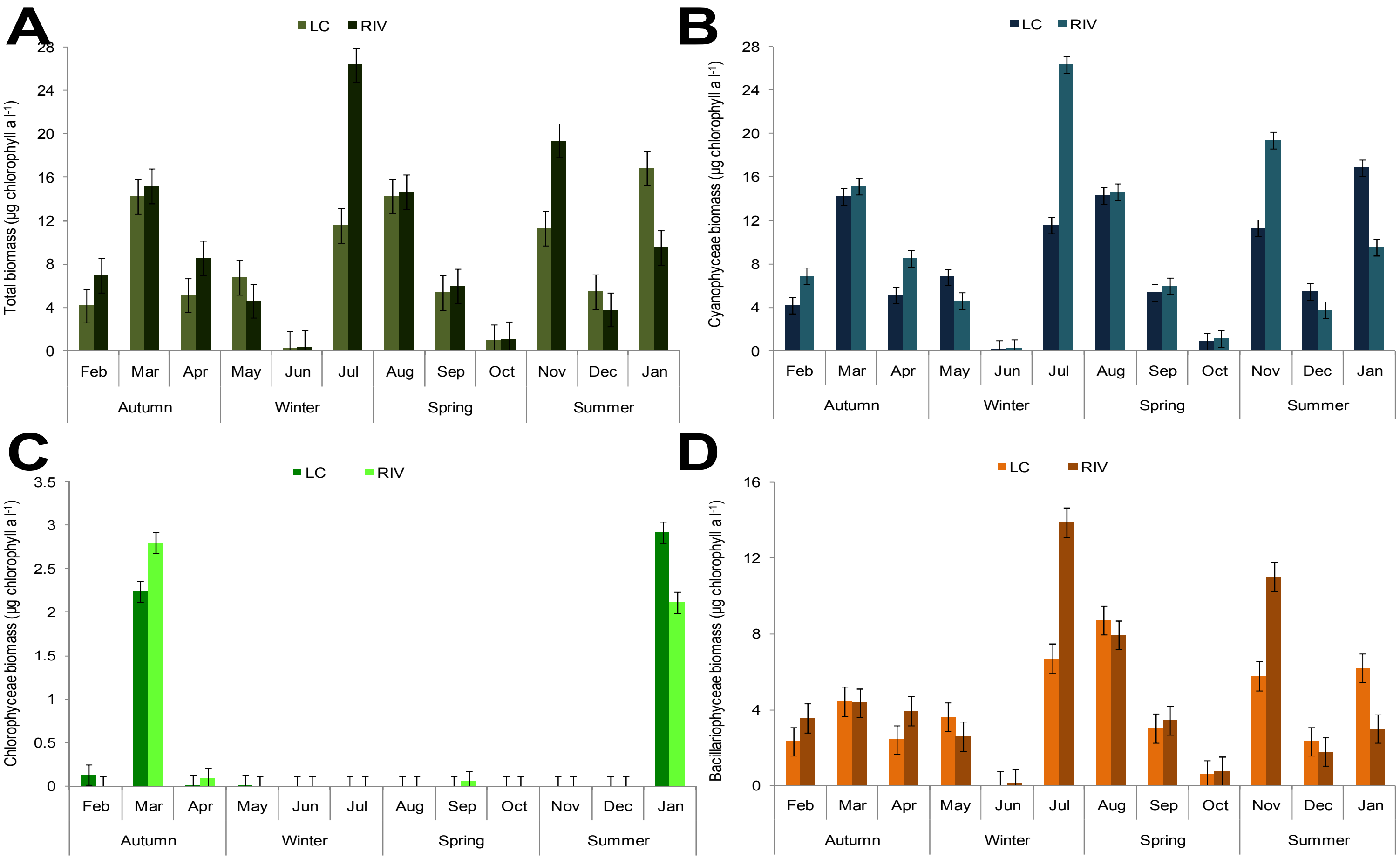

Figure 4.4. Monthly variations in A. total phytoplankton biomass and those of B. Cyanophyceae, C. Bacillariophyceae, and D. Chlorophyceae in lacustrine and riverine habitats in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars

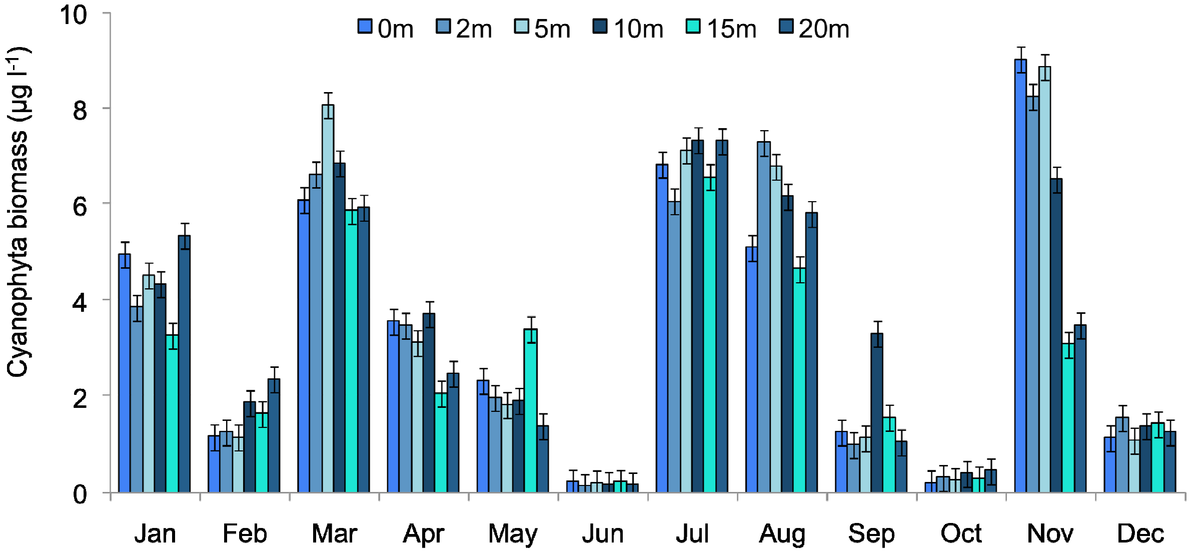

Figure 4.5. Monthly variations in Cyanophyceae biomass with water depth in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars

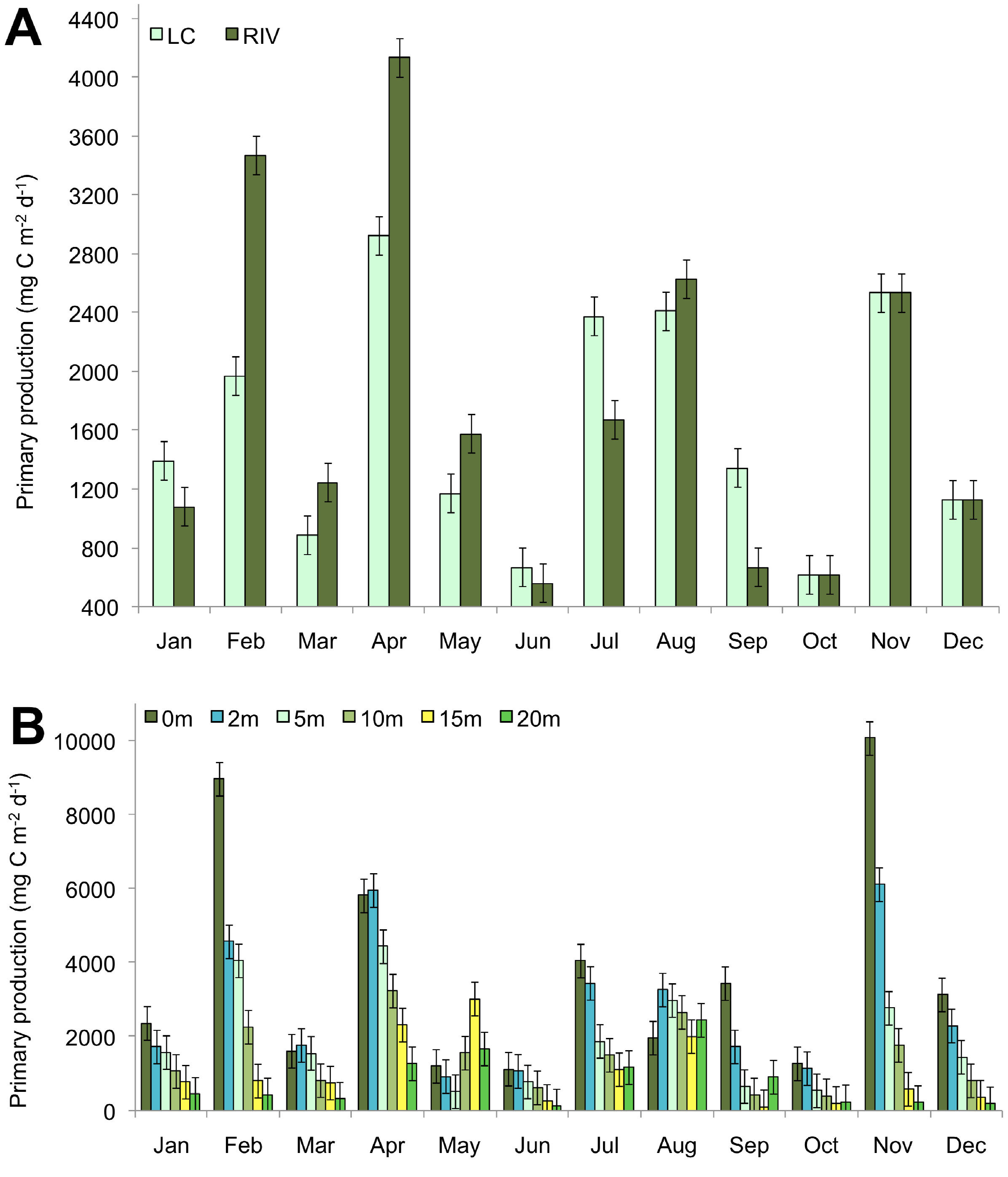

Figure 4.6. Monthly variations in primary production in A. lacustrine and riverine habitats and B. different water depths in the Sanyati Basin of Lake Kariba. Average standard error of differences shown by bars

4.4. Discussion

Cyanophyceae contributed 68.6 ± 1.9% of the total phytoplankton biomass in the lake's five basins during summer, closely corresponding with Ramberg's (1987) and Cronberg's (1997) reports that Cyanophyceae comprises between 70% and 80% of the total phytoplankton biomass in the entire lake during the summer rainy season. The highest summer-time Cyanophyceae percentage of the total phytoplankton biomass was observed in Basin 5 (84.0%), followed by Basin 1 (72.6%) and Basin 3 (72.3%). The high Cyanophyceae percentage in Basin 5 was attributed to localised pollution from discharge of partially treated sewage effluent, averaging 3.6 metric per day into the lake (Mulendema, 2000), and that in Basin 1 due to the nutrient-rich Zambezi River inflow (Marshall, 1982). In Basin 3 the high Cyanophyceae biomass is due to wind-induced wave action along its exposed shoreline, especially during the hot, dry months of August to October (Coche, 1974), causing upwelling of nutrients known to stimulate primary production (Mtada, 1987; Van Ruth, 2009). However, the reported hydrological gradient of decreased nutrient concentrations, with increasing distance from the Zambezi River inflow, (Coche, 1974; Masundire, 1997; Cronberg, 1997) was not reflected in a corresponding reduction in total phytoplankton biomass, which displayed an increase from Basins 1 to 3 and a subsequent decline from basin 4 to 5.

Chlorophyceae contributed on average only 8.1 ± 0.8% of the total phytoplankton biomass in the five lake basins during summer, which contrasted with Ramberg's (1987) and Cronberg's (1997) observations that Chlorophyceae co-dominate with Cyanophyceae during summer. Laboratory experiments have demonstrated that the optimum growth temperatures for Chlorophyceae are between 20 and 25°C (Sibanda, 2003; Senerpont-Domis *et al.*, 2007). Seventy three percent (73%) of summer water temperatures at or near the surface of Lake Kariba often exceed 25°C (Magadza, 2008; Tumbare, 2008). These high temperatures and photo-inhibition of algal photosynthesis in surface waters by the high summer light intensities (Cronberg, 1997) may also explain the lower Chlorophyceae biomasses recorded at shallower water depths in the lake in late summer (February and March). Photo inhibition of phytoplankton photosynthesis at solar irradiances exceeding 2 000 μE m^{-2} s^{-1} have been observed in the surface waters of Lake Tanganyika, this reflected in an increased fraction of light-acclimated pico phytoplankton in the phytoplankton biomass (Stenuite *et al.*, 2009). Similarly, in Lake Malawi, small-sized (<2 μm) light-acclimated phytoplankton in the lake surface water account for 30-50% of the total phytoplankton chlorophyll (Guildford *et al.*, 2007). Ninety-seven percent of the phytoplankton quantum yields measured in this study were below 0.83, which indicated that the phytoplankton were under some environmental stress (Falkowski and Raven, 1997). However, the precise cause of this stress is unclear, but does seem partly related to photo inhibition of phytoplankton photosynthesis, since Chlorophyceae biomasses and those of the Cyanophyceae were also negatively ($P \leq 0.01$) correlated with photosynthetic active radiation (PAR).

In Lake Kariba's Basin 5, there were distinct seasonal trends in phytoplankton biomass and primary production. Four distinct peaks in total phytoplankton biomass and primary production were observed in this basin. A July-August peak was observed, which concurred with an August peak normally observed in the lake after turn-over (Masundire, 1994, 1997), this resulting from the release of nutrients trapped in the hypolimnion caused by stratification break-down in June-July (Ramberg, 1987; Masundire, 1997). The November and January peaks were caused by local flooding discharging nutrient-rich water as run-off into the lake during the summer rainy season, whilst the March to April peak resulted from annual flooding of the Zambezi River (FAO, 2009) carrying large amounts of nutrient-rich sediments into the lake (Marshall, 1982). Ramberg (1987) and Cronberg (1997) also reported two well-defined maxima in phytoplankton biomass in the Sanyati Basin, the first lasting three to four months during the summer rainy season and comprising mainly Cyanophyceae (70-90%) and Dinophyceae (13%), the second lasting one to two months during the dry winter season and comprising Bacillariophyceae co-dominating with Cyanophyceae (Ramberg, 1987; Cronberg, 1997). The July-August maxima in Bacillariophyceae biomass also observed in Basin 5 during the dry winter season concurred with these previous reports (Ramberg, 1987; Cronberg, 1997).

However, substantial Bacillariophyceae biomasses were also measured in this lake basin during the summer (November-April) rainy season, a possible consequence of the phytoplankton analyzer's inability to distinguish between Dinophyceae (yellow algae) and Bacillariophyceae (brown algae) as was also found by Hart and Wragg (2009). Nevertheless, Cronberg (1997) did previously report a trend of increasing dinoflagellate species in Lake Kariba with a dominance of up to 62% in the summer season, this feature seemingly manifested in this study. The observed seasonal changes in relative abundance of different phytoplankton groups in Lake Kariba are also common in other African lakes such as Malawi, Tanganyika and Victoria, where Cyanophyceae dominate during summer stratification and Bacillariophyceae dominate during stratification break-down in winter (Cronberg, 1997; Lung'ayia *et al.*, 2001; Stenuite e*t al.*, 2009). However, slightly different seasonal patterns have been reported in other African lakes such as Lake Ogelube in Nigeria, where the phytoplankton biomass during the summer rainy season comprises mainly Chlorophyceae, followed in decreasing order of abundance by the Cyanophyceae and Bacillariophyceae - this sequence changing in the dry winter season when the relative abundance of Bacillariophyceae exceeds that of Cyanophyceae (Nweze, 2006).

The measured range in total phytoplankton biomass in Lake Kariba's Basin 5 of 0.1 to 77.7 µg chlorophyll a l^{-1} in this study exceeded that of 2 to 11 µg chlorophyll a l^{-1} measured in 1990 by Lindmark (1997), but was much lower than that of 200 to 1 300 µg chlorophyll a l^{-1} measured in 1983 by Ramberg (1987) and Cronberg (1997), indicating an approximate 95.1% decline in phytoplankton biomass since 1983. Similarly, in Lake Tanganyika it has been reported that phytoplankton biomass has declined by 70% between 1975 and 2000 (Verburg *et al*., 2003), this decline accompanied by substantial changes in phytoplankton composition. The formerly dominant Cryptophyceae and the Chrysophyceae, comprising 34% of the total phytoplankton biomass in the north basin in 1975, reduced to 3% in 2000 (Verburg *et al*., 2003), with Bacillariophyceae biomasses reduced by 44% in the winter season and by 88% in the summer season over this 25-year period (Verburg *et al*., 2003; Hardy *et al*., 2005). These changes in phytoplankton biomass in Lake Tanganyika have been attributed to warming of the upper waters during the past century that have intensified stratification and diminished mixing of shallow and nutrient-rich deeper waters, which has lead to decreased primary production and an expansion of the anoxic water mass (Descy *et al*., 2006). As a consequence, pico-phytoplankton are presently dominant in Lake Tanganyika, contributing up to 70% of the total phytoplankton biomass (Descy *et al*., 2005; Stenuite *et al*., 2009). This feature was also noted recently in Lake Kivu (Sarmento *et al*., 2008), whose waters have warmed up by an average of 0.5°C over the 55-year period from 1937 to 2002 as a consequence of elevated temperatures attributed to global warming (Halbwachs *et al*., 2002).

Measured total phytoplankton biomass and primary production rates in Lake Kariba compared favourably with those reported for other oligotrophic African lakes such as Cleveland Dam, Lakes Albert and George (Table 4.3), even though other techniques (light and dark bottle O_2 production, ^{14}C uptake) were applied in measuring primary production. In addition, Lake Malawi's average primary production of 4 600 mg C m^{-2} d^{-1} (Guildford *et al*., 2007) and Lake Tanganyika's current primary production of between 340 and 4 300 mg C m^{-2} d^{-1} (Vuorio *et al*., 2003; Stenuite *et al*., 2007) were nearly twice that measured in Lake Kariba. However, much higher primary production rates have been reported in eutrophied African lakes such as Lake Chivero, where these average 23 300 mg C m^{-2} d^{-1} (Ndebele and Magadza, 2005) and in Lake Victoria, where these average 29 100 mg C m^{-2} d^{-1} (Silsbe, 2004), with an associated phytoplankton biomass of 10^4 mg l^{-1}, the highest among natural tropical African lakes (Ochumba and Kibaara, 1989; Sarmento *et al*., 2006). It is important to note, however, that whilst reflecting the range in production across the lakes, the sampling methods used to measure primary production differed from the light and dark bottle method to the fluorescence method or the uptake of inorganic carbon using isotope tracers (^{13}C, ^{14}C), such that minor discrepancies may be expected in comparing the results. Primary production in Lake Kariba has undergone a 50% reduction from a previously reported average of 0.42 g C m^2 d^{-1} (Cronberg 1997) to the current measured average of 0.24 ± 0.01 g C m^2 d^{-1} this attributed to an upward shift in the depth of the thermocline associated with an average temperature increase of 1.9°C (see Chapter 3) and a 50% reduction in the depth of the euphotic zone from previously reported depths of 31.8 m between 1965 and 1966 (Coche 1974) and 17.9 m between 1986 and 1989 (Magadza *et al*. 1989), to the current estimated depth of 15 m, the latter derived from a plot of average primary production against dissolved oxygen in Lake Kariba, from which was estimated the compensation depth Z_c at which oxygen evolution during photosythetic carbon assimilation balanced respiratory oxygen uptake (Figure 4.7).

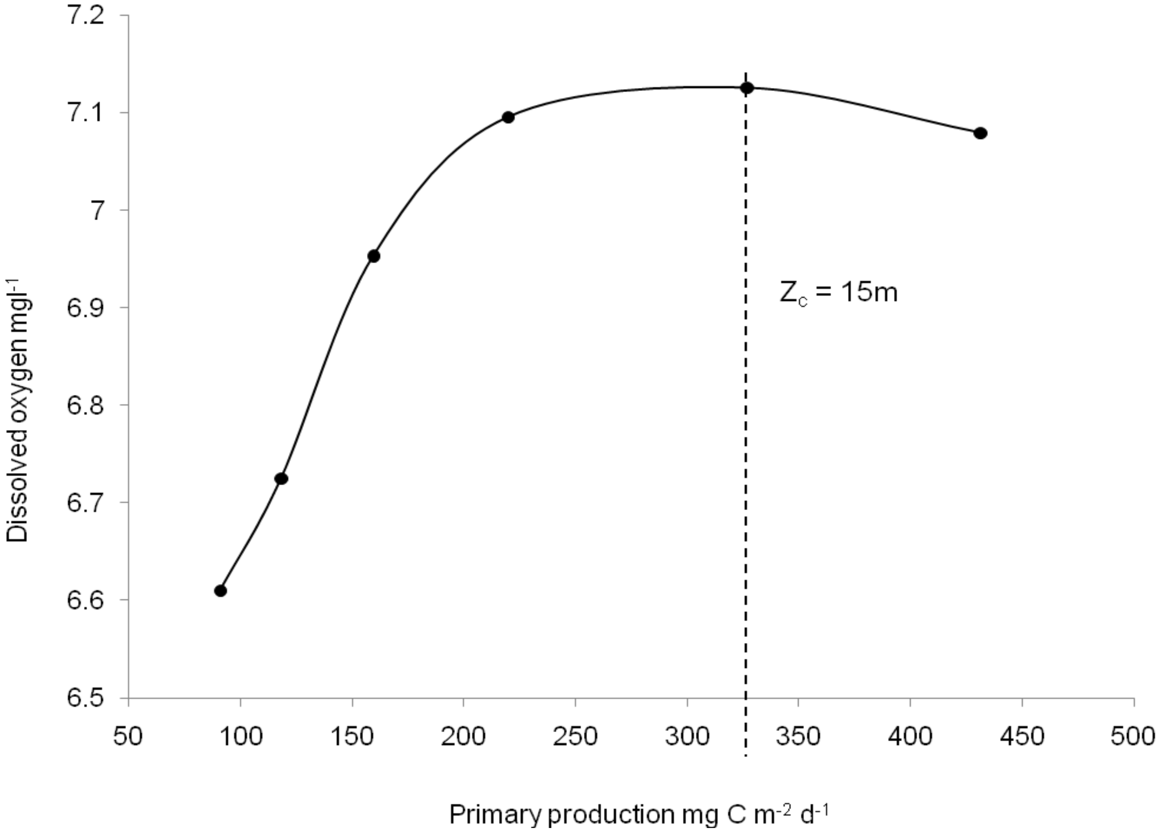

Figure 4.7. A plot of primary production against dissolved oxygen in Lake Kariba's Sanyati Basin. Z_c is the compensation depth at which oxygen evolution during photosynthetic carbon assimilation balances respiratory oxygen uptake

Diminished phytoplankton production rates have also been reported in Lakes Kivu and Tanganyika, these attributed to upward shifts in the thermocline associated with warming of the waters, slower mixing rates, and a reduction in the volume of mixed layer (O'Reilly *et al*., 2003; Verburg *et al*., 2003; Descy *et al*., 2006; Stenuite *et al*., 2007; Verburg and Hecky, 2009).

Table 4.3. Comparison of average biomass (chlorophyll a) and primary production levels in some major African lakes

Lake	Country	Year	Chlorophyll a ($\mu g\ l^{-1}$)	Primary production (mg C $m^{-2}\ d^{-1}$)	Source
Kivu	DRC/Rwanda	2003- 2005	2.2	620	Sarmento *et al*., 2009
Cleveland	Zimbabwe	2005- 2006	8.2	120	Ndebele, 2009
George	Uganda	1967- 1968	10.0	134	Ganf, 1975
Kariba	Zambia/Zimbabwe	2007-2009	10.6	233	Present study
Tanganyika	Tanganyika	2002-2003	6.7	434	Stenuite *et al*., 2007
Malawi	Malawi	1997- 2000	4.0	463	Guildford *et al*., 2007
Baringo	Kenya	2003	55.0	480	Schager and Oduor, 2003
Nakuru	Kenya	2000-2003	16.0	1 960	Ballot *et al*., 2004
Naivasha	Kenya	2000	130.0	2 000	Hubble and Harper, 2002
Chivero	Zimbabwe	2002- 2003	43.0	2 330	Ndebele and Magadza, 2005
Victoria	Kenya/Uganda	2001-2002	72.0	2 906	Silsbe, 2004

Similarly, in Lake Malawi decreased primary production rates have been attributed to increasing temperatures, causing a warmer lake and consequently a shallower, more stable thermocline, and restricted nutrient fluxes from the hypolimnion to the surface mixed layer (Vollmer *et al*., 2002, 2005; Guildford *et al*., 2007). These findings are corroborated by geochemical records obtained from sediment cores of changes in Lake Malawi over the last 730 years, caused by natural climatic forcing and anthropogenic activities. These seemingly cosmopolitan declines in primary production in oligotrophic African lakes with climate warming have potentially deleterious consequences for the fish stocks and human livelihoods.

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Chapter 5

Phytoplankton species richness and abundance in Lake Kariba's Sanyati Basin

Abstract

This study examined spatial, temporal and depth variations in phytoplankton species richness and abundance in Lake Kariba, compared these with those in other tropical African lakes, and established whether any changes determined in phytoplankton composition might be linked to climate warming. Phytoplankton species richness and concentrations were enumerated microscopically in water samples, collected at 2-monthly intervals over a 24-month period at six different depths from five stations located in lacustrine and riverine habitats in Lake Kariba's Sanyati Basin. Cyanophyceae comprising 18 species exhibited the highest relative cellular concentration (78.05%), followed by Chlorophyceae with 40 species (9.7%), Dinophyceae with four species (7.2%), Bacillariophyceae with 10 species (1.7%), Euglenophyceae with three species (1.6%), Chrysophyceae (1.3%) and Xanthophyceae (0.45) with one species each. The relative concentration of Cyanophyceae dominated by *Cylindrospermopsis raciborskii* has increased from a previously reported 50-65% to the current 78%. This was accompanied by a shift in Cyanophyceae maximum as previously reported summer stratification peak to the present winter turnover peak. Also, relative concentrations of Bacillariophyceae and Dinophyceae have declined from previously reported 18% and 13% to the present 1.7% and 7.2% respectively. These reduced concentrations are associated with changes in species dominance, the previously reported dominant Bacillariophyceae species *Aulacoseira granulata* replaced by *Cymbella affinis,* and the previously reported dominant Dinophyceae species *Peridioniopsis* sp. replaced by *Peridinium gatunense* in present populations. In addition, the previously reported common Bacillariophyceae genera, such as *Fragilaria* and *Synedra,* were absent in the present populations. In addition, the previously reported high Chlorophyceae species richness, especially among small-celled chlorococcales, was also observed in present populations. However, there was a notable increase in the total numbers of Chlorophyceae species, from the previously reported 30 species to the 40 species in present populations. In contrast, the previously reported 41 Cyanophyceae species and eight Euglenophyceae species have declined to 18 and three respectively in present populations. Noteworthy also was the absence in current populations of certain orders, such as the Tetrasporales in the Chlorophyceae, the Desmidiales in the Desmidiaceae, as well as members of the Cryptophyceae, Haptophyceae and Raphidophyceae previously recorded in the lake. These shifts in phytoplankton concentrations and species composition to less palatable Cyanophyceae that are competitively superior at higher temperatures, were attributed to decreased

nutrient availability particularly that of nitrogen associated with shallower more stable thermoclines, due to elevated water temperatures with climate warming. The increase in Cyanophyceae with decreased nitrogen levels was expected but not that with decreased phosphorus concentrations.

5.1. Introduction

Most African lakes have a well-established seasonality in phytoplankton abundance, governed mainly by climate and the stratification cycle (Talling, 1966; Schargel and Oduor, 2001; Ndebele-Murisa *et al*., 2010). The most significant phytoplankton classes are Cyanophyceae, Chlorophyceae, Bacillariophyceae and Dinophyceae, with other classes, such as Euglenophyceae and Xanthophyceae, less abundant and least frequent. The general annual cycle of thermal stratification in African lakes includes a short phase of partial vertical mixing, which is often accompanied, or immediately followed, by a peak of phytoplankton abundance to which Bacillariophyceae make a major contribution (Chale, 2004). A second peak dominated by Cyanophyceae and co-dominated by Chlorophyceae often develops after stratification (Chale, 2004). Although the dominant species may differ, this seasonal pattern is prevalent in lakes such as Kariba, Kivu, Malawi, Tanganyika and Victoria, where Cyanophyceae dominate during summer stratification and Bacillariophyceae during winter at turn-over (Hecky and Kling, 1987; Bootsma, 1993; Patterson and Katchinjika, 1995; Cronberg, 1997; Cocquyt and Vyverman, 2005; Sarmento *et al*., 2008). However, in some cases such as in Lake Ogelube (Nigeria), a slightly different seasonality occurs, where Chlorophyceae (mostly desmids) are most abundant during the rainy season, followed in decreasing order of abundance by Cyanophyceae, Bacillariophyceae, Euglenophyceae, Dinophyceae, Cryptophyceae, Chrysophyceae and Xanthophyceae (Nweze, 2006). This order changes in the dry season, when the relative abundance of Bacillariophyceae is greater than that of Cyanophyceae, and Dinophyceae greater than that of Euglenophyceae (Nweze, 2006).

Inter-annual variations in phytoplankton composition and biomass in temperate regions are known to reflect changes in climate (Lehman *et al*., 1998). On the other hand, relatively few data exist on the influence of climate variability on phytoplankton composition and seasonality in tropical African lakes. Despite the research gap, African lakes are known to be potentially highly sensitive to climate change (Johnson and Odada, 1996), as small variations in climate cause wide fluctuations in the thermocline over a narrow range of high water temperature (O’Reilly *et al*. 2003; Moss, 2007; Stenuite *et al*., 2007). Reduced depths of light-transparent epilimnia, due to shallower thermoclines in response to elevated temperatures, can potentially adversely affect phytoplankton in deep, tropical African lakes. Indeed, thermal stratification, which isolates nutrients from the euphotic zone, is strongly linked to hydrodynamic and climatic conditions in Lake Tanganyika (Plisnier *et al*., 1999), whilst fisheries data from this lake show significant correlations with climatic (ENSO) data over the last 40 years (Stenuite *et al*., 2007). In addition, it is known that as water temperatures increase, phytoplankton succession follows a progression from Bacillariophyceae through to Chlorophyceae to Cyanophyceae (Pliński and Jóźwiak, 1999). The preponderance of Cyanophyceae at higher water temperatures (> 25ºC) has led to concerns that increased water temperatures due to global warming could result in a decline in the production of palatable Chlorophyceae, leading to decreased zooplankton production and a consequent decline in fish stocks (IPCC, 2007). This suggests that moderate warming could destabilise plankton seasonality and biomass, thereby potentially reducing water quality and food resources for higher trophic levels such as planktivorous fish, as seen in shallow cold-water ecosystems (Strecker *et al*., 2004).

Lake Kariba contains a diverse phytoplankton species assemblage, which has been monitored since 1959. Studies have shown that the existing phytoplankton community, comprising some 155 species, has progressed from a riverine-dominated species complement rich in Chlorophyceae (desmids) and large phytoplankton species normally associated with enriched waters, to a lacustrine-adapted species complement comprising small-celled chlorococcal Chlorophyceae, with Cyanophyceae dominating in summer and Bacillariophyceae co-dominating with Cyanophyceae during the winter turn-over (Thomasson, 1965, Mitchell, 1969; Bowmaker, 1973; Hancock, 1979; Thomasson, 1980; Ramberg, 1984, 1987; Cronberg, 1997). However, it is unclear whether any changes in phytoplankton species composition, abundance and seasonality have taken place in Lake Kariba since the last long-term study conducted by Cronberg (1997) in the Sanyati Basin between 1986 and 1990 (Mhlanga, 2001a, b). Consequently, this study examined current spatial, temporal and depth variations in phytoplankton species richness and abundance in Lake Kariba's Sanyati Basin, compared these with those in other tropical African lakes, and ascertained whether measured changes in phytoplankton composition might be linked to climate warming.

5.2. Methods and materials

5.2.1. Study area

The study site comprised the Sanyati Basin (B5), where most long-term phytoplankton studies have previously been conducted (Ramberg, 1984, 1987; Cronberg, 1997). The basin is located at the north-eastern end of Lake Kariba, a 5 364 km^2, 97 m (maximum) deep artificial reservoir created on the Zambezi River between 1955 and 1960 that borders Zambia and Zimbabwe. The history of the lake is detailed in World Commission on Dams (2000).

5.2.2. Experimental design and sampling stations

Phytoplankton measurements were conducted at 2-monthly intervals over a 24-month period, extending from March 2007 through to February 2009 at five sampling stations in Basin 5, where the majority of previous long-term phytoplankton studies have been conducted (Ramberg, 1984, 1987; Cronberg, 1997). Three of these sampling stations were located at the margins of the lake basin in close proximity to the Charara, Gache-gache and Sanyati River inflows and designated riverine habitats. The other two sampling stations traversed the centre of the basin and were designated lacustrine habitats. Figure 5.1 shows the sampling stations in the Sanyati Basin of the lake.

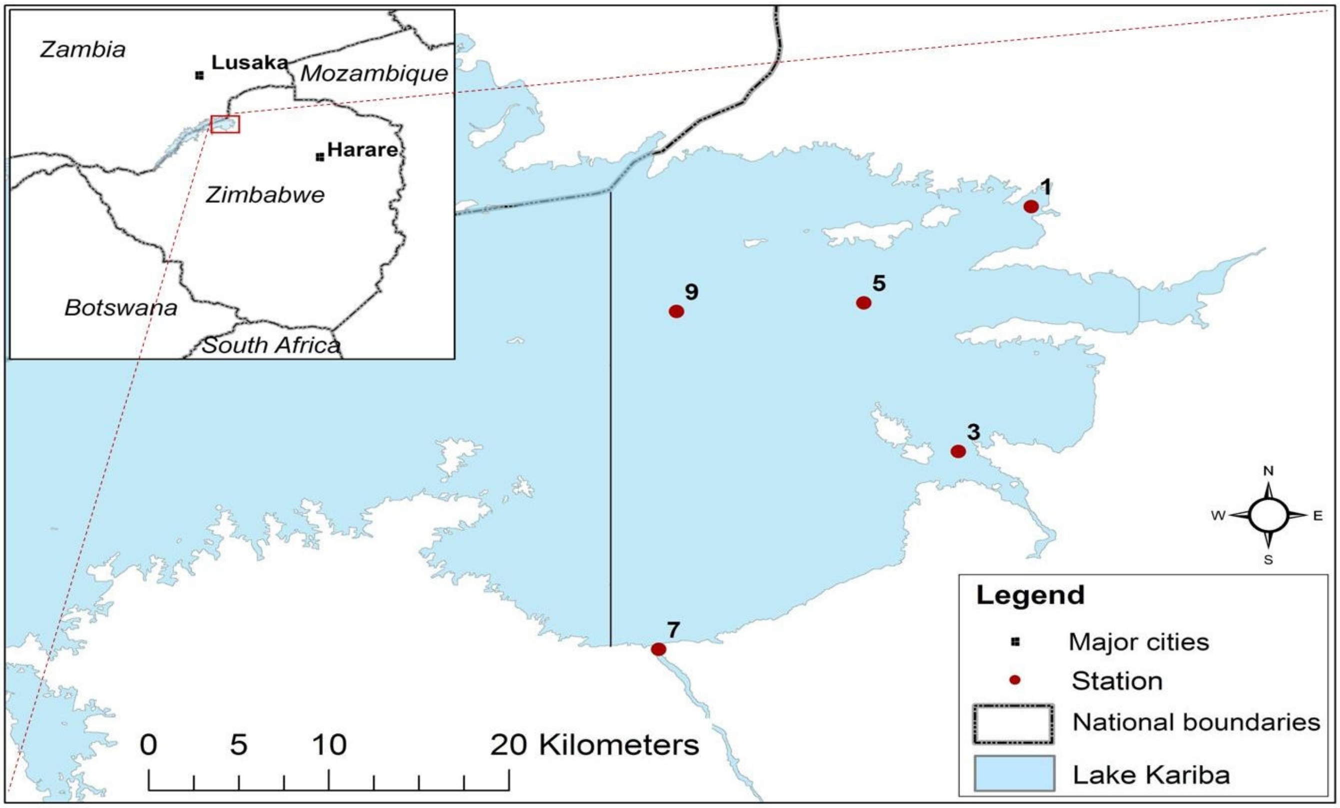

Figure 5.1. Distribution of 5 sampling stations in Lake Kariba's Sanyati Basin, with those located in the centre of the lake designated lacustrine and those located along the lake margin in proximity to river inflows designated riverine

5.2.3. Phytoplankton species richness and cellular concentrations

Two 20-litre water samples were collected from the six different depth zones (0, 2, 5, 10, 15 and 20 m) at each sampling station with a Ruttner flask, at 2-monthly intervals spanning a 24-month period from March 2007 to February 2009. Based on preliminary sampling and past studies, the thermocline depth below which there is negligible primary production rarely exceeded 20 m and this formed the rationale for the maximum depth sampled. The water samples were filtered through a 22 μm mesh to form a concentrate of phytoplankton from the 20 litres of water and this sub-sample was preserved with Lugol's solution. Phytoplankton species in the filtered water samples were identified under an inverted light microscope, using descriptions provided by Prescott (1964), Cronberg (1997) and John *et al.* (2002), and enumerated in counting chambers as described by Utermöhl (1958). Identification of some Bacillariophyceae and Dinophyceae when possible was done to species level with the assistance of a Scanning Electronic Microscope (SEM), which provides three-dimensional images of cellular surface structures (Montagnes and Taylor, 1994). Phytoplankton species richness was expressed as the total number of species per litre of water sample, and concentrations as the numbers of individuals of each species per litre of water sample.

5.2.4. Statistical analysis

The experimental design was not fully balanced, due to unequal numbers of measurements. Consequently, within each of the seven phytoplankton classes (Bacillariophyceae, Chlorophyceae, Chrysophyceae, Cyanophyceae, Dinophyceae, Euglenophyceae and Xanthophyceae), a REML (residual maximum likelihood) variance component analysis (repeated measures mixed model) tested for significant differences in species richness and cellular concentration between months, riverine and lacustrine habitats, water depth and their interactions, using the Wald X^2 statistic generated by REML (GENSTAT Discovery Edition 3, VSL Lty, UK). Habitat and water depth were fitted in the fixed model and months in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This is based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is equal to two. Relative concentrations of each species were calculated as a percentage of the total number of species counted.

5.3. Results

5.3.1. Species richness in different phytoplankton classes

The total of 77 phytoplankton species were recorded in the Sanyati Basin, which comprised 40 species of Chlorophyceae, 18 species of Cyanophyceae, 10 species of Bacillariophyceae, four species of Dinophyceae, three species of Euglenophyceae, one species of Xanthophyceae, and one species of Chrysophyceae. Species names and authorities are tabulated in Appendices 5.1 to 5.3. Scanning electron microscopic images of cellular surface structures of some Bacillariophyceae, Chlorophyceae, and Dinophyceae species used in their identifications, are presented in Appendices 5.4 to 5.6.

Significant ($P \leq 0.001$) monthly differences in species richness were observed in all seven phytoplankton classes (Table 5.1). Cyanophyceae and Bacillariophyceae displayed significant ($P \leq 0.05$) dips in species richness in June and July, with Bacillariophyceae exhibiting a significant ($P \leq 0.05$) drop in species richness in June and in November as well (Figures 5.2A & B). In contrast, Chlorophyceae, Euglenophyceae and Chrysophyceae displayed significant ($P \leq 0.05$) peaks in species richness in June and July, with Xanthophyceae also exhibiting a significant ($P \leq 0.05$) peak in species richness in July (Figures 5.2A & C). Chlorophyceae displayed a secondary significant ($P \leq 0.05$) peak in species richness in September (Figure 5.2A), with Dinophyceae exhibiting a significant ($P \leq 0.05$) peak in species richness in September and in October (Figure 5.2B). Phytoplankton species richness differed significantly ($P \leq 0.05$) between riverine and lacustrine waters in the Bacillariophyceae and Euglenophyceae, with both of these phytoplankton classes displaying higher species richness in riverine than lacustrine waters. However, there were significant ($P \leq 0.001$) interactions between month and habitat for Euglenophyceae, Chrysophyceae and Cyanophyceae species richness (Table 5.1). Chrysophyceae and Euglenophyceae species diversities were significantly ($P \leq 0.05$) higher in lacustrine than riverine waters in June and July only, with Cyanophyceae species richness significantly ($P \leq 0.05$) higher in lacustrine than riverine waters in January and November only, with the converse apparent in February, April, and December. In addition, there was a significant ($P \leq 0.01$) interaction between month and water depth for Bacillariophyceae species richness (Table 5.1), which peaked at 2 m water depth in February, May, August and December, at 5 m water depth in June, at 10 m water depth in March, and at 15 m water depth in October (Figure 5.6A).

5.3.2. Cellular concentrations and species composition of different phytoplankton classes

Overall, the Cyanophyceae had the highest cellular concentrations, followed by the Chlorophyceae, Dinophyceae, Euglenophyceae, Chrysophyceae, Bacillariophyceae and Xanthophyceae (Figures 5.3A, 5.4A, 5.5A). The 20 most common phytoplankton species with relative abundances above 0.45% collectively comprised 91.9% of the total phytoplankton population, whilst the top five Cyanophyceae species made up more than 75% (76.1%) of the total phytoplankton concentrations (Table 5.2).

In all seven phytoplankton classes, cellular concentrations differed significantly ($P \leq 0.001$) monthly (Table 5.3). Cyanophyceae displayed significant ($P \leq 0.05$) peaks in cellular concentration during winter in June and August (Figure 5.3A), these due mainly to increased cellular concentrations of the dominant species *Cylindrospermopsis raciborskii* (Figure 5.3B), which comprised 66.2% of the total phytoplankton population (Table 5.2). Chlorophyceae exhibited a significant ($P \leq 0.05$) peak in cellular concentration during early autumn in March (Figure 5.3A), due mainly to increased cellular concentrations of *Cosmarium botrytis* (Figure 5.3C), and also a second significant (P ≤ 0.05) peak in cellular concentration during early winter in June, due to increased cellular concentrations of both *C. botrytis* and *Mougetia capucina* (Figure 5.3C). Also, Dinophyceae displayed a significant (P ≤ 0.05) peak in cellular concentration during early winter in June (Figure 5.4A), due predominantly to massively increased cellular concentrations of *Peridinium gatunense,* with relatively smaller increases in cellular concentrations also apparent in *Ceratium hirundinella* and *Ceratium furcoides* (Figure 5.4B). Similarly, Euglenophyceae and Chrysophyceae both displayed significant (P ≤ 0.05) peaks in cellular concentration during early winter in June (Figure 5.5A), those of the Euglenophyceae due predominantly to considerably increased cellular concentrations of *Euglena acus* (Figure 5.5B), and those of the Chrysophyceae due entirely to increased cellular concentrations of *Dinobryon sertularia* (Figure 5.5D). Bacillariophyceae exhibited a significant (P ≤ 0.05) peak in cellular concentration during late autumn in May (Figure 5.4A), due mainly to substantially increased cellular concentrations of *Cymbella affinis* (Figure 5.4B). Xanthophyceae exhibited significant (P ≤ 0.05) peaks in cellular concentration during midwinter in July and also during summer in December (Figure 5.5A), these due entirely to increased cellular concentrations of *Tribonema* sp. (Figure 5.5C).

There were significant (P ≤ 0.05) interactions between month and habitat for Cyanophyceae, Dinophyceae and Euglenophyceae cellular concentrations (Table 5.3), those of Cyanophyceae significantly (P ≤ 0.05) higher in riverine and lacustrine waters in June, July and August, and those of Euglenophyceae significantly (P ≤ 0.05) higher in riverine and lacustrine waters in June only. In addition, there were significant (P ≤ 0.001) interactions between month and water depth for Bacillariophyceae and Cyanophyceae cellular concentrations (Table 5.3). Bacillariophyceae cellular concentrations peaked at 2 m water depth in May, August, October and December, at 5 m water depth in February, June and September, at 10 m water depth in March, and at 15 m water depth in November (Figure 5.6B). Cyanophyceae cellular concentrations peaked at 2 m water depth in July and August, at 5 m water depth in December and January, at 10 m water depth in March and May, at 15 m water depth in June, and at 20 m water depth in October and November (Figure 5.6C).

Table 5.1. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth and their interactions on phytoplankton species richness in different taxonomic classes in Lake Kariba's Sanyati Basin. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001

		Wald χ^2statistic						
REML	df	Bacillariophyceae	Chlorophyceae	Chrysophyceae	Cyanophyceae	Dinophyceae	Euglenophyceae	Xanthophyceae
Main Effects								
Month	11	**98.34*** **	**47.75*** **	**183.24*** **	**132.51*** **	**46.21*** **	**74.60*** **	**120.03*** **
Habitat	1	**5.90* **	0.02	0.00	0.64	2.87	**4.23* **	0.00
Depth	5	7.60	5.71	0.00	7.31	10.28	2.60	0.08
2-way interactions								
Month x Habitat	11	8.71	17.09	**40.41*** **	**35.58*** **	13.65	**23.22* **	11.04
Month x Depth	55	**84.27** **	43.55	66.75	53.95	38.28	35.74	61.24
Habitat x Depth	5	1.86	5.77	0.01	6.92	9.26	2.58	0.03
3-way interactions								
Month x Habitat x Depth	53	58.63	43.44	35.44	44.70	40.86	28.39	57.19

Table 5.2. Relative concentrations in decreasing order of the 20 most common phytoplankton species

Species	**Class/Order**	**Relative concentration (%)**
1. *Cylindrospermopsis raciborskii*	Cyanophyceae/ Nostocales	66.20
2. Microcystis aeruginosa	Cyanophyceae/ Chroococcales	2.79
3. *Peridinium gatunense*	Dinophyceae/ Peridiniales	2.65
4. *Anabaena flos aquae*	Cyanophyceae/ Nostocales	2.50
5. *Microcystis flos aquae*	Cyanophyceae/ Chroococcales	2.38
6. *Anabaena circunalis*	Cyanophyceae/ Nostocales	2.29
7. *Ceratium furcoides*	Dinophyceae/ Gonyaulacales	1.88
8. *Euglena acus*	Euglenophyceae/ Euglenales	1.74
9. *Dinobryon sertularia*	Chrysophyceae/ Chromunales	1.64
10. *Ceratium hirundinella*	Dinophyceae/ Gonyaulacales	1.63
11. *Peridioniopsis* sp.	Dinophyceae/ Peridiniales	1.26
12. *Staurastrum johnsonii*	Chlorophyceae/ Zygnematales	0.67
13. *Coelastranum microponum*	Chlorophyceae/ Chlorocoocales	0.61
14. *Oedogonium* sp.	Chlorophyceae/ Oedogoniales	0.60
15. *Aulacoseira granulata*	Bacillariophyceae/ Alacoiseirales	0.57
16. *Cosmarium botrytis*	Chlorophyceae/ Zygnematales	0.55
17. *Anabaena catenula*	Cyanophyceae/ Nostocales	0.51
18. *Trachelomonas caudatum*	Euglenophyceae/ Euglenales	0.48
19. *Mougetia capucina*	Chlorophyceae/ Zygnematales	0.48
20. *Chlorella vulgaris*	Chlorophyceae/ Volvocales	0.46
Total		**91.89**

Table 5.3. Wald χ² statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth and their interactions on phytoplankton cellular concentrations in different taxonomic classes in Lake Kariba's Sanyati Basin. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001

		Wald χ^2statistic						
REML	df	Bacillariophyceae	Chlorophyceae	Chrysophyceae	Cyanophyceae	Dinophyceae	Euglenophyceae	Xanthophyceae
Main effects								
Month	11	**46.13*****	**64.13*****	**33.54*****	**56.89*****	**64.25*****	**147.57*****	**39.68*****
Habitat	1	0.01	0.73	0.31	**15.09*****	0.06	0.49	1.03
Depth	5	**17.69****	**17.09***	4.14	**34.63*****	4.11	**97.33*****	0.95
2-way interactions								
Month x Habitat	11	18.33	11.64	11.37	**19.36***	**21.05***	**824.84***	11.65
Month x Depth	55	**179.40*****	50.52	35.72	**109.51*****	51.00	4.24	60.98
Habitat x Depth	5	6.60	6.88	2.79	5.38	6.14	**833.44*****	7.98
3- way interactions								
Month x Habitat x Depth	53	**80.00****	43.63	37.33	49.55	26.35	34.68	58.69

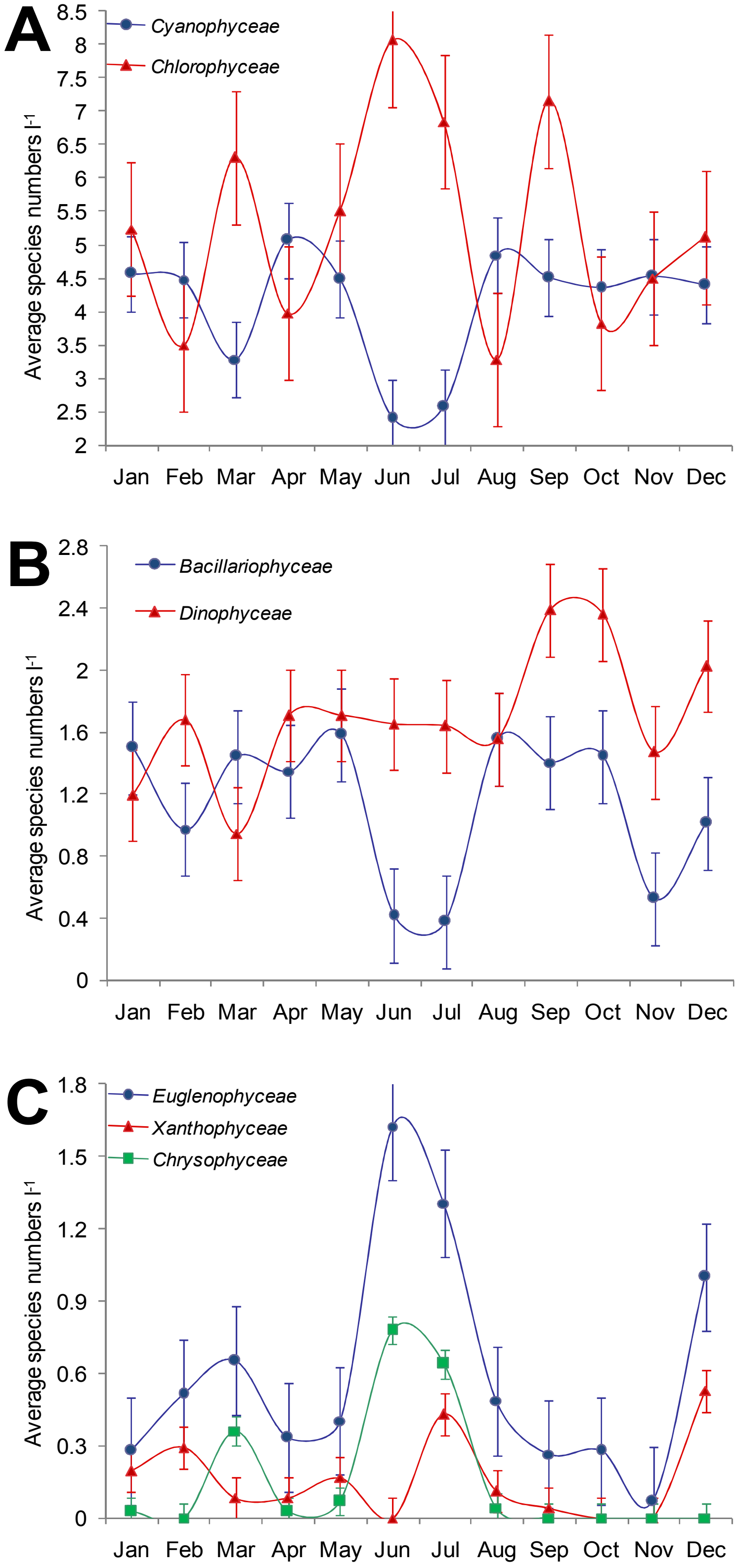

Figure 5.2. Monthly variation in species richness of A. Cyanophyceae and Chlorophyceae, B. Bacillariophyceae and Dinophyceae and C. Euglenophyceae, Xanthophyceae and Chrysophyceae. Standard error of differences shown by bars

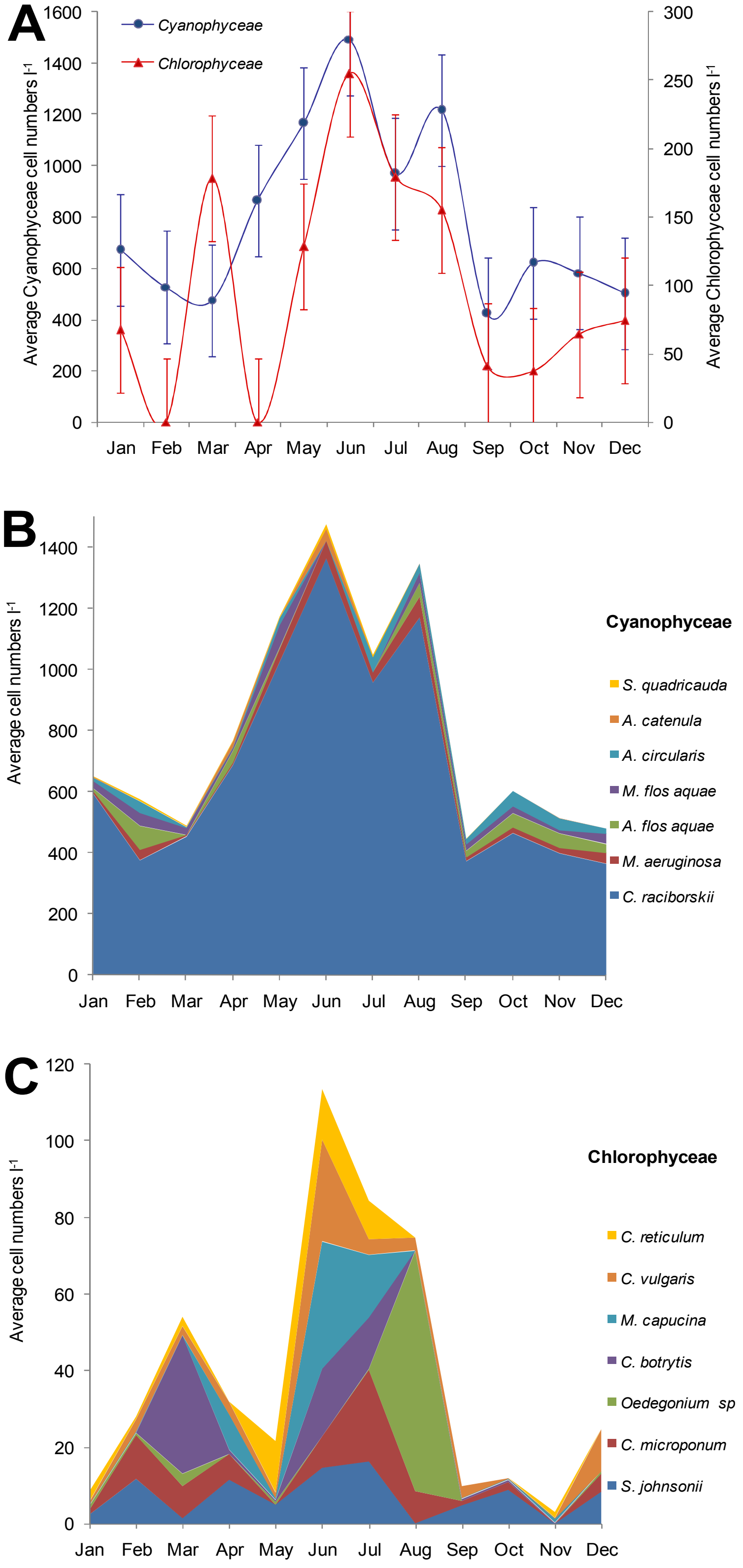

Figure 5.3. Monthly variation in cellular concentrations of A. Cyanophyceae and Chlorophyceae, and cellular concentrations of most common species of B. Cyanophyceae and C. Chlorophyceae. Standard error of differences shown by bars

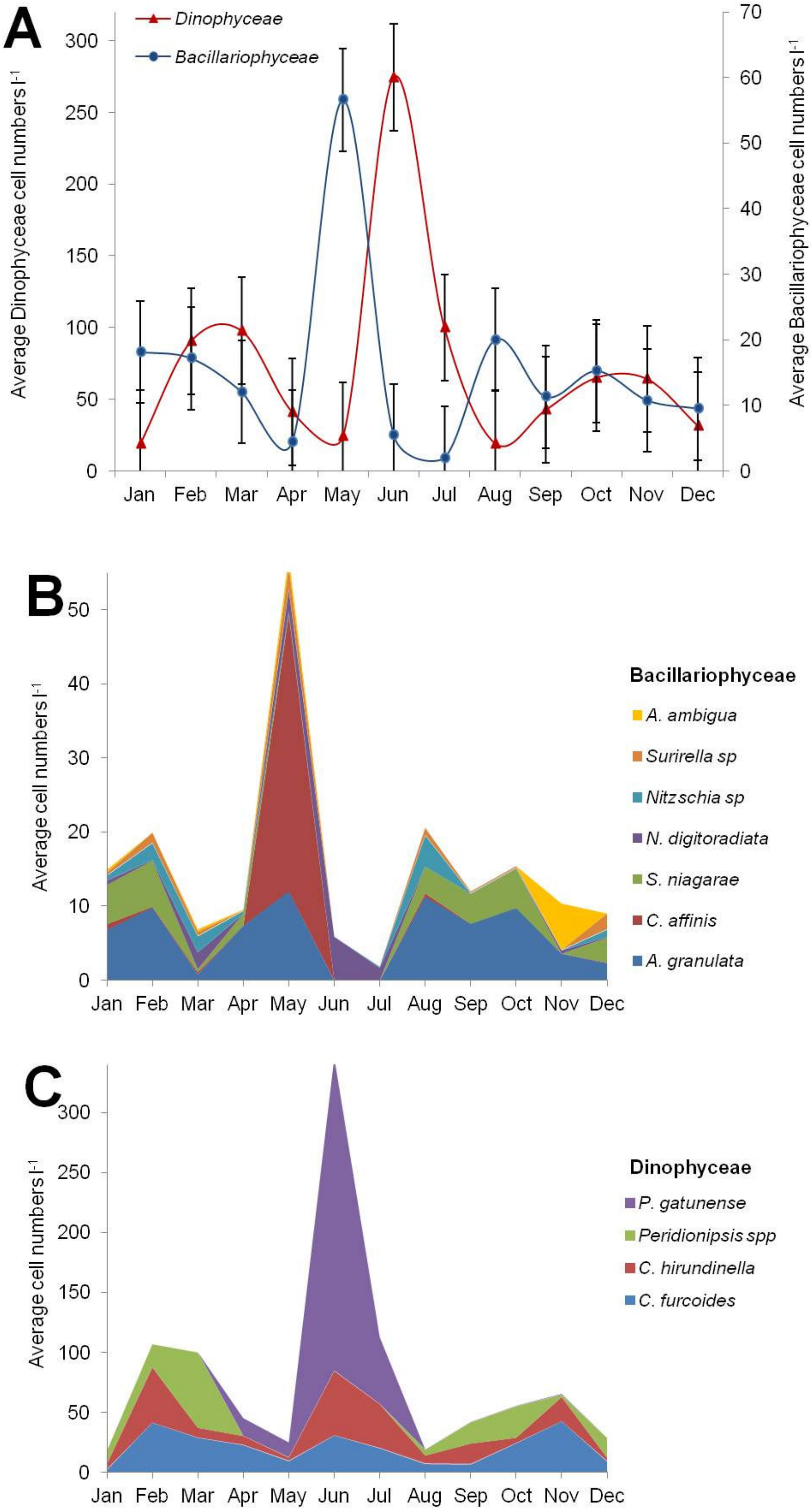

Figure 5.4. Monthly variation in cellular concentrations of A. Dinophyceae and Bacillariophyceae, and cellular concentrations of most common species of B. Dinophyceae and C. Bacillariophyceae. Standard error of differences shown by bars

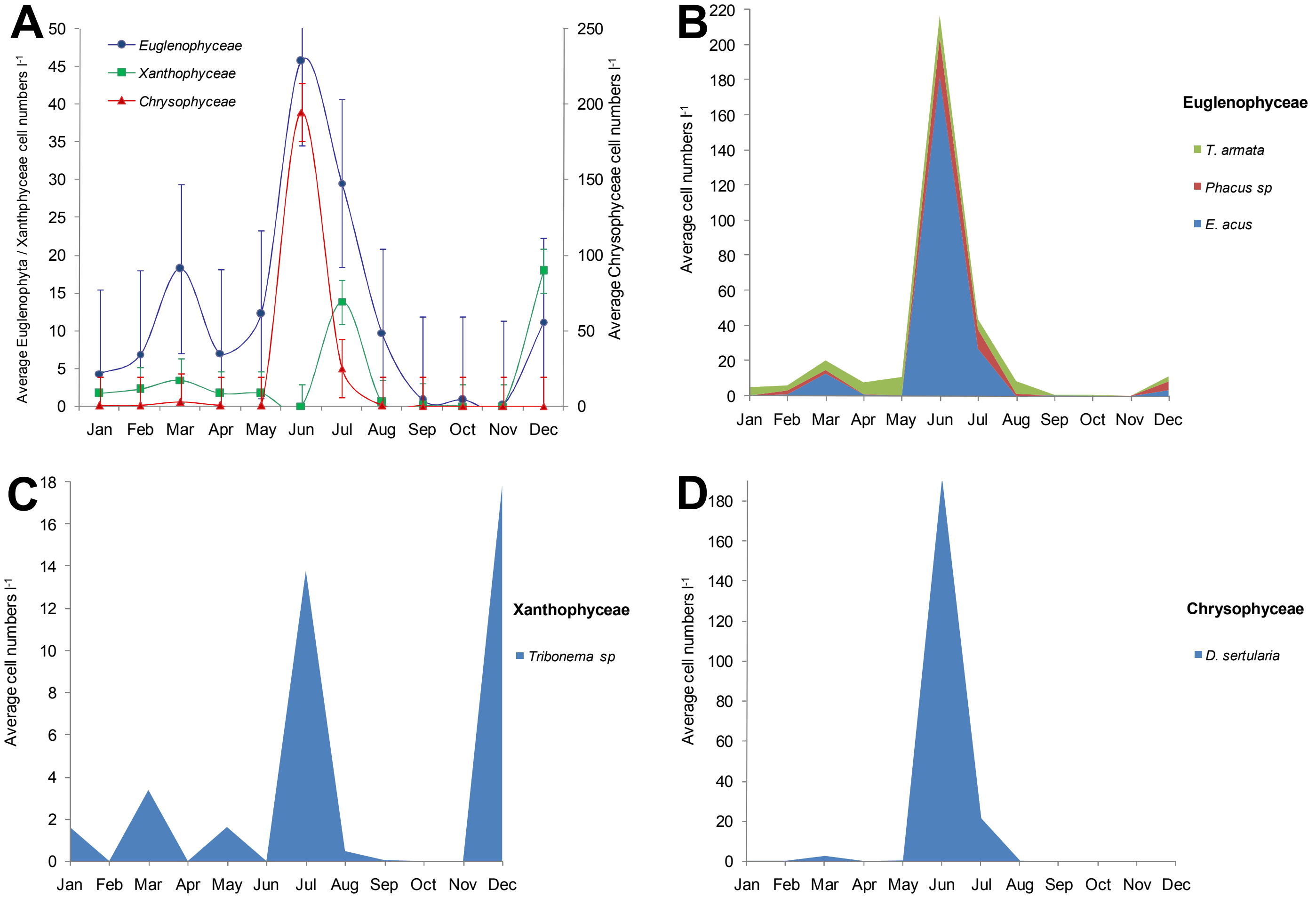

Figure 5.5. Monthly variation in cellular concentrations of A. Euglenophyceae, Xanthophyceae and Chrysophyceae, and cellular concentrations of most common species of B. Euglenophyceae, C. Xanthophyceae and D. Chrysophyceae. Standard error of differences shown by bars

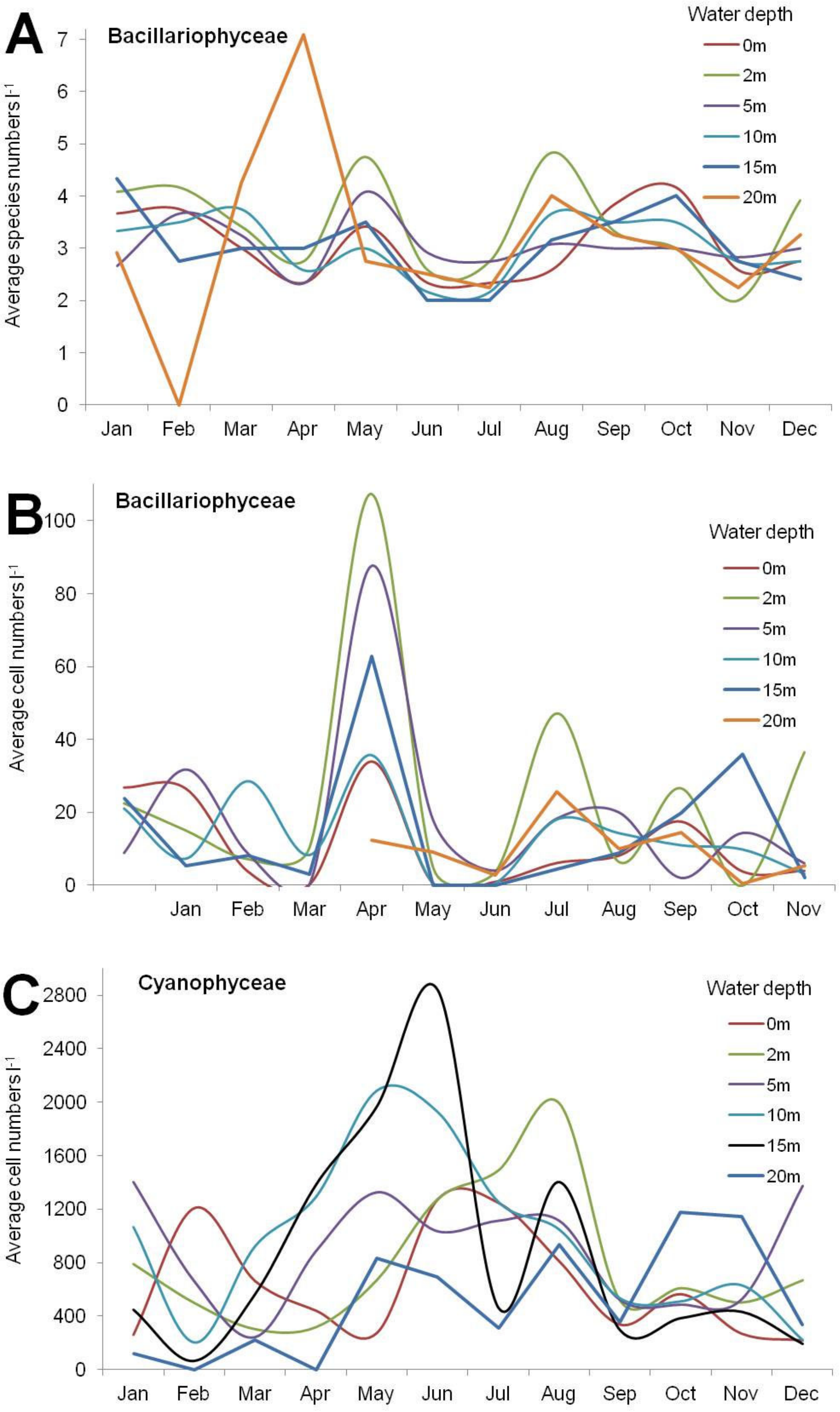

Figure 5.6. Monthly changes in species richness and cellular concentrations of Bacillariophyceae (A and B) and Cyanophyceae (C) at different water depths

5.4. Discussion

The dominance of Cyanophyceae in Lake Kariba is consistent with earlier studies (Thomasson, 1980; Ramberg, 1984, 1987; Cronberg, 1997), and a common feature in several other deep tropical African lakes such as Lakes Kivu, Malawi, Tanganyika and Victoria (Talling and Lemoalle, 1998; Chale, 2004). This Cyanophyceae dominance relative to other algal classes is likely due to the nitrogen-fixing capability of many Cyanophyceae species, which provides them with a competitive advantage over other phytoplankton taxa, particularly in systems where N has been shown to be limiting for phytoplankton growth such as in Lakes Kariba, Malawi, Naivasha and Tanganyika (Hubble and Harper, 2002; Chale, 2004; Moyo, 1991; Guildford *et al.,* 2003*;* Ndebele, 2007; De Wever *et al*., 2008). In Lake Kariba, the presence of heterocysts and specialised nitrogen-fixing akinetes occur on the dominant Cyanophyceae *C. raciborskii*, (John *et al*., 2002), whose concentrations also correlate highly with temporal variations in biological nitrogen fixation (Moyo, 1997). In fact, the Cyanophyceae species complement in Lake Kariba resembles that in Lake Victoria, where the low total nitrogen to total phosphorus molar ratio (Gikuma-Njuru and Hecky, 2004) is indicative of N-limitation that favours heterocystous N-fixing Cyanophyceae (Mugidde, 2001; Mugidde *et al*., 2003).

Noteworthy was the substantial increase in the relative concentration of Cyanophyceae in Lake Kariba, from the previously reported 50-65% (Ramberg, 1987; Cronberg, 1997) to the current 78%. This increase was accompanied also by a shift in Cyanophyceae concentrations, from a previously reported summer stratification peak to a winter turnover peak in current populations. In addition, there have been substantial reductions in the relative concentrations of Bacillariophyceae and Dinophyceae, previously reported as 18% and 13% between 1982 and 1984 (Ramberg, 1987) to 1.7% and 7.2% in current populations. These reduced concentrations are associated with changes in species dominance. The previously reported dominant Bacillariophyceae species *Aulacoseira granulata* was replaced by *Cymbella affinis,* and the previously reported dominant Dinophyceae species *Peridioniopsis* sp. replaced by *Peridinium gatunense* in present populations. In addition, the previously reported common Bacillariophyceae genera such as *Fragilaria* and *Synedra* in the Lake Sanyati Basin (Hancock, 1979; Ramberg, 1987; Cronberg, 1997) were absent in present populations (Appendix 5.3). Also, the previously reported high Chlorophyceae species richness, especially among small-celled Chlorococcales in Lake Kariba's Sanyati Basin (Ramberg, 1987; Cronberg, 1997), was also observed in current populations. However, there was a notable increase in the total numbers of Chlorophyceae species, from the previously reported 30 species in the lake between 1982 and 1984 to the 41 species recorded in the lake between 1986 and 1990, and the 40 species recorded in present populations (Table 5.4). In contrast, the previously reported 41 Cyanophyceae species and the eight Euglenophyceae species in the lake between 1986 and 1990 have declined to 18

Cyanophyceae species and three Euglenophyceae in present populations, the existing species numbers in these two algal classes similar to those recorded between 1982 and 1984 (Table 5.4). Noteworthy also was that certain orders, such as the Tetrasporales in the Chlorophyceae, the Desmidiales in the Desmidiaceae, as well as members of the Cryptophyceae, Haptophyceae and Raphidophyceae, which were previously recorded in the lake, were not observed in the lake water in present populations (Table 5.4). Results of these studies were comparable as they comprised similar sampling locations and depth intervals, though there were slight differences in sampling frequency, i.e monthly in four studies, every four months in the fifth and every second month in the current study.

Table 5.4. A comparison of the total numbers of phytoplankton species present in different algal classes and orders recorded in Lake Kariba at different intervals between 1959 and 2009

CLASS/Order	Interval					
	1959[a]	1959-1964[b]	1968-1970[c]	1982-1984[d]	1986-1990[e]	2007-2009[f]
CYANOPHYCEAE	11	16	15	15	41	18
CHLOROPHYCEAE	-	-	-	30	41	40
Chlorococcales	23	22	36	15	42	22
Volvocales	5	4	2	4	6	3
Tetrasporales	2	1	-	4	2	0
DINOPHYCEAE	4	4	5	11	6	4
EUGLENOPHYCEAE	6	2	4	3	8	3
CHRYSOPHYCEAE	4	1	-	4	16	1
XANTHOPHYCEAE	-	-	2	-	-	1
CRYPTOPHYCEAE	-	-	-	6	4	0
DESMIDIACEAE						
Desmidiales	106	9	68	7	14	0
RAPHIDOPHYCEAE	-	-	-	-	3	0
HAPTOPHYCEAE	-	-	-	1	1	0
TOTAL	161	59	132	100	184	92

[a]Thomasson (1965), [b]Douglas (1969), [c]Thomasson (1980), [d]Ramberg (1987), [e]Cronberg (1997), [f]Present study

The observed increased concentrations of Cyanophyceae and decreased concentrations of Bacillariophyceae in Lake Kariba concur with similar phytoplankton compositional changes observed in other African lakes. A typical example is Lake Victoria, where the Bacillariophyceae species *Aulacoseira* and many Chlorophyceae species are presently rare, whilst heterocyst-forming Cyanophyceae, such as *Anabaena* and *Microcystis,* are proliferating due to eutrophication (Haande *et al*., 2010). Similarly, increased concentrations of the Cyanophyceae species *Microcystis aeruginosa* and *Anabaenopsis arnoldii* in the alkaline Lake Turkana have been attributed to nutrient enrichment, (Mageed and Heikal, 2006), with *Microcystis* forming a dominant component of other hyper-eutrophic lakes such as Chivero and Victoria (Ochumba and Kibaara, 1989; Magadza, 2003; Mhlanga *et al*., 2006), due to its ability to rapidly exploit available nutrients (Harding, 1997). Similarly, in Lake Malawi the Cyanophyceae species *Anabaena* and *Cylindrospermopsis* have recently become more pervasive, due to nutrient enrichment caused by increased anthropogenic activities in the lake's catchment (Hecky and Kling, 1987; Bootsma, 1993; Patterson and Katchinjika, 1995). Conversely, Bacillariophyceae concentrations and phytoplankton primary production rates have decreased substantially in Lake Tanganyika, by 44% in the mixing season and by 88% in the stratified season between 1975 and 2000 to 2001, due to decreased mixing caused by stronger stratification as a result of a 0.9°C warming of the epilimnion waters (Verburg *et al*., 2003). This increase in the temperature gradient within the water column has reduced nutrient exchange rates between the shallow and deep waters of the lake. However, reduced upwelling due to decreased winds have also been reported to reduce nutrient levels, and therefore primary production in Lake Tanganyika (O'Reilly *et al*., 2003), as well as changes in silica levels and water transparency (Sarvala *et al.,* 2007).

The increased concentrations of Cyanophyceae species, especially that of *C. raciborskii* in Lake Kariba, the recent occurrence of *C. raciborskii* in Lake Malawi (Patterson and Katchinjika, 1995), and the increased abundance of closely related *Cylindrospermopsis* species in Lake Victoria since the late 1980's (Mugidde, 1993; Guildford *et al*., 1999; Haande *et al*., 2010), have raised concerns for water quality due to toxin production by species of *Cylindrospermopsis* (Ndebele and Magadza, 2006). *C. raciborskii* displays a high growth rate at water temperatures above 23°C (Fabbro and Duivenvoorden, 1996; Hawkins *et al*., 1997; Saker *et al*., 1999; Saker and Griffiths, 2001), is capable of growing at photosynthetic photon flux densities below 25 μE $s^{-1,}$ and in nitrogen-impoverished waters, due to its ability to fix atmospheric nitrogen (Padisák and Istvánovics, 1997; Bouvy *et al*., 1999; Briand *et al*., 2002). These features, and this species' ability to rapidly exploit nutrients during upwelling (Reynolds, 1984, 1989), especially phosphorus inputs which favour increases in nitrogen fixing Cyanophyceae (Hendzel *et al*., 1994), and its ability to migrate up and down the water column with the aid of trichomes (Ramberg, 1987), explains its proliferation in Lake Kariba and its reported increased abundance in reservoirs and rivers in Australia, Brazil, Florida, South Central Europe, Kenya, South Africa, and China (Carmichael *et al*., 2001; Chorus, 2001; Ballot *et al*., 2003, 2005; Janse and Kriel, 2008; Chen *et al*., 2009).

The observed decline in Bacillariophyceae concentrations as a whole, and also among individual species such as *Cymbella, Pinnularia* and *Navicula,* recorded at lower concentrations in present populations in Lake Kariba than previously reported (Phiri *et al*. 2006), have been attributed to elevated water temperatures and altered dissolved oxygen profiles associated with climate warming (Magadza, 2008). Bacillariophyceae tend to dominate under conditions of low temperature and light, high water turbulence, and nutrient concentrations (Tallberg, 2000), while high temperatures indirectly favour Cyanophyceae and inhibit Chlorophyceae (Schargel and Oduor, 2001). Indeed, the observed decreased concentrations of Bacillariophyceae and Dinophyceae in Lake Kariba, and increased concentrations of Chlorophyceae and Cyanophyceae which are competitively superior at higher temperatures (Pliński and Jóźwiak, 1999; Sibanda, 2003), may explain the observed shift in phytoplankton species composition in Lake Kariba, normally associated with increasing temperatures, nitrogen limitation and phosphorus loading (Senerpont-Domis *et al*., 2007). In fact, warming has been observed in several African freshwater lakes (Bootsma, 1993; O'Reilly *et al*., 2003; Sarmento *et al*., 2006). Water temperatures in the epilimnion of Lake Kivu have increased by 0.5°C between 1972 and 2002 (Lorke *et al*., 2004), this associated with nutrient declines and a potential reduction in phytoplankton production (Sarmento *et al*., 2006, 2007, 2008). In the deep, meromictic Lake Tanganyika, increased warming by 0.2°C at 1 000 m and 1.3°C at the water surface (Verburg and Hecky, 2009) has increased water column stability and decreased vertical mixing, thereby reducing nutrient loading to the upper mixed layer, resulting in decreased phytoplankton abundance and increased dissolved silica, both indicative of declining primary production associated with the warming of the waters (O'Reilly *et al*., 2003; Stenuite *et al*., 2007; Verburg and Hecky, 2009). In addition, shifts in phytoplankton composition to less palatable Cyanophyceae, that are competitively superior at higher temperatures, have been shown to suppress total zooplankton biomass (Doney, 2006), with potential adverse effects on fish production. Indeed, fisheries data from Lake Tanganyika show significant correlations with climatic data over the last 40 years (Stenuite *et al*., 2007), suggesting that moderate warming could destabilise phytoplankton dynamics, thereby potentially reducing water quality and food resources for higher trophic levels such as planktivorous fish, as seen in shallow cold-water ecosystems (Strecker *et al*., 2004).

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Appendix 5.1. A list of Chlorophyceae species and their average concentrations in the Sanyati Basin of Lake Kariba (2007-2009)

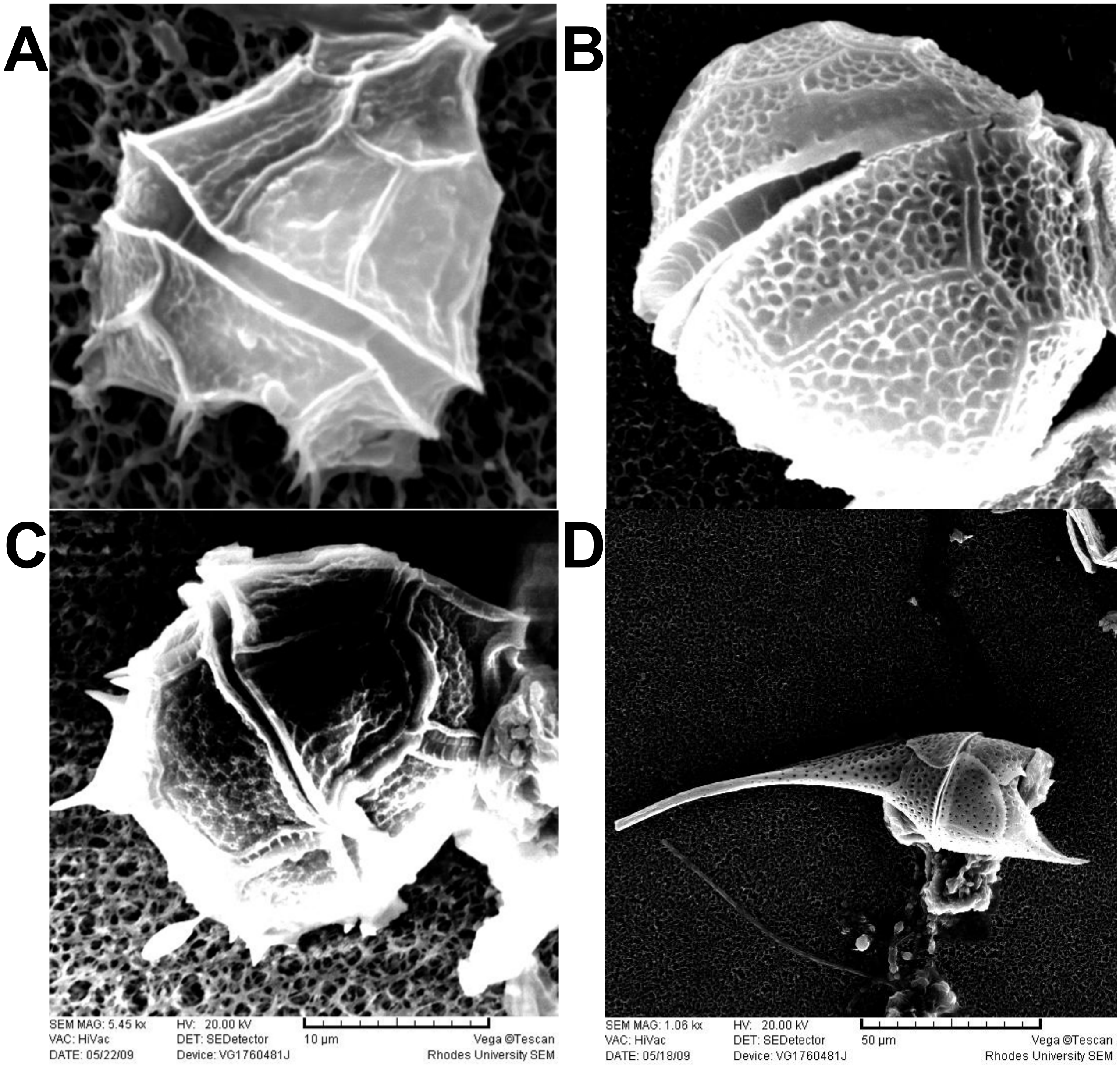
Class/Order/Species	**Average concentration (cells l^{-1})**	**Class/Order/Species**	**Average concentration (cells l^{-1})**
CHLOROPHYCEAE			
Chlorocoocales		**Oedogoniales**	
Actinastrum hantzschii Lagerheim	0.2	*Oedogonium* sp.	6.2
Cerasterias sp.	1.7		
Ankistrodesmus falcatus (Corda) Ralfs	1.1	**Volvocales**	
Ankistrodesmus gracilis (Reinsch) Korshikov	0.1	*Chlamydomonas* sp.	0.6
Colestrium sp.	1.3	*Chlorella vulgaris* Beyerinck	11.7
Monoraphidium contortum (Thuret) Komárková-Legnerová	0.6	*Volvox aureus* Ehrenberg	0.0
Muriella magna F.E. Fritsch & R.P. John	0.3		
Nephrochlamys sp.	9.6	**Zygnematales**	
Nephrocytium schilleri (Kamm.) Comas	5.5	*Closteriopsis* sp.	2.8
Oocystis sp.	0.5	*Closterium acutum* Brébisson	14.0
Pediastrum pulex Meyen	1.1	*Closterium kützingii* Brébisson	7.4
Pediastrum ellipticum (Ehrenberg) Hassall ex Ralfs	0.2	*Cosmarium botrytis* Menegh.	5.9
Pediastrum simplex (Meyen) Lemmermann	6.3	*Cosmarium monoliforme* (Turp.) Ralfs	1.3
Pediastrum tetras (Ehrenberg) Ralfs	2.9	*Euastrum pinnatum* Ralfs	2.2
Scenedesmus aculeolatus Reinsch	0.4	*Eustaropsis* sp.	0.3
Scenedesmus dejectus Brébisson	3.1	*Gonatozygon aculcatum* Hastings	3.2
Scenedesmus falcatus Chodat	1.3	*Micramasterias* sp.	6.2
Scenedesmus quadricauda (Turp.) Brébisson	3.8	*Mougetia capucina* Bory.	5.0
Scenedesmus microspina Chodat	0.3	*Staurastrum gracile* Lemmermann	6.7
Tetraedron minimum (A. Braun) Hansg.	3.6	*Staurastrum johnsonii* West & G.S. West	13.6
Treubaria triappendiculata Bern.	6.7	*Staurastrum limneticum* Schmidle	10.0
Ulothrix sp.	0.4	*Staurastrum* sp.	10.8

Appendix 5.2. A list of Cyanophyceae species and their average concentrations in the Sanyati Basin of Lake Kariba (2007-2009)

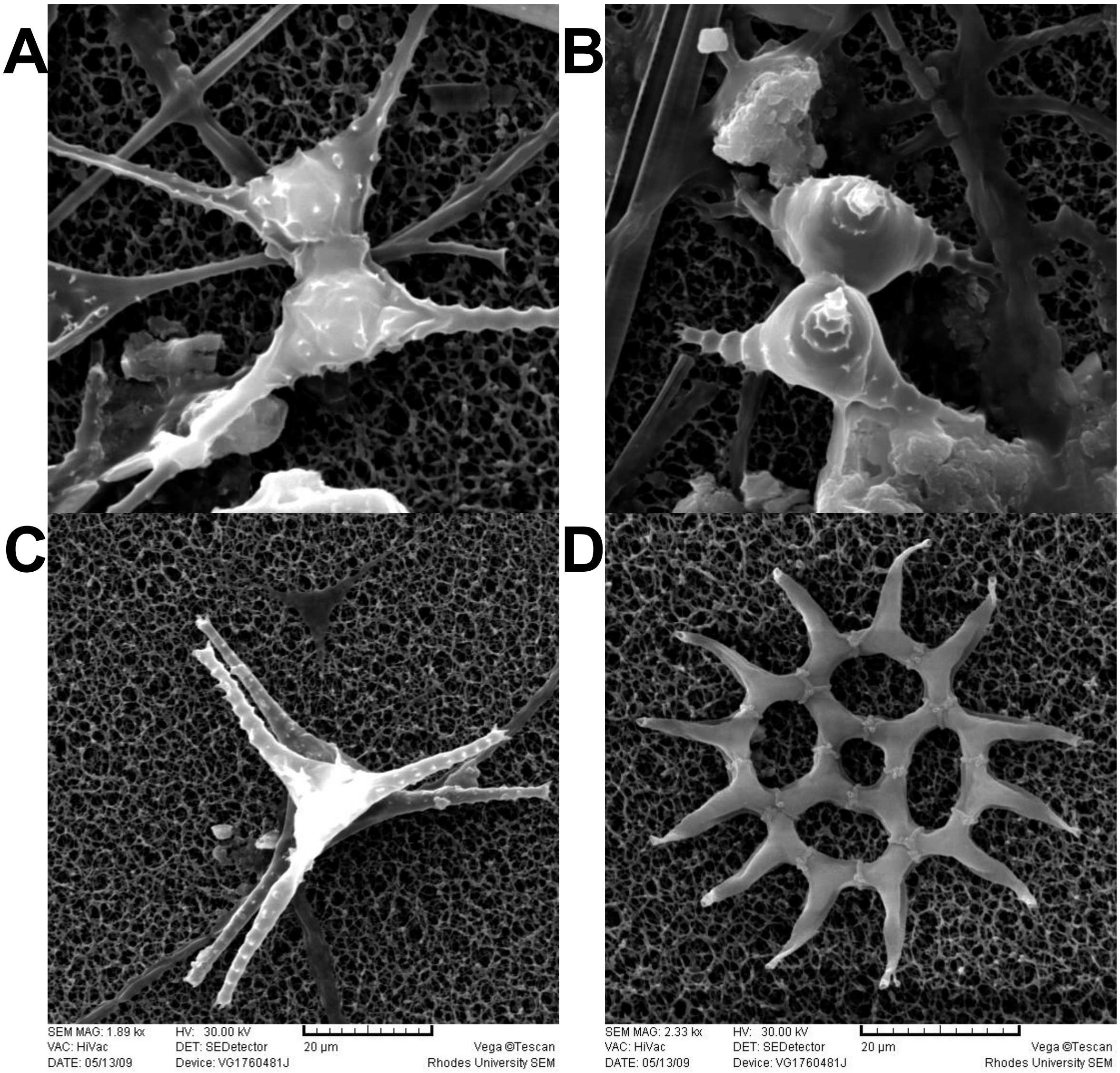
Class/Order/Species	**Average Concentration (cells l⁻¹)**
CYANOPHYCEAE	
Chroococcales	
Aphanocapsa incerta (Lemmermann) Cronberg & Komárek	0.6
Chroococcus turgidus (Kützing) Näg.	1.0
Merispomedia glauca (Ehrenberg) Näg.	1.0
Microcystis aeruginosa Kützing	29.2
Microcystis flos aquae (Wittr.) Kirchner	24.9
Microcystis wesenbergii (Komárek) (Komárek)	0.6
Spirulina laxissima G.S. West	1.1
Nostocales	
Anabaena catenula (Kützing) Bornet & Flahault	5.3
Anabaena circularis (Kützing) Hansg.	24.2
Anabaena flos aquae (Lyngbye) Brébisson	26.1
Aphanizomenon flos aquae Ralfs	1.1
Cylindrospermopsis africana Komárek & Kling	0.6
Cylindrospermopsis raciborskii (Woloszynska) Seenaya & Subba Raju	690.4
Nostoc sp.	0.8
Oscillatoriales	
Lyngbya sp.	1.1
Oscillatoria agardhii Gom.	0.9
Oscillatoria limosa (Dillw.) Ag.	0.4
Planktothrix agardhii (Gomont) Anagnostidis & Komárek	0.2

Appendix 5.3. A list of Bacillariophyceae, Dinophyceae, Euglenophyceae, Chrysophyceae and Xanthophyceae species and their average concentrations in the Sanyati Basin of Lake Kariba (2007-2009)

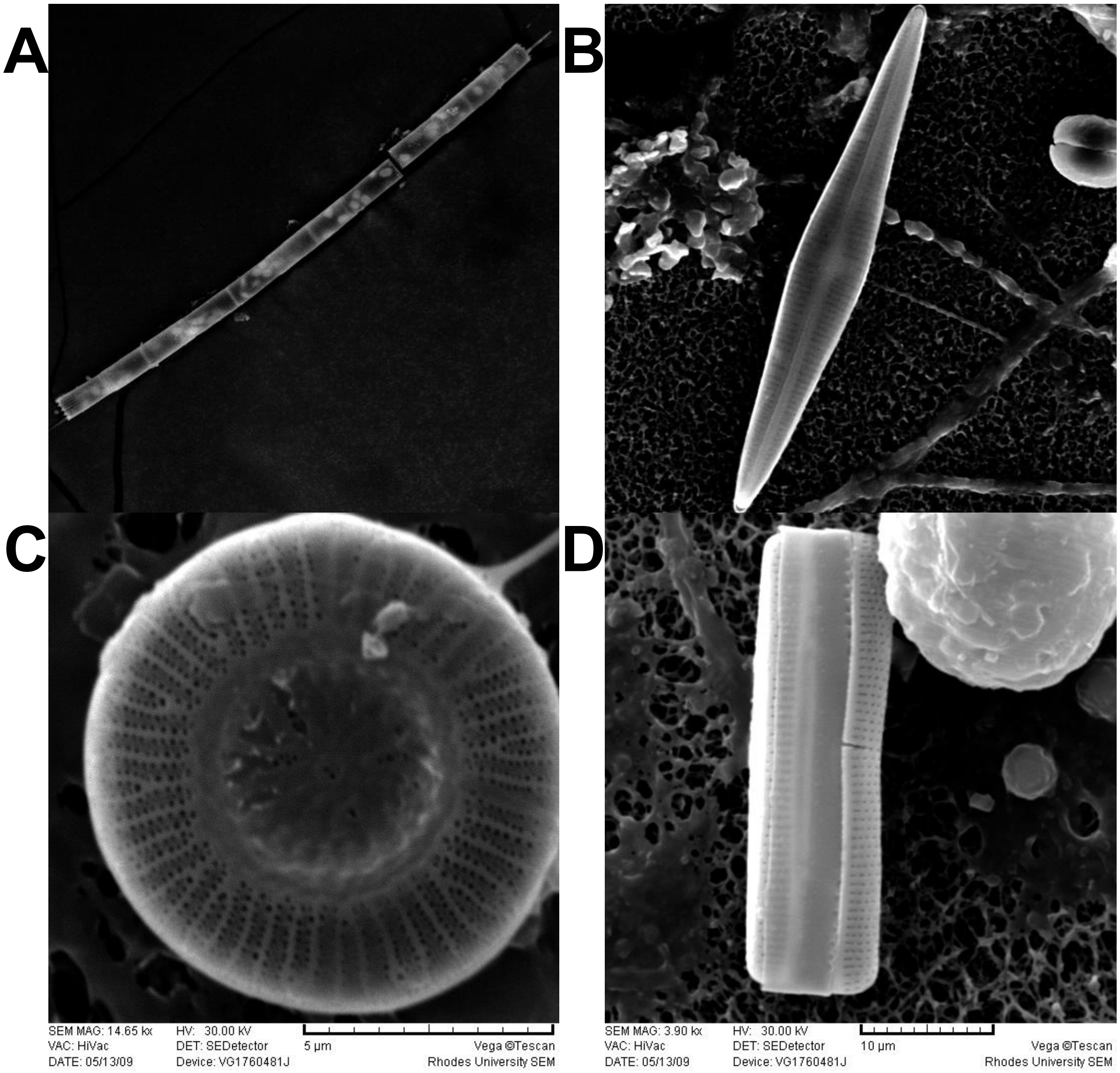
Class/Order/Species	**Average concentration (cells l⁻¹)**
Bacillariophyceae	
Aulacoseira agassizii (Ostenef.) Simonsen	0.5
Aulacoseira ambigua (Grunow) Simonsen	0.7
Aulacoseira granulata (Ehrenberg) Simonsen	5.9
Cyclotella stelligera (Cleve & Grunow) Van Heurck	2.7
Cymbella affinis Kützing	3.4
Navicula digitoradiata (Gregory) Ralfs	1.2
Nitzschia sp.	0.9
Pinnularia viridis (Nitsch.) Ehrenberg	0.6
Surirella sp.	0.8
Stephanodiscus nyassae Klee & Casper	2.5
Dinophyceae	
Ceratium furcoides (Lev.) Langh.	19.6
Ceratium hirundinella O.F. Müller	17.0
Peridinium gatunense Nygaard	13.1
Peridiniopsis sp.	27.6
Euglenophyceae	
Euglena acus (O.F. Müller) Ehrenberg	18.2
Phacus anomalus F.E. Fritsch & M.F. Rich.	3.7
Trachelomonas armata (Ehrenberg) F. Stein	5.0
Chrysophyceae	
Dinobyron sertularia Ehrenberg	17.1
Xanthophyceae	
Tribonema sp.	3.9



Appendix 5.4. Scanning Electron Microgram (SEM) images of Dinophyceae species; A. *Peridionipsis* sp., B. *Peridinium gatunense,* C. *Ceratium furcoides and* D. *C. hirundinella* (short horns on the apotheca) sampled in the Sanyati Basin of Lake Kariba



Appendix 5.5. Scanning Electron Microgram (SEM) images of Chlorophyceae species of A. *Staurastrum johnsonii*, B. *S. gracile*, C. *S. limnetica* and D. *Pediastrum simplex* sampled in the Sanyati Basin of Lake Kariba



Appendix 5.6. Scanning Electron Microgram (SEM) images of Bacillariophyceae species of A. *Aulacoseira granulata*, B. *Navicula digitoradiata*, C. *Cyclotella stelligera* and D. *Aulacoseira* sp. sampled in the Sanyati Basin of Lake Kariba

Chapter 6

Zooplankton species richness and concentrations in Lake Kariba

Abstract

This study examined spatial, temporal and depth variations in zooplankton species richness and concentrations in Lake Kariba, compared these with those in other tropical African lakes, and ascertained whether measured changes in zooplankton composition might be linked to climate warming. Zooplankton species richness and concentrations were enumerated microscopically in water samples collected in midwinter and midsummer at six different depths at 17 sampling stations distributed across Lake Kariba's five basins, with a more extensive sampling regime conducted at 2-monthly intervals over a 24-month period at five sampling stations distributed across the lake's Sanyati Basin. The whole lake samples comprised 77 species, including 48 species of Rotifera of which *Keratella cochlearis* was the most abundant, 15 species of Copepoda of which *Thermocyclops albidus* was the most abundant, 14 species of Cladocera of which *Bosmina longirostris* was the most abundant. In the Sanyati Basin, 52 species were enumerated, comprising 38 Rotifera, eight Copepoda, six Cladocera, of which *B. longirostris* was the most abundant Cladocera, *T. albidus* and *Tropodiaptomus congruens* the most abundant Copepoda, and *K. cochlearis* the most abundant Rotifera taxa. All three zooplankton classes displayed concentration peaks in August, following stratification breakdown which were consistent with earlier reports. However, only the Copepoda exhibited the summer peak in the present study, implying a change in the seasonality and a decline in concentration of the zooplankton during summer. Comparisons of the current zooplankton assemblage with that of the past revealed overall lower concentrations than those in previous studies, with substantial decreases in the Cladocera of up to 93.3% and increases in the Rotifera species richness and concentrations which constituted 64.4% of total zooplankton counts. In addition, a number of zooplankton species seem to have disappeared in Lake Kariba's waters. These include the midge larvae *Chaoborus anomalis*, *C. ceratopogones* and *C. edulis*, and the Cladocera *Ceriodaphnia dubia,* whilst only *Bosmina longirostris* has remained dominant among the Cladocera, though higher densities of the Bosminidae were recorded in earlier studies. The zooplankton composition of Lake Kariba is similar to that of other African lakes, with differences in species richness attributed to predation, predominantly by the clupeid sardine, *Limnothrissa miodon,* and recent changes in lake water physical and chemical properties, especially elevated water temperatures, the latter affecting phytoplankton composition and biomass.

6.1. Introduction

Lake Kariba is an artificial reservoir that was created between 1958 and 1963 primarily to generate hydro-electricity. In creating the lacustrine environment, an empty pelagic zone was formed comprising 70% of the lake. In 1968 the Tanganyika sardine, *Limnothrissa miodon* (Boulenger) was introduced at Sinazongwe in Zambia (Bell-Cross and Bell-Cross, 1971) to fill the empty pelagic zone, then thought to be 'teeming' with zooplankton (Begg, 1976). Since then, the sardine has developed into a successful commercial industry and is largely zooplanktivorous, whilst most of the zooplankton is largely planktivorous (Masundire, 1991; Mandima, 1999). Several studies (King, 1971; Bowmaker, 1973; Begg, 1974, 1976; Mills, 1977; Cochrane, 1978, 1984; Magadza, 1980; Marshall, 1980; Masundire, 1991, 1994, 1997; Harding and Rayner, 2001) have investigated zooplankton dynamics and the predator-prey relationships between the plankton and sardine.

Initial investigations by Fryer (1957) involved the collection of free-living micro-Crustacea from the flooded backwaters of the Zambezi River. Seven species of Cladocera were recorded, dominated by *Diaphanosoma excisum* and *Moina micrura,* five species of Cyclopoids dominated by *Mesocyclops major*, the Calanoid *Tropodiaptomus* cf. *kraepelini,* and the Decapod shrimp *Caridina nilotica* (JFRO Annual Report, 1959). Between May 1959 and September 1963, Thomasson (1965) recorded a complement of four Protozoa and 34 Rotifera, the most common of which were *Branchionus falcatus*, *Keratella tropica*, *Lecane bulla*, *Filinia opoliensis* and *Hexarthra mira,* and 13 Cladocera, the most common of which were *Diaphanosoma excisum*, *Chydorus sphaericus*, *Daphnia lumholtzi* and *Bosmina longirostris*, as well as one Calanoid (*Tropodiaptomus* cf. *kraepelini*), one Cyclopoid (*Mesocyclops major*), and one *Chaoborus* sp. Harding and Rayner (2001) examined samples collected from the Kariba Gorge outflow and all inflowing rivers in the lake. Species of *Ceriodaphnia* occurred frequently, of which *C. quadrangula* was most common, followed by *Bosmina longirostris* and *Diaphanosoma excisum*. Among the Copepoda, *Thermodiaptomus mixtus* was the most common. Harding and Rayner (2001) concluded that the zooplankton composition of the lake was typical of warm water bodies similar to those found in sub-Saharan artificial tropical lakes.

The zooplankton concentration in Lake Kariba varies in response to phytoplankton biomass, and it is has been suggested that zooplankton production is determined to a larger extent by phytoplankton availability than fishing pressure and predation (Marshall, 1984, 1997; Paulsen, 1994), with a distinct correlation also evident between zooplankton biomass and river inflows (Begg, 1974; Magadza, 1980; Masundire, 1992; Chifamba, 2000). Noteworthy is that the Cladocera species has declined since the introduction of the Tanganyika sardine, whilst that of Copepoda has remained relatively stable (Cochrane, 1978; Masundire, 1989; Marshall, 1991). At the same time, *L. miodon* populations*,* assessed from recorded catches per unit effort, have also steadily declined in the lake since 1986 (LKFRI, 2010), which does not readily explain the concomitant decline in zooplankton concentration. In view of this ambiguity, this study examined the current species composition and seasonal concentration of zooplankton in Lake Kariba, compared these with previous records and those in other tropical African lakes, and ascertained whether any measured changes in zooplankton composition might be linked to climate warming.

6.2. Methods and materials

6.2.1. Study area

The study area was Lake Kariba (16º 28' S; 26º 40' to 29º 03'E), whose catchment spans an area of 185 000 km² comprising 60% of the entire Zambezi River Basin (Tumbare, 2000). The lake was constructed in 1958, primarily to generate electricity for Zambia and Zimbabwe; then known as Northern and Southern Rhodesia (World Dams Commission, 2000; Magadza, 2006).

6.2.2. Experimental design and sampling stations

Two separate studies measured zooplankton species richness and concentrations at six different depths (0, 2, 5, 10, 15, 20 m) at 17 sampling stations distributed across the entire length of the lake, from Basin 1 in the south-west to Basin 5 in the north-east (Figure 6.1). In the first study, zooplankton measurements were conducted twice annually, namely during lake turnover in midwinter (July) and again during lake stratification in midsummer (February), at four sampling stations located in Basin 1, three in Basin 2, one in Basin 3, four in Basin 4, and five in Basin 5. In the second study, zooplankton measurements were conducted at 2-monthly intervals over a 24-month period, extending from March 2007 through to February 2009, at five sampling stations in Basin 5, where the majority of previous long-term zooplankton studies have been conducted (Magadza, 1980; Masundire, 1989, 1991, 1994, 1997). Three of these sampling stations were located at the margins of the lake basin in close proximity to the Charara, Gache-gache and Sanyati River inflows and were designated riverine habitats. The other two sampling stations traversed the centre of the basin, and were designated lacustrine habitats.

6.2.3. Zooplankton species richness and concentration

For taxonomic analysis, two sets of 20l water samples were collected with a Ruttner sampler from each of the six depth zones described above and at each sampling station. The water was filtered through a 64 µm mesh and preserved with 70% alcohol within five minutes after the collection to prevent tissue damage by autolysis and bacterial action, and transported to the laboratory.

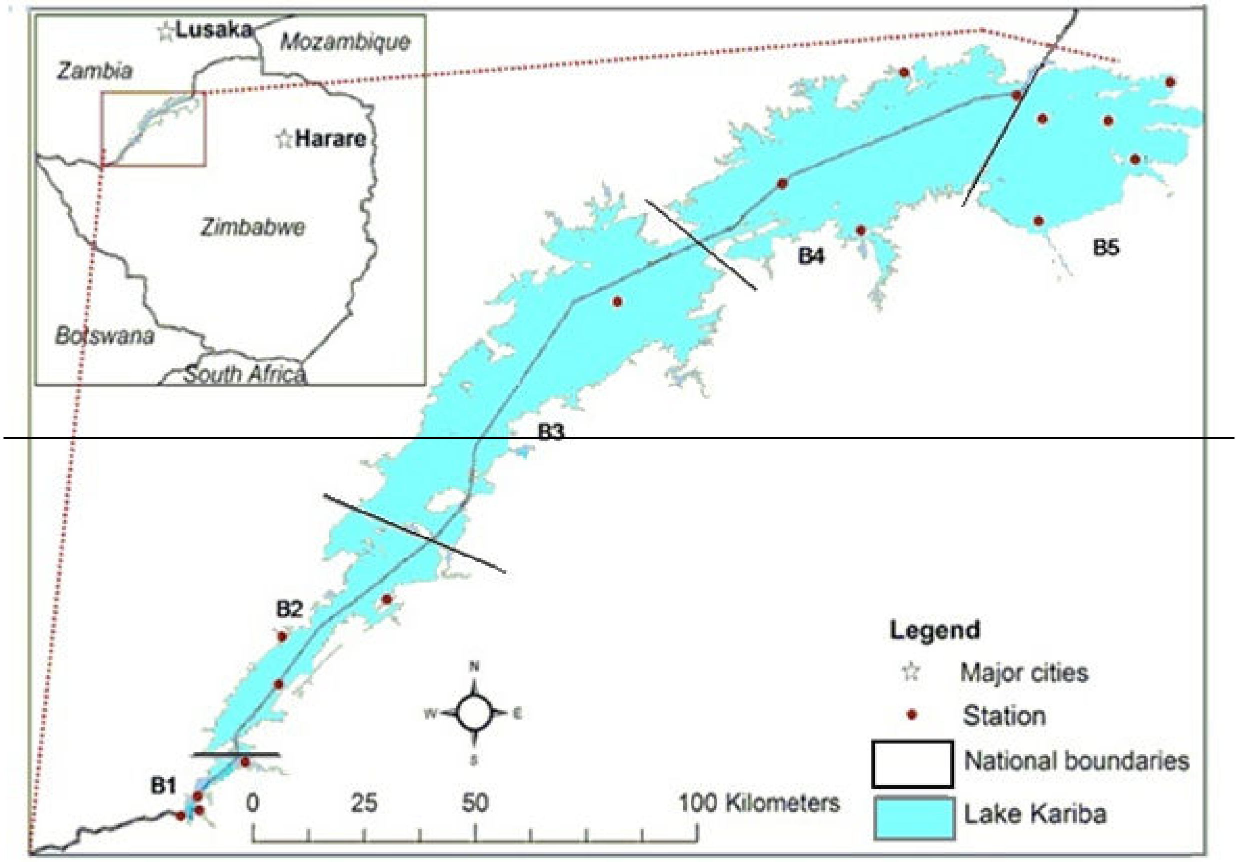


Figure 6.1. Distribution of 17 sampling stations for zooplankton assays in Lake Kariba's five basins

In the laboratory the zooplankton samples were thoroughly shaken to achieve a uniform distribution of the organisms. Sample volumes for microscopic examination were adjusted, based on visual estimates of organism concentrations (Edmondson, 1971), 5 ml sample volumes for high organism concentrations and up to 20 ml sample volumes for low organism concentrations. The samples were transferred to sedimentation chambers using a Socorex adjustable volume pipette with a 3 mm-diameter tip, and allowed to sediment for at least one hour.

Zooplankton species and their concentrations were enumerated microscopically with the aid of a Nikon Diaphot-TMD inverted microscope at 100 x magnification, the species identified with the aid of diagrams and descriptions presented in published keys (Mellanby, 1983; Fernando *et al*., 2002). All the crustacean plankton in the sedimentation chambers were enumerated in compliance with published guidelines (Edmondson and Winberg, 1971; Edmondson, 1974; Bottrell *et al*., 1976;

Downing and Rigler, 1984). Zooplankton species richness was expressed as the number of species per litre of water sample, and concentrations as the number of individuals of each species per litre of water sample.

The biomasses of five dominant zooplankton species were determined as bio-volumes, using body measurements presented in Carpentier *et al.* (1999) and Hillenbrand *et al*. (1999). Body lengths of crustacean zooplankton, excluding furcal setae, shell spines or other appendages, were precisely measured with the aid of an ocular micrometer eye-piece. Measurements were performed on at least 20 individuals of each species and the means used to compute their bio-volumes using formulae based on their geometric shapes (Table 6.1), and the computed biovolumes converted to biomasses applying a published conversion factor as shown in the table below (Wetzel and Likens, 1991).

Table 6.1. Formulae applied for calculation of bio-volumes of six dominant zooplankton species in Lake Kariba (l= length μm^{-1}, w= width μm^{-1} and d= diameter μm^{-1})

Species	Geometric shape	Formulae
Bosmina longirostris	Sphere	$\pi /6. d^3$
Horaella brehmi	Prolate spheroid	$\pi /6. w^2. l$
Keratella cochlearis	Prolate spheroid	$\pi/6. w^2. l$
Lecane bulla	Prolate spheroid	$\pi /6. w^2. l$
Thermocyclops oblongatus	Cone+1/2 sphere	$\pi /12. w^2.(l+w)$

6.2.4. Statistical analysis

The experimental design was not fully balanced, due to unequal numbers of measurements. Consequently, within each of the three zooplankton taxonomic classes (Cladocera, Copepoda, Rotifera) a REML (residual maximum likelihood) variance component analysis (repeated measures mixed model) tested for significant differences in total zooplankton species richness and concentrations between seasons, months, lake basins, water depth, habitat and their interactions, using the Wald X^2 statistic generated by REML (GENSTAT Discovery Edition 3, VSL Lty, UK). In the first REML analysis of the 17 sampling stations distributed across the entire lake, lake basins and water depth were fitted in the fixed model, and replicated winter and summer seasons in the random model. In the second REML analysis of the five sampling stations in the Sanyati Basin, the lacustrine and riverine habitats and water depth were fitted in the fixed model, and replicated months in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This is based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is equal to two.

6.3. Results

6.3.1. Whole lake zooplankton species richness

A total of 77 zooplankton species were indentified in the lake, comprising 48 Rotifera species, 15 Copepoda species and 14 Cladocera species. Species' names and authorities are presented in Appendices 6.1 to 6.2. Scanning Electron Microscopic images of some Copepods, and a Rotifera showing the appendages used in their identification, are illustrated in Appendices 6.4 to 6.6.

Zooplankton species richness differed significantly ($P < 0.001$) between winter and summer seasons in all taxonomic classes, and between lake basins for Rotifera (Table 6.2). However, there were significant ($P \leq 0.001$) interactions between season and lake basin for Cladocera and Copepoda species richness, between lake basin and water depth for Cladocera species richness, and between season, lake basin and water depth for Cladocera and Copepoda species richness (Table 6.2). Peak Cladocera species richness was observed in Basin 4 at 15 m and 20 m depths during winter only and the peak richness at these two depths was significantly ($P \leq 0.05$) higher than those in Basins 1, 3 and 5, but not Basin 2 (Figures 6.2A & B). In contrast, peak Copepoda species richness was observed in Basin 1 at 2 m and 5 m depths during summer, the peak richness at these two depths significantly ($P \leq 0.05$) higher than those in all other basins (Figure 6.2C & D). Peak Rotifera species richness was observed in Basin 3 during summer and Basin 5 during winter, the peak winter richness significantly ($P \leq 0.05$) higher than those in Basins 2, 3 and 4, but not Basin 1, with the peak winter species richness not significantly ($P \geq 0.05$) different from those in the other four basins (Figure 6.3).

6.3.2. Whole lake zooplankton concentrations

Zooplankton concentrations in all taxonomic classes differed significantly ($P < 0.001$) between winter and summer (Table 6.3). However, there were significant ($P \leq 0.001$) interactions between season and lake basin, and also between season, lake basin and water depth, for zooplankton concentrations of all three taxonomical classes (Table 6.3). Cladocera concentrations peaked at 10 m water depths in both Basins 1 and 3 during summer and winter respectively, the peak summer and winter concentrations significantly ($P \leq 0.05$) higher than those in the other lake basins (Figures 6.4A & B), due mainly to increased concentrations of the dominant species *Bosmina longirostris* (Figure 6.6A). Copepoda concentrations peaked at 2 m water depth in Basin

1 during summer, the peak summer concentration significantly (P ≤ 0.05) higher than those in the other lake basins (Figures 6.4C & D), due mainly to increased concentrations of the dominant species *Thermodiaptomus congruens* (Figure 6.6B). No significant (P ≥ 0.05) differences in Copepoda concentrations were evident between the five lake basins in winter (Figures 6.4C & D). Rotifera concentrations peaked at depths of 0 to 2 m depth in Basin I during summer (Figure 6.5A & B), the peak summer concentrations at these shallow depths dominated by *Bosmina quadridentata* and *Keratella serrulata* (Figure 6.6C), and significantly (P ≤ 0.05) higher than those at all depths in the four other basins during both summer and winter (Figure 6.5A & B).

Table 6.2. Wald χ^2 statistics derived from REML (repeated measures mixed model), which tested the effects of season, lake basin and water depth and their interactions on zooplankton species richness in different taxonomic classes in Lake Kariba. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P <0.001

		Wald χ^2statistic		
REML	df	Cladocera	Copepoda	Rotifera
Main effects				
Season	1	**16.21*** **	**7.12***	**7.83****
Basin	4	2.06	6.80	**22.41*****
Depth	5	5.07	5.47	8.98
2-way interactions				
Season x Basin	4	**27.58*****	**16.64***	5.98
Season x Depth	5	1.82	0.73	2.27
Basin x Depth	20	**34.35***	20.74	10.1
3-way interactions				
Season x Basin x Depth	20	**44.17****	**35.7***	10.41

Table 6.3. Wald χ^2 statistics derived from REML (repeated measures mixed model), which tested the effects of season, lake basin and water depth and their interactions on the concentration of zooplankton individuals in different taxonomic classes in Lake Kariba. Values presented in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P <0.001

		Wald χ^2statistic		
REML	df	Cladocera	Copepoda	Rotifera
Main effects				
Season	1	**9.28****	**7.94***	**25.88*****
Basin	4	8.84	5.45	7.90
Depth	5	9.95	3.67	7.03
2-way interactions				
Season x Basin	4	**25.14*****	**15.49****	**11.77***
Season x Depth	5	3.13	1.21	**12.12***
Basin x Depth	20	**74.17*****	25.17	13.05
3-way interactions				
Season x Basin x Depth	20	**99.25*****	**38.24****	**36.46***

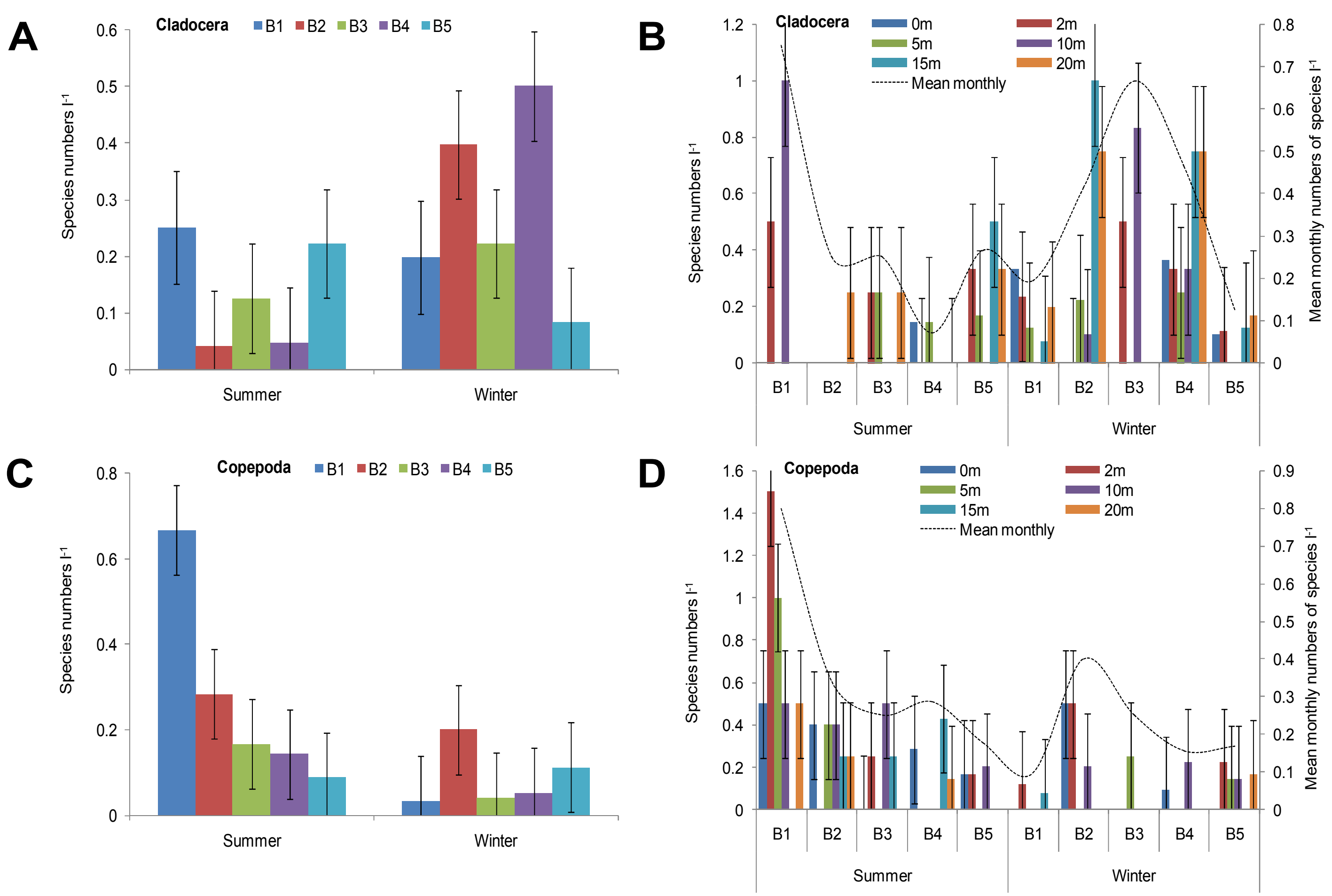


Figure 6.2. Seasonal and seasonal versus depth variations in A & B Cladocera and C and D Copepoda species richness in different lake basins. Standard error of differences shown by bars

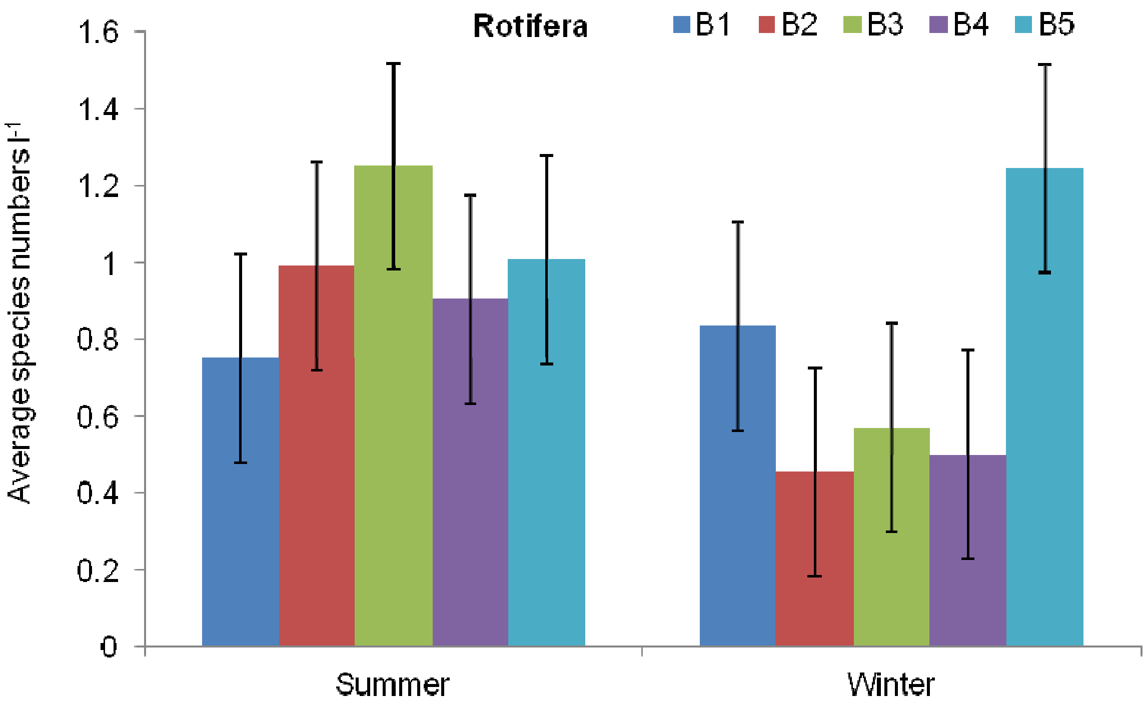


Figure 6.3. Seasonal variations in Rotifera species richness in different lake basins. Standard error of differences shown by bars

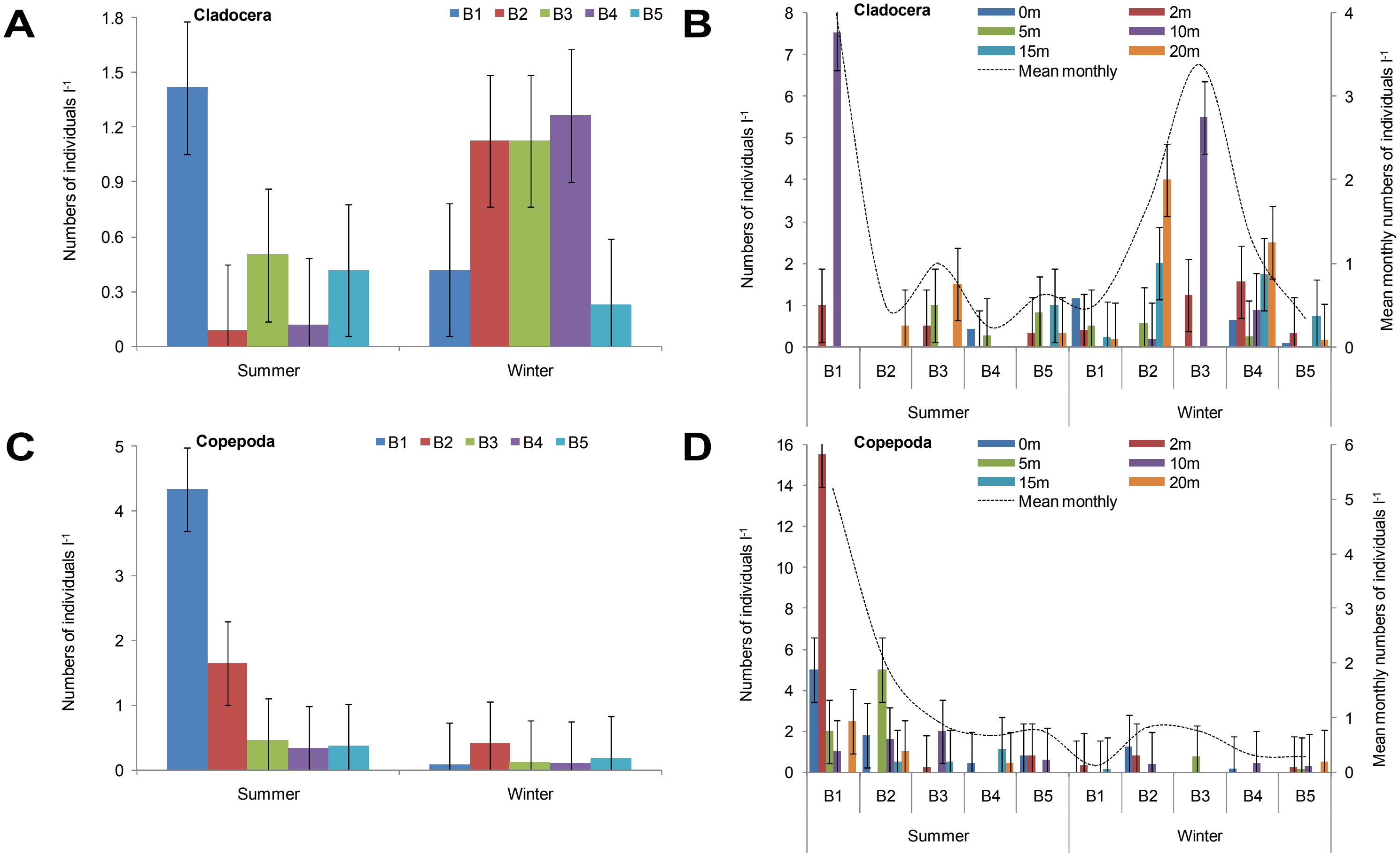


Figure 6.4. Seasonal and seasonal versus depth variations in A & B Cladocera and C and D Copepoda concentrations in different lake basins. Standard error of differences shown by bars

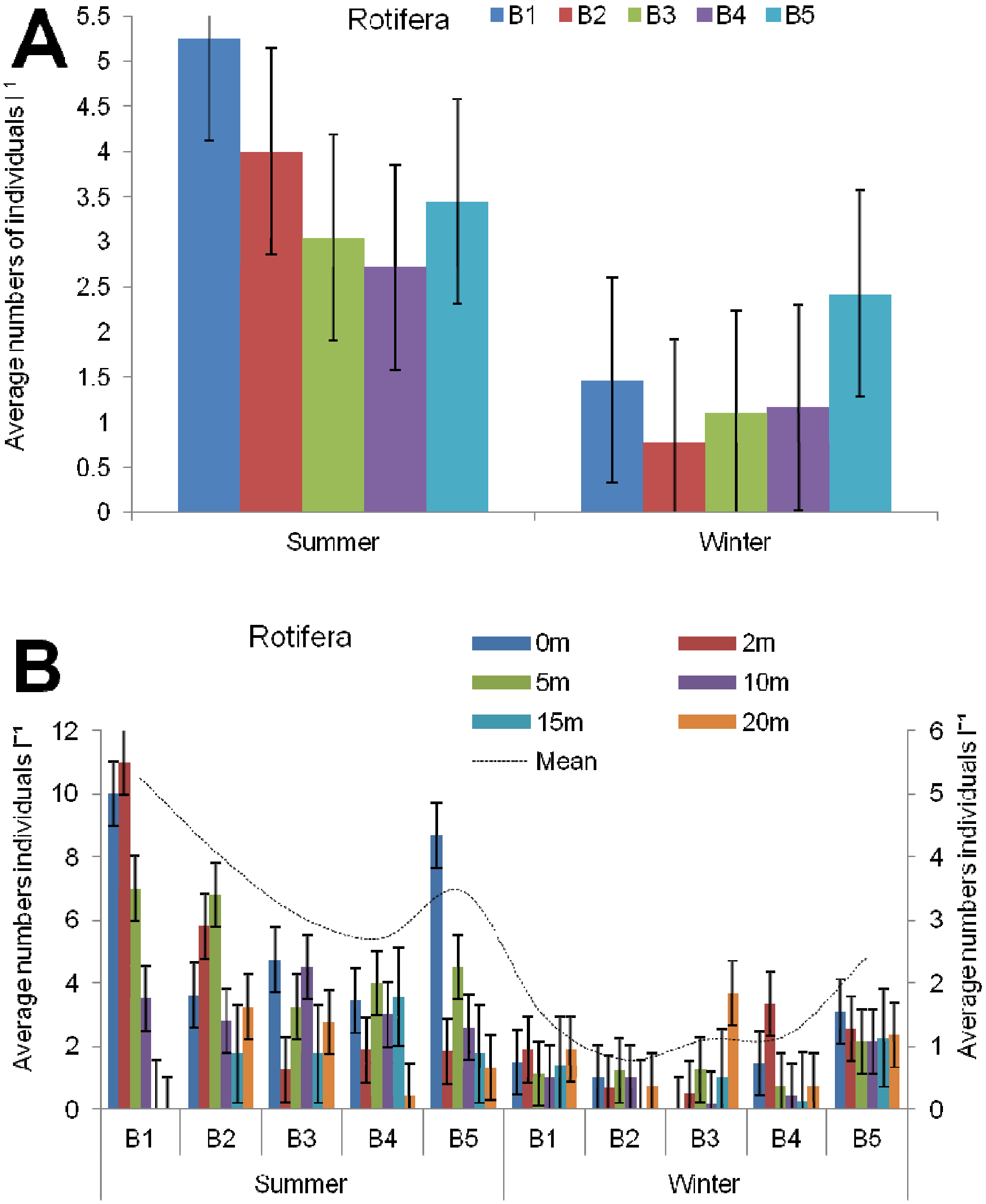


Figure 6.5. Seasonal variations in A. Rotifera species concentrations and B. seasonal versus depth variations in Rotifera species concentrations in different lake basins. Standard error of differences shown by bars

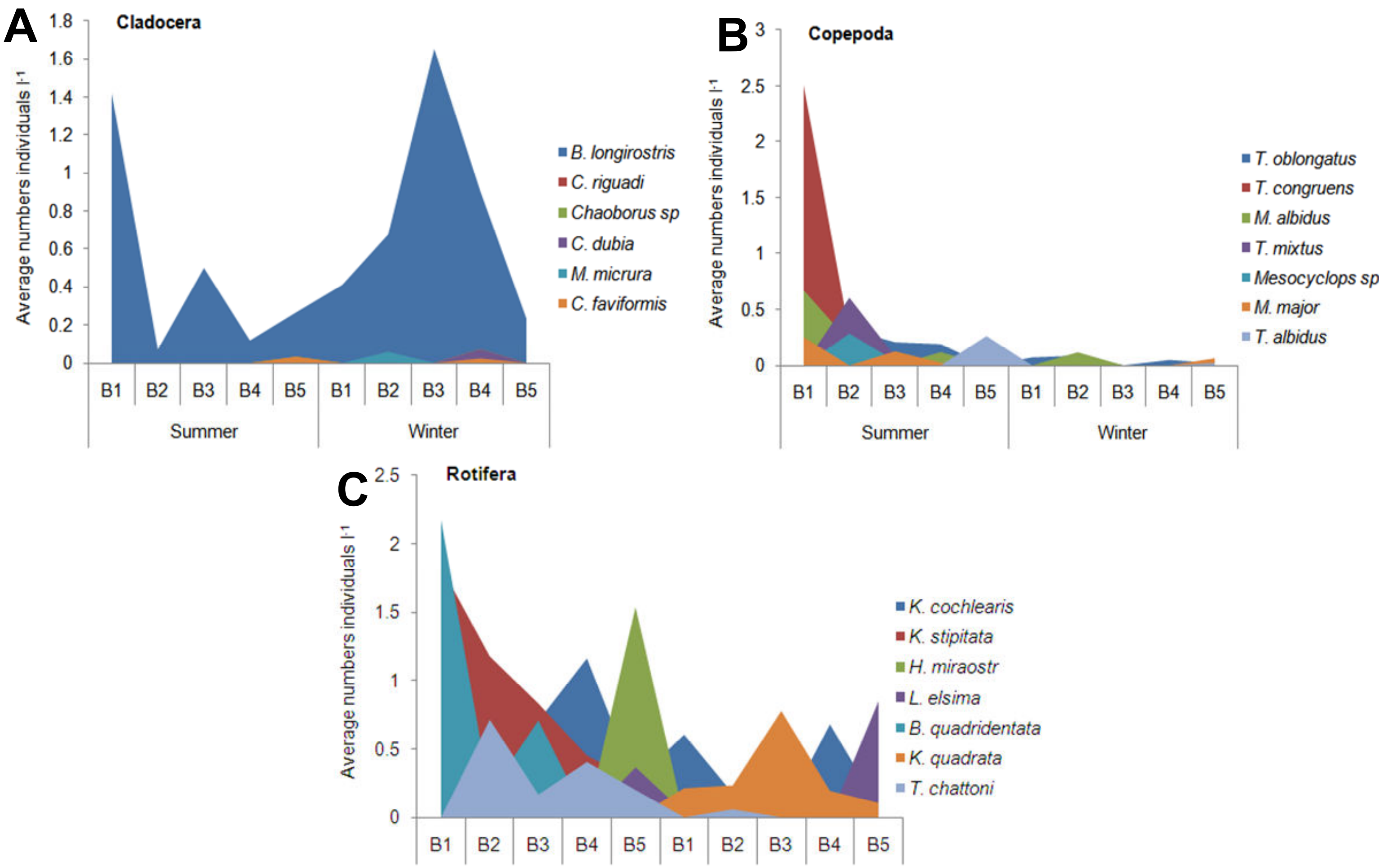


Figure 6.6. Seasonal variation in concentrations of the most common A Cladocera, B. Copepoda and C. Rotifera species in different lake basins

6.3.3. Sanyati Basin zooplankton species richness

A total of 52 zooplankton species were recorded in the Sanyati Basin, of which 38 comprised Rotifera, eight Copepoda and six Cladocera of which *K. cochlearis*, *B. longirostris* and *T. albidus/Tropodiaptomus congruens* were the most abundant in the Rotifera, Copepoda and Cladocera respectively. The three most abundant species, collectively making up 57.3% of the total zooplankton population in the basin, comprised the Rotifera *Keratella cochlearis* (30.3%), and the Cladocera *Bosmina longirostris* (7.9%). There were significant ($P \leq 0.001$) interactions between month, habitat, and water depth for Cladocera, Copepoda species richness (Table 6.4). Cladocera species richness in the lacustrine habitat at the lake centre peaked at 10 m to 20 m water depths in July and August, whereas in riverine habitats along the lake margins, Cladocera species richness peaked at 2 m to 5 m water depths in March, at 10 m water depth in September, and at 15 m water depth in December (Figure 6.7A). Copepoda species richness in the lacustrine habitat peaked at the water surface to 5 m water depth in March, whereas in the riverine habitat Copepoda species richness peaked at 5 m to 15 m water depth in March, at the water surface to 2 m water depth in April, and at 10 m to 15 m water depth in June (Figure 6.7B). Rotifera species richness displayed no significant ($P \geq 0.05$) differences between lacustrine and riverine habitats, with species richness peaking at the water surface in June and October, and declining with increasing water depth (Figure 6.8A).

6.3.4. Sanyati Basin zooplankton concentrations and bio-volumes

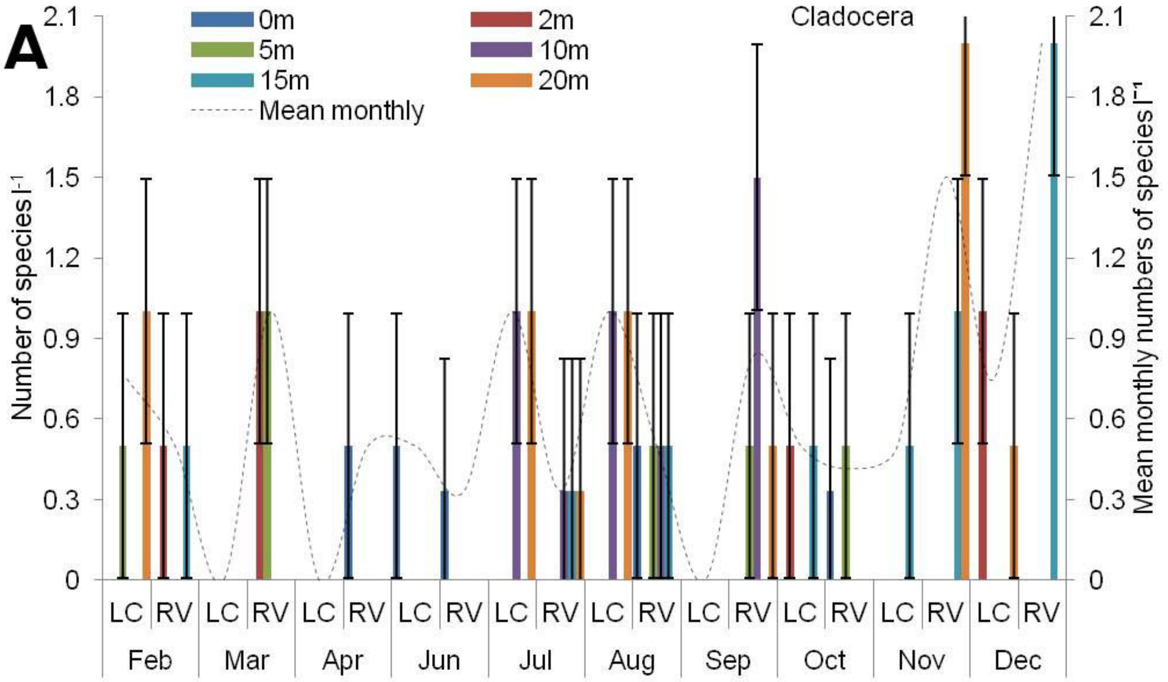
The highest Cladocera concentrations were observed at 10 m water depth during August, (Figure 6.9A) and dominated by *Bosmina longirostris* (Figure 6.10A). However, overall there were no statistically significant ($P \geq 0.05$) differences in Cladocera concentrations between month, water depth, lacustrine and riverine habitats (Table 6.5). Copepoda concentrations displayed significant ($P \leq 0.001$) interactions between month, water depth, lacustrine and riverine habitats (Table 6.5). Copepoda concentrations in the lacustrine habitat peaked at 20 m water depth in August and at 2 m water depth in November (Figure 6.9B), the August peak concentrations dominated by *Thermocyclops albidus* and the November peak by *Thermodiaptomus congruens* (Figure 6.10B). In the riverine habitat, Copepoda concentrations peaked at 5 m water depth in March, at the water surface in April, and at 15 m water depth in June (Figure 6.9B), the March peak dominated by *Thermodiaptomus congruens* and the April and June peaks by *Thermocyclops albidus.* The highest Rotifera concentrations were observed in surface waters during August (Figure 6.8B) and dominated by *Keratella cochlearis* (Figure 6.10C), with concentrations declining significantly ($P \leq 0.05$) with increasing water depth (Table 6.5). The Copepoda *Thermocyclops oblongatus* displayed the highest average bio-volume (3 695 462 x 10^3 µm^3) per individual, followed by the Cladocera *Bosmina longirostris* (3 479 142 x 10^3 µm^3) and the Rotifera*'s Horaella brehmi* (139 724 x 10^3 µm^3) *Lecane bulla* (78 539 x 10^3 µm^3) and *Keratella cochlearis* (51 413 x 10^3 µm^3).

Table 6.4. Wald χ^2 statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth, and their interactions on zooplankton species richness in different taxonomic classes in the Sanyati Basin of Lake Kariba. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001

		Wald χ^2 statistic		
REML	df	Cladocera	Copepoda	Rotifera
Main effects				
Month	9	8.52	**37.81*** **	**84.98*** **
Habitat	1	**3.98***	2.65	2.54
Depth	5	8.28	9.27	**11.32***
2-way interactions				
Month x Habitat	9	9.96	7.74	16.27
Month x Depth	45	59.56	**94.52*** **	47.35
Habitat x Depth	5	4.62	**23.00*** **	7.60
3-way interactions				
Month x Habitat x Depth	45	**85.19*** **	**86.77*** **	44.37

Table 6.5. Wald χ^2 statistics derived from REML (repeated measures mixed model), which tested for the effects of month, habitat, water depth, and their interactions on zooplankton concentrations in different taxonomic classes in the Sanyati Basin of Lake Kariba. Values presented in bold significant at *P <0.05, **P <0.01, ***P <0.001

		Wald χ^2statistic		
REML	df	Cladocera	Copepoda	Rotifera
Main effects				
Month	9	11.79	**24.56***	**38.86*** **
Habitat	1	0.74	0.11	0.57
Depth	5	3.31	8.47	**11.33***
2-way interactions				
Month x Habitat	9	8.69	**19.69***	10.99
Month x Depth	45	42.92	**113.57*** **	28.08
Habitat x Depth	5	1.81	**25.72*** **	1.78
3-way interactions				
Season x Habitat x Depth	45	48.14	**85.04*** **	28.81



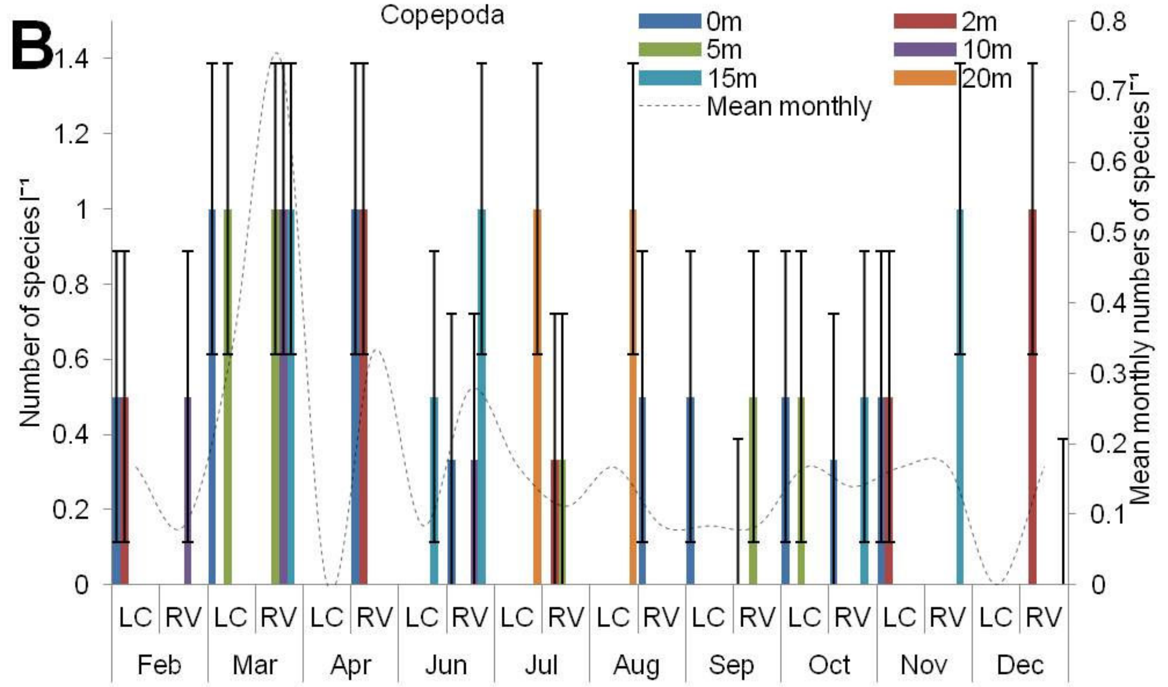
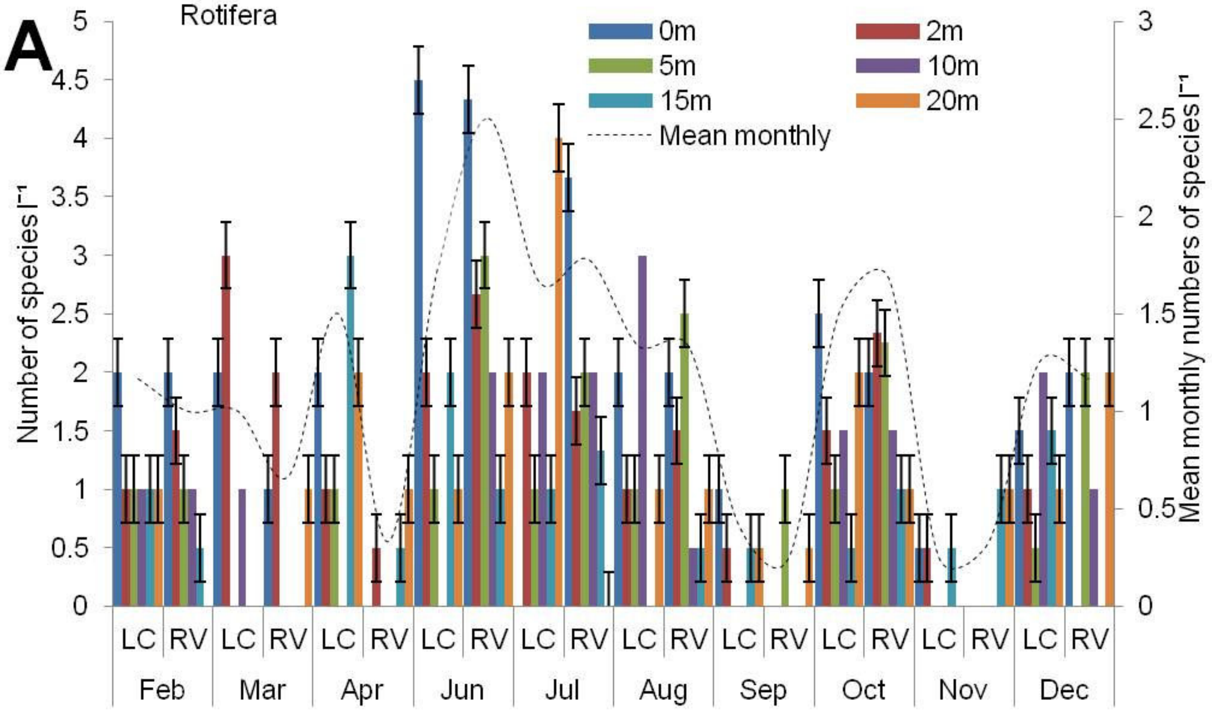


Figure 6.7. Monthly variations versus habitat in A. Cladocera and B. Copepoda with water depth in the Sanyati Basin. Standard error of differences shown by bars



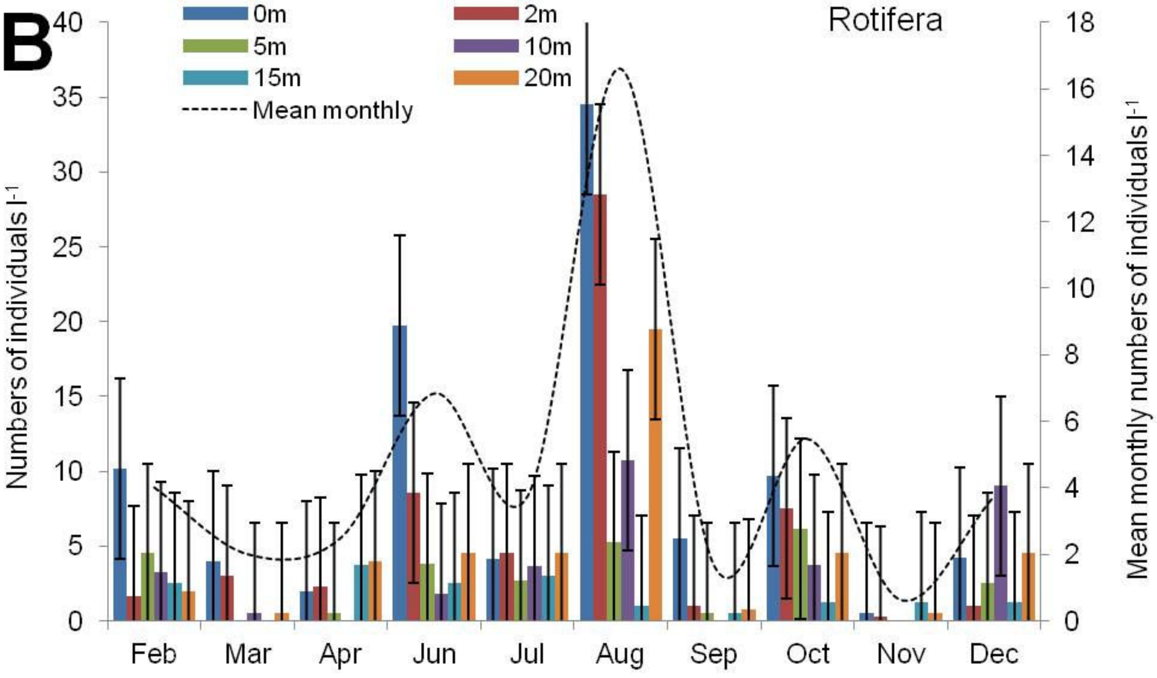


Figure 6.8. Monthly variations versus habitat in Rotifera A. species richness and B. individual concentrations with water depth in the Sanyati Basin. Standard error of differences shown by bars

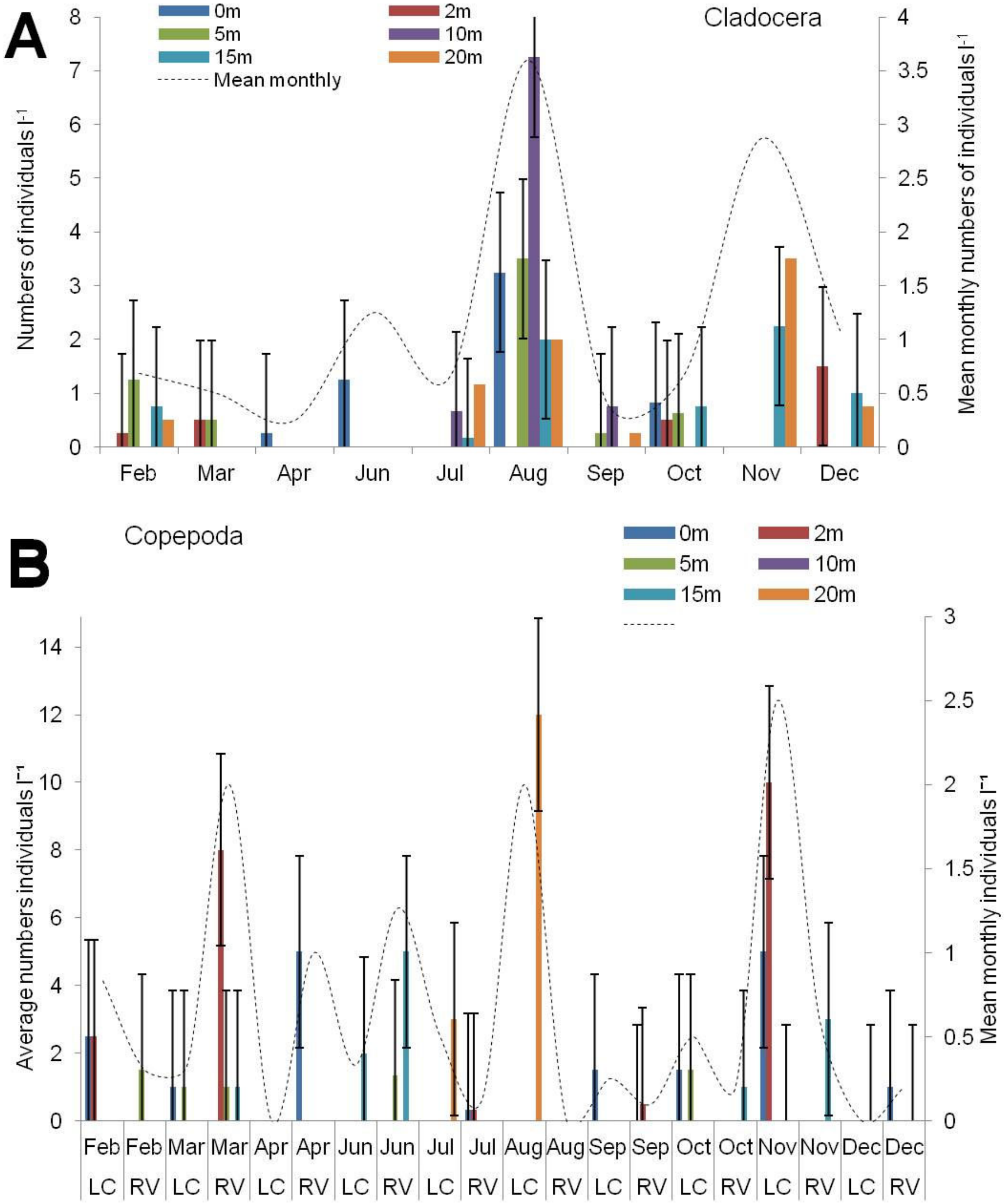


Figure 6.9. Monthly variations in A. Cladocera and B. monthly variations and habitat in Copepoda with water depth in the Sanyati Basin. Standard error of differences shown by bars

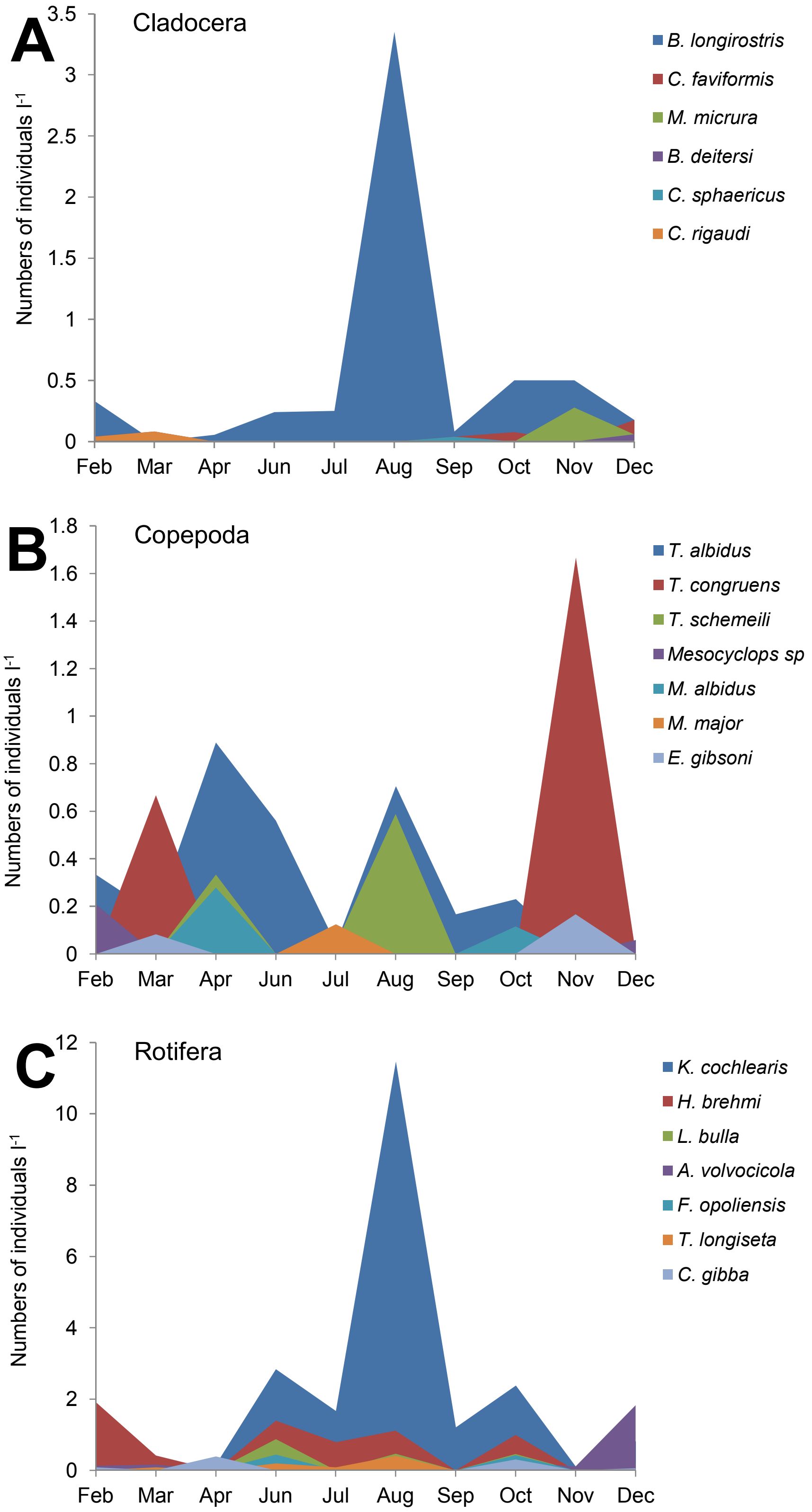


Figure 6.10. Monthly variation in concentrations of the most common A. Cladocera, B. Copepoda and C. Rotifera species in the Sanyati Basin

6.4. Discussion

Begg (1976) and Masundire (1997) found that Basin 1 exhibited the highest zooplankton species richness and concentrations, with these declining from the Zambezi River inflow in Basin 1 to Basin 4 along a decreasing nutrient concentration gradient. These findings were partly corroborated by this study, where only summertime Copepoda species richness and summertime Copepoda and Rotifera concentrations declined consistently between Basins 1 and 4. The observed summertime depth variations in zooplankton concentrations were attributed to changes in thermocline depth, which mostly confined the zooplankton to the epilimnion. Indeed, during summer when temperature stratification in the monomictic Lake Kariba intensifies and the hypolimnion becomes devoid of oxygen, zooplankton migrations are limited to the depth of the thermocline, as the deeper layers become less accessible to large zooplankton because of the lack of oxygen and food resources. This is evident from the majority of summer-time zooplankton peaks occurring in the 0 to 2 m water depth zone. However, wintertime Copepoda concentrations in the Sanyati basins peaked at 20 m water depth in lacustrine waters in August and at 15 m water depth in riverine waters in June. These findings supported those of Begg (1976), who reported that the most extensive depth migrations were by species of Copepoda, such as *Mesocyclops leuckadi*. This is due to the fact that adult Copepods can survive at oxygen-depleted water depths that are inaccessible to fish (Strickle *et al*., 1989), with Kizito (1998) reporting adult Copepoda survival for eight days at dissolved oxygen concentration as low as 0.50 mg l^{-1} in Lake Kivu. However, it is important to note that zooplankton is negatively phototactic with vertical migration behavior, and so resides at deeper places during the day. Therefore, with the current sampling scheme, some species might have been missed. Equally important to note, is that larger sized renders visual predation easier, forcing these macrozooplankton to 'shelter' in darker waters.

The observed peak in zooplankton concentration during winter turnover following stratification breakdown concurred with earlier studies that attributed this peak to increased phytoplankton abundance (Marshall, 1988; Masundire, 1997; Mandima, 1999). Similar zooplankton population peaks associated with winter turn-over have been reported in other monomictic lakes, such as Lakes Chad, Naivasha and Ziway (Mavuti and Litterick, 1981; Infante, 1982; Saint-Jean, 1983; Saunders and Williams, 1988; Belay, 1988), and in some meromictic tropical lakes such as Lakes Malawi and Valencia in Venezuela (Twombly, 1983; Saunders and Williams, 1988). Also, Lake Kivu's total crustacean concentration increases to a distinct seasonal maximum, following a rise of zooplankton production associated with a deep epilimnetic mixing in the dry season from August to September (Isumbisho *et al*., 2006). Masundire (1994) argued that the August peaks, as well as the secondary peaks observed in Lake Kariba during the rainy season (December-April), coincide with corresponding peaks in total phytoplankton biomass, with the mid-year peaks coinciding with a peak in Bacillariophyceae biomass. However, only the Copepoda exhibited a summer concentration peak in the present study, implying a change in the seasonality and a decline in concentration of the zooplankton during summer. This may well be explained by climate warming and the decline in the thermocline depth. Similarly, a decline in zooplankton during the rainy season has been observed in Lake George and Cabora Bassa (Burgis, 1971; Gliwicz, 1986). Decreased zooplankton productivity and biomass in Lake Kariba have often been observed in poor rainy seasons (Mills, 1977; Marshall, 1980, 1982, 1985) that are associated with decreased nutrient levels into the lake (Magadza, 1980; Marshall, 1982), and it is possible that this factor may also have contributed to the observed declines in zooplankton during this season in Lake Kariba.

Comparisons of measured zooplankton concentrations with those previously reported (Begg, 1976; Cochrane, 1978; Magadza, 1980; Marshall, 1980; Green, 1985 and Masundire, 1989, 1994; Mandima, 1999; Harding and Rayner, 2001) indicate a decline in zooplankton concentrations in the lake since 1975. However, Cladocera were exceptions, as this group displayed slightly elevated concentrations during 1986 and 2001 respectively, though these both declined thereafter to the present date (Figure 6.11). Cladocera were the most abundant group in 1975 (Cochrane, 1978), but their numbers have decreased by 93.3%, from over 15 individuals per litre to the present date of less than one individual per litre in the lake (Figure 6.11). Despite the overall reductions in zooplankton concentrations in Lake Kariba since 1975, substantial increases in species' richness have occurred among some zooplankton groups. For example, in 1975 only one cyclopoid, *Mesocyclops leuckartii* (later correctly identified as *Mesocyclops* sp. by Mandima, 1999) was reported in the lake (Begg, 1976), whereas in 1979 two calanoids (*Thermodiaptomus syngenes, Tropodiaptomus hutchinsonii*) and four cyclopoids (*Macrocyclops albidus*, *Mesocyclops leuckartii*, *Thermocyclops emini, and Thermocyclops oblongatus)* were reported *(*Magadza, 1980). However, in the present study, 11 calanoid species and four cyclopoid species were observed in the lake, with only one calanoid *M. albidus* and one cyclopoid *T. oblongatus*, previously recorded in the lake water, still present. However, the Cladocera species complement observed in the present study was similar in composition to that previously reported (Magadza, 1980; Masundire, 1994; Mandima, 1999), but the species in the current study were present at much lower concentrations.

In addition, several other zooplankton species, such as the dipterans *Chaoborus anomalis*, *Chaoborus ceratopogones* and *Chaoborus edulis* and the Daphnids, *Daphnia longispina, Ceriodaphnia dubia* and *Daphnia lumholtzi,* the largest Cladoceran in the lake which were previously reported in the lake (Magadza, 1980; Masundire, 1994; Green, 1985; Mandima, 1999), seem to have disappeared from Lake Kariba's especially in the Sanyati Basin, with only one unidentified *Chaoborus* species recorded in the lake in the present study. Apparently, some *Chaoborus* species do occur in the lake's littoral zone, a habitat where they seemingly avoid predation by *L. miodon* (Phiri, pers. comm.). *Daphnia lumholtzi* was occasionally recorded from some river-mouth locations in B5 and in the Mwenda River Mouth (Mills, 1977), and only in B2 (Masundire, 1997) but not in the pelagic zones of the other basins. This was consistent with the present study, though significantly lower numbers were recorded. All these zooplankton species are edible to *Limnothrissa* (Cochrane 1978, 1984; Mandima, 1999; Zengeya and Marshall, 2008). Only *Bosmina longirostris* has remained the dominant Cladocera species in the lake since the mid 1970's, though currently present at much lower concentrations than in the past. The observed retention of *Bosmina longirostris*'s dominance in Lake Kariba since 1975, despite its reduced concentration, may be explained by its ability to undergo cyclomorphic changes, such as increased translucency of head and reduction in body size, that diminish its likelihood of predation (Mellanby, 1983; Masundire, 1997).

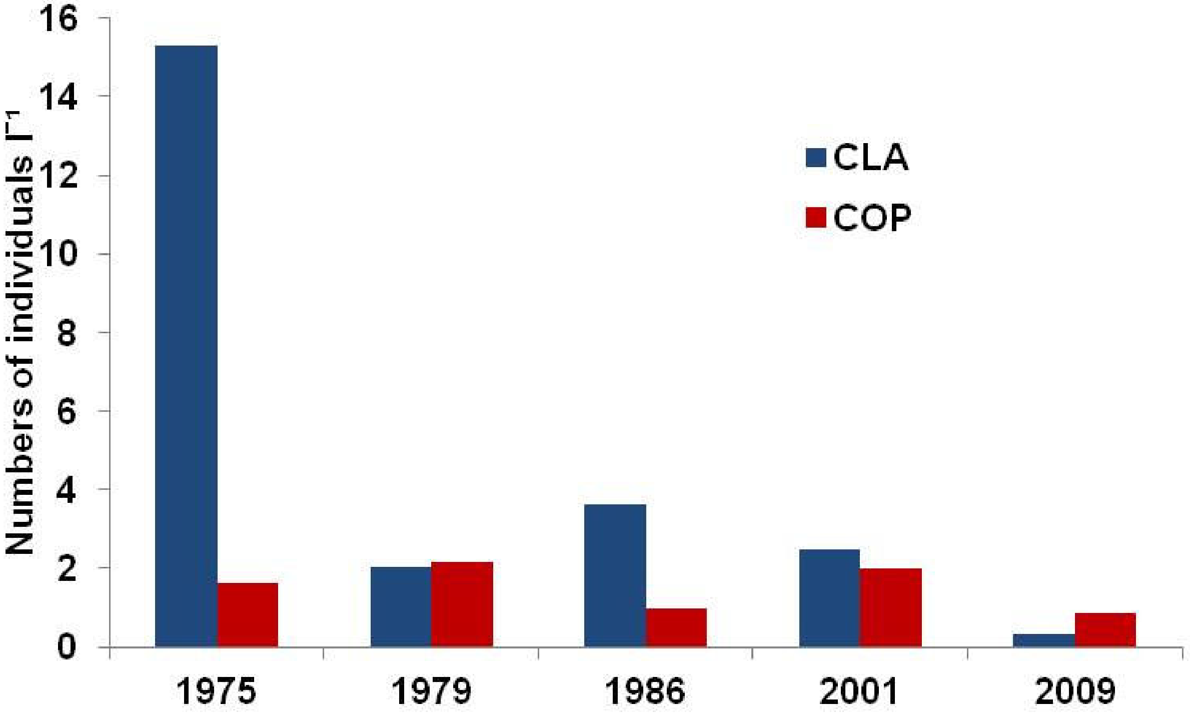


Figure 6.11. Variation in the concentration of two major zooplankton groups in Lake Kariba (1975-2009). CLA= Cladocera; COP= Copepoda. Source of data: Cochrane (1978), Marshall (1980), Masundire (1989) and Harding and Rayner (2001) and present study

The observed declines in Cladocera concentrations in Lake Kariba have been attributed to predation by fish, interspecific competition, elevated water temperature, and diminished phytoplankton abundance of especially palatable forms. The introduction of the sardine *L. miodon* into Lake Kariba resulted in a subsequent decline in *Daphnia* spp. concentrations (Green, 1985), with the presence of this and other species of Cladocera, such as *Bosminopsis deitersi* and *Bosmina longistrosis,* observed in *L. miodon* stomach constituents (Bell-Cross and Bell-Cross, 1971; Begg, 1976; Cochrane, 1978, 1984; Marshall, 1984, 1985, 1988; Machena, 1988; Fernando, 1994; Moyo, 1994; Sanyanga, 1996; Mandima, 1999; Chifamba, 2000; Moyo and Fernando, 2000; Zengeya and Marshall, 2008). Similarly, in Lake Tanganyika the elimination of another Cladocera species (*Chaoborus* sp.) has been blamed on predation by two endemic clupeids (Lowe-McConnell, 1987). Also, in Lake Kivu the introduction of *L. miodon* has resulted in the disappearance of *Daphnia curvirostris* (Isumbisho *et al*., 2006), this accompanied by a decline in total zooplankton biomass (Isumbisho *et al*., 2006), though the total Cladocera species complement remained fairly constant (De Iongh *et al*., 1983). Furthermore, fluctuations in abundance of predatory fish and invertebrates (Fryer, 1997; Phoon *et al*., 2004) in Lake Victoria have resulted in corresponding changes in zooplankton population structure, from that dominated in the 1930s and 1950s by large-bodied Calanoid and Cladocera species to those presently dominated by small-bodied species (Worthington, 1931; Rzoska, 1957, Mwebaza-Ndaula, 1994; Gophen *et al.*, 1995; Wanink, 1998). Also, in Ethiopia's Lake Alemaya (Lemma, 2003), the Bitter Lakes (Hobæk *et al*., 2002), and in Egypt's Lake Nasser (El Shabrawy and Dumont, 2003), the decline or rare occurrence of Cladocera has been attributed to predation by fish and invertebrates.

Apart from predation by fish, inter-specific competition may also lead to structural changes in the zooplankton populations. Among the Cladocera, *Daphnia* are the most efficient grazers, but competitive grazing superiority is strongly linked to vulnerability to predation, with efficient grazers the first victims of predators (Bengtsson, 1978). Cladocera in this study were not characterised by reduced species richness but by lower concentrations than in previous studies, this evident from the rarity of larger-sized *Ceriodaphnia dubia* and *Daphnia longispina* species that were abundant during the late 1970's (Magadza, 1980), with smaller Moinids currently more prevalent, the latter a consequence of higher predation levels among larger-sized species (Dumont, 1994).

There is also evidence that elevated water temperatures may affect zooplankton concentrations. Experimental warming of zooplankton populations in microcosms have shown diminished total zooplankton biomass, with large Cladocera species such as *Daphnia pulex* declining in abundance and smaller Rotifera species such as *Keratella cochlearis* and *Conochilus unicornis* increasing in abundance (Strecker *et al*., 2004). This trend is also evident in Lake Kariba, where large-sized Cladocera have declined and small-sized Rotifera and *Keratella* sp. are presently most abundant, these changes associated with an average 1.9°C temperature increase in the lake's epilimnion since the 1960s. Associated with reductions in zooplankton biomass with elevated water temperatures is an altered phytoplankton species composition towards high temperature-tolerant, normally unpalatable or large-size species (Doney, 2006). Similarly, Beisner *et al*. (1997) showed that zooplankton biomass, consisting of *D. pulex*, declined significantly in mesocosms that were heated from 18°C to 25°C. Overexploitation of food resources, increased metabolic costs, and a shift toward inedible filamentous Cyanophyceae were considered to be the primary causes of the decline and of the extinction of daphnids in the warmed mesocosms (Beisner *et al*. 1997). Cyanophyceae are particularly unpalatable and even toxic to zooplankton (Carmichael and Falconer, 1993; Christoffersen, 1996; Carmichael, 1997; Codd *et al*., 1999; Chorus, 2001; Ballot *et al*., 2005; Ndebele and Magadza, 2006), and their increased concentrations in Lake Kariba may also be linked to the overall decrease in zooplankton concentrations.

Changes in phytoplankton biomass have also been reported to affect zooplankton abundance, which is arguably determined more by food availability than fishing pressure and predation in Lake Kariba (Marshall, 1984; Paulsen, 1994). This argument is corroborated by Masundire (1990, 1991), who found the mean length of *Bosmina* responded more to the availability of food than predation pressure by *L. miodon*, whereas in Lake Kivu measurement of zooplankton body sizes indicated that fish predation affected mainly the Cladoceran *Diaphanosma excisum*, with larger Copepoda species escaping predation by migrating to the deep mixolimnion during daytime (Isumbisho *et al*., 2006). In the Hartbeespoort Dam, the primary determinant of zooplankton composition, size and biomass is also their food source, which comprises largely unpalatable Cyanophyceae dominated by small size (0.1 µm) *Microcystis* sp. (Van Ginkel *et al*., 2001). As a consequence, the zooplankton community comprises predominantly small-sized Copepoda, with larger-sized zooplankton such as *Chaoborus* sp. more common in deep waters where they escape from fish predation (Hely-Hutchinson, 1985).

The high species richness of Rotifera observed in Lake Kariba conforms to previous reports on zooplankton taxa in this lake and other tropical African lakes such as Chivero (Elenbaas and Grundel, 1994), Albert (Green, 1972) and Constance (Walz *et al*., 1987), where Rotifera is the most species rich zooplankton group. In fact, zooplankton populations of most tropical and subtropical lakes and reservoirs are dominated by rotifers (Figure 6.12) regardless of trophic state, but due to their small size and mass, they often contribute little to the biomass but can be very productive with high production/biomass (P/B) ratios (Marshall, 1997). In Kariba, the most abundant Rotifera species (*Keratella cochlearis)* had a total biomass up to 70 times smaller than that of the most abundant Cladocera (*B. longirostris)* and Copepoda (*T. oblongatus),* whose ability to utilise non-algal resources such as bacteria, ciliates and detritus (Mandima, 1999) may explain their relatively small changes in concentration in Lake Kariba since 1975.

Rotifera are especially tolerant of temperature variations (Barnes, 1968), as they undergo cyclomorphogenic changes under harsh conditions (Hickman *et al*. 2001), and this could explain their richness and high concentrations in Lake Kariba and other tropical African lakes where temperature is the most influential factor in the production chain (Karenge and Kolding, 1995; Chifamba, 2000). Cyclomorphosis could also perhaps explain the peak in Rotifera concentration at the water surface and at 2 m, observed in Basins 1 to 3 where temperatures normally exceed

30°C. In addition, cyclomorphosis has also been observed in the Cladocera *Daphnia cucullata* and a whole lot of daphnid species (Laforsh and Tollrian, 2004).

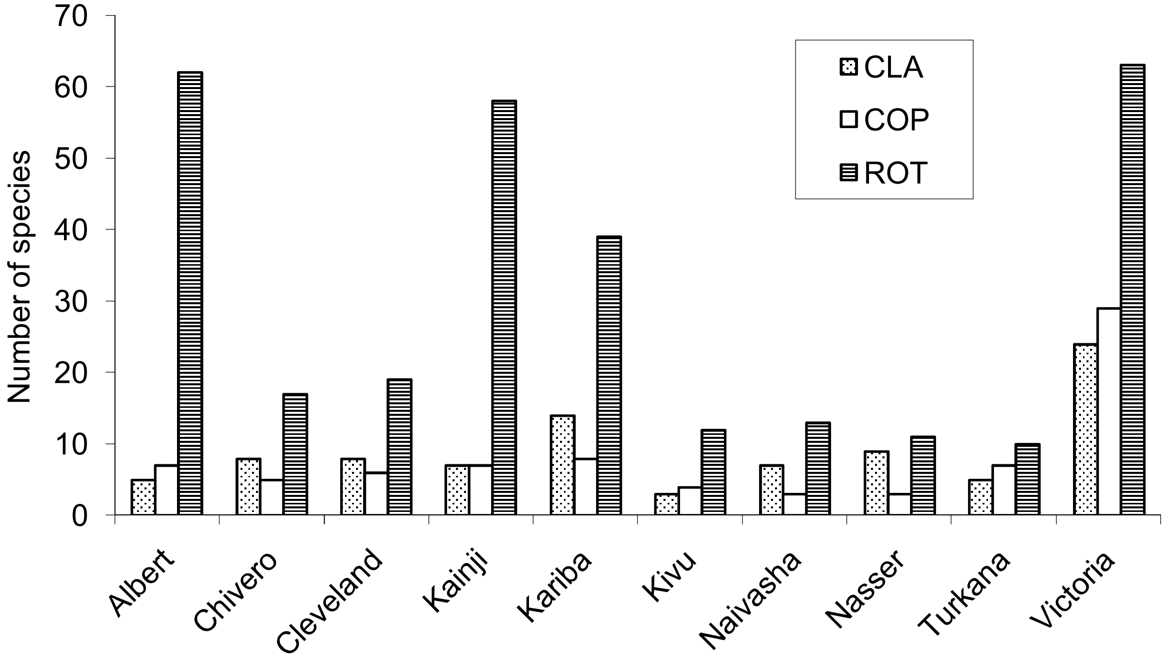


Figure 6.12. A comparison of the species richness of three major zooplankton groups in ten tropical water bodies: Lakes Albert, Chivero, Cleveland Dam (Elenbaas and Grundel, 1994), Kainji, Kariba (this study), Kivu (Isumbisho *et al*., 2006), Naivasha (Uku and Mavuti, 1987), Nasser (Mageed and Heikal, 2006), Turkana (Green, 1985) and Victoria (Mutune *et al*., 2007)

The estimation of zooplankton bio-volume (Hillenbrand *et al*., 1999) has proven to be a relatively easy measurement of zooplankton fresh biomass. The present range in zooplankton biomass was within the range recorded by Magadza (1980), who recorded an overall standing crop of zooplankton in the Sanyati Basin as ranging from 0.26 to 15.9 mg m^3 with an average of 2.76 mg m^{3,} as well as Masundire (1994), who reported a range of 0 to 26 mg m^{3,} with *B. longistrosis* and *Ceriodaphnia cornuta* and calanoids adults exhibiting the highest biomass. However, the biomass levels recorded in the present studies are significantly lower in comparison to those of earlier studies, suggesting a decrease in the zooplankton biomass of Lake Kariba since these past studies.

As the zooplankton of Lake Kariba is changing, there is a need to understand these changes in view of the success of the fish industry, particularly of *Limnothrissa miodon*, which primarily feeds on plankton and is dependent on adequate zooplankton production (Mandima, 1999; Zengeya and Marshall, 2008). Temporal variations may depend on changes in availability of edible phytoplankton and micro-zooplankton, which often vary, depending on physical processes that drive nutrient availability and depth of the mixed layer, which are known to be key factors determining primary production in tropical lakes (Beadle, 1981; Hecky and Kling, 1987; Sarmento *et al*., 2006). In addition, the influence of climate variability and climate changes in and around the lake need to be taken into account more extensively, as these are known to directly impact the limnology of lake waters as well as the phytoplankton community, since both factors determine zooplankton production. The generation times of many zooplankton, for instance, are primarily determined by temperature (Bottrell *et al*. 1976). Therefore, it seems highly likely that the zooplankton of Lake Kariba is being affected by climate warming through the reduction of nutrient inflows and therefore availability, coupled with the consequent, adverse effect on the phytoplankton productivity, whilst other factors (fish predation, inter-specific competition) act as secondary factors that shape the zooplankton community.

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Personal communication

Phiri C. Dr. (2009). University Lake Kariba Research Station, Kariba, Zimbabwe

Appendix 6.1. A list of Rotifera species in Lake Kariba (2007-2009). Species with an asterisk (*) denote species found in lake basins other than the Sanyati (Basin 5)

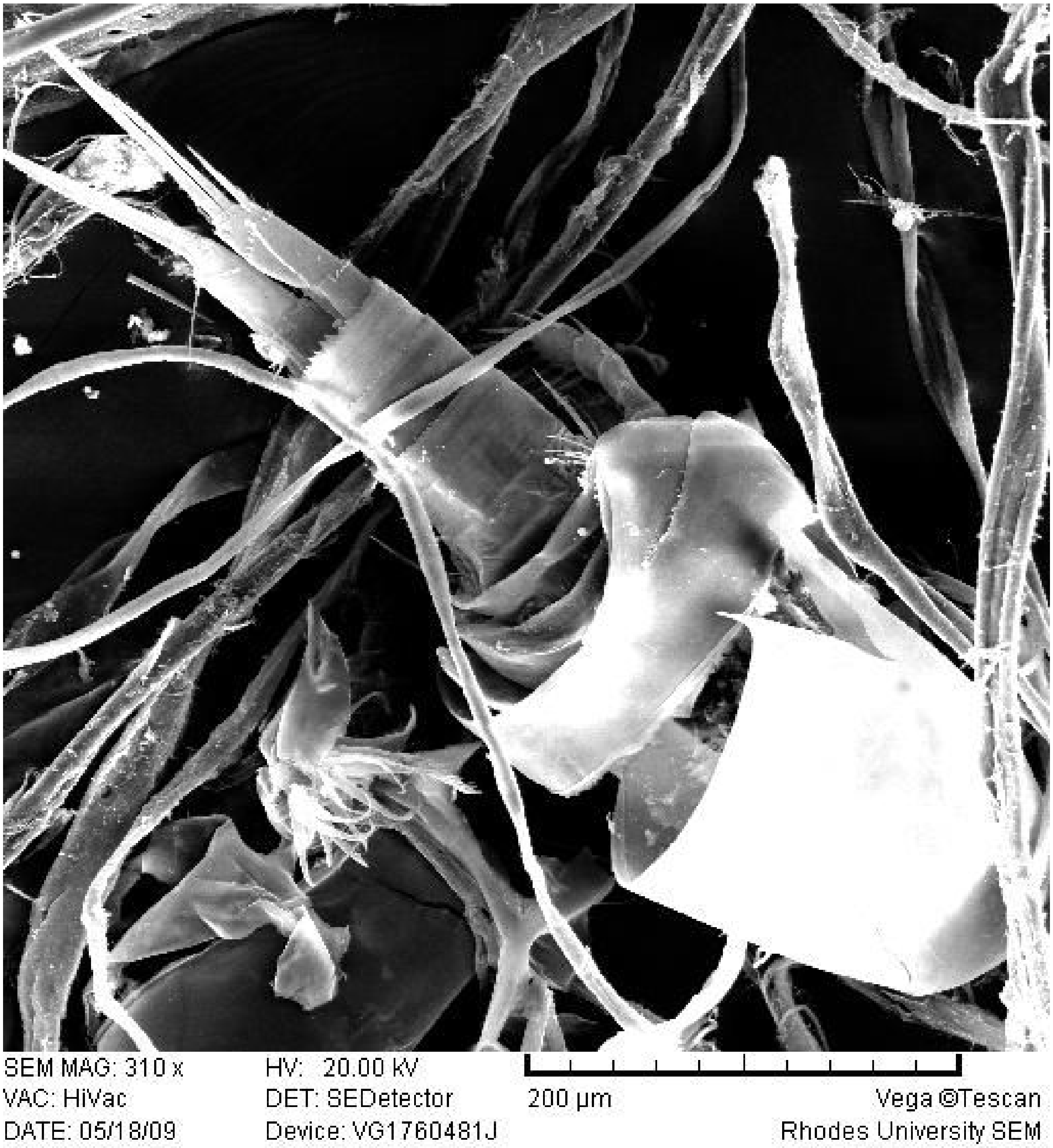
Species	Average concentration (individuals l^{-1})	**Species**	Average concentration (individuals l^{-1})
ROTIFERA		**ROTIFERA**	
Anuraeopsis fissa Gosse	0.009	*Horaella brehmi* Donner	0.068
Ascomorphella sp. Wiszniewski	0.012	*Horaella thomassoni* Koste*	0.001
Ascomorphella volvocicola Plate	0.009	*Lecane bulla* Gosse	0.018
Asplanchna brightwelli Gosse*	0.012	*Lecane elasma* Harring & Myers*	0.166
Asplanchna priodonta Gosse	0.050	*Lecane quadridentata* Ehrenberg	0.023
Asplachnopus sp. Guerne	0.006	*Keratella cochlearis* Gosse	0.507
Branchionus bidentata Anderson	0.012	*Keratella quadrata* Müller	0.151
Branchionus falcatus Zacharias	0.074	*Keratella serrulata* Ehrenberg	0.040
Branchionus havaniensis Lindeman	0.059	*Keratella tropica* Apstein	0.348
Branchionus quadridentata Hermann	0.163	*Keratella valga,* Ehrenberg	0.039
Cephalodella gibba Ehrenberg	0.045	*Macrochaetus* sp. Perty *	0.003
Collurela adriatica Ehrenberg	0.003	*Mytilina mucronata* Müller*	0.015
Conochilus sp. Ehrenberg*	0.003	*Notommata* sp. Ehrenberg	0.006
Cyrtonia tuba Ehrenberg	0.006	*Octoctrocha* sp. Thorpe	0.001
Eosophora sp Ehrenberg*	0.009	*Philodina* sp. Ehrenberg	0.006
Epiphanes clavulata Ehrenberg	0.021	*Ploesma citrina* Ehrenberg	0.005
Epiphanes senta Müller	0.012	*Ploesma* sp. Herrick	0.005
Euchlanis dilatata Ehrenberg	0.012	*Proales fallaciosa* Wulfert	0.009
Filinia cylindrica Bory de St. Vincent*	0.003	*Trichocerca chattoni* de Beauchamp*	0.145
Filinia longiseta Ehrenberg	0.001	*Trichocerca cylindrica* Imhof	0.042
Filinia minuta Smirnov	0.021	*Trichocerca elongata* Gosse	0.003
Filinia opoliensis Zacharias	0.015	*Trichocerca longiseta* Schrank	0.009
Hexarthra sp. Schmarda	0.012	*Trichocerca multicrinis* Kellicott	0.084
Hexarthra mira Hudson	0.193	*Trichocerca ruttneri* Donner *	0.003

Appendix 6.2. A list of Cladocera, Copepoda in the Sanyati Basin of Lake Kariba (2007-2009). Species with an asterisk (*) denote species found in lake basins other than the Sanyati (Basin 5)

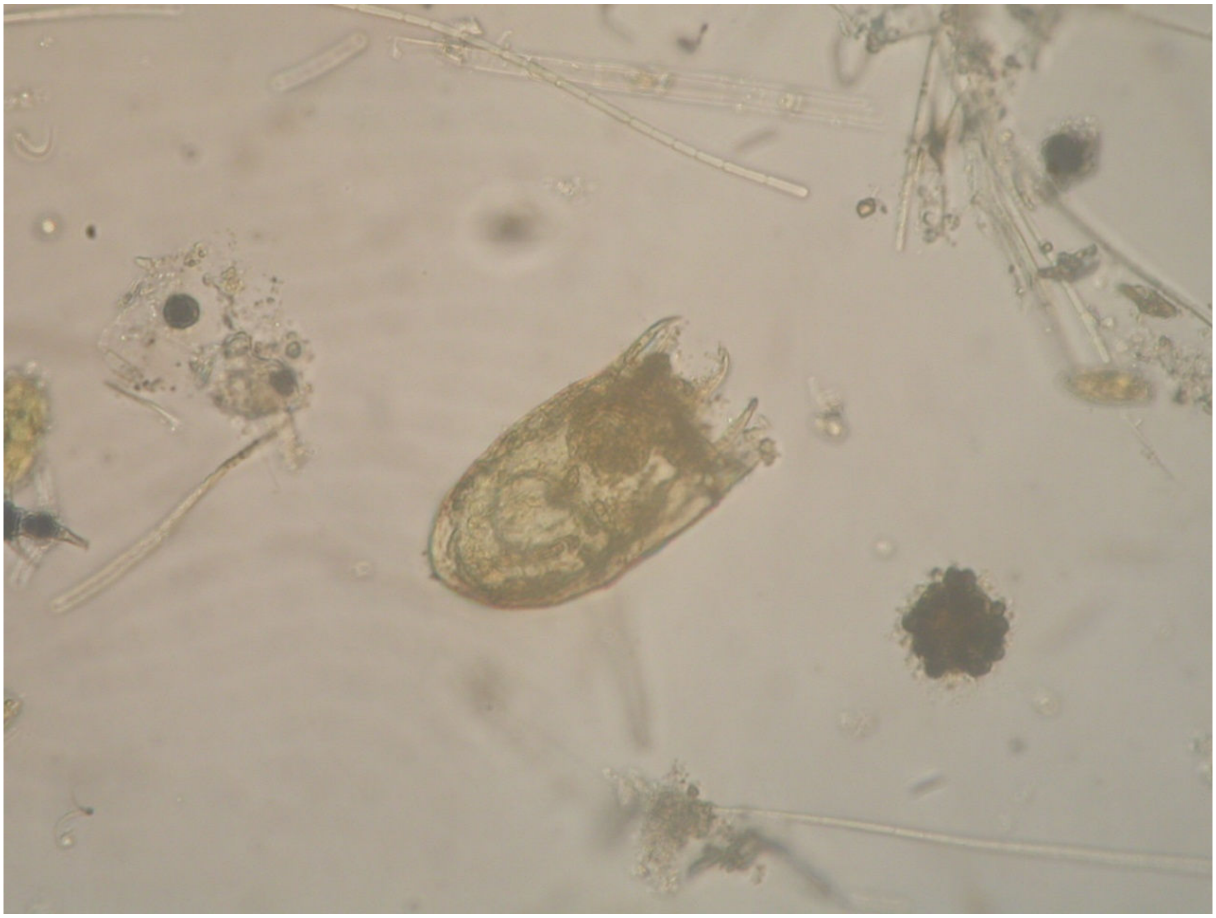
Species	Average concentration (individuals l^{-1})	**Species**	Average concentration (individuals l^{-1})
BRANCHIOPODA **CLADOCERA**		**COPEPODA** **CYCLOPODA**	
Bosmina longirostris O.F. Müller	0.522	*Ergasiloides macrodactylus* Sars*	0.030
Bosminopsis deitersi Richard	0.010	*Eucyclops gibsoni*	0.020
Ceriodaphnia dubia Richard*	0.001	*Macrocyclops albidus* Jurine	0.068
Ceriodaphnia rigaudi Richard	0.012	*Macrocyclops major* Jurine*	0.006
Chaoborus sp. *	0.012	*Mesocyclops* sp. Sars	0.042
Chydorus faviformis Birge	0.003	*Mesocyclops* leuckartii Claus Kurz	0.027
Chydorus sphaericus O.F. Müller	0.010	*Microcyclops* sp. *	0.009
Daphnia longispina O.F. Müller *	0.006	*Thermocyclops albidus* Mrazek	0.030
Daphnia lumholtzi Sars*	0.015	*Thermocyclops oblongatus* Mrazek *	0.125
Daphnia pulex Leydig*	0.006	**CALANOIDA**	
Diaphanosoma excisum Sars*	0.006	*Metadiaptomus capensis* G.O. Sars*	0.009
Eurycercus lamellatus O.F. Müller*	0.003	*Metadiaptomus colonialis* Van Douwe*	0.006
Moina micrura Kurz	0.006	*Thermodiaptomus corniculata* Keifer*	0.018
Moina tenuicornis Sars*	0.001	*Tropodiaptomus hutchinsonii* Keifer	0.018

Appendix 6.3. A comparison of Cladocera and Copepoda species complements in the Sanyati Basin between 1976 and 2009. '+g' = organism identified to genus level, '+' = organism present, '_' = absent and 'o. i. a. c.o.' = organism identified as copepods only

Species	Begg (1976)	Magadza (1980)	Masundire (1994)	Mandima (1999)	Mhlanga (2001)	Present study
Cladocera						
Bosmina longirostris	+	+	+	+	+	+
Bosminopsis deitersi	-	-	-	+	-	+
Ceriodaphnia cornuta	-	-	+	+	+	-
Ceriodaphnia dubia	-	+	-	-	-	-
Ceriodaphnia rigaudi	-	-	-	-	-	+
Chydorus faviformis	-	-	-	+	-	+
Chydorus sphaericus	-	-	-	-	-	+
Daphnia lumholtzi	-	-	+	+	-	-
Daphnia longispina	-	+	-	-	-	-
Diaphanosoma excisum	-	+	+	+	+	-
Moina micrura	-	-	+	+	+	+
Copepoda			o.i.a.c.o		o.i.a.c.o.	
Ergasilus sieboldi	-	-		-		+
Eucyclops gibsoni	-	-		-		+
Macrocyclops albidus	-	+		+g		+
Mesocyclops leuckartii	+	+		+g		-
Mesocyclops major	-	-		+g		+
Thermocyclops emini	-	+		+g		-
Thermocyclops oblongatus	-	+		+g		+
Thermodiaptomus mixtus	-	-		+g		+
Thermodiaptomus syngenes	-	+		+g		-
Tropodiaptomus	-	+		+g		-
Tropodiaptomus schemeili	-	-		+g		-



Appendix 6.4. SEM image of *Thermocyclops* sp. captured from Sampling Station 38 (Zambezi River Mouth) of Basin 1 in February 2009



Appendix 6.5. Photograph of *Keratella quadrata* (centre) sampled from Station 1 (Charara River Mouth) in October 2008; Magnification = X 400 with *Cylindrospermopsis* sp. (rods) in the background and *Microcystis* sp. colony (bottom right corner)

Appendix 6.6. SEM image of *Mesocyclops* sp. sampled from Sampling Station 7 (Sanyati River Mouth) in December 2008

Chapter 7

Associations between climate, water environment, plankton, and fish production

7.1. General Discussion

This study's review of phytoplankton dynamics in tropical African lakes detailed the different dynamics influencing phytoplankton in them. These included changing environments due to climate warming and anthropogenic influences that impact on stratification cycles, which then govern phytoplankton seasonality and nutrient dynamics, which in turn influence phytoplankton biomass. The limnological changes observed in Lake Kariba were diminished nitrogen and dissolved oxygen concentrations, increased acidity (decreased pH), water temperatures, phosphorus concentrations and conductivities, as well as a more stable and prolonged thermocline.

The decline in overall nutrient levels in the lake epilimnion is due to the more stable thermocline associated with an average of 0.34°C per decade increase in air temperature in the Zambezi Valley, this nearly double the IPCC (2007) global average of 0.2°C per decade, and an 0.63 mm yr^{-1} reduction in annual precipitation, accompanied by a 25% increase in pan evaporation. The elevated air temperatures have altered the lake's thermal properties, reflected as an average 1.9°C temperature increase in the lake's epilimnion since the 1960's, and a reduction in the depth of the thermocline evident from the smaller metalimnion temperature gradient, and an upward movement of the depleted (<2 mg l^{-1} DO) oxygen layer. As a consequence, the volume of the epilimnion has shrunk by 80%, resulting in a 50% reduction in the euphotic zone and a rapid decline in overall nutrient levels, especially nitrogen concentrations which presently are lower than those previously measured in the 1960s and 1980s. These changes in lake thermal properties have negatively affected plankton and fish production. Phytoplankton biomass and primary production rates in Lake Kariba have declined by 95% and 57% since the last long-term phytoplankton study of 1986 to 1990 (Cronberg, 1997), such declines also reported in other tropical African lakes and attributed to climate warming (O'Reilly *et al.*, 2003; Verburg *et al.*, 2003; Verburg and Hecky, 2009). The correspondence observed between seasonal changes in phytoplankton productivity, rainfall, and temperature, both in Lake Kariba and in other tropical African lakes, such as Malawi and Tanganyika (Vollmer *et al.*, 2002, 2005; O'Reilly *et al.*, 2007; Stenuite *et al.*, 2007) point to a causal connection between climate, nutrients, and primary productivity.

Water temperature is considered the predominant factor affecting plankton production in tropical African lakes such as Lake Malawi (Vollmer *et al.*, 2002, 2005) and Lake Tanganyika (O'Reilly *et al.*, 2003; Verburg *et al.*, 2003; Descy *et al.*, 2006; Guildford *et al.*, 2007; Stenuite *et al.*, 2007; Verburg and Hecky, 2009). It affects not only phytoplankton biomass and species dominance but also phytoplankton photosynthetic efficiency, as demonstrated by O'Reilly *et al*. (2003) in Lake Tanganyika. In this study, phytoplankton analyser-enumerated Cyanophyceae and Chlorophyceae biomasses were positively correlated with lake water temperatures in the range of 19.7 to 32.3ºC, though the converse was evident with respect to the microscopically-enumerated Cyanophyceae and Chlorophyceae concentrations and those of the Dinophyceae and Chrysophyceae (Table 7.1). The observed positive correspondence between Cyanophyceae biomass and water temperature concurred with previously reported positive responses to elevated water temperature by species of Cyanophyceae (Robarts and Zohary, 1987) with, for example, *Microcystis* sp. reported growing best at water temperatures of 30ºC to 35ºC (Imamura, 1981). Indeed, the dominant Cyanophyceae *Cylindrospermopsis raciborskii* present in Lake Kariba grows optimally at water temperatures of 25°C to 30°C (Briand *et al*., 2004). This species' rapid spread and invasive behaviour is attributed to its physiological tolerance to high light intensities and water temperatures (Komárek, 2002), which, together with its low palatability and allelopathy (Branco and Senna 1994; Figueredo *et al*., 2007), may explain its geographical expansion with climate warming (Padisák, 1997; Briand *et al*., 2004).

Phytoplankton analyser-enumerated Bacillariophyceae biomasses were negatively correlated with water temperature, with the converse also evident with respect to the microscopically enumerated Bacillariophyceae concentrations. The negative correspondence observed between Bacillariophyceae biomass and water temperature supported the proposal that, with elevated water temperatures, phytoplankton succession follows a progression from Bacillariophyceae through to Chlorophyceae to Cyanophyceae, including a decline in larger-size species (Pliński and Jóźwiak, 1999). The proposed progression of Chlorophyceae to Cyanophyceae with elevated water temperature is supported by studies of mixed algal cultures of Chlorophyceae and Cyanophyceae from Lake Chivero, in which it was found that elevated water temperatures in the range 21 to 26ºC increased the biomass of Cyanophyceae and decreased that of the Chlorophyceae, with the former gaining a selective advantage at 22°C and the latter at 26°C (Sibanda, 2003). Noteworthy also was the exceptionally low contribution by Chlorophyceae to total phytoplankton biomass, even though this class possessed the highest species richness. The high Chlorophyceae species richness conforms to previous reports (Cronberg, 1997), though the relative contributions by Chlorophyceae and Bacillariophyceae to total phytoplankton biomass has decreased slightly since the 1980's (Ramberg, 1987). The current ratio of 1:4:10 for the Chlorophyceae, Bacillariophyceae and Cyanophyceae biomasses represents a skewed distribution, slightly different to that of 1:3:8 reported by Ramberg (1987) for the same taxa.

Table 7.1. t-statistics for Pearson correlations between measured biomasses and concentrations of different phytoplankton and zooplankton taxa and lake water physical and chemical properties. Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001

Taxa	**Lake water physical and chemical properties**								
	Temp	pH	DO	Cond	TDS	Total N	PO_4^{3-}	DOC	PAR
Phytoplankton biomass (μg Chlorophyll l^{-1})					**$t_{1,434}$**				
Cyanophyceae	**2.67****	**2.23***	**-2.40****	**-3.48*****	1.47	1.29	**-2.29***	**-4.14*****	-1.39
Bacillariophyceae	**-5.15*****	**1.70***	-1.01	-1.37	1.61	**4.11*****	-0.99	**-3.36*****	-1.26
Chlorophyceae	**7.43*****	**-4.78*****	-0.26	**-2.89****	**1.81***	**4.66*****	0.28	0.35	**-3.86*****
Phytoplankton concentration (individuals l^{-1})					**$t_{1,434}$**				
Cyanophyceae	**-3.59*****	-0.81	**2.25***	**3.03****	-1.05	**3.13*****	0.46	0.26	-0.27
Bacillariophyceae	**2.39****	**2.01***	-1.38	**2.67****	-0.09	**1.69***	-1.08	**-1.87***	-0.28
Chlorophyceae	**-3.30*****	-0.97	**2.48****	1.42	1.16	**4.42*****	**2.29***	-0.95	**1.70***
Dinophyceae	**-1.71***	0.17	**4.00*****	-0.86	0.61	0.82	**1.83***	-1.31	1.20
Euglenophyceae	1.36	-0.66	1.55	-0.22	0.67	**1.89***	**2.96****	-0.66	-0.91
Chrysophyceae	**-2.50****	-1.15	**3.04****	-0.37	**2.01***	**2.33****	**4.33*****	-1.10	0.05
Zooplankton concentration (individuals l^{-1})					**$t_{1,309}$**				
Cladocera	**-2.77****	-0.68	-0.55	-0.57	-0.96	**2.99****	-0.64	0.11	**-2.29***
Copepoda	1.36	0.30	-1.64	-0.40	**-1.74***	1.05	-0.28	-0.46	**2.09***
Rotifera	**2.39****	0.70	1.53	-0.96	**-1.80***	**2.96****	-0.80	0.68	0.43

These altered ratios indicate slight increases in Cyanophyceae and Bacillariophyceae biomasses, relative to the Chlorophyceae, with the unexpected small relative increase in Bacillariophyceae due possibly to the inability of the phytoplankton analyser to distinguish Bacillariophyceae from Dinophyceae with similar absorption spectra (Mantoura *et al*., 1997).

It has been argued that the effects of elevated water temperature on phytoplankton are often reflected as changes in community composition rather than in overall biomass (Doney, 2006; Thompson *et al*., 2008), since phytoplankton communities often show greater diversity of species during periods of high temperature (Egborge, 1974). Also, warming often results in the replacement of large phytoplankton taxa by smaller taxa (Sommer and Lengfellner, 2008). For example, Strecker *et al*. (2004) observed that warming altered Chlorophyceae composition by favouring smaller-sized phyto-flagellates (*Mallomonas*, *Synura*, *Trachelomonas*) over larger, filamentous Chlorophyceae (*Mougetia*, *Phymatodocas*). In this study also, substantially lower *Mougetia* concentrations were observed at warmer water temperatures during summer (15.8 cells l^{-1}) than during winter (0.2 cells l^{-1}). In addition, smaller (≤ 2 μm) picophytoplankton species including mostly single-celled synechococcoid species and Cyanophyceae and several chlorococcal species such as *Chlorella* and *Choricystis* (Reynolds *et al*., 2002), proliferated in Lake Kariba during summer, with fewer larger species (*Ceratium*, *Microcystis*, *Peridinium* and *Volvox*), comprising mostly unpalatable Cyanophyceae and Dinophyceae apparent.

It has been reported that Bacillariophyceae biomass and phytoplankton primary production has decreased substantially in Lake Tanganyika, due to diminished mixing of lake water caused by reduced wind action and a 0.9°C warming of the epilimnion, which collectively have intensified stratification and reduced nutrient, especially silica, levels (O'Reilly *et al*., 2003; Verburg *et al*., 2003; Sarvala *et al.,* 2007). These findings, and the increase in Cyanophyceae and decline in winter Bacillariophyceae biomasses also observed in Lake Kariba in this study, repudiated Cronberg's (1997) assertion of steady phytoplankton seasonality. In fact, weekly observations on primary production and phytoplankton densities in Lake Kinneret (Israel) over a 35-year period have revealed deviations from the predictable *Peridinium gatunense* blooms during spring, and the intensified *Aulacoseira granulata* blooms during winter (Zohary 2004). Also, in this lake palatable nanoplankton present in the high summer phytoplankton biomass have been replaced by less palatable forms, and there has been a new appearance and an increase in absolute biomass of toxin-producing, nitrogen-fixing cyanobacteria (Zohary, 2004).

Unlike water temperature, total nitrogen levels in Lake Kariba water were positively correlated with both phytoplankton analyser enumerated biomasses and microscopically enumerated concentrations in all phytoplankton classes, except in the Cyanophyceae (Table 7.1). The ability of heterocyst-forming Cyanophyceae to fix nitrogen may partly explain the absence of a positive correlation between phytoplankton analyser-enumerated Cyanophyceae biomasses and lake water nitrogen levels. Conversely, the positive correlation observed between microscopically enumerated Cyanophyceae concentrations and total N concentrations may reflect migration of some flagellated Cyanophyceae, up and down the water column in response to nutrient supply. In Lake Kariba it has been reported that the waters are principally P-limited for most of the year (Moyo, 1991; Magadza, 1992). This report is supported by the significant positive correlations observed between ortho-phosphate levels in Lake Kariba water and microscopically enumerated Chlorophyceae, Dinophyceae, Euglenophyceae and Chrysophyceae concentrations, though a significant negative correlation was observed between ortho-phosphate levels and phytoplankton analyser-enumerated Cyanophyceae biomasses (Table 7.1). Improved phytoplankton photosynthetic rates and growth in tropical waters have been attributed to an increased nutrient supply during the rainy season (Melack, 1979), with peak phytoplankton biomasses in the Wetlands Lakes of North Africa corresponding with elevated phosphorus levels (Fathi *et al*., 2001). In fact, phytoplankton community composition is affected by nutrient supply in several tropical African lakes. In Lake Victoria, for example, increased concentrations of heterocyst-forming Cyanophyceae such as *Anabaena* and *Microcystis,* and decreased concentrations of Bacillariophyceae such as *Aulacoseira,* have been reported in response to elevated nutrient levels (Haande *et al*., 2010). Also, increased concentrations of the Cyanophyceae *Microcystis aeruginosa* and *Anabaenopsis arnoldii* in response to nutrient enrichment, have been reported in the alkaline Lake Turkana (Mageed and Heikal, 2006), with *Microcystis* also forming a dominant component of the hyper-eutrophic Lakes Chivero and Victoria (Magadza, 2003; Mhlanga *et al*., 2006; Ochumba and Kibaara, 1989), due to its ability to rapidly exploit available nutrients (Harding, 1997). Similarly, in Lake Malawi the Cyanophyceae *Anabaena* and *Cylindrospermopsis* have recently become more pervasive, due to nutrient enrichment caused by increased anthropogenic activities in the lake's catchment (Hecky and Kling, 1987; Bootsma, 1993; Patterson and Katchinjika, 1995).

There was relatively poor correspondence between other lake-water physical and chemical properties (TDS, DOC, PAR) and phytoplankton abundance. The positive correlations found between dissolved oxygen concentrations and phytoplankton analyser-enumerated Cyanophyceae biomasses, and microscopically enumerated Cyanophyceae, Chlorophyceae, Dinophyceae and Chrysophyceae concentrations (Table 7.1), seemingly reflected photosynthetic oxygen evolution by the phytoplankton.

Also, photosynthetic active irradiances were negatively correlated with phytoplankton analyser-enumerated Chlorophyceae biomasses, which pointed to possible photo-inhibition of phytoplankton photosynthesis at high solar irradiances, though the weak positive correlation observed between microscopically enumerated Chlorophyceae concentrations and photosynthetic active irradiances did not entirely support this premise.

It has been reported that phytoplankton growth is limited at photosynthetic active irradiances above 615 µE m^{-2} s^{-1} (Domingues *et al*., 2011), yet in this study photosynthetic active irradiances exceeding 2 000 µE m^{-2} s^{-1} were frequently recorded in Lake Kariba's surface waters. At such high irradiances, photo inhibition of phytoplankton photosynthesis has been observed in surface waters of Lake Awassa (Ethiopia), where the vertical distribution of phytoplankton is typical of light-inhibited photosynthetic activity on all but overcast days (Kifle and Belay, 1990). Similarly, in Lake Tanganyika, high photosynthetic active irradiances in surface waters are associated with an increased fraction of light-acclimated pico phytoplankton in the phytoplankton biomass (Stenuite *et al*., 2009), whereas in Lake Malawi small-size (<2 µm) light-acclimated phytoplankton in the lake surface water account for 30-50% of the total phytoplankton chlorophyll (Guildford *et al*., 2007). In contrast, Schager and Oduor (2007) found no photo inhibition of phytoplankton in Lakes Bogoria, Nakuru and Elmentaita in Kenya, where phytoplankton photosynthesis is likely more severely inhibited by the high water salinities.

With respect to the zooplankton, the negative correlations found between water temperature and Cladocera concentrations, and opposing positive correlation between water temperature and Rotifera concentrations, conformed to results obtained from experimental warming of zooplankton populations in microcosms. These have shown that large Cladocera species, such as *Daphnia pulex,* decline in abundance, and smaller Rotifera species, such as *Keratella cochlearis* and *Conochilus unicornis,* increase in abundance with warming (Strecker *et al*., 2004). Similarly, Beisner *et al*. (1997) showed that zooplankton biomass, consisting of *Daphnia pulex*, also declined significantly in mesocosms that were heated from 18°C to 25°C. These findings were further supported by the observed decline in large-sized Cladocera associated with an average 1.9°C temperature increase in Lake Kariba's epilimnion since the 1960s, while small-sized Rotifera species have remained in abundance. Over-exploitation of food resources, increased metabolic costs, and a shift toward inedible filamentous Cyanophyceae are considered to be the primary causes of the decline in large Cladocera species with warming (Beisner *et al*. 1997). Cyanophyceae are particularly unpalatable and even toxic to zooplankton (Carmichael and Falconer, 1993; Christoffersen, 1996; Carmichael, 1997; Codd *et al*., 1999; Chorus, 2001; Ballot *et al*., 2005; Ndebele and Magadza, 2006), and their increased concentrations in Lake Kariba may also be linked to the overall decrease in zooplankton concentrations.

Classical models of phytoplankton-zooplankton interactions show that adverse conditions lead to reduced phytoplankton species richness and biomass, which in turn result in diminished zooplankton and fish production (Marshall, 1997). Thompson (2009) proposed that the impact of adverse conditions on higher trophic organisms, such as zooplankton and fish, would be proportionately greater than on phytoplankton, as demonstrated in warming experiments (Petchey *et al*., 1999; Strecker *et al*., 2004; Daufresne *et al*. 2009). In Lake Kariba, early winter peaks in phytoplankton biomass were closely followed by late winter peaks in zooplankton biomass and *Limnothrissa miodon* (Kapenta) fish catches per unit effort (Figure 7.1A). The negative correspondence between the other zooplankton classes and phytoplankton, (Table 7.2) can be explained by the preferential feeding on larger phytoplankton by adult Copepoda and on smaller phytoplankton by adult Cladocerans (Sommer *et al*., 2001). The recent proliferation of small-sized phytoplankton in Lake Kariba is a likely consequence of the diminished Cladocera populations with climate warming, due to their greater sensitivity to elevated water temperatures as discussed above. Also, Cyanophyceae are generally considered unpalatable to zooplankton because of their large size, poor nutritional content, and high toxicity, yet the increased Cyanophyceae biomass in Lake Kariba has been accompanied by an increase in Rotifera species richness and abundance, which suggests that Rotifera are tolerant of Cyanophyceae as a food source. This suggestion is supported by Soares *et al*. (2010), who recently reported that the Cyanophyceae *Cylindrospermopsis raciborskii,* the most abundant phytoplankton in Lake Kariba, is less harmful to Rotifera taxa such as *Keratella* sp. However, it is important to note that negative correlation values can be reflecting a lagged effect between food and grazer and/or an avoidance of the named ‘food’.

The observed decline in zooplankton biomass and altered zooplankton composition, towards increased abundance of small-sized Rotifera over the large-sized Copepoda and Cladocera in Lake Kariba, point to a control by phytoplankton caused by the proliferation of unpalatable species, such as *Microcystis*, *Ceratium* and *Peridioniopsis,* on zooplankton abundance, rather than to predation by *Limnothrissa miodon* (Kapenta) in compliance with the cascade hypothesis (Paulsen, 1994; Marshall, 1997). This, despite the reported close correspondence between the movement of the sardine *Limnothrissa miodon* (‘Kapenta’) and zooplankton in Lake Kariba (Begg 1976), the distribution of both, however, highly patchy (Magadza, 1980; Lindem, 1988; Marshall, 1988).

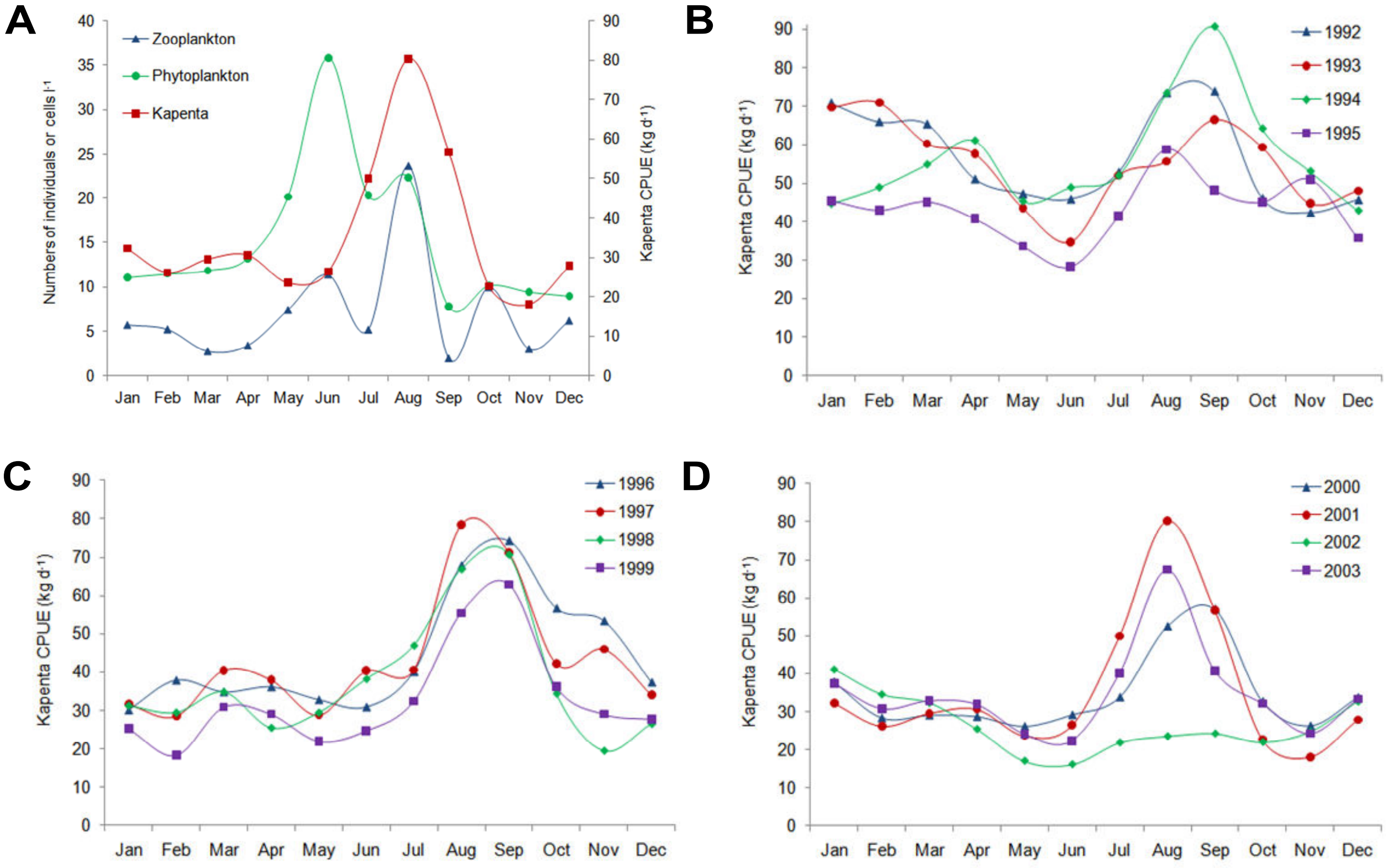


Figure 7.1. Monthly variation in A. phytoplankton cellular, zooplankton individuals' concentration and Kapenta catch (CPUE kg d^{-1}) in the Sanyati Basin coincident with this study, and Kapenta CPUE from B. 1992 to 1995, C. 1996 to 1999 and D. 2000 to 2003 in the whole lake.

Table 7.2. t-statistics for Pearson correlations between measured concentrations of different phytoplankton and zooplankton taxa. Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001

Phytoplankton class	Zooplankton class		
	Cladocera	Copepoda	Rotifera
Cyanophyceae	$t_{1,303} = 0.76$	$t_{1,303} = -0.01$	$t_{1,303} = -0.12$
Bacillariophyceae	$t_{1,303} = -0.77$	$t_{1,303} = 1.35$	$t_{1,303} = 1.43$
Chlorophyceae	$t_{1,303} = -1.26$	$t_{1,303} = -0.46$	$t_{1,303} = 0.19$
Dinophyceae	$t_{1,303} = -1.20$	$t_{1,303} = -0.41$	$t_{1,303} = 1.49$
Euglenophyceae	$t_{1,303} = -0.17$	$t_{1,303} = -0.05$	$t_{1,303} = -0.21$
Chrysophyceae	$t_{1,303} = -0.53$	$t_{1,303} = 0.39$	$t_{1,303} = -0.07$

Seasonal changes in plankton and fish production are effected by water circulation and availability of nutrients in the water column, which in turn are determined by stratification and variations in temperature. Begg (1976) reported increased zooplankton abundance during circulation, and Mtada (1987) found a high negative correlation between thermal stratification and monthly Kapenta catches, which were reduced during periods of strong thermal stratification and increased during circulation in Lake Kariba. Therefore, peaks in phytoplankton biomass (Ramberg, 1987; Cronberg, 1997) and zooplankton production (Magadza, 1980; Masundire, 1989, 1991, 1992, 1994, 1997) in Lake Kariba coincide with nutrient fluxes caused by both river inflow and turnover, and these in turn are followed by peaks in fish production (Marshall, 1982; Zengeya and Marshall, 2008). Similarly, an increase in pelagic plankton biomass at the end of the dry season during the windy period of August/ September in Lake Kivu has been associated with a Kapenta peak (De Iongh, 1983; Sarmento *et al.*, 2006, 2008, 2009a, 2009b).

Historical records of Kapenta catches per unit effort over the period 1974 to 2003 point to a consistent decline in Kapenta catches since 1986 (Figure 7.2A) in all the basins (Figure 7.2B), in all the four seasons (Figure 7.2C), with the largest decline apparent during early winter in June (Figure 7.2D). The regression functions, derived from least squares regressions of Kapenta catch per unit effort against years (Table 7.4), predict negligible Kapenta fish yields in the lake by the year 2020 in Basin 5, 2012 in Basin 4, 2025 in Basin 3, and 2016 in Basin 2. Previous studies have reported that Kapenta yields vary according to changes in lake water levels, with periods of drought being characterised by low catches (Marshall, 1982 and 1988; Karenge, 1992; Magadza, 1994; Karenge and Kolding, 1995), presumably because the nutrient supply to the lake is reduced by decreased river inflows. Marshall (1982) reported a significant correlation between Kapenta catches and rate of Sanyati River inflow, though not with the rate of the Zambezi River inflow which contributes over 70% of the water flowing into Lake Kariba. However, Chifamba (2000) found that correlations between mean length of Kapenta and various environmental and hydrological factors in Lake Kariba were mostly insignificant. In this study, mostly negative correlations were found between Kapenta catch per unit effort and lake water levels (Table 7.3). Similarly, Stauch (1977) reported a significant inverse correlation between falling lake levels in Lake Chad and increased fish catches between 1969 and 1974, this attributed to the concentration of fish stocks and the increased ease of fish capture, as in subsequent years the fish yields fell sharply. Also, fish yields in the shallow Lake Chilwa in Malawi have been reported to vary with lake level (Furse *et al*., 1979), with cichlid fish catches in Lake Malawi shown to be predictable three years in advance from recorded level changes in the lake (Tweddle and Magasa, 1989). In addition, a linear correlation between commercial fish catch rates and the previous years' mean lake level have been observed over a 16-year period in Lake Turkana in Kenya (Kolding 1989, 1992), with variations in water levels of a Tasmanian lake also reported as the principal factor dictating the dynamics of trout populations (Davies and Sloane, 1988).

Table 7.3. t-statistics for Pearson correlations between measured Kapenta catch (CPUE kg month-1) and temperature, rainfall and lake level. Values in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$. The Kapenta catch statistics returned by commercial fishing companies between 1974 and 2003 to the Lake Kariba Fisheries Research Station and expressed as kg wet weight of Kapenta caught per standard unit net panel 45.7 m in length

Basin	Max temp	Min temp	Rainfall	Lake level
Basin 5	$t_{1,214} = -0.268$	$t_{1,214} = -0.3727$	$t_{1,214} = -0.4725$	$t_{1,214} = \mathbf{-3.835***}$
Basin 4	$t_{1,214} = \mathbf{-2.839**}$	$t_{1,214} = \mathbf{-3.420***}$	$t_{1,214} = -0.984$	$t_{1,214} = \mathbf{-2.725**}$
Basin 3	$t_{1,214} = \mathbf{-4.663***}$	$t_{1,214} = \mathbf{-5.504***}$	$t_{1,214} = \mathbf{-3.481***}$	$t_{1,214} = -1.1721$
Basin 2	$t_{1,214} = \mathbf{-3.120**}$	$t_{1,214} = \mathbf{-2.539**}$	$t_{1,214} = -0.262$	$t_{1,214} = \mathbf{-3.542***}$
Basin 1	$t_{1,104} = -0.486$	$t_{1,104} = -0.269$	$t_{1,104} = 1.132$	$t_{1,104} = \mathbf{-2.533**}$

Table 7.4. t-statistics for slopes and intercepts of least squares regressions of Kapenta catch (CPUE kg month^{-1}) against year for the period 1986 to 2004. Values in bold significant at $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$

Basin	Intercept	t-statistic	Slope	t-statistic
Basin 5	3821.0862	$\mathbf{t_{1,216} = 7.983***}$	-1.8920	$\mathbf{t_{1,216} = -7.884***}$
Basin 4	3367.5357	$\mathbf{t_{1,216} = 9.661***}$	-1.6740	$\mathbf{t_{1,216} = -9.578***}$
Basin 3	2525.6650	$\mathbf{t_{1,216} = 6.274***}$	-1.2471	$\mathbf{t_{1,216} = -6.179***}$
Basin 2	3018.2032	$\mathbf{t_{1,216} = 8.269***}$	-1.4971	$\mathbf{t_{1,216} = -8.181***}$
Basin 1	1061.8651	$t_{1,106} = 1.736$	-0.5155	$t_{1,106} = -1.683$

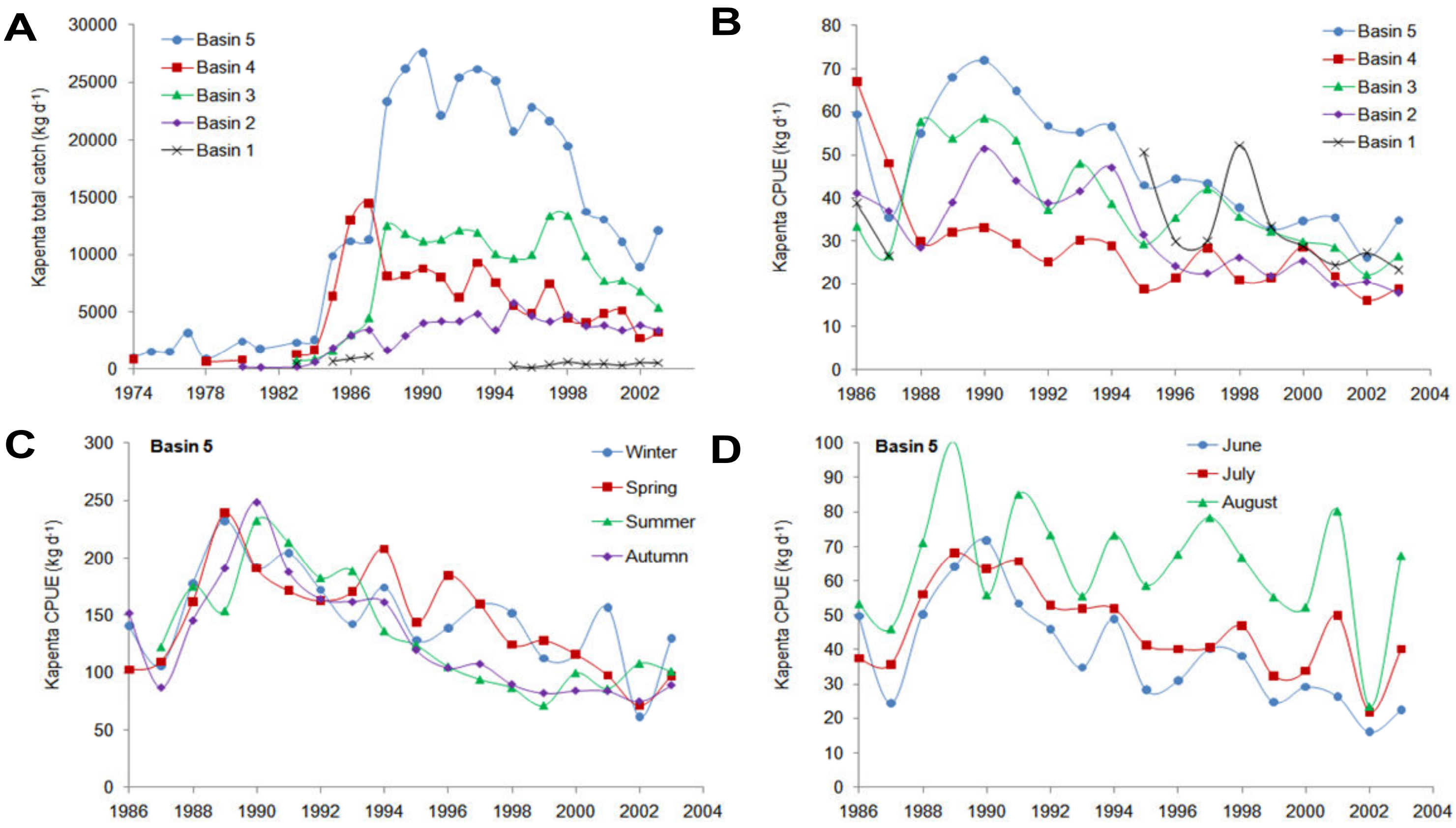


Figure 7.2. Annual variation in Kapenta catch (CPUE kg d^{-1}) in A. different basins of Lake Kariba from 1974 to 2003, and from B. 1986 to 2003 in the whole lake, C. in different seasons in the Sanyati Basin, and D. from June to August in the Sanyati Basin

Apart from lake water level, significant negative correlations were also found between measured Kapenta catches and maximum daily temperatures in three of five of Lake Kariba's basins (Table 7.3), which strongly point to climate warming as the driving force negatively affecting fish production in Lake Kariba, since water levels in this lake are inversely related to temperature and rainfall and pan evaporation rates (Vörösmarty *et al*., 2000). An ECOPATH model applied to analyse biomass flows of different trophic levels (phytoplankton, periphyton, zooplankton, plants, crocodiles and fish) in Lake Kariba revealed that, over the period 1983 to 1989, zooplankton were being fully utilised by the introduced Kapenta and other endemic fish in the lake, and that the phytoplankton were present in just sufficient quantity to feed the zooplankton (Machena *et al*., 1993; Moreau *et al*., 1997). This seemingly no longer applies, as the observed increased abundance of unpalatable Cyanophyceae and decreased abundance of more palatable Chlorophyceae and Bacillariophyceae in Lake Kariba since the 1980's corresponds with a decline in zooplankton production and fish stocks. The continued zooplankton survival in Lake Kariba, despite the decline in palatable phytoplankton, is due to the ability of zooplankton to utilise alternate food sources such as bacteria, detritus, and suspended organic material, a feature reported in both Lakes Tanganyika (Moreau *et al*., 1993) and Turkana (Christensen and Pauly, 1993).

7.2. Conclusion

Changes in the physical and chemical properties of Lake Kariba, reflected as elevated temperatures, phosphorus, TDS and conductivity levels, and conversely declined nitrogen, pH and DO concentrations, are linked to climate warming, which was measured as a 1.9°C increase in the lake waters since the 1960's. The changes in the physical and chemical parameters are reflected in the phytoplankton community as reduced primary production rates and phytoplankton biomass, as well as a shift in the phytoplankton seasonality and abundance, with increased dominance of Cyanophyceae and decreased dominance of Bacillariophyceae and Chlorophyceae. The changes in the phytoplankton, ostensibly affecting the zooplankton community and shown as overall declined zooplankton biomass, but particularly of the large-sized Cladocera and Copepoda with the small-sized Rotifera proliferating. The changes in the plankton, in turn, are shown to be adversely affecting the Kapenta fish stocks, where substantial declines have been recorded since the 1970's. The use of multi-disciplinary, multi-trophic studies, ranging from microbial food to fish communities constituting a baseline of all organisms in the lake, is recommended in order to devise management strategies in line with the changes observed in the lake.

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