

TROPHIC CHARACTERISATION OF THE DOMINANT FISHES IN THE VICTORIA AND KYOGA LAKE BASINS

BY

**MBABAZI DISMAS
BSC. EDUC., MSC. (MAK)**

**A THESIS SUBMITTED TO THE GRADUATE SCHOOL FOR THE AWARD OF
THE DEGREE OF DOCTOR OF PHILOSOPHY OF MAKERERE UNIVERSITY**

DECEMBER, 2004

© MBABAZI DISMAS

ACKNOWLEDGEMENTS

I am grateful to my supervisors, Dr. Makanga, B. and Dr. Orach-Meza F. for their dedicated guidance through this study.

I am indebted to the Director and staff of Fisheries Resources Research Institute (FIRRI), Jinja who supported me at various levels both materially and morally during this study. I am particularly grateful to Dr. Ogutu-Ohwayo, R. former Director, FIRRI for encouraging and introducing me to this quite challenging and very important study. Dr. Balirwa J.S. Acting Director FIRRI, tirelessly provided both personal and administrative support towards completion of this study. This study would not have been accomplished without the support of my field team (Namulemo G., Muhumuza E., Luyiga J., Okello W., Baliise C and Mwogeza H.) who assisted in various ways during data collection. I am specifically grateful to Mr. Wandera S.B. for the continued guidance in fish identification and Sekiranda S. for the help on maps.

University of Waterloo, Ontario, Canada provided a home outside Uganda. I owe a debt of gratitude to Prof. Robert E. Hecky who made my dream about application of stable isotope studies in food web studies a reality. Hecky developed a special interest in this study, readily provided guidance/advice in addition to financial support when needed. My interaction with Prof. Bill W. Taylor made multivariate statistics user friendly. Dr. P. Verburg introduced me to stable isotope sample preparation and/or preparing them, the times I was not physically at University of Waterloo. I learnt a lot through interactions with the Graduate students in Biology Department. I am grateful to M. Sairah and G. Silsbe who made sure that I was comfortable both academically and socially through out my two study visits. Dr. S. Guildford, Dr. G. Dixon provided office /Laboratory space. Mr. William Mark and staff of the Environmental Stable Isotope Laboratory (EIL), Department of Earth sciences, for analyzing samples.

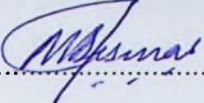
My investigations have prospered from discussions with the various colleagues and friends in particular Profs. L. Chapman, O. Seehausen, D. Schindler, L. Kaufman, Drs J. Schwarz and L. Muhoozi. I am grateful for their advice and for reviewing the tedious draft manuscripts.

A special acknowledgment is directed to my family members especially my brother F. Nkurunungi and Uncle S. Mugisha Nyanda for their support and encouragement during my study period. I also thank my wife Midius and Children (Pascal and Thereza) for the patience and understanding for the long times I was away from home.

I wish to acknowledge the Lake Victoria Environmental management project (LVEMP) GEF/ World Bank funded, for financial support. In addition, this study has been sustained by the National Agricultural Research Organisation (NARO) my employer to whom I am grateful.

DECLARATION

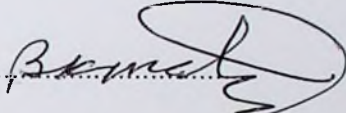
I, MBABAZI DISMAS declare that this thesis is my original work and has not been submitted for a degree in any other University.

Signed.....

Dated.....31st August, 2005

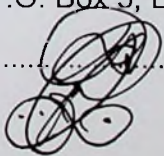
This Thesis has been submitted for examination with our authority as University supervisors,

1. Dr. Makanga, Boniface (PhD, MSc., BSc., Dip. Educ.)
Associate Professor,
Zoology Department, Makerere University,
P.O. Box 7062, Kampala.

Signed.....

Dated.....2nd Sept 2005

2. Dr. Orach-Meza Faustin (PhD, MSc., BSc.,)
Executive Secretary,
Lake Victoria Environmental Management Project (LVEMP),
P.O. Box 5, Entebbe.

Signed.....

Dated.....31st Aug. 2005

DEDICATION

This work is dedicated to my late parents Teddy and Pascal Rwebishengye who laboured much to enable me go through school but could not live long to see the fruits of their efforts.

COPY RIGHT

No part of this Thesis may be reproduced, stored in any retrieval system, or transmitted in any form or by any means: electronic, mechanical, photocopying, recording, or otherwise, without the prior written permission of the author or Makerere University on that behalf.

TABLE OF CONTENTS

	PAGE
ACKNOWLEDGEMENTS.....	ii
DECLARATION.....	iv
DEDICATION.....	v
COPY RIGHT.....	vi
TABLE OF CONTENTS.....	vii
LIST OF TABLES.....	x
LIST OF FIGURES.....	xii
LIST OF APPENDICES.....	xvi
LIST OF ABBREVIATIONS.....	xvii
ABSTRACT.....	xviii
CHAPTER ONE.....	1
1.0 Background.....	1
1.1.0 Introduction.....	4
1.1.1 The food web structure in the pre-Nile perch Lake Victoria.....	4
1.1.2 The current food web structure of Lake Victoria.....	6
1.2.0 Literature Review.....	9
1.2.1 The role of fish and fisheries in trophic interactions and food web structure.....	9
1.2.2 Food chains and food webs in establishing trophic relationships.....	13
1.2.3 Use of stable Nitrogen and Carbon isotope ratios in food web studies.....	14
1.3.0 Research Problem.....	17
1.4.0 Objectives.....	18
1.5.0 Thesis Structure.....	19
CHAPTER TWO.....	20
2.0 Materials and Methods.....	20
2.1.0 Choice of the Study Area.....	20
2.2.0 Study Area.....	21
2.2.1 Koki drainage system lakes.....	24
2.2.2 Nabugabo drainage system lakes.....	25
2.2.3 Kyoga drainage system lakes.....	27
2.2.4 Lake Victoria.....	29
2.3 Field sampling.....	33
2.4.0 Laboratory Procedures.....	35
2.4.1 Fish species identification.....	35
2.4.2 Diet trophic positions and food chain length.....	35
2.4.3 Dietary stomach content analysis.....	36
2.4.4 Stable isotope analyses.....	36
2.5.0 Data analysis.....	37
2.5.1 Species richness and abundance.....	37
2.5.2 Dietary data and trophic groups.....	37
2.5.3 Stable isotopes, food sources and trophic relationships.....	39
2.5.4 Estimation of trophic positions based on diet.....	39
2.5.5 Estimation of trophic positions and Food chain length based on $\delta^{15}\text{N}$ signatures.....	41
CHAPTER THREE.....	44

3.0	Trophic analysis of the fish communities in the Victoria and Kyoga basin lakes based on stomach contents	44
3.1	Introduction	44
3.2	Diet analysis of fishes	48
3.2.1	Koki drainage system lakes.....	48
3.2.2	Nabugabo drainage lakes	50
3.2.3	Kyoga drainage system lakes	53
3.2.4	Inshore areas of the northern portion of Lake Victoria	58
3.3	Trophic groups of fishes	61
3.3.1	Koki drainage system lakes.....	61
3.3.2	Nabugabo drainage system lakes	65
3.3.3	Kyoga drainage system lakes	67
3.3.4	Inshore areas of northern portion of Lake Victoria	72
3.5	Fish species and spatial trophic diversities	77
3.6	Discussion and conclusions	81
3.6.1	Discussion	81
3.6.2	Conclusions.....	88
CHAPTER FOUR		90
4.0	Stable isotopes of carbon and nitrogen as indicators of trophic structure and food sources of the fish communities in the Victoria and Kyoga basin lakes	90
4.1	Introduction.....	90
4.2	Carbon sources	94
4.2.1	Koki drainage system lakes.....	94
4.2.2	Nabugabo drainage system lakes	97
4.2.3	Kyoga drainage system lakes	99
4.2.4	Inshore areas of northern parts of Lake Victoria	103
4.3	Trophic positions, relationships and $\delta^{15}\text{N}$ signatures among fishes.....	105
4.3.1	Koki drainage systems lakes.....	108
4.3.2	Nabugabo drainage system lakes	109
4.3.3	Kyoga drainage system lakes	111
4.2.4	Inshore areas of northern parts of Lake Victoria	112
4.2.5	Spatial variability in the basal $\delta^{15}\text{N}$ signatures among lakes	114
4.4	Food chain length	115
4.4.1	Factors affecting food chain length	116
4.5	Discussion and Conclusions	120
4.5.1	Discussion.....	120
4.5.2	Conclusions.....	126
CHAPTER FIVE		127
5.0	Trophic relationships as the basis for fisheries ecosystem management in the Victoria and Kyoga basin lakes.....	127
5.1	Introduction.....	127
5.1.1	Quantification of trophic relationships	128
5.1.2	Dietary groups and food sources	132
5.1.3	Trophic or dietary shifts.....	134
5.1.5	Trophic/feeding patterns	140
3.1.5	Trophic positions.....	142
5.2	Factors that influence trophic structure and food web complexity.....	146
5.2.1	Fishing.....	147
5.2.2	Direct additions or losses of biota	149
5.2.3	Eutrophication	150

5.2.4 Habitat diversity and fish food webs152

5.2.4.1 Aquatic macrophytes152

5.2.4.2 Rocky habitats154

5.2.5 Catchments' disturbances155

5.2.6 Human influences157

5.3.1 Implications for ecosystem based fisheries management159

REFERENCES161

APPENDICES193

LIST OF TABLES

TABLE	TITLE	PAGE
2.1	Drainage, lake/area, species richness, species abundance, selected physicochemical parameters, food chain length and riparian characteristics and associated human activities (August 2001 to May 2004). Surface areas for lakes Kyoga and Victoria sampled parts refer to the total areas of entire lakes.....	31
2.2	Estimated trophic position values for the prey items used to calculate trophic position of fishes based on diet modified from Vander Zanden and Rasmussen (1996).....	40
3.1	List of fish species and food items included in dietary analysis from August 2001 to May 2004, text code and former taxonomic genera. The size classes for <i>L. niloticus</i> were determined based on total length (TL) in cm according to Ogutu-Ohwayo (1994). Note the absence of a dot in text codes for food items.....	46
3.2	Fish stomach contents (proportion of volume) in diets of fishes pooled from all sites within the individual Koki drainage system lakes from August 2001 to August 2003. Number of stomachs with food, total number of fish observed and trophic positions of fishes are presented in the final three columns.....	49
3.3	Fish stomach contents (proportion of volume) in diets of fishes pooled from all sampled sites within lakes from the Nabugabo drainage system from August 2001 to August 2003. Number of stomachs with food, total number of fish observed and trophic positions of fishes are presented in the final three columns.....	51
3.4	Fish stomach contents (proportion of volume) in diets of fishes pooled from all sampled sites within lakes in the Kyoga drainage system from August 2001 to May 2004. Number of stomachs with food, total number of fish observed and trophic positions of fishes represented in the final three columns.....	55
3.5	Fish stomach contents (proportion of volume) in diets of fishes pooled from all sampled sites in inshore areas of northern portion of Lake Victoria from August 2001 to August 2003. Number of stomachs with food, total number of fish observed and trophic positions of fishes given in right most columns.....	59
3.6	Trophic groups of the dominant fish species/size groups encountered in the Victoria and Kyoga basin lakes from August 2001 to May 2004 (Kachera = KR, Mburo = MR, Kayugi = KG, Kanyanja = KJ, Nabugabo = NB, Nawampasa = NS, Nakuwa = NW, Bisina = BS, Kyoga-Iyingo = KI, Kyoga-Bukungu = KB, Napoleon = NP, Thruston Bay = TN and Hannington Bay = HG)...	78

4.1 A list of fish species or their length size classes and potential food sources included in stable isotope analysis (August 2001 - May 2004), text code and former taxonomic genera. Note the absence of a dot in text codes for food items..... 92

4.2 The trophic position of the dominant fish species encountered in the Victoria and Kyoga basin lakes (August 2001 to August 2003) determined using the primary consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relationship according to Vander Zanden and Rasmussen (1999)..... 107

LIST OF FIGURES

FIGURE	TITLE	PAGE
2.1A	A map of showing part of the studied lakes in the Victoria and Kyoga basins, indicating landing sites where fish samples were obtained and sampling sites where experimental collection of fish and possible food sources was done.....	22
2.1B	A map of Uganda showing the location of the drainage systems studied in fig. 2.1A (A= Koki, B= Nabugabo, C= Kyoga) and D = norther portion of Lake Victoria indicating landing sites where fish samples were obtained and sampling sites where experimental collection of fish and food sources was done.....	23
3.1	(A) UPGMA cluster diagram showing the similarity in diets of fishes using the Bray-Curtis distance measure. At ≤ 0.60 diet similarity three cluster groups of fishes were possible at $P < 0.05$; U indicates location of ungrouped fishes; Lake Kachera = KR and Lake Mburo = MR. (B). A DCA scatter plot showing the spatial patterns between 18 food sources (Δ) and nine fish species from Koki drainage system lakes (eigen values: 0.58 and 0.38 for DCA 1 and DCA 2 respectively; fishes are indicated by ($\bullet$) from Lake Kachera, ($\blacksquare$) from Lake Mburo and all text codes Table 3.1).....	64
3.2	(A) UPGMA cluster diagram showing the similarity in diets of fishes using the Bray-Curtis distance measure. At ≤ 0.67 diet similarity 7cluster groups of fishes were possible, Lake Kayugi = KG, Lake Kayanja = KJ and Lake Nabugabo = NB. (B). A DCA scatter plot showing the spatial patterns between 25 food sources (Δ) and 19 fish species from Nabugabo drainage system lakes (eigen values: 0.67 and 0.47 for DCA 1 and DCA 2 respectively; fishes are indicated by ($\blacksquare$) from Lake Kayugi, ($\bullet$) from Lake Kayanja, ($\blacktriangle$) from Lake Nabugabo and all text codes Table 3.1).....	66
3.3A	UPGMA cluster diagram cluster diagram showing the similarity in diets among 35 fish species using Bray- Curtis distance measure from the Kyoga drainage system. At ≤ 0.52 diet similarity 16 cluster groups of fishes were possible and U indicates location of the ungrouped fish species. (Nawampasa = NS, Nakuwa = NW, Bisina = BS, Kyoga-lyingo = KI, Kyoga-Bukungu = KB and other text codes Table 3.1).....	70
3.3B	A DCA scatter plot showing the spatial patterns between 26 food sources (Δ) and 30 fish species/size groups from the Kyoga drainage system lakes eigen values: 0.78 and 0.54 for DCA 1 and DCA 2 respectively; fishes are indicated by ($\blacksquare$) from Lake Nawampasa, ($\bullet$) from Lake Nakuwa, ($\blacklozenge$) from	

	Bisina, (▲) from Lake Kyoga-Iyingo, (▼) from Lake Kyoga-Bukungu and all text codes Table 3.1.....	71
3.4A	A. UPGMA cluster diagram showing the similarity in diets of 23 fish species/ size groups using Bray- Curtis distance measure from the northern portion of Lake Victoria. At ≤ 0.60 diet similarity 7 cluster groups were possible and U indicates location of the ungrouped fish species (Napoleon Gulf = NP, Thruston Bay = TN, Hannington Bay = HG and other text codes Table 3.1).....	74
3.4B	A DCA scatter plot showing spatial patterns between 23 food sources (Δ) and 23 fish species/size groups from the inshore areas of the northern portion of Lake Victoria (eigen values: 0.72 and 0.33 for DCA 1 and DCA 2 respectively, fishes are indicated by (▲) from Napoleon Gulf, (■) from Thruston Bay, (●) from Hannington Bay and all text codes Table 3.1).....	75
3.5	(A) Trophic diversity by number of species from the studied lakes in the Victoria and Kyoga basin lakes (August 2001 to May 2004) and (B) comparison of the current data with pre-perch Lake Victoria situation (KR =Kachera, MR = Mburo, KG = Kayugi, KJ = Kyanja, NS = Nawampasa, BS = Bisina, NW = Nakuwa, KI = Kyoga-Iyingo, KB = Kyoga-Bukungu, NP = Napoleon gulf, TN = Thruston bay, HG = Hannington Bay and VR = Pre-perch Lake Victoria. Data on pre-perch boom is only on haplochromines 1984 and are from (Goldschmidt, 1996).....	80
4.1	The mean $\pm$ sd of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for nine fish species and 10 potential food sources from Koki lakes. Note the lighter and high variation in $\delta^{13}\text{C}$ of food web structure of L. Kachera compared to Lake Mburo. Overlapping sd in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and sd were only calculated for organisms that raised three individuals (See Table 4.1for a key to labels).....	96
4.2	The Mean $\pm$ sd of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the 18 fish species and 12 food sources from Nabugabo lakes. Note the lighter and heavier $\delta^{13}\text{C}$ of the fish food webs of Kayugi and Kyanja respectively. Overlapping sd in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and sd were only calculated for organisms that raised three individuals (See Table 4.1for a key to labels).....	98

4.3	The Mean $\pm$ sd of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the 32 fish species and 18 food sources from Kyoga lakes. Note the lighter $\delta^{13}\text{C}$ of the fish food webs of Nawampasa compared to the rest of the lakes. Overlapping sd in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and sd were only calculated for organisms that raised three individuals (See Table 4.1for a key to labels).....	102
4.4	The Mean $\pm$ sd of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for 25 fish species and 15 food sources from inshore areas of northern part of Lake Victoria. Note the relatively lighter $\delta^{13}\text{C}$ of the fish food webs Hannington Bay compared to Napoleon gulf and Thruston Bay. Overlapping sd in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and sd were only calculated for organisms that raised three individuals (See Table 4.1for a key to labels).....	104
4.5	Relationships between $\delta^{15}\text{N}$ signatures of <i>O. niloticus</i> and phytoplankton across the examined lakes in the Victoria and Kyoga basin lakes (August 2001 to September 2003). Error bar represent 1sd. Note the high variation in $\delta^{15}\text{N}$ signatures in phytoplankton compared to <i>O. niloticus</i> . The thick continuous line represents the 3.4‰ fractionation line.....	115
4.6	Relationships between food chain length and water transparency (secchi depth) in lakes (A) without and (B) with Nile perch in the examined Victoria and Kyoga basin lakes (August 2001 to August 2003).....	117
4.7	Relationships between food chain length and water transparency (secchi depth) in lakes (A) without and (B) with Nile perch in the examined Victoria and Kyoga basin lakes (August 2001 to August 2003).....	118
4.8	The relationship between species richness and water transparency (secchi depth) in (A) Nile perch free and (B) Nile perch lakes examined in the Victoria and Kyoga basin lakes (August 2001 to August 2003). Note the small and large effect of water transparency in the Nile perch free and Nile perch lakes respectively on species richness. The least-square regression line is shown ($P<0.001$).....	119
5.1	Seasonal variation (volumetric mean $\pm$ SE) in the relative importance of main food items in stomachs of <i>O. niloticus</i> (pooled across size classes) from the littoral zone of	

northern Lake Victoria between 1995 and 1996 (Bairwa, 1998).....	138
--	-----

5.2	Comparison of mean estimates of fifteen fish species common to at least three study sites, calculated using dietary and $\delta^{15}\text{N}$ methods. Error bars represent 1 sd. The solid diagonal line represents the 1:1 line.....	145
-----	--	-----

LIST OF ABBREVIATIONS

CAP	=	Community Analysis Package
DCA	=	Detrended Correspondence Analysis
FAO	=	Food Agricultural Organisation
FIRRI	=	Fisheries Resources Research Institute
GEF	=	Global Environmental Facility
IAEA	=	International Atomic Energy Agency
ILEC	=	International Lake Environment Committee
LVEMP	=	Lake Victoria Environmental Management Project
NARO	=	National Agricultural Research Organisation
NMFS	=	National Marine Fisheries Service
NOAA	=	National Oceanic and Atmospheric Administration
NRC	=	National Research Council
sd	=	Standard Deviation
UPGMA	=	Uweighted Pair Group Method Using Arithmetic Averages

ABSTRACT

This study examined the trophic structure of the fishes present in lakes Victoria and Kyoga, and the less impacted satellite lakes in the two basins using a combination of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes, and stomach content analyses between 2001 and 2004.

Both stomach content and stable isotope analyses revealed that fish had a varied diet, which in part was influenced by their species and size, but in general displayed a lack of specialization. Invertebrates constituted the most important dietary component of most fish species (>50%) with the exception of the tilapiine species in the less disturbed lakes without Nile perch. Fish formed another important dietary item, especially for the predatory Nile perch the basis of the current fishery in lakes where it is found. Phytoplankton and detritus formed the basal carbon supporting the fish communities among the examined lakes. Ontogenetic dietary shift was only evident from stomach content analysis for Nile perch (*Lates niloticus*), consuming mainly invertebrates at a total length of (< 20 cm) and fish (between 20 and < 60 cm) but neither of the size groups were purely invertebrate eaters or piscivores. The high $\delta^{15}\text{N}$ signatures (7.35 – 8.28 ‰) and trophic positions (2.5 – 2.6) of the *Rastrineobola argentea* found in stomachs of Nile perch ($\leq 20\%$), in comparison to those of Nile perch (5.35 – 9.30 ‰ and 2.1 – 3.3 respectively) rules them out as major diets contributing to its somatic growth. It was apparent that the trophic structure of the examined lakes/areas was not structured in a simple linear fashion, but indicated omnivory, hence the $\delta^{15}\text{N}$ did not exhibit a typical assumed shift of 3-4 ‰ per trophic level. Based on $\delta^{15}\text{N}$ signatures the longest food chain lengths were recorded in Thruston Bay Lake Victoria (1.7) followed by lakes Bisina, Kayugi and Napoleon Gulf in Lake Victoria (1.5), Nawampasa (1.4) and the shortest were recorded in lakes Nabugabo and Nakuwa (≤ 0.7). Noteworthy, lakes Nabugabo and Nakuwa, with the shortest food chain lengths, like the main lakes, contain the predatory Nile perch. The $\delta^{13}\text{C}$ of the fishes in the main lakes ranged from -21.7 to -14.8 ‰ and -25.4 to -13.8 ‰ in lakes Victoria and Kyoga respectively and from -28.1 to -6.7 ‰ in the satellite lakes. Among the satellite lakes in the Lake Victoria basin, Nabugabo recorded the least range for $\delta^{13}\text{C}$ (-21.6 to -19.7 ‰) and Lake Kachera the largest range (-20.5 to -9.4 ‰). In the Kyoga lake basin, Lake Bisina

recorded the largest range in $\delta^{13}\text{C}$ (-25.9 to 11.3 ‰) and Lake Nawampasa the least (24.4 to 21.7 ‰).

The littoral areas of Lake Victoria and the satellite lakes without Nile perch were characterized by substantially longer food chains than those lakes with the Nile perch in the same drainage systems. The broad ranges in $\delta^{13}\text{C}$ are an indication of a wide range of food sources in the aquatic systems including external inputs. This study has indicated the importance of non-commercial fish species and other biota in trophic interactions as well as the potential factors that may affect ultimate energy sources supporting commercially important stocks.

CHAPTER ONE

1.0 Background

Natural communities are assemblages "bound together by a web of complex interactions" (Charles Darwin, 1859)

There are about 25000 different known fish species of which 15000 are marine and nearly 10000 are fresh water (Nelson, 1994). Despite the abundance and diversity of fish, most fisheries target a few species. Fish are generally valued for their qualities as goods, selected by human preferences, in form of food protein, fishmeal, fish oil, game fish, medicine and for aquaculture production (Holmlund and Hammer, 2001). Further, recreational fishing in lakes and rivers is a major tourism activity (FAO, 1996; Postel and Carpenter, 1997). Fish are also integral parts of ecosystems as components of key food web interactions.

Fish play active roles in the maintenance of aquatic ecosystems and in the provision of a range of ecosystem services (Holmlund and Hammer, 2001). Ecosystem services have been defined as "conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life" (Daily, 1997). This includes the life-support functions (Odum, 1989) of ecosystems and nature's capacity to provide aesthetic and cultural quality to human life (Daily, 1997). Holmlund and Hammer (2001) categorized ecosystem services provided by fish into two: 1) Fundamental ecosystem services (e.g., nutrient cycling) which are essential for ecosystem function and resilience, and often have no market value, and 2) Demand-derived ecosystem services (e.g., recreational values) which serve human values and demands. Fundamental services are a prerequisite for human existence whether humans are aware of them or not. Nevertheless, all demand-derived ecosystem services depend on natural systems of which the fundamental ecosystem services provided by fish form a major component in aquatic ecosystems (Holmlund and Hammer, 2001).

Studies of ecosystems are often impeded by the unclear boundaries of many ecosystem types. Lakes provide useful model ecosystems because they are discrete, self-contained ecosystems with relatively well-defined boundaries.

Thus studies of lakes have played an important role in the development of ecological theory (e.g., Forbes, 1925, Lindeman, 1942, Carpenter *et al.*, 1985), although lakes are also complex ecosystems composed of distinct interconnected macrohabitats with diverse biological, physical and chemical processes (Schindler and Scheuerell, 2002; Lewin *et al.*, 2004).

Increasing attention has been given to the impact of fishing on ecosystems with the main major emphasis being put on resource sustainability, biodiversity conservation and environmental protection (Garcia and Newton, 1997; Gislason *et al.*, 2000; Pauly *et al.*, 2002). Conventionally, fisheries management focuses on single species and generally assumes that the productivity of that stock is only a function of its inherent population characteristics. However the inter-dependence of all ecosystem components is increasingly recognised and an ecosystem is considered as a new level of management to be taken into account according to the FAO Code of Conduct for responsible Fisheries (FAO, 1995; Kaufman *et al.*, 2004). Incorporation of such whole-ecosystem considerations into resource decision-making is called "ecosystem-based management," in which human activities are managed within the context of naturally dynamic and integrated ecosystems (Langton and Haedrich, 1997; NMFS 1998; Juda, 1996; Okey and Harrington, 1999; Kaufman *et al.*, 2004).

Recently, there has been considerable interest in ecosystem approaches to fisheries management (e.g., Christensen *et al.*, 1996; Larkin, 1996; Jennings and Kaiser, 1998; NRC, 1999). However, the implementation of broader ecological considerations has not become widespread in fisheries management even though it has been emphatically advocated (NMFS, 1999; NRC, 1999) and mandated (NOAA, 1996). Recognizing the importance of ecological processes in the regulation of fish populations is a key step to a broader approach of fisheries management. However ecosystem-based management should be an adaptive process and will require periodic evaluation and modification to incorporate new scientific information as it becomes available. This approach is needed because, ecosystems are not static, and human impacts also change with technology and continued population growth (Witherell *et al.*, 2000).

Fish conservationists suggest that in determining what constitutes sustainable levels, fisheries management should put into account methods of exploitation, target species and changing environmental conditions. For instance,

resource removal that may have minimal impacts on ecosystem function and overall biodiversity under relatively pristine conditions could potentially have devastating effects in ecosystems already stressed by pollution, eutrophication, and alterations to primary or ecologically linked habitats. For scientific, institutional, philosophical, or logistical reasons, ecological factors are often omitted in fishery management. In some cases this is justifiable, but in most cases omitting ecological considerations is irresponsible (Link, 2002).

Trophic interactions play a major role in aquatic ecosystems (Carpenter *et al.*, 1985; Vander Zanden *et al.*, 1999). A trophic interaction or "link" occurs between species when a member of one species consumes a member of another or the same (cannibalistic) species (Martinez *et al.*, 1999). Food web relationships always involve a number of species and links with top predators, intermediate, and basal species (Briand and Cohen, 1984). In trophic relationship studies, food webs are always based on either taxonomic or trophic groupings of species (Martinez *et al.*, 1999). Taxonomic groups of species are organisms classified by taxonomists to belong to a specific group (Gaston, 1996). Trophic groups of species contain organisms that appear to eat and be eaten by the same species within a food web (Cohen and Briand, 1984). Recent research indicates that variation in trophic structure of ecological systems described in terms of trophic groups of species is generally easier to explain, than the same structure described in terms of taxonomic groups of species (Martinez, 1994; Martinez *et al.*, 1999). The trophic habits of fish have consequences for other aspects of their biology, e.g. accumulation of contaminants (Kidd *et al.*, 1995, Vander Zanden and Rasmussen 1996; Kidd *et al.*, 2001), life history patterns and growth (Martin, 1966, Shuter *et al.*, 1998).

Fish are important consumers in aquatic food webs (Bax, 1991) and at the whole system scale; predation by fishes alters community structure and nutrient cycling. Thus both direct and indirect predation effects are expressed in population structure, community composition and productive processes at all trophic levels (Kitchell *et al.*, 1994). Fisheries can also alter food web interactions because they target certain species that have important trophic effects on entire food webs. Thus future management of tropical fish stocks and aquatic ecosystems that support them will require greater knowledge of food web ecology. For example, commercial exploitation of marine fish stocks has changed

food web structure and dominant species in many regions of the world (Parsons, 1996). Likewise, the introduction of exotic piscivores into tropical Lake Gatun in Panama (Zaret and Paine, 1973) and Lake Victoria in Africa (Kaufman, 1992, Goldschmidt, 1996) was followed by altered food web structure, and changes in important features of aquatic and terrestrial ecosystems.

This thesis examines the trophic relationships among fish assemblages in lakes Victoria, Kyoga and their less impacted satellite lakes in their basins, with the specific aims of describing the trophic positions of dominant fishes and their food sources to provide a baseline for assessing the current disturbances especially food chain length in the Victoria and Kyoga main lakes and future disturbances in aquatic systems as a whole.

1.1.0 Introduction

1.1.1 The food web structure in the pre-Nile perch Lake Victoria

Lake Victoria formerly supported important fisheries, based on herbivores and detritus feeders of the family Cichlidae. Fisheries based on such short food chains are ecologically the most efficient (Barel *et al.*, 1985). The Victoria food web and fishery contained an ecologically and phylogenetically diverse group of fishes (Greenwood, 1981). The fish fauna was dominated by a diversified, presumably monophyletic species flock of haplochromine cichlids (Meyer *et al.*, 1990). The most recent estimates of Lake Victoria's pre-Nile perch species flock comprised over 500 species that occupied spectacular variety of niches in the lake (Greenwood, 1974; 1981; Seehausen, 1996; Seehausen *et al.*, 1997; Witte *et al.*, 1992b; Kaufman and Ochumba, 1993).

Prior to the stockings of exotic fish species (Nile perch, *Lates niloticus* and four tilapiines Nile tilapia, *Oreochromis niloticus*, *Oreochromis leucostictus*, *Tilapia zillii* and *Tilapia rendalli*), the Victoria and Kyoga lake basins had extremely a high diversity of fish species comprising many trophic groups, with many endemic fish species that were found only in these lakes. Two endemic tilapiine species, *Oreochromis esculentus* and *Oreochromis variabilis* were unique to the Victoria and Kyoga basins and were the most important commercial species in these lakes (Graham, 1929; Worthington, 1929). Other species, such

as *Protopterus aethiopicus*, *Bagrus docmak*, *Clarias gariepinus*, *Barbus* spp, mormyrids, *Synodontis* spp, *Schilbe intermedius* and *Rastrineobola argentea*, were also abundant (Graham, 1929; Worthington, 1929; 1932; Kudhongania & Cordone, 1974). The rivers of the Victoria Lake basin also had a number of riverine species and the most commercially important were *Labeo victorianus* and *Barbus altianalis* (Graham, 1929; Lowe-McConnell, 1997).

Prior to Nile perch introduction in Lake Victoria, the top predatory fishes on haplochromines were: catfishes like *B. docmak*, several *Clarias gariepinus*, *P. aethiopicus* and *Schilbe intermedius*. The other predators were fish eating birds (*Phalacrocorax africanus*, *Phalacrocorax carbo*, *Ceryle rudis*), otters (Goldschmidt *et al.*, 1990; Goudswaard and Wanink, 1993) and piscivorous haplochromines (Witte and Van Oijen, 1990). The phytoplankton was directly grazed by the tilapiine species (Ligtvoet and Witte, 1991).

Lake Kyoga, downstream of Lake Victoria, and Lake Nabugabo, formerly connected to Victoria, also had endemic haplochromine species (Worthington 1929, Trewavas 1933, Greenwood 1965, 1966, Kendall, 1969) that occupied all consumer trophic levels and played an important role in the flow of energy in the ecosystem of these lakes. The haplochromines converted numerous food sources including detritus, algae, zooplankton, insect larvae and molluscs, into fish protein for consumption at higher trophic levels (Christian, 1995). They were crucial in transfer of energy in the ecosystem, as well as contributing to the high biodiversity associated with the lake basin. The fishes were important as human food and provided outstanding opportunities for studying evolutionary processes and community ecology (Lowe- Mc Connell, 1987). Haplochromine studies have also played a major role in illustrating how organisms undergo adaptive radiation to produce new species, and how a trophically diverse fish assemblage can utilize a diversity of food resources in an ecosystem.

Changes in the food web of Lake Victoria (East Africa) during the last 40 years are among the most dramatic known in ecology (Kaufman, 1992; Lowe-McConnell 1994). By the 1960's, stocks of the native tilapiines and other large fish species of Lake Victoria had been reduced by overfishing (Jackson 1971, Ogutu-Ohwayo 1990a). Nile perch and four tilapiine species were introduced into many of the lakes in the Victoria and Kyoga basin, including the main lakes Victoria and Kyoga in 1950's and early 1960's, respectively to improve the

declining fisheries. As a result of overfishing and introduction of exotic fishes, populations of most of the native species declined and many species became rare (Witte *et al.* 1992 a, b, Kaufman, 1992). Most notable was the disappearance of over 50% of the 600 plus species of the endemic haplochromine cichlids (Kaufman, 1992; Kaufman *et al.*, 1997). Although environmental changes and local overfishing played a role in the decline of native fish stocks (Jackson 1971, Ogutu - Ohwayo 1990 a; Hecky, 1993, Hecky *et al.*, 1994), the Nile perch predation was the most likely key factor (Ogari & Dadzie 1988, Ligtoet & Mkumbo 1990; Ogutu – Ohwayo, 1990 b; Witte *et al.* 1992 a, b). The introduced tilapiines impacted and displaced endemic tilapiines mainly through competition and possibly hybridisation as has been observed in other similar ecosystems (Juliano, 1998).

1.1.2 The current food web structure of Lake Victoria

With the establishment of the introduced species in Lake Victoria especially the Nile perch, the trophic ecology of the system changed, through both predator–prey and competitive interactions, and the removal of various trophic groups from the food web (Reinthal and Kling, 1994). The Nile perch boom also coincided with changes in the trophic composition of the haplochromine cichlid assemblage, with strong reduction in numbers of the then dominating piscivores and apparent extinction of prawn eaters, whereas, other groups such as algae scrapers and insectivores were less affected (Seehausen, 1999). The Nile perch further disrupted the ecosystem by simplification of the food web through elimination of haplochromines from many interactions and shortening of food chains to the Nile perch (Campbell *et al.*, 2003). Detritivore and phytoplanktivore groups, which together constituted 50% of the total haplochromines fish biomass in Lake Victoria between 1968 and 1971 (Kudhongania and Cordone, 1974), declined in the early 1980's to less than 1% (Witte *et al.*, 1992 a,b). The haplochromines were the main initial prey items of the Nile perch in Lake Victoria until they were almost eradicated (Gee, 1969; Hughes, 1986; Ogari and Dadzie, 1988; ligtoet and Mkumbo, 1990; Ogutu-Ohwayo, 1990c). Decimation of haplochromines caused Nile perch to switch to alternative prey items, such as prawn *Caridina nilotica* (Goldschmidt *et al.*, 1993,

Hecky 1993), native cyprinid *R. argentea* and cannibalism of its own young (Witte *et al.*, 1992b). The native fishes had occupied virtually all trophic levels, including phytoplanktivores, zooplanktivores, insectivores, molluscivores, detritivores, and piscivores and maintained an efficient flow of organic matter in the system. This study supported by earlier studies indicate that, in the present food web of Lake Victoria, the Nile perch is the dominant top predator, marginalizing the few remaining piscivores and eats few *R. argentea* (Crul, 1998; Campbell *et al.*, 2003). The detritivorous /phytoplanktivorous haplochromines have been replaced by the prawn *C. nilotica* and herbivorous zooplankton, and the zooplanktivorous haplochromines by *R. argentea*. The indigenous tilapiine species have been marginalized by the introduced Nile tilapia. The Nile tilapia particularly the young ones, live in the littoral and sublittoral regions of the lake and have minimal overlap with Nile perch (Lowe-McConnell, 1997; Welcomme, 1988; Ogutu-Ohwayo, 1990a). The two species also coexist in lakes Albert and Turkana. The present system is also characterized by extensive cannibalism within the Nile perch population, which starts at very young stages (Crul, 1998). Whereas the haplochromines converted numerous protein sources into fish protein for consumption by higher trophic levels, Nile perch now eats quite a lot of its own juveniles in addition to invertebrates which have filled the trophic niches left vacant through loss of haplochromines (Christian, 1995). Several other changes have also been observed at the top of the food pyramid, e.g. the pied Kingfisher (*C. rudis*), shifted from the diet of mainly haplochromines to one that consists exclusively of *R. argentea* (Wanink and Goudswaard, 1994). Similar diet shifts were also found for the Great cormorant *P. carbo*, and the long-tailed cormorant *P. africanus* (Goudswaard and Wanink, 1993). Currently, humans through fishing comprise another dominant component of the Lake Victoria food web, and fisheries have the potential to further alter community structure and dynamics (Kitchell *et al.*, 1997).

The reduction of species and trophic groups, and associated alterations in food webs have been accompanied by increasing algal blooms (Ochumba & Kibara 1989; Hecky and Bugenyi, 1992; Mugidde, 1993) and deoxygenation of the deeper waters of the lake. This has sometimes been associated with mass fish kills in Lake Victoria (Hecky *et al.*, 1994). Primary production doubled, and algal biomass increased eight to ten fold, accompanied by a shift in algal

composition from dominance of diatoms to cyanobacteria (Hecky, 1993; Mugidde, 1993). The process of eutrophication preceded the introduction of Nile perch and its population boom in the 1980's. Paleolimnological studies demonstrate that algal changes began as early as the 1930's and deoxygenation was increasingly prominent by the 1950's in parts of Lake Victoria at certain times of the year (Hecky, 1993, Lipiatou *et al.*, 1996, Verschuren *et al.*, 2002). By the 1980's deoxygenation was already pronounced (Verschuren *et al.*, 2002). The increased turbidity and deoxygenation, caused by eutrophication, probably started the breakdown of the complexity of the food web through a combination of demersal haplochromine displacement and increased invertebrate abundance (Hecky, 1993). It could have also reduced the effectiveness of cichlid visual signals between mates, leading to the breakdown of reproductive barriers and consequent loss of cichlid species in the lake (Seehausen *et al.*, 1997a). The turbid environment and reduced light penetration probably favoured the predator Nile perch because of its ability to feed at low light intensity and the detritivorous invertebrates that do not require light to find food but with serious consequences to many haplochromines with physiological inability to find prey in the poor light environment (Seehausen *et al.*, 2003). Predation by the introduced Nile perch (Ogutu-Ohwayo, 1990 a,b) and the reduction of good quality food for the native fishes that followed the dominance of cyanobacteria in Lake Victoria, may have contributed to the reduction or loss of native planktivorous haplochromines and tilapiine cichlids (Mugidde, 2001). The declining water quality in Lake Victoria has been recognized as contributing directly to the loss of fish habitat, diversity and deterioration of other uses of the lake (Bugenyi and Balirwa, 1989). The accumulation of excess organic matter in the water column (Hecky, 1993), is an indication that much of the organic matter produced in the lake is not being channelled efficiently through the food web accumulates in the hypolimnion where it causes deoxygenation. Eutrophication and depletion in stocks of this trophically diverse fish community by Nile perch changed the food web of the lake (Hecky, 1993, Campbell *et al.*, 2003) and reduced grazing pressure and the overall ecological efficiency through shortening of the food chains in the lakes.

1.2.0 Literature Review

1.2.1 The role of fish and fisheries in trophic interactions and food web structure

Ecologists and limnologists must recognize that fisheries and the cascade of food web effects they induce are a major cause of changes in aquatic systems (Goldschmidt *et al.*, 1993). Numerous studies demonstrate that fish and fisheries play an important role in the structure and function of aquatic ecosystems (e.g. Carpenter and Kitchell, 1988). This role has not been adequately investigated in most ecosystems. Populations of fish and other aquatic ecosystem components can be affected by the gear selectivity, magnitude, timing, location, and methods of fish removals (Witherell *et al.*, 2000). Fisheries can also affect aquatic ecosystems by vessel disturbance, nutrients, introduction of exotic species, pollution, unobserved mortality, and habitat alteration (Orach-Meza and Saila, 1978; Coleman and Williams, 2002; Schindler *et al.*, 1993; Witherell *et al.*, 2000; Blaber, *et al.*, 2000). The change in the integrity of the habitat and the loss of disproportionately rich feeding areas (Costa and Elliot, 1991) will ultimately affect the nursery function of near shore areas (Blaber *et al.*, 2000). The abundance and diversity of aquatic invertebrates in the interface zone are crucial links in the food chains of littoral fish (Baliwa, 1995). Throughout the world, many invertebrate bait organisms are collected from soft substrata by digging, affecting the target organisms, the structure of the substratum, and its community (Olive, 1993; Beukema, 1995; Dahl *et al.*, 1994). It has long been recognized that benthic production can be a substantial contributor to whole-lake primary and secondary production (Forbes, 1925, Lindeman, 1942). Benthic and pelagic energy flows and processes can be coupled in a variety of ways including cross-habitat foraging by fishes (Blumenshine *et al.*, 1997; Vadeboncoeur *et al.*, 2002; Schindler and Scheuerell, 2002). Furthermore, piscivores often forage broadly upon pelagic and benthic fishes, as well as benthic and terrestrial invertebrates, thereby linking pelagic and benthic food chains (Schindler *et al.*, 1996; 1997). Howell (1985) showed that digging for bait worms resulted in increased bioavailability of heavy metals. Post harvest processes such as fish processing release wastewater and organic pollutants that may have significant and long-

lasting effects (Blaber *et al.*, 2000). Many fishes exhibit flexible feeding habits and undergo diet shifts that deviate from their presumed food chain (Jeppesen *et al.*, 1997a).

Feeding in fishes can regulate trophic structure and thus influence the stability, resilience, and food web dynamics of aquatic ecosystems. These regulatory influences also change as fish pass from one life stage to another (Carpenter *et al.*, 1992; Post *et al.*, 1997). Resilience in this context means the ability to replace lost resource from a given aquatic ecosystem. Top predators in food webs can have substantial effects on species in the lower levels of a food web (Paine, 1980; Power, 1990; Carpenter and Kitchell, 1993; Schmitz *et al.*, 1997; Persson, 1999). Most trophic levels in natural systems are heterogeneous, in that, they consist of many species that differ in a number of ecological characteristics, including vulnerability to predators, use of resources and response to abiotic factors (Osenberg and Mittelbach, 1996; Polis and Strong, 1996; Persson, 1999). An important feature of heterogeneous trophic levels is that a decrease in one species at a trophic level due to predation may to a certain extent be compensated by a concomitant increase in another species less sensitive to predation at the same trophic level (Lovgren and Persson, 2002). An example of such compensation was the replacement of detritivorous/phytoplanktivorous haplochromines by *Caridina nilotica* and the zooplanktivorous haplochromines by the *R. argentea* with the establishment of the Nile perch in Lake Victoria (Crul, 1998).

The feeding pattern of fishes can influence the temporal availability of nutrients and the potential for algal blooms to occur in lakes, because fish mineralize nitrogen and phosphorus through excretion and defecation, thereby making these nutrients available for primary production (Schindler, 1992; Schindler *et al.*, 1993).

Aquatic systems are often connected to each other and even systems that seem to be closed are open and connected to other systems and can be influenced by processes taking place outside the system under study (Orach-Meza and Saila, 1978; Polis and Strong, 1996; Polis *et al.*, 1997; Loeb *et al.*, 1998; Schindler and Scheuerell, 2002). Mobile consumers may also connect habitats by foraging in one habitat and defecating in another (Schindler *et al.*, 1996; Polis *et al.*, 1997; Schindler and Scheuerell, 2002). Within lakes, animal

movements including inshore-offshore fish and horizontal zooplankton migrations link the littoral and pelagic habitats both in terms of prey consumption and translocation of nutrients (Carpenter *et al.*, 1992; Kitchell *et al.*, 1994; Schindler *et al.*, 1996; Vanni, 1996; Jeppesen *et al.*, 1997a,b; Persson and Crowder, 1997). This coupling also involves ontogenetic habitat shifts in juvenile fish between pelagic and vegetated habitats (Persson and Crowder, 1997). Flow of resources between habitats has been identified to be of major importance to trophic interactions in several systems including terrestrial islands (Polis and Hurd, 1996), streams (Nakano *et al.*, 1999), and lakes (Hecky and Hesslein, 1995, Schindler *et al.*, 1996).

Currently, humans are a dominant component of most aquatic food webs, and fisheries have the potential to further alter community structure and dynamics. Most of the lakes in the Victoria and Kyoga basin are characterised by excessive overexploitation and fishing mortalities (e.g. Muhoozi, 2002). Overexploitation stems not only from need but also from the “tragedy of the global commons”, that is, the inability of governments to adequately regulate use of common property resources (Hardin, 1966). Commercial fishing, whether large-scale industrial fisheries or small-scale operations, commonly overexploits fish stocks, in some cases collectively causing trophic mining (Pauly *et al.*, 1998). The complex nature of fishing effects on ecosystems became entrenched in the environmental consciousness when it became clear that fishing could cause imbalances in the most basic of species interactions and predator-prey relationships. In fresh waters, fish can be important in nutrient dynamics, and sometimes most of the pelagic phosphorous is stored in fish biomass (Bartell and Kitchell, 1978; Schindler *et al.*, 1993). In addition to the direct removal of the target fish species, considerable removal of nutrients by fisheries landings has been reported in fresh waters (Sarvala *et al.*, 1984) and in marine systems (Hjerne and Hansson, 2002).

Frequently the most abundant fish species are seriously reduced through overfishing (FAO, 2000; Steele and Schumacher, 2000). Fishing pressure usually supercedes ecological processes, and causes a notable decline in benthic megafauna and habitat complexity (Jennings and Polunin, 1996; Collie *et al.*, 1997; Malakoff, 1997; Auster and Langton, 1999). Removal of fish with key characteristics and functions from the ecosystem may result in loss of resilience

and in ecosystem changing from one equilibrium state to another (Holling, 1986; Chapin *et al.*, 1997, Grime, 1997; Tilman *et al.*, 1997). Like in many aquatic bodies fishing down food webs occurs as the fishery concentrates on the top predators and subsequently more abundant prey species of these predators (Pauly, *et al.*, 1998; Steele and Schumacher, 2000). Additionally, the resurgence of a predator population after a release of fishing pressure may have a strong impact on the depressed or highly susceptible prey populations (Carpenter and Kitchell, 1993). Fishing pressure on upper and mid trophic level fishes can significantly alter energy flow and biomass at lower trophic levels in lake ecosystems (Link, 2002). Decline in abundance of primary consumers removes important forage species for organisms higher in the food web, again with cascading effects (Dayton *et al.*, 1995; Jennings and Kaiser, 1998). In addition to acute effects on fish stocks, reductions in biogenic structures, habitat complexity, fauna biomass and benthic community diversity, have been documented in heavily fished or dredged areas (Auster *et al.*, 1996; Collie *et al.*, 1997). Many of the impacted benthic species are important prey items for the other commercially and ecologically valuable fish species (Garrison and Link, 2000). This decreases both structural and functional diversity of ecosystems, presumably also decreasing their resilience or ability to replenish lost resources (Coleman and Williams, 2002). The effects of nutrient dynamics show the importance of fish as ecosystem components and limnologists are already taking advantage of this in lake biomanipulation, (i.e. reducing the effects of eutrophication by modifying food web structure (Stenson *et al.*, 1978; Carpenter *et al.*, 1985; Hansson *et al.*, 1998).

Fish consumers can be viewed as trophic levels and fishing gear (e.g., nets) as a size-selective predator fully as effective as those described from the principles of predation outlined in textbooks (Ricklefs, 1990; Diana, 1994; Stone, 1995). Fishing is therefore one of the ecological forces and is among the most important regulators of trophic dynamics in the tropical Lake Victoria ecosystem (Kitchell *et al.*, 1997).

1.2.2 Food chains and food webs in establishing trophic relationships

There has been increasing recognition of the importance of food web structure in regulating a wide range of ecological patterns and processes (Hairston *et al.*, 1960; Paine, 1966; 1980; Pimm, 1982; Carpenter *et al.*, 1985; Rasmussen *et al.*, 1990; Persson *et al.*, 1992; Hairston and Hairston 1993; Persson *et al.*, 1996; Schindler *et al.*, 1997). Studies attempting to describe food web structure have generally been based on either food chains or food webs. Food chain studies assign species to one of several discrete trophic levels (Hairston *et al.*, 1960; Oksanen *et al.*, 1981; Persson *et al.*, 1992; Abrams., 1993, Goldschmidt., 1996, Namulemo, 1997 and Mbabazi., 1999). The concept of discrete trophic levels is commonly used in ecological studies and has been used successfully in studies predicting contaminant bioaccumulation in top predators (Rasmussen *et al.*, 1990; Cabana and Rasmussen, 1994; Kidd *et al.*, 1995; Swanson *et al.*, 2003). Furthermore, trophic levels provide the framework for studies of cascading trophic interactions (Carpenter *et al.*, 1985; Wootton and Power, 1993) and ecological energetics and efficiencies (Lindeman, 1942; Kerr and Martin, 1970). The trophic level concept, however, is limited by the strict use of discrete trophic levels and its limited ability to capture the complex interactions and trophic omnivory that are prevalent in many ecosystems (Paine, 1988; Polis and Strong, 1996; Persson, 1999; Vander Zanden and Rasmussen, 1999). In contrast, food web studies capture the complexity of trophic relationships in nature (Sprules and Bowerman, 1988). Although food web studies recognize and quantify important attributes such as omnivory, cannibalism and reciprocal predation (Sprules and Bowerman, 1988, Polis, 1991), designation of "trophic linkages" is a subjective process that fails to consider the energetic or functional importance of the represented trophic connections (Paine, 1988, Polis, 1991, Vander Zanden and Rasmussen, 1996). Omnivory is important in trophic interactions and has been found to stabilize simple food chains (McCann and Hastings, 1997; Sterner, *et al.*, 1997; Holyoak and Sachdev, 1998). Cannibalism is a special form of omnivory, where the species feeds both on its own kind and other food sources (Polis *et al.*, 1989).

Food chains and food webs represent extreme end points of models used to represent trophic relationships and both approaches have the potential to

misrepresent the pathways of trophic transfer and energy flow through ecosystems (Murdoch, 1996; Kling *et al.*, 1992; Vander Zanden and Rasmussen, 1996). Recent critiques and studies of highly resolved food webs indicate a variety of problems, including poor taxonomic resolution, inconsistent sampling effort and general incompleteness of the food web data (Winemiller, 1990; Hall and Raffaelli, 1991; Martinez, 1991; Polis, 1991; Hall and Raffaelli, 1993; Polis and Strong, 1996; Polis and Winemiller, 1996; Goldwasser and Roughgarden, 1997).

In response to these problems, numerous authors have called for food web approaches that quantify energy flow and the importance of feeding interactions (Cohen *et al.*, 1990; Kenny and Loehle, 1991; Martinez, 1991).

Use of quantitative gut content data and weighted average formulas to assign organisms, a continuous measure of trophic position which represents the mean path length leading to a consumer, provides energetically based representations of trophic relationships, thereby serving as a compromise between discrete food chain and food web models (Levine, 1980; Vander Zanden and Rasmussen, 1996; 1999; Vander Zanden *et al.*, 1997; Vander Zanden *et al.*, 1999; Jepsen and Winemiller., 2002).

1.2.3 Use of stable Nitrogen and Carbon isotope ratios in food web studies.

The use of stable isotopes to study the trophic interactions of fish is generally increasing (Gu *et al.*, 1996b; Jennings *et al.*, 1997; Vander Zanden *et al.*, 1997). It is becoming increasingly common to use stable isotope ratios in mass-balance equations in order to estimate dietary composition, carbon flows or dietary overlap (Havelange *et al.*, 1997).

Traditionally trophic interactions in fresh water food webs have been defined using dietary analyses of fish stomachs or gut contents or from the presence of organisms within a system. As discussed earlier, the Lake Victoria food web structure has shifted based on information on the volume and composition of the fish catch in the lake, as well as on the stomach contents of fish (Balirwa, 1998; Ogutu-Ohwayo, 1995; Wanink, 1998). Studies based on stomach content analysis revealed a higher trophic diversity among

haplochromines of the Kyoga satellite lakes compared with the main lakes Kyoga (Mbabazi, 1999; Mbabazi *et al.*, 2004) and Victoria (Namulemo, 1997).

While dietary analysis provides valuable taxonomic information on fish diets, it is simply "a snap-shot" technique, that enables analysis of the dietary intake of an individual over the previous few hours and it is also often difficult to identify masticated food items accurately (Hynes, 1950). However conclusions can be drawn from repeated diet studies which are often rare in such studies. The dietary studies can be complimented by analyses of stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope ratios of biota to characterise food web structure and trophic interactions (Peterson and Fry, 1987). Food sources often have specific isotopic signatures that are acquired by consumers (Fry, 1988). If two individuals consume two separate food sources with differing isotopic compositions, they will have different isotopic signatures.

Nitrogen isotopes consistently fractionate in organisms: ^{14}N is selectively eliminated while ^{15}N is selectively retained in body tissues. At every successive trophic transfer, $\delta^{15}\text{N}$ values in the tissue of biota increase. Many studies find the average $\delta^{15}\text{N}$ difference between an animal and its food source is approximately 3 to 4 ‰. (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001). This consistent change provides a powerful analytical tool to quantify relative trophic position or dietary changes in fish (Cabana and Rasmussen, 1994). However use of $\delta^{15}\text{N}$ signatures of consumers as a measure of trophic position neglects intrasystem variation in $\delta^{15}\text{N}$ values characterizing organisms at the base of the food web. Cabana and Rasmussen (1996) found that the lake-specific mean primary consumer varied from 1-13 ‰. Thus, interpreting the $\delta^{15}\text{N}$ of a consumer relative to an appropriate baseline $\delta^{15}\text{N}$ value provides a reliable and quantitative measure of trophic position, defined as a noninteger value reflecting the energy-weighted mean number of trophic transfers between the basal resources and the consumer (Vander Zanden and Rasmussen, 1999). Unlike previous isotopic food web studies, use of this baseline standardization method allows comparative food web studies (Cabana and Rasmussen, 1996; Vander Zanden *et al.*, 1997).

In contrast carbon isotopes fractionate very little in biota, with 1‰ enrichment in $\delta^{13}\text{C}$ per trophic level (Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001). Because of these low fractionation rates, the stable carbon

isotope values of organisms reflect the average $\delta^{13}\text{C}$ of their diets. $\delta^{13}\text{C}$ values can vary at the base of the food web due to differences in photosynthetic C-fixation, growth rates, CO_2 concentration and pH, and these differences are passed on up in the food chain, indicating the origin of organic carbon in organisms at higher trophic levels (Hecky and Hesslein, 1995). In lakes, $\delta^{13}\text{C}$ is useful for differentiating between two major sources of available energy, littoral (near shore) production from attached algae and its detritus, and pelagic (open water) production from phytoplankton, because the base of the littoral food web tends to be enriched in ^{13}C (less negative $\delta^{13}\text{C}$) relative to the base of the pelagic food web (Hecky and Hesslein, 1995; France, 1995a; Post, 2002). Aquatic macrophytes such as water hyacinth and papyrus also provide distinctive $\delta^{13}\text{C}$ inputs because both use atmospheric CO_2 but different photosynthetic pathways (hyacinth C-3 and papyrus C-4 photosynthesis) (Hecky and Hesslein, 1995).

The value of $\delta^{13}\text{C}$ can vary widely among primary producers within a system, and the factors influencing variation in $\delta^{13}\text{C}$ are fairly well understood. The biota inhabiting the different depths of stratified lakes has been observed to be ^{13}C depleted, due to algal uptake of respired CO_2 , which is more abundant in deeper waters of stratified lakes (Rau, 1978; 1980). Benthic algae tend to be enriched in ^{13}C relative to phytoplankton due to a CO_2 boundary layer effect, which causes diffusion limitation to benthic algal cells in oligotrophic lakes (France, 1995a; b; Hecky and Hesslein, 1995). Additionally, algal use of carbonate as a carbon substrate results in enriched $\delta^{13}\text{C}$ values (Hecky and Hesslein, 1995).

Much less is known about the factors influencing variation in $\delta^{15}\text{N}$ values at the lower levels of the food web compared with $\delta^{13}\text{C}$ (Vander Zanden and Rasmussen, 1999). Cabana and Rasmussen (1996) report a wide range of variation in $\delta^{15}\text{N}$ values of primary consumers and showed the 68% of the among-variation in primary consumer $\delta^{15}\text{N}$ is explained by human population density in the watershed. Nitrogen transformation processes such as denitrification and ammonification occur in the suboxic profundal zones of stratified lakes. These processes are accompanied by considerable N isotope fractionation, resulting in a ^{15}N -enriched pool of inorganic N available for uptake by primary producers (Wada and Hatori, 1978; Macko and Estep, 1985; Owens,

1987). In contrast, Nitrogen fixation yields a ^{15}N signal near atmospheric N_2 i.e., 0 ‰

While it is relatively straight forward to use stable isotope ratios to evaluate food web structure and material flow within a single system (e.g., Peterson *et al.* 1985; Keough *et al.*, 1996; Hannson *et al.*, 1997), many critical questions in ecology are best answered through comparisons across multiple systems (e.g. Kling *et al.*, 1992; Post *et al.*, 2000). When comparing among ecosystems, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of a single organism alone provides little information about its source of carbon. This is because there is considerable variation among ecosystems in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the base of the food web from which organisms draw their nitrogen and carbon ($\delta^{15}\text{C}_{\text{base}}$ and $\delta^{13}\text{C}_{\text{base}}$; Rounick and Winterbourn, 1986; Zohary *et al.*, 1994; Cabana and Rasmussen, 1996; MacLeod and Barton, 1998; Kitchell *et al.*, 1999; Vander Zanden and Rasmussen, 1999). With an appropriate isotopic baseline and an appreciation of the underlying assumptions, stable isotopes can help answer some of the difficult questions in food web ecology (France, 1999; Post, 2002). For example, in aquatic systems, most primary producers and detrital energy sources have high temporal variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, complicating their direct use as baseline indicators for secondary consumers that integrate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ over much longer time periods (Cabana and Rasmussen, 1996; O'Reilly *et al.*, 2002). Furthermore, $\delta^{15}\text{N}_{\text{base}}$ and $\delta^{13}\text{C}_{\text{base}}$ can be spatially variable both within a lake (France, 1995a; Vander Zanden and Rasmussen, 1999) and among lakes (Cabana and Rasmussen, 1996; del Giorgio and France, 1996). Cabana and Rasmussen (1996) suggested the use of long-lived primary consumers to quantify $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in aquatic food webs because the temporal variance of their isotopic signature is much lower than that of primary producers (Cabana and Rasmussen, 1996). They should also reflect the spatial variation within and among lakes (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999).

1.3.0 Research Problem

The need for ecosystem-based management is widely recognised and accepted, but ecosystem models have not yet proved themselves as

management tools (Mace, 2001). Moreover, there is still great uncertainty as to how to implement an effective ecosystem management on poorly known aquatic ecosystems (Beamish and Mahnken, 1999). To implement ecosystem-based management, a good understanding of the influences that regulate species naturally in the ecosystem is required (Beamish and Mahnken, 1999). It is then of prime necessity to improve our knowledge on these complex and poorly understood aquatic ecosystems. This study characterized the trophic structure and positions of the different fish species and/ or food chain lengths in the different aquatic ecosystems that are at different anthropogenic levels in the Victoria and Kyoga lake basins.

1.4.0 Objectives

The Victoria and Kyoga basin lakes have values that contribute to the Ugandan government's efforts of increasing food security, poverty reduction, economic growth and conserving the natural resource base. They are critical sources of freshwater for humans and domestic animals, cheap high quality protein, income, medicine and employment for the communities around these lakes.

The overall objective of this study was to examine the trophic positions and food webs of the dominant fish species in the Victoria and Kyoga Lake basins to provide insight into how changes in fish fauna can result from a reduced variety of carbon sources and changing food chain lengths in these lakes. This was specifically achieved by examining:

- a) The trophic composition of dominant fish species,
- b) The food sources and trophic interactions among fishes in lakes with and without Nile
- c) The trophic positions of the individual fish species
- d) The food chain lengths among the fishes in the different lakes.

1.4.1 Hypotheses

- a) The presence of Nile perch reduces the trophic position of the native species in lakes where it is found;
- b) The presence of Nile perch reduces the food chain lengths in lakes where it is found;
- c) Species richness has no effect on food chain lengths among lakes;
- d) Water transparency has no effect on food chain lengths among lakes.

1.5.0 Thesis Structure

This chapter discusses the trophic interactions and food webs before and after Nile perch introduction, the utilisation of food chain and food web approaches in trophic relationships, use of dietary stomach content and stable isotopes analyses in establishing trophic positions and food webs.

The second chapter describes the study lakes, the methods used in field sampling, laboratory analyses of diet using both stomach contents, and nitrogen and carbon stable isotope methods in determining trophic positions and food chain lengths.

The third Chapter describes and discusses the diet and trophic composition of the different fishes in the study sites based on stomach content analysis.

The fourth chapter describes carbon sources, trophic relationships and trophic positions of the fish species and the fish food chain lengths in the study sites based on stable isotope analysis.

The fifth chapter synthesizes out puts from the previous chapters with other information and suggests recommendations for steps towards developing an ecosystem based management approach for these aquatic ecosystems.

CHAPTER TWO

2.0 Materials and Methods

2.1.0 Choice of the Study Area

The Victoria and Kyoga Lake basins had a similar native fish fauna (Graham, 1929; Worthington, 1929). The two lakes have had similar history with Nile perch being introduced and having similar impacts in the two lakes. For ichthyogeographical purposes, the two lakes can be considered to be similar (Kudhongania *et al.*, 1992; Mbabazi, 1999). Lake Kyoga lies downstream of Lake Victoria and fish propagules could conceivably move from Lake Victoria down the Nile to the Lake Kyoga satellite complex, but not upstream due to water falls along the river (e.g. Ripon and Bujagali fall). Evolution of Lake Victoria haplochromines therefore proceeded downstream in Lake Kyoga, and the Lake Kyoga complex has been described both as refugium for Lake Victoria functional diversity (Kaufman, 1997; Kaufman *et al.*, 1997) and as a significant fishery resource (Kudhongania *et al.*, 1992; Ogutu-Ohwayo, 1995). Victoria and Kyoga Lake basins have many satellite lakes which are separated from the main lakes by swamps which are at different levels of anthropogenic impacts, encompassing environmental conditions extending from pristine to highly impacted and dominated by either the introduced species especially Nile perch as the top predators or Nile perch free with native species such as *Protopterus aethiopicus* and haplochromines (Table 2.2).

It was therefore considered that understanding of these lakes in a watershed context incorporating interconnections among lakes, as opposed to lake-by-lake basis would contribute to the knowledge base required to solve some of the problems experienced in lakes Victoria and Kyoga, especially the reduction in trophic groups, which seems to have shortened the food chain lengths of lakes.

2.2.0 Study Area

The study focused on eight satellite lakes, five and three from the Victoria and Kyoga Lake basins respectively, which were grouped into three categories according to their drainage systems. Since aquatic systems are confined to the interconnecting swamps, streams and rivers between water bodies; lakes within a watershed provided a unique study system. The two drainage systems comprised the satellite lakes from the Lake Victoria basin i.e Koki, with lakes Kachera and Mburo; Nabugabo, with lakes Kayugi, Kayanja and Nabugabo main. The third drainage system comprised satellite lakes from the Lake Kyoga basin i.e. Kyoga; with Lakes Nawampasa, Nakuwa and Bisina. Some data were also collected in the main lakes Victoria and Kyoga. In Lake Kyoga, which is part of the Kyoga drainage system described above, data were collected from the North Eastern part (Iyingo) and the Western part of the lake off Victoria Nile from Bukungu landing site East-wards. The North Eastern part (Iyingo) is adjacent to Lake Nawampasa but separated by thick papyrus and the two systems are linked through a channel (Figure 2.1A). The inshore areas of northern Lake Victoria were the fourth drainage system and data were collected from Napoleon Gulf, Thruston and Hannington Bays that are at different levels of human interference.

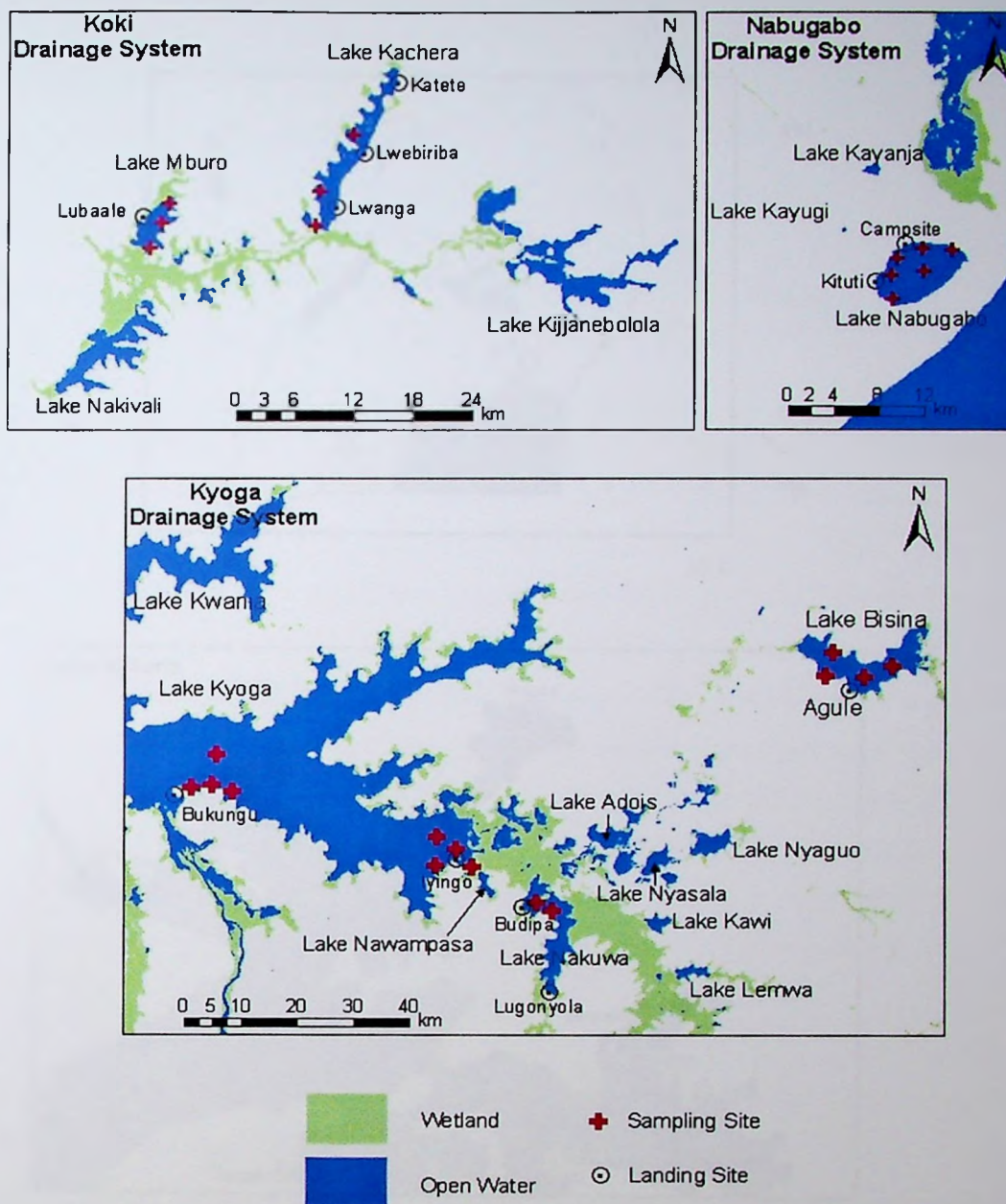


Figure 2.1. A map showing part of the studied lakes in the Victoria and Kyoga basins, indicating landing sites where fish samples were obtained and sampling sites where experimental collection of fish and possible food sources was done. Source of digital Map (National Biomass, 1995)

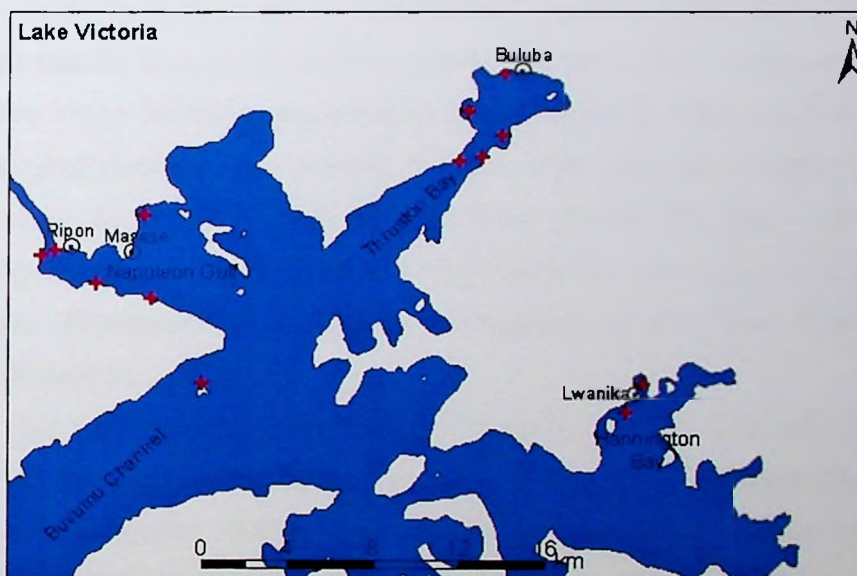
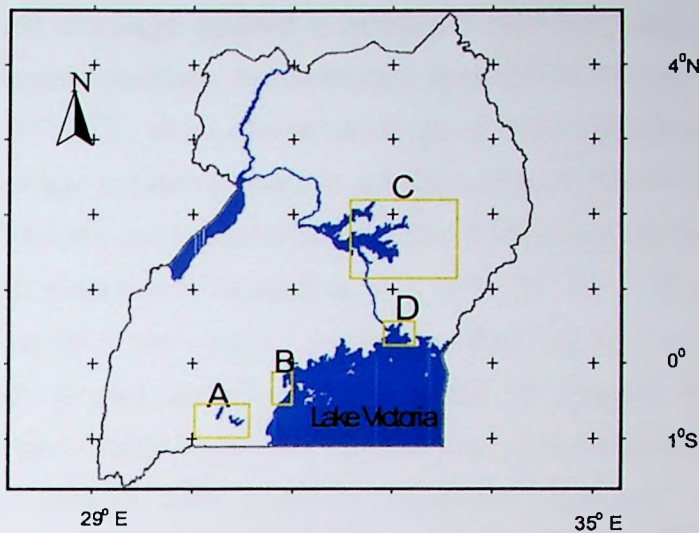


Figure 2.1B. A map of Uganda showing the location of the drainage systems studied in Fig. 2.1A (A=Koki, B= Nabugabo, C= Kyoga and D=Northern portion of Lake Victoria) indicating landing sites where fish samples were obtained and sampling sites where experimental collection of fish and possible food sources was done. Source of Digital map for Lake Victoria (Silsbe, 2003)

2.2.1 Koki drainage system lakes

The Koki drainage system is located ~ 226 Km, west of Kampala city, in Rakai and Mbarara districts, between latitudes 00°40"S and 01°35"S; longitudes 30°50"E and 31°50"E, at an elevation range of 1230 m (Atlas of Uganda, 1967). The Koki drainage system covers a surface area of about 570 Km². Two lakes (Kachera and Mburo) were sampled from this drainage system.

(1) Lake Kachera is located at 00° 35'S; 31° 07' E (Fig. 2.1A), has a total surface area of 36.3 km², and a maximum depth of 4.1 m. It has a maximum length of 20.0 km and width of 3.5 km (Atlas of Uganda, 1967). The size and shape of the lake varies from time to time due to floating islands. The shoreline vegetation is fringed with papyrus (*Cyperus papyrus*), reeds (*Phragmites mauritanus*), forest, and scattered banana plantations. Lake Kachera is shared by the districts of Mbarara and Rakai and borders Lake Mburo national park and is exposed to very many anthropogenic factors. The communities around Lake Kachera have for long depended on fishing as a major economic activity. The non fishing communities around the lake are either traditional cattle keepers or cultivators, but most of the communities around the lake now practice mixed farming combining both livestock management and crop cultivation to varying degrees (Marquardt *et al.*, 1994; Kamugisha *et al.*, 1997; Namara and Infield, 1998; Emerton, 1999).

(2) Lake Mburo is located at 00 40'S; 30° 56' E in Mbarara District (Fig. 2.1A) in an area owned in precolonial days by the traditional King, the Omugabe of Nkore (Mugisha, 2003), has a total surface area of 10.4 km², a maximum length of 6.0 km and width of 3 km (Atlas of Uganda, 1967). However, the size and shape vary from time to time due to floating islands. The inhabitants (Bahima) around the lake primarily use the riparian land for pastoralism. Until the intervention of colonial government fishing was not an important economic activity in the lake (Mugisha, 2003). In 1983 Lake Mburo was gazetted as a national park (Burgis *et al.*, 1987) and therefore fishing was restricted. Following the eviction of the last residents in 1997 there is no permanent human settlement in the 260 km² Lake Mburo National Park, apart from approximately 50 Uganda Wildlife Authority (UWA) staff and 100 or so workers and fisherfolk who temporarily reside at Lubale Landing site (Emerton, 1999). The economic

benefits accruing from fisheries activities were valued at Ush 108.1 million in 1997, 7.6 million of which went to the national park as house maintenance fees, boat fees, and fuel wood fee for processors, and the rest to Department of Fisheries Resources (Emerton, 1997). The National park is characterised by high densities of animals most of which are native and the lake harbours large populations of hippopotamuses most of the day hours.

2.2.2 Nabugabo drainage system lakes

The Nabugabo drainage system is located ~ 150 Km, west of Kampala city, in Masaka district, between latitudes $00^{\circ}17''\text{S}$ and $00^{\circ}24''\text{S}$; longitudes $31^{\circ}51''\text{E}$ and $31^{\circ}54''\text{E}$, at an elevation range of 1159 to 1162 m (Atlas of Uganda, 1967; Ramsar Convention Bureau, 2004). The Nabugabo drainage system with a surface area of 220 Km^2 is also one of the sites designated as wetlands of international importance in Uganda (Ramsar Convention Bureau, 2004). Three lakes (Kayugi, Kayanja and Nabugabo) with similar fish fauna except Nabugabo where Nile perch was introduced were sampled from this drainage system.

(1) Lake Kayugi is located at $00^{\circ} 19'1\text{S}$ $31^{\circ} 51'1\text{E}$ and at an elevation 1162 m, has a surface area of about 0.2 km^2 (Fig. 2.1A). Lake Kayugi is separated from Lake Manywa by a 0.5 Km extensive thick papyrus swamp, and is connected to Lake Nabugabo via River Juma. Lake Kayugi has a maximum depth of about 3.0 m. River Kagona feeds the swamp around lakes Kayugi and Manywa from the Northwest (Ogutu-Ohwayo, 1993). Lake Kayugi is mainly used by communities for subsistence fishing and has a maximum of four fishing rafts. Lake Kayugi also provides an example where cultural norms help in conservation of biodiversity. On Lake Kayugi women are barred from getting into contact with the lake, where as in Africa generally women are charged with the duty of collecting domestic water. Due to the cultural norms associated with Lake Kayugi, it is less used as a direct source of water for domestic purposes, besides there is a borehole adjacent to the lake.

(2) Lake Kayanja is located at $00^{\circ} 17'1\text{S}$ $31^{\circ} 52'1\text{E}$, at an elevation of 1159 m, Fig. 2.1A (Atlas of Uganda, 1967) and has a surface area of about 1.2 km^2 with a maximum depth of about 3.0 m (Ogutu-Ohwayo, 1993). Apart from the eastern shoreline, an extensive *Loudentia phragmitoides* dominated swamp

surrounds the lake. The swamp around this lake is fed by Rivers Nzonsemu and Kikoma from the North-West and drains North-Eastwards via River Kanywa and the adjoining swamp, into Nakiga Bay of Lake Victoria (Ogutu-Ohwayo, 1993). The dissolved oxygen (DO) levels in the lake are high in the open water (surface values of 7 mgL^{-1}), and the lake appeared to be well mixed (Chapman and Hulen, 2001). Lake Kayanja like Lake Kayugi is used for subsistence fishing (maximum of two dug out canoes), but unlike lake Kayugi, it is extensively used for watering domestic animals especially cattle.

(3) Lake Nabugabo the largest among the Nabugabo drainage system is located at $00^{\circ} 22' 1'' \text{S } 31^{\circ} 54' 1'' \text{E}$ at an elevation of 1159 m (Atlas of Uganda, 1967). Lake Nabugabo is shallow with a surface area of 24 km^2 and mean depth of 4.5 m and maximum depth of 7 m. It lies within an extensive marsh that was formerly a bay on the western shore of Lake Victoria (Worthington 1932; Greenwood 1965; Ogutu-Ohwayo 1993) (Figure. 2). Lake Nabugabo was formed when a sand bar separated a portion of Lake Victoria during a water level recession about 4000 years ago (Trewavas, 1933; Beadle, 1981; Kendall, 1969; Ramsar Convention Bureau, 2004). The lake has no surface out flow apart from seepage through the sand bar into Lake Victoria (Greenwood, 1965; Ogutu-Ohwayo, 1993). The lake margin is primarily dominated by hippo grass *Vossia cuspidata*, papyrus and *Miscanthidium violaceum* (Visser, 1964). The lake also contains emergents such as water lilies (*Nymphaea lotus* and *N. caerulea*) and submerged *Ultricularia spp*; but the open waters characterize the largest portion of the lake (Visser, 1964; Schofield and Chapman, 1999). Nile perch was introduced in Lake Nabugabo in 1960 and 1963 to assess the effects its introduction would have on fish faunas similar to that of Lake Victoria (Gee, 1964). Four tilapiine species *O. niloticus*, *O. leucostictus*, *T. zillii* and *T. Rendalli* were also introduced or gained access to this lake around the same time (Welcome, 1964; 1967; Ogutu-Ohwayo, 1993). Unlike the smaller lakes (Kayanja and Kayugi), Lake Nabugabo is extensively used by local communities for subsistence and commercial fishing, source of water, handicraft materials (mats, hats, roof thatch) and fishing floats and rafts. There are also an increasing number of holiday and conference centers. Boating and swimming are popular, as the lake has a reputation for being free of schistosomiasis (bilharzia) (Ramsar Convention Bureau, 2004).

2.2.3 Kyoga drainage system lakes

The Kyoga drainage system is located between latitudes 001°N and $02^{\circ}30'\text{N}$; longitudes $32^{\circ}45'\text{E}$ and $34^{\circ}25'\text{E}$, at an elevation range of 914 to 1048 m (Atlas of Uganda, 1967). The Kyoga drainage system lakes and the associated wetlands cover a surface area of 4700 Km^2 (ILEC, 2001). The Kyoga drainage system consists of the main Lake Kyoga, Lake Kwanja and a series of smaller lakes, which are separated from the main lake by swamps (Fig. 2.1A). Four lakes (Nawampasa, Nakuwa, Bisina and Kyoga main) were sampled from this system.

(1) Lake Nawampasa is a small lake, located 130 km north east the town of Jinja, in Kamuli district at $01^{\circ} 16' \text{N}$ $33^{\circ} 21' \text{E}$ and elevation 1037 m (Atlas of Uganda, 1967). It has a surface area of about 8 km^2 ; with a mean depth of 2.6 m and maximum depth of 3.1 m (Fig. 2.1A). Lake Nawampasa is internationally recognized because it still contains remnants of the beautiful cichlid populations once found in lakes Victoria and Kyoga (Mbabazi, 1999; Mbabazi *et al.*, 2004). The lake currently is dominated by open waters and has numerous floating vegetation islands. Lake Nawampasa formerly comprised of three ecological zones (Mbabazi 1999).

- (i) An open water section in the middle of the lake,
- (ii) A belt of dense aquatic macrophytes that consisted of the submerged *Ceratophyllum sp.* and floating water lilies, mainly *Nymphaea sp.* and
- (iii) The zone between the clear open water and aquatic macrophytes surrounded by turbid waters.

The shoreline vegetation is mainly hippo grass (*Vossia cuspidate*), *Miscanthidium sp.* and *C. papyrus* on the end where there is a channel that connects the lake to the main Lake Kyoga. Some stationary mats of water hyacinth are already present at the various entry points into the lake.

(2) Lake Nakuwa one of the large lakes among the Kyoga drainage system lakes, located 132 km north east the town of Jinja, at $01^{\circ} 09' \text{N}$ $33^{\circ} 21' \text{E}$, an elevation 1037 m, surface area of 200 km^2 and an average depth of 3.3 m (Fig. 2.1A; Atlas of Uganda, 1967). It is shared by the districts of Kamuli, Pallisa and Soroti. The lake is free of submerged and floating macrophytes, with lots of floating papyrus (sudds). Papyrus, hippo grass and reeds dominate the shoreline

vegetation. Lake Nakuwa like the main lake Kyoga was stocked with the Nile perch and the tilapiine species namely *O. niloticus*, *O. leucostictus* and *Tilapia zilli* in the general stocking exercise of small lakes and dams in the early 1970's (Baliirwa, personal communication).

(3) Lake Bisina, is another large lake, located 272 km north east the town of Jinja, in the shadow of Mt. Elgon at $01^{\circ} 38'N$ $33^{\circ} 58'E$ and elevation 1048 m and which has tiny crater lakes high in the mountains. Lake Bisina has a surface area of 308 km^2 (Atlas of Uganda, 1967) and a maximum depth of 3.5 m. Districts of Kumi (south) and Katakwi (North) border Lake Bisina. Lake Bisina like the main lakes Victoria and Kyoga was stocked with Nile perch and the tilapiines (*O. niloticus*, *O. leucostictus* and *T. zilli*) in the early 1970's. Lake Bisina, like Lake Nawampasa, still has beautiful remnant species/groups of cichlid haplochromines that occurred in lakes Victoria and Kyoga. Lake Bisina is known by local inhabitants to have supported a Nile perch fishery however; this study did not record any Nile perch through out the survey. The lake is characterized by a variety of habitat types ranging from submerged aquatic macrophytes dominated by *Najas horrida* and *Ceratophyllum spp.* some floating water lilies (*Nymphaea spp.*). Most of the lake's shoreline is fringed with hippo grass (*Vossia cuspidata*) and a very small portion of cattail (*Typha domingensis*). The human populations surrounding the lake are mainly pastoralist communities keeping cattle and goats but also do some crop cultivation.

(4) Lake Kyoga is the largest lake in the entire Kyoga drainage system, with surface area of 2047 km^2 , located at, $01^{\circ}58'N$ $32^{\circ}83'E$, and elevation of 914m (Figure 2.1A; Uganda Atlas, 1967). It has an average depth of 4 m and a maximum depth of 7 m. Lake Kyoga lies in the flooded branches of the low west flowing Kafu river and receives the out flow from the Victoria Nile as it turns out of the lake northward and then westward over the low northern end of the Rift escarpment via the Murchishon falls and pours into lake Albert (Atlas of Uganda, 1967). Most of the shoreline of Lake Kyoga main is fringed with mainly papyrus interspaced with hippo grass, reeds, and scanty unhealthy looking Water hyacinth. Sampling for this study concentrated around the North Eastern part of the lake around Iyingo landing site and the Western part beginning from Bukungu landing site east-wards (Fig. 2.1A).

2.2.4 Lake Victoria

Lake Victoria formed its own drainage system, located between latitudes $00^{\circ} 20' \text{N}$ - $03^{\circ} 00' \text{S}$ and longitudes $31^{\circ} 39' \text{E}$ - $34^{\circ} 53' \text{E}$, elevation 1134 m (Hecky and Bugenyi, 1992; Crul, 1995; Balirwa, 1998; Muhoozi, 2002), is the largest tropical lake in the world with a surface area, 68,800 km² (Bootsma and Hecky, 1993) and supports the largest freshwater fishery on the planet with annual catches of 300 to 500 thousand tonnes (Ogutu-Ohwayo, 1994; ILEC, 2001). Three countries, Tanzania (51%), Kenya (6%) and Uganda (43%) share Lake Victoria. The lake is roughly square in shape; its greatest length and width being about 400 and 320 km respectively. Much of the lake is relatively shallow with the deepest part (96 m) being the northeast (Johnston *et al.*, 2000). The shallow depth and long retention time (residence and flushing times of 23 and 123 years respectively) mean that any environmental disturbances, such as contaminant input or phytoplankton blooms, exhibit strong impacts relatively rapidly (Bootsma and Hecky, 1993). The lake receives nearly 80% of its water inputs from rain directly to the surface; a similar amount is lost through evaporation (Bootsma and Hecky 1993). The lake bottom is mainly covered by a thick layer of organic mud, but with patches of hard substrate, sand or rock (Scholtz *et al.*, 1990). The coastline is indented with many bays and gulfs which increases perimeter area ratio and therefore increased changes of allochthonous inputs (Gasith and Hasler, 1976; Schindler and Scheuerell, 2002). Three areas (Napoleon Gulf, Thruston and Hannington Bays) of Lake Victoria were sampled by the current study (Fig.2.1B).

Napoleon Gulf is located in southeastern Uganda at $00^{\circ} 20' \text{N}$; $33^{\circ} 15' \text{E}$ and leads to the source of the Nile River located near the town of Jinja (Fig. 2.1B). The Gulf has a mean depth of 8.8 m and maximum depth of 14 m (Silsbe, 2004). Napoleon Gulf is eutrophic, with a highly convoluted shoreline and numerous bays which provide a range of aquatic ecosystems from wetland to pelagic (Campbell *et al.*, 2003) and associated biota. Samples were collected from six experimental sites that represented the major habitat types of the gulf based on shoreline characteristics such as papyrus/waterhyacinth, papyrus/water hyacinth/banana plantations, steep slope/rocky/forest/reeds, hippo grass/ambachi/water, hippo grass.rocky and rocky habitats.

Thruston Bay is located 37km east of Jinja town, in Mayuge district, northeast of Napoleon Gulf at $00^{\circ} 26'N$; $33^{\circ} 20'E$ (Fig.2.1B). The Bay is approximately 1650 hectares and has a mean depth of 3.3 m and the maximum depth of 11 m (Wanda, 2003). Thruston Bay is semi urban with a hospital, schools and a landing site. Thruston Bay has a large wetland littoral region dominated by the macrophytes papyrus, reeds, cattail, hippo grass and water hyacinth. Three distinct shoreline types were distinguished and were sampled to represent the Bay; these were; a rocky reeds-hippo grass, papyrus—dominated sub-bay, rocky papyrus shoreline, forested shoreline and rocky - steep slope with scattered hippo grass shoreline.

Hannington Bay is located 79 km east of Jinja town, in Mayude district, south east of Thruston Bay at $00^{\circ} 18'N$; $33^{\circ} 26'E$ (Fig. 2.1B). The Bay has a mean depth of 3.2 m and the maximum depth of 10 m. Hannington Bay relative to Napoleon Gulf and Thruston Bay, is categorised as rural. Due to logistical reasons only two sites were sampled and comprised two distinctive shoreline types; a papyrus-dominated sub-bay with small patches of hippo grass and papyrus dominated and hippo grass / reeds.

Drainage, lake/site, species richness, species abundance, selected physicochemical parameters, food chain length and riparian characteristics and associated human activities (August 2001 to May 2004). Surface areas for lakes Kyoga and Victoria sampled parts refer to the total areas of entire lakes.

Drainage	Lake/site	Total no. of species	Most abundant species/taxa (Weight)	Most abundant Species/taxa (number)	Area (Km ²)	Depth (m)	Secchi depth (m)	DO (mgL ⁻¹)	Temp (°C)	pH	Chla (ugL ⁻¹)	Food Chain Length	Shoreline characteristics and activities
Koki	Kachera	10	<i>P. aethiopicus</i>	Haplochromines	36.3	1.71	0.29	5.48	23.47	7.73	121.60	0.8	Mixed farming, intensive fishing.
	Mburo	10	<i>P. aethiopicus</i>	Haplochromines	10.4		0.50	4.70	23.30	6.90	49.97	1.1	Protected area, sheltered, minimal fishing
Nabugabo	Kayugi	12	Haplochromines	Haplochromines	0.2							1.5	Completely sheltered by papyrus, almost no fishing
	Kayanja	15	<i>O. esculentus</i>	Haplochromines	1.2		0.63				27.11	1.3	Thinly sheltered one side and the other completely open, cattle keeping, minimal fishing
	Nabugabo	16	<i>L. niloticus</i>	<i>L. niloticus</i>	24		0.88				17.38	0.7	Deforestation, papyrus harvesting, urban beach development
Kyoga	Nawampasa	36	Haplochromines	Haplochromines	8	1.65	1.09	5.76	27.50	8.04	18.01	1.4	Completely sheltered, mixed farming, minimal fishing
	Nakuwa	13	<i>L. niloticus</i>	<i>S. afroffischeri</i>	200	1.90	0.66	7.55	28.70	8.24	64.34	0.5	Mixed farming, papyrus harvesting, intensive fishing, suddes
	Bisina	38	Haplochromines	Haplochromines	308		2.86	5.78	27.18	7.81	5.56	1.5	Thinly sheltered by scattered <i>Vossia</i> sp, Typha sp, mixed farming, navigation, almost no fishing

Drainage	Lake/site	Total no. of species	Most abundant species/taxa (Weight)	Most abundant Species/taxa (number)	Area (Km ²)	Depth (m)	Secchi depth (m)	DO (mgL ⁻¹)	Temp (°C)	pH	Chla (ugL ⁻¹)	Food Chain Length	Shoreline characteristics and activities
	Kyoga-Iyingo	21	<i>L. niloticus</i>	<i>L. niloticus</i>	2,047	2.95	0.71	4.14	27.45	7.70	32.16	0.8	Mixed farming, papyrus harvesting, navigation, sudds, intensive fishing
	Kyoga-Bukungu	17	<i>L. niloticus</i>	<i>L. niloticus</i>		3.50	1.04	7.39	26.27	8.01			Mixed farming, papyrus harvesting, navigation, sudds, intensive fishing
Victoria	Napoleon Gulf	32	Haplochromines	Haplochromines	68,800	8.8	1.35		24.55		24.30	1.5	Mixed farming, breweries, fish factories, hotels, beach developments, urban, navigation
	Thruston Bay	29	<i>L. niloticus</i>	<i>L. niloticus</i>		3.30	0.83	7.43	26.80	8.88	32.68	1.7	Sugar cane plantations, Hospital, intensive fishing, navigation
	Hannington Bay	19	<i>L. niloticus</i>	Haplochromines		2.13	0.77			7.92		0.9	Mixed farming, sand mining, navigation, intensive fishing, papyrus harvesting

2.3 Field sampling

The representative dominant taxa for the analysis of trophic levels and potential food or carbon sources were collected from two to six pre-selected sites at various distances from the shoreline to the open water of each of the sampled lakes between August 2001 and August 2003. Additional sampling was done for the western part of the Lake Kyoga (Bukungu) in the months of February and April 2004 to get an idea into within lake differences. The representative taxa included fish, macro-invertebrates and primary producers.

Fish for stomach content and stable isotope analyses were collected every three months, using experimental multifilament gill nets with stretched mesh sizes ranging from 25.4 mm to 203.2 mm. The gill nets increased by 12.7 and 25.4 mm intervals from 25.4 to 139.7 mm and 152.4 to 203.2 mm respectively. The nets were set overnight at two to six pre-selected stations at various distances from the shore line (0-5m), 50 m, 200m and > 200m to the open water depending on the size of the lake and based on the habitat types that were available in the lake, for approximately 12 hours. Some fish specimens were also obtained from local fishers who used a range of fishing gears and methods such as gill nets, beach seines, cast nets, hook and line, long lines and locally constructed basket traps.

Upon retrieval, fish specimens were sorted into their taxonomic groups, to species level whenever possible. The total length of the individual specimens was measured to the nearest centimetre (cm) and the number, and weights of each taxon were recorded.

The fishes were cut open, their stomachs dissected out and their degree of fullness determined (Bagenal, 1978). Stomach fullness was assessed at four levels by visually determining the level of stomach fullness of the abdominal cavity. A subjective scale of scores ranging from empty (0) to full (1) stomachs was used (Bagenal, 1978; Baliwa, 1998). Stomach fullness was necessary in the estimation of volumetric dietary contributions to fish. The stomachs of the large predatory fishes (e.g. Nile perch) were dissected in the field for assessment and examination of stomach contents while the stomachs of herbivorous fishes especially tilapiines were labelled and preserved for later laboratory analysis (e.g. Duque and Winemiller, 2003). Stomach contents for the large predatory species were identified to the lowest possible taxonomic level, focusing particularly on the identification of fish prey

to species or to genus and where the fish prey were overdigested, they were grouped as unidentified fish remains.

The Invertebrate preys were generally lumped into family or order and occasionally genus or species level. For the Nile perch a dominant predator individual fishes were divided into length categories to account for ontogenetic shifts in diet (Ogutu-Ohwayo, 1994). The fishes (especially haplochromines, not identified in the field), were preserved in 10% formaldehyde solution, labelled with habitat and date of capture and transported to the laboratory where further identifications and remaining stomach content analysis were done.

A skinless white muscle tissue was cut from the dorsal anterior part of each fish species or size class, placed in an aluminium dish and sun dried to constant weight in an experimental plexglass-drying box. Tissues were only got from the dorsal anterior part of the fish to avoid bias in isotope ratios that occur when using different tissues with variable turnover times (Tieszen *et al.*, 1983 Fry and Parker., 1979; Rau *et al.*, 1983, 1992; Thomas and Cahoon., 1993; Cabana and Rasmussen., 1994; Jennings *et al.*, 1997). White muscle also tends to be less variable in terms of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than other tissues (Pinnegar and Polunin., 1999). In Additional sampling for Lake Kyoga (Bukungu) fish samples for suspected piscivorous predators representing the possible size classes were selected for stable isotope analysis and their lengths were recorded.

Aquatic macro-invertebrates were collected as potential prey from same sites as for fish within each lake (two sweeps per site). Macro-invertebrates were sampled using a pond net (mesh size 330 μm) and sorted live into different taxa. Samples of molluscs and other epiphytic invertebrates were hand picked. Benthic invertebrates in the profundal zone were sampled with a Ponar grab (Beaudoin *et al.*, 2001). Invertebrates were kept alive in filtered lake water as separate individual taxa in containers for 6 h in order to let their guts clear (Zah *et al.*, 2001, Jones and Waldron, 2003). All molluscs were removed from their shells. Invertebrate samples from the different sites were pooled to raise enough biomass for stable isotope analysis. The invertebrate samples were sun dried and treated as above for fish.

The leaves and stems of the dominant macrophytes were hand picked along the shoreline, on water and/or under the water surface depending on whether the plant was floating or submerged. The macrophyte samples were

thoroughly washed and sun dried as above, for fish and invertbrates (Jones and Waldron, 2003).

Phytoplankton samples were obtained from vertical hauls of a 10 μm mesh plankton net beginning from about a depth 1.5 m to the surface in all the sampled lakes. Samples from different stations were pooled to ensure sufficient biomass for stable isotope analysis. Phytoplankton were filtered out of lake water with a pre-combusted GF/F (1.2 μm) filter paper and dried over silica gel overnight.

All the dried samples were kept in scintillation vials and transported for further analysis at the Environmental Isotope Laboratory (Department of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada).

2.4.0 Laboratory Procedures

2.4.1 Fish species identification

Fish specimens that were not identified in the field were sorted into taxonomic groups to genus or species level where possible. If a fish did not fit the described characters of a species, it was assigned a "chironym" or a working name given in parenthesis. Morphological characteristics of small fishes were examined with the help of a binocular microscope. The species that were not identified both in the field and laboratory were compared with specimens of described species present in the FIRRI museum.

2.4.2 Diet trophic positions and food chain length

A combination of nitrogen and carbon stable isotopes (Owens, 1987, Vander Zanden *et al.*, 1997) with the traditional dietary stomach content analyses (Hynes, 1950, Balirwa, 1984, 1998; Winemiller, 1990) were used to quantify diet, trophic positions of the different fish species and the fish food chain length in the examined lakes (Vander Zanden *et al.*, 1999; Lake *et al.*, 2001).

2.4.3 Dietary stomach content analysis

The preserved fishes (small or herbivorous) were treated as follows; the fish were cut open, the stomach of each fish was dissected out and its degree of fullness determined as above. Both the preserved stomachs and those stomachs got from the preserved fish were slit open and the contents emptied onto a petri dish, flooded with water and examined first under a binocular microscope (magnification X 50). The larger food items were sorted out of what appeared to be phytoplankton or detrital material, identified to the highest degree of taxonomic resolution possible given the material's state of digestion. Based on relative sizes of ingested items, the larger organisms were thoroughly mixed with water and two sub samples were separately examined on a slide under a compound microscope (up to magnification X 600) (Balirwa, 1984, 1998). Only those food items located in within the stomach were considered ingested and quantified. For all the analysed stomachs of fish species or size groups, the percentage composition by bulk or volume were assessed by sorting out food items and estimating how much they contributed to the total contents (Balirwa, 1984, Winemiller, 1990). Constituents within each sample were quantified using a modified version of the points method (Swynnerton and Worthington, 1940; Hynes, 1950). The dietary component with the highest volume was allocated 16 points. Subsequently every other dietary component was awarded 16, 8, 4, 1 or 0 points depending on the relative importance of the food item in the stomach (Hynes 1950, Genner *et al.*, 1999). Most of the invertebrate dietary items were aggregated into taxonomic orders for further analysis (Duque and Winemiller, 2003).

2.4.4 Stable isotope analyses

Sun dried skinless white dorsal anterior muscle tissues (fillet) from individual fishes were re-dried when necessary in an oven at 60°C and pulverized into fine powder to homogenize the samples by using a Resch 2000 ball mill grinder. About 1 mg ($\pm$ 0.05 mg) of powdered samples was placed into tin capsules of 5 X 3.5 mm that were immediately sealed. Stable nitrogen and carbon isotope analyses were performed on this sample. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were determined using the Micromass VG-Isochrom Continuous Flow system Isotope Ratio Mass

spectrometer (CF-IRMS). Analyses were carried out at the Environmental Isotope Laboratory, Department of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada. The ratios of the stable isotopes were expressed in delta (δ) notation, defined as the difference, parts per thousand (‰ or “per mil”) between the isotopic ratio of the sample and the standard, and will be calculated as:

$$\delta^{15}\text{N or } \delta^{13}\text{C} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \quad (1)$$

Where $R = {}^{15}\text{N}/{}^{14}\text{N}$ for $\delta^{15}\text{N}$ or $R = {}^{13}\text{C}/{}^{12}\text{C}$

The standard material is Pee Dee belemnite (PDB) limestone for $\delta^{13}\text{C}$ (Craig, 1957), and atmospheric nitrogen for $\delta^{15}\text{N}$ (Peterson and Fry, 1987; Ehleringer and Rundel, 1989; Gearing, 1991). The working standards used followed the International Atomic Energy Agency (IAEA) standards, CH6 ($\delta^{13}\text{C} = -10.4\text{‰}$), N1 ($\delta^{15}\text{N} = 0.36\text{‰}$) and N2 ($\delta^{15}\text{N} = 20.3\text{‰}$), and the in-house standards, EIL-70 (powdered lipid-extracted Lake Ontario walleye; $\delta^{13}\text{C} = -19.34\text{‰}$, $\delta^{15}\text{N} = 16.45\text{‰}$ and EIL-72 (powdered Whatman cellulose fibre; $\delta^{13}\text{C} = -25.4\text{‰}$).

2.5.0 Data analysis

2.5.1 Species richness and abundance

Species richness was determined based on the number of species recorded as present in the lake or areas during the study period based on the experimental surveys and unpublished FIRRI data. The most abundant fish species or taxa by lake or area were estimated by determining the average fresh weight or number of each fish species or taxa through out the sampling period. The data was presented in tabular form.

2.5.2 Dietary data and trophic groups

Resource use by the individual fish species or size groups was expressed as percentage composition of prey item to the total volume of the stomach based on

points of the food item and was presented in tabular form. Data were pooled for each species for the different stations within the lake or area for the entire sampling period since the aim was to determine the time-averaged trophic structure and energy sources of the fish communities. Of the total of 13046 specimens representing 125 species or size groups, only 5513 representing 76 fish species or size groups, had three or more stomachs with food or prey and were subjected to further analyses (Chapter 3).

The unweighted arithmetic average clustering also called "UPGMA" ("Uweighted Pair-Group Method using Arithmetic averages") using the Bray-Curtis measure of community distance or dissimilarity, Equation (2) (Rohlf, 1963; Sneath and Sokal, 1973; Pielou, 1984; Legendre and Legendry, 1998) and Detrended Correspondence Analysis DCA (Hill and Gauch, 1980; Gauch, 1982) using DECORANA program were applied to diet data in order to classify the different consumers into distinct trophic groups. Common ordinations and classification clusters could have been helpful in making an argument that trophic groups do or do not exist in the different lakes; however considering the differences in species assemblages a drainage system approach was adopted.

Trophic groups were established in two ways using relative abundance dietary data for the fishes in the different drainage systems coded from Tables 3.1 to 3.4. Initially the UPGMA cluster analysis was used to group the fishes and DCA was then used to simultaneously display the factor scores of the fishes and the diets or food sources coded from cluster group membership in the same multivariate space (Luczkovich *et al.*, 2003). In the resulting scatter plots, the promiximity of points or factor scores for each taxon indicated the similarity of the fishes with respect to other fishes and their food sources and proximity of food sources indicated similarity of their consumers. All multivariate analyses were conducted using Community analysis Package version 2.0-(CAP 2.0) (Henderson and Seaby, 2002).

$$\text{Bray-curtis dissimilarity distance} = \frac{\sum_{i=1}^n |s_{i1} - s_{i2}|}{\sum_{i=1}^n (s_{i1} + s_{i2})} \quad (2)$$

Where s_{i1} , and s_{i2} are the abundancies of diet item i in fish species 1 and 2 respectively.

2.5.3 Stable isotopes, food sources and trophic relationships

Considering the large study area, large number of species and reliability of stable isotope technique, where available a maximum of three individuals per fish species or taxon were analysed, otherwise one or two specimens were also considered. The trophic importance of specific food items to consumers was assed using a dual isotope approach, taking into account of the combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of consumers and prey and the fractionation expected to occur for each isotope (Herwig *et al.*, 2004). We assumed a trophic enrichment of +1‰ for each trophic transfer for $\delta^{13}\text{C}$ (DeNiro and Epstein, 1978, Vander Zanden and Rasmussen, 2001) and 3.4‰ for each trophic transfer for $\delta^{15}\text{N}$ (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 1996; 1999; 2001; Post, 2002).

The mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of the fish or taxa were plotted against one another to give an over view of the trophic structure in the sampled lakes or areas (Chapter 4). The heavier ^{15}N accumulates in consumers as nitrogen moves up the food web, and as a result, top consumers tend to have greater $\delta^{15}\text{N}$ signatures than consumers near the base of the food web. From the observed high omnivory and $\delta^{15}\text{N}$ overlap, this study did not use $\delta^{15}\text{N}$ signatures as a direct measure of discrete trophic level, but calculated a realized trophic position as a continuous variable for each fish species described in detail section 2.5.5 below.

2.5.4 Estimation of trophic positions based on diet

A continuous measure of trophic position of the individual fish species was calculated from using the estimates of the trophic positions of prey organisms (Winemiller, 1990; Vander Zanden and Rasmussen 1996). Considering the complexity of specific trophic interactions among invertebrates, which dominated the diet of most fishes. Trophic positions of prey items were assigned based on dietary stomach analysis (Chapter 3) and $\delta^{15}\text{N}$ signatures (Chapter 4) according to a classification modified from Vander Zanden and Rasmussen (1996). The simplest possible assumptions used in estimation of trophic position of prey items used in this

study are summarized (Table 2.1). A major limitation to this method was that it assumes and simplifies trophic interactions of lower food webs to determine the trophic positions.

Trophic position of each fish species in the sampled lakes or areas was then calculated from dietary data and trophic position estimates for prey items (Table 2.1) using the formula.

$$TP_{\text{fish}} = \sum (Vi Ti) + 1 \quad (3)$$

Where TP_{fish} = mean trophic position of the fish consumer population, Vi = volumetric contribution of the i th prey item, Ti = trophic position of the i th food item and 1 = assumed trophic position of primary producers.

Table 2.2 Estimated trophic position values for the prey items used to calculate trophic position of fishes based on diet modified from Vander Zanden and Rasmussen (1996).

Prey category	Estimated trophic position	Includes
Fish	2.5	Tilapines
	3.5	Haplochromines, <i>Clarias</i> sp, <i>Barbus</i> sp, <i>Brycinus</i> sp, <i>Lates</i> sp, <i>R. agentea</i> , <i>A. frenatus</i> , un identified fish
Peadophages	3.0	Fish eggs, fish embryos
Crustaceans	2.5	Zooplankton, Ostracods, crabs
Omnivorous zoobenthos	2.5	Trichoptera, Ephemeroptera, Hemiptera, Nematocera, Coleoptera, Diptera, Oligochaeta, Hirudinea,
Predatory zoobenthos	3.0	Odonata, Hirudinea,
Detitivores/herbivores zoobenthos	2.0	Isoptera, Millipedes,
Molluscs	2.0	Gastropoda
Prawn	2.0	<i>Caridina</i>
Protozoa	2.0	Ciliates
Primary	1.0	Detritus, phytoplankton, higher plants,

2.5.5 Estimation of trophic positions and Food chain length based on $\delta^{15}\text{N}$ signatures

The $\delta^{15}\text{N}$ signatures cannot be used directly to represent the trophic position, since the $\delta^{15}\text{N}$ of primary producers are highly variable among systems (Kling *et al.*, 1992; Kline *et al.*, 1993; Cabana and Rasmussen, 1996) and within systems (Toda and Wada, 1990; Gu *et al.*, 1994; Cabana and Rasmussen, 1996). In this study the $\delta^{15}\text{N}$ signatures of primary producers varied from -9.18 to 8.4 ‰, therefore a continuous measure of trophic position was determined using equation (2) (Vander Zanden and Rasmussen 1996, 1999, Jepsen and Winemiller, 2002, Post 2002). For $\delta^{15}\text{N}$ values to provide a measure of the trophic position of a fish consumer, they were interpreted relative to the lake specific $\delta^{15}\text{N}$ signature representing the base of the food web (hereafter referred to as the baseline $\delta^{15}\text{N}$) (Cabana and Rasmussen, 1996; Vander Zanden *et al.*, 1999, Post, 2002). The observed spatial variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for most primary producers complicates their direct use as indicators of $\delta^{13}\text{C}_{\text{base}}$ and $\delta^{15}\text{N}_{\text{base}}$ for secondary consumers that integrate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ over a much longer time periods (Cabana and Rasmussen, 1996) as typical example. Based on stomach contents and $\delta^{15}\text{N}$ signatures, therefore, this study interpreted the $\delta^{15}\text{N}$ of all the other fishes relative to the baseline $\delta^{15}\text{N}$ determined from selected tilapiine species. The selected tilapiine species were the most appropriate because they relatively large and long-lived primary consumers and integrate temporal variability in primary producer $\delta^{15}\text{N}$ compared to planktonic primary consumers. The tilapiine species were generally herbivores or included a larger proportion of algae in their diets (Chapter 3); generally occupied similar and/or low food web positions based on $\delta^{15}\text{N}$ signatures (Chapter 4) and were common to most examined lakes or areas. The best options for estimating the baseline $\delta^{15}\text{N}$ would have been herbivorous snails because they are relatively long lived primary consumers but were not common to all most examined lakes or areas.

A method that uses the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ information to correct for within and among variation in primary consumer developed by VanderZanden and

Rasmussen (1999) was adopted by this study. The method estimated trophic position in three stages: it generated a primary consumer $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ relationship described by equation (4), used the $\delta^{13}\text{C}$ signature of a primary consumer (selected tilapia species) to define the appropriate baseline $\delta^{15}\text{N}$ value equations (4, 5 and 6) and estimated the trophic position of fish consumers using equation (7).

$$\delta^{15}\text{N}_{pcon} = \frac{6.34}{1 + \exp[9.67 + (0.356 \times \delta^{13}\text{C}_{pcon})]} \quad (4)$$

Where $n = 78$; $r^2 = 0.40$; $F = 71.73$; $df = 4, 74$; $p < 0.001$; $\exp(x) = e^x$; $\delta^{15}\text{N}_{pcon}$ = the $\delta^{15}\text{N}$ of the primary consumer and $\delta^{13}\text{C}_{con} = \delta^{13}\text{C}$ of the primary consumer.

The residual for each of the primary consumers (tilapia species) were calculated from their obtained $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values using equation (5)

$$resid = \delta^{15}\text{N}_{pcon} - \frac{6.34}{1 + \exp[9.67 + (0.356 \times \delta^{13}\text{C}_{pcon})]} \quad (5)$$

Where "resid" is the residual value from equation (4). The mean residual value (U_{resid}) of all the tilapia species was calculated for each lake.

From equations (4) and (5) an appropriate baseline $\delta^{15}\text{N}$ for each of the individual fish species in the examined lakes were obtained by Equation (6)

$$\delta^{15}\text{N}_{corrected} = \frac{6.34}{1 + \exp[9.67 + (0.356 \times \delta^{13}\text{C}_{fish})]} + U_{resid} \quad (6)$$

Where, $\delta^{15}\text{N}_{corrected}$ is the lake specific baseline $\delta^{15}\text{N}$ signature of the individual fish species, and U_{resid} is the lake specific deviation from the general $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ relationship.

The species trophic position (TP_{fish}) was finally determined relative to the baseline value from Equation (6) using the formula as:

$$TP_{fish} = \frac{\delta^{15}\text{N}_{fish} - \delta^{15}\text{N}_{corrected}}{3.4} + 2 \quad (7)$$

Where, TP_{fish} is the trophic position of fish, $\delta^{15}N_{\text{fish}}$ is the $\delta^{15}N$ of fish, 3.4 is the enrichment in $\delta^{15}N$ per trophic level between fish and food source (Vander zanden and Rasmussen, 1996, 1999, 2001, Post 2002) and 2 is the assumed trophic level position of primary consumers (tilapiine species) used to estimate $\delta^{15}N_{\text{baseline}}$ signatures.

Food chain length for further analysis was only estimated from the trophic positions got from $\delta^{15}N$ signatures because examination stomach contents sometimes provides information on what a consumer has recently eaten but isotopic composition of a consumer reflects its assimilated diet over a period determined by the turnover rate of the tissues (Davenport and Bax, 2002). Food chain length was taken as the difference between the highest trophic positions of fish and the primary consumer (selected tilapiine species) in the examined lakes or areas.

A linear regression analysis (Draper and Smith, 1981) was used to examine the relationship between trophic positions got from dietary and stable isotope analysis, food chain length and lake/food web characteristics such as species richness and transparency.

In all the analyses lakes were grouped into those with Nile perch and those without.

CHAPTER THREE

3.0 Trophic analysis of the fish communities in the Victoria and Kyoga basin lakes based on stomach contents.

3.1 Introduction

Trophic relationships comprise the framework upon which fish communities are organized. Fisheries biologists have long appreciated the importance of feeding and food habits to the ecology and production dynamics of fish stocks (Keast, 1977; Dill, 1983; Ross, 1986; Gerking, 1994). Likewise, there is recognition that feeding activities of fish often have significant impacts on their prey (Northcote, 1988). The strong effects of introduced predatory fish have been shown to deplete not only their immediate supply, but also modify the aquatic food web (Zaret and Paine, 1973; Ogutu-Ohwayo, 1985; Witte *et al.*, 1992a; b; Carpenter and Kitchell, 1993; Kaufman, 1993; Kitchell *et al.*, 1997; Jennings and Kaiser, 1998; Forgaty and Murawski, 1998; Liao *et al.*, 2002). Fishery removals of top predators may also have strong effects on trophic structure of a system because the reduction in predator abundance can have cascading impacts on the lower food webs (Carpenter and Kitchell, 1993, Kitchell *et al.*, 1997; Garrison and Link, 2000). Competition has also been advanced as another process that can restructure food webs. For example, in the Lake Victoria basin there is evidence to suggest that the introduced Nile perch has competed with the native top predators such as the catfishes (Olowo and Chapman, 1999; Goudswaard and Witte, 1997), piscivorous haplochromine cichlids, and introduced tilapiines competing with the phytoplanktivores haplochromine cichlids (seehausen *et al.*, 1997b). As a result, knowledge of diet composition, in terms of relative importance of different prey items of a fish species at a specific locality, is useful in assessing its ecological function and impact. It is also useful, for construction of ecological models, defining the nutritional requirements of potential aquaculture species, and thus guiding management efforts aimed at increasing fish production.

While fisheries management can regulate the removal of biomass of target species, internal ecosystem dynamics, such as predator prey and competitive interactions, ultimately determine the recovery of fish communities (Jennings and

Kaiser, 1998). Accurate quantification of fish diets and feeding patterns therefore provides the basis for understanding trophic interactions in aquatic food webs (Garvey *et al.*, 1998; Vander Zanden *et al.*, 2000). Diet composition can supplement other techniques that track feeding patterns, such as stable isotopes, to evaluate effects on trophic interactions of ontogeny, habitat alteration, or the establishment of exotic species (Chipps and Garvey in press).

Diet studies of lakes in the Victoria and Kyoga basin lakes of East Africa have focused primarily on species of commercial interest, and their effects on inter-specific interactions in individual Victoria or Kyoga basin lakes (Bairwa, 1984; 1998; Mwebaza-Ndawula, 1984; Ogutu-Ohwayo, 1985; 1994; Olowo and Chapman, 1999; Kitchell, *et al.*, 1997; Chapman *et al.*, 2003; Mbabazi *et al.*, 2004). Less commercially important species and lower trophic levels, i.e. those compartments that sustain the trophic webs and fisheries, have received, in general, little attention (Christensen, 1995; Cartes and Maynou, 2001). This study indicated a high percentage of fish with empty stomachs from the overall drainage systems (Koki 76%, Nabugabo 69%, Kyoga 73%, and Victoria 77%), which may reflect sampling regimes and the diets of the fishes. The high percentages of empty stomachs also indicate one of the main short-coming in the use of stomach contents in diet studies.

This chapter describes food utilization in fish communities in lakes of the Victoria and Kyoga basin that have experienced different levels of human interference. It also describes food items in stomachs and identifies the trophic groups in the communities by determining the dietary similarity among the various fish species. The detailed materials and methods used in the study are fully described (Chapter 2).

Table 3.1 List of fish species and food items included in dietary analysis from August 2001 to May 2004, text code and former taxonomic genera. The size classes for *L. niloticus* were determined based on total length (TL) in cm according to Ogutu-Ohwayo (1994). Note the absence of a dot in text codes for food items.

Family	Species (author)	Former Genera	Text Code
Characidae	<i>Brycinus jacksonii</i> (Boulenger, 1912)	<i>Alestes</i>	B.j
	<i>Brycinus sadleri</i> (Boulenger, 1906)	<i>Alestes</i>	B.s
Bagridae	<i>Bagrus docmak</i> (Forsskål, 1775)		B.d
Centropomidae	<i>Lates niloticus</i> ($\geq 60 < 100$ cm) (Linneas, 1758)		L.n-L
	<i>L. niloticus</i> ($\geq 20 < 60$ cm)		L.n-M
	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)		L.n-S
Cichlidae	<i>Oreochromis esculentus</i> (Graham, 1928)		O.e
	<i>Oreochromis leucostictus</i> (Trewavas, 1933)		O.l
	<i>Oreochromis niloticus</i> (Linneas, 1758)		O.n
	<i>Oreochromis variabilis</i> (Boulenger, 1906)		O.c
	<i>Tilapia zillii</i> (Gervas, 1848)		T.z
	<i>Astatotilapia "fattooth"</i>	<i>Haplochromis</i>	A.t
	<i>Astatotilapia "kyogaastato"</i>	"	A.k
	<i>Astatoreochromis alluaudi</i> (Pellegrin,	"	A.a
	<i>Astatotilapia aneocolor</i> (Greenwood, 1973)	"	A.c
	<i>Astatotilapia latifasciata</i> (Regan, 1829)	"	A.l
	<i>Astatotilapia nubila</i> (Boulenger, 1908)	"	A.n
	<i>Astatotilapia velifer</i> (Trewavas, 1933)	"	A.v
	<i>Astatotilapia</i> sp.	"	A.s
	<i>Gaurochromis simpsoni</i> (Greenwood, 1965)	"	G.s
	<i>Haplochromis lividus</i>	"	H.l
	<i>Harpagochromis micheali</i> (Trewavas, 1928)	"	H.m
	<i>Harpagochromis squamipinnis</i> (Regan, 1921)	"	H.s
	<i>Harpagochromis squamulatus</i> (Regan, 1922)	<i>Haplochromis</i>	H.q
	<i>Harpagochromis guiarthi</i> (Pellegrin, 1913)	"	H.g
	<i>Lipochromis cryptodon</i> (Greenwood, 1959)	"	L.c
	<i>Lipochromis maxillaris</i> (Trewavas, 1928)	<i>Haplochromis</i>	L.m
	<i>Paralabidochromis "redfin"</i>	"	P.f
	<i>Paralabidochromis "blackpara"</i>	"	P.x
	<i>Paralabidochromis beadlei</i>	"	P.d
	<i>Paralabidochromis "big eye"</i>	"	P.e
	<i>Paralabidochromis crassilabris</i> (Boulenger, 1906)	"	P.d
	<i>Paralabidochromis "sheller"</i>	"	P.h
	<i>Paralabidochromis rockribensis</i>	"	P.r
	<i>Prognathochromis "shovelmouth"</i>	"	P.g
	<i>Prognathochromis argenteus</i> (Regan, 1922)	"	P.t
	<i>Prognathochromis pellegrini</i> (Regan, 1922)	<i>Haplochromis</i>	P.p
	<i>Prognathochromis stilleto</i>	"	P.i
	<i>Prognathochromis venator</i> (Greenwood, 1965)	"	P.v
	<i>Psammochromis riponians</i> (Boulenger, 1914)	<i>Haplochromis</i>	P.n
	<i>Pyxichromis orthostoma</i> (Regan, 1922)		P.o
	<i>Ptyochromis sauvegai</i> (Pfeffer, 1896)	"	P.s
	<i>Xystichromis phytophagus</i> (Greenwood, 1966)	<i>Haplochromis</i>	X.p
Clariidae	<i>Clarias alluaudi</i> (Boulenger, 1906)		C.a

Family	Species (author)	Former Genera	Text Code
	<i>Clarias gariepinus</i> (Burchell, 1822)		C.g
	<i>Clarias liocephalus</i> (Boulenger, 1898)		C.l
Cyprinidae	<i>Barbus altianalis</i> (Boulenger, 1900)		B.a
Mastacembelidae	<i>Caecomastacembelus frenatus</i> (Gosse, 1986)	<i>Mastacembelus</i>	A.f
Mochokidae	<i>Synodontis afrofischeri</i> (Hilgendorff, 1888)		S.a
	<i>Synodontis victoriae</i> (Boulenger, 1906)		S.v
Momyridae	<i>Gnathonemus victoriae</i> (Ruppell, 1832)		G.v
	<i>Mormyrus kannume</i> (Forsskål, 1775)		M.k
	<i>Petrocephalus catostoma</i> (Steindacher, 1914)		P.c
Propteridae	<i>Protopterus aethiopicus</i> (Heckel, 1851)		P.a
Schilbidae	<i>Schilbe intermedius</i> (Rüppell, 1832)		S.i

Food item	ID CODE
Detritus	Ds
Phytoplankton	Pk
Macrophytes	Vp
Ciliates	Ct
Zooplankton	Zn
Ephemeroptera	Ea
Coleoptera	Ca
Nematocera	Na
Isoptera	Is
Odonata	Od
Trichoptera	Ta
Chironomids	Cd
Chaoborus	Cb
Hirudinea	Hd
Oligochaetes	Os
Molluscs	Ml
<i>Caridina nilotica</i>	Cn
Fish eggs/embryo	Fe
<i>R. argentea</i>	Rs
<i>L. niloticus</i>	Ln
<i>B. sadleri</i>	Br
Tilapiine	Tp
Haplochromine	Hp

3.2 Diet analysis of fishes

The diets of the 76 fish species from 10 lakes representing four drainage systems in the lake Victoria and Kyoga basins showed that fishes consumed a wide variety of food resources, with the highest dietary richness (34 different prey resources) in the Kyoga drainage lakes and the least (23 different prey resources) in the Koki drainage lakes (Tables 3.1 – 3.5).

3.2.1 Koki drainage system lakes

In the two Koki lakes that were sampled (lakes Mburo and Kachera), the 9 fish species examined consumed a total of 23 different prey or food resources (Table 3.2). In both lakes studied, insects were the most important prey by volume (50%) for most fishes with the exception of *Oreochromis esculentus* and *Oreochromis niloticus* whose main primary food was algae, however these fishes still included at least 10% insects in their diet (Table 3.2).

Fish formed another important component of the diet for *Harpagochromis squamipinus* ($\geq 13\%$), *Clarias gariepinus* ($\geq 13\%$) and *Protopterus aethiopicus* ($> 8\%$). Molluscs were also important in the diet of *P. aethiopicus* ($\geq 10\%$) in both lakes and formed the largest component in the diet of *Clarias liocephalus* ($\geq 35\%$) in Lake Kachera. Molluscs did not appear to contribute to the diet of *H. squamipinus* in Lake Kachera, but contributed ($\geq 10\%$) to the same species in Lake Mburo (Table 3.2).

Table 3.2. Fish stomach contents (proportion of volume) in diets of fishes pooled from all sites within the individual Koki drainage system lakes from August 2001 to August 2003. Number of stomachs with food, total number of fish observed and trophic positions of fishes are presented in the final three columns.

Fish species	Lake	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Macrophytes	Ciliate	Crabs	Unidentified insects	Ephemeroptera	Coleoptera	Nematocera	Hemiptera	Isoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Sandgrains	Molluscs	Fish eggs/embryo	Millipedes	Unidentified fish	Sample size (food)	Sample size (total)	Trophic position
<i>A. alluaudii</i>	Mburo	-	-	-	-	-	-	-	-	0.35	0.11	0.22	-	-	-	0.14	-	0.18	-	-	-	-	-	-	19	71	3.6
<i>A. aneocolor</i>	Kachera	0.09	-	-	-	-	0.15	-	-	0.05	-	-	-	-	-	0.12	0.24	-	-	-	0.03	-	0.31	-	27	233	3.4
	Mburo	-	-	-	-	-	0.14	-	-	0.06	0.24	-	-	-	-	0.12	0.02	-	-	-	-	0.34	-	0.06	26	501	3.3
<i>C. gariepinus</i>	Kachera	-	-	-	-	-	0.03	-	0.05	-	-	-	-	-	-	0.13	0.20	0.04	-	-	0.01	-	0.40	0.08	22	113	3.3
	Mburo	-	-	-	-	-	-	-	-	0.09	-	-	-	0.52	-	0.16	0.04	-	0.04	-	0.02	-	-	0.13	26	119	3.6
<i>C. loiocephalus</i>	Kachera	-	-	-	-	-	0.11	-	-	-	-	-	0.28	-	-	0.22	0.04	-	-	-	0.35	-	-	-	6	24	3.2
<i>H. squamipinnis</i>	Kachera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	0.33	-	-	-	-	-	0.33	3	44	4.0
	Mburo	-	-	-	-	-	0.12	-	-	0.30	-	-	-	-	-	0.15	0.02	-	0.03	-	0.12	-	-	0.25	39	285	3.5
<i>O. esculentus</i>	Kachera	0.19	0.13	0.17	0.07	0.02	0.15	0.15	-	-	-	-	-	-	-	0.13	-	-	-	-	-	-	-	-	55	213	2.3
	Mburo	0.10	0.09	0.14	0.05	0.02	0.27	0.08	-	-	-	-	-	-	-	0.11	0.15	-	-	-	-	-	-	-	138	435	2.5
<i>O. leucostictus</i>	Kachera	0.04	0.01	0.02	0.01	-	0.30	-	-	-	-	-	-	-	-	0.53	0.09	-	-	-	-	-	-	-	24	203	2.9
	Mburo	0.17	0.01	0.02	0.01	-	0.05	-	-	0.46	-	-	-	-	-	0.16	0.12	-	-	0.01	-	-	-	-	26	104	3.1
<i>O. niloticus</i>	Kachera	0.08	0.08	0.13	0.04	0.01	0.28	-	-	-	-	-	-	-	-	0.28	0.10	-	-	-	-	-	-	-	65	139	2.6
	Mburo	0.12	0.12	0.17	0.06	0.02	0.13	0.02	-	0.02	-	-	-	-	-	0.11	0.06	-	-	0.17	-	-	-	-	90	185	2.3
<i>P. aethiopicus</i>	Kachera	0.09	-	-	-	-	0.12	-	-	0.03	-	-	-	-	0.07	0.14	-	0.33	-	0.01	0.13	-	-	0.08	54	131	3.3
	Mburo	0.02	-	-	-	-	0.16	-	-	0.14	0.05	-	-	-	-	0.08	-	0.27	-	-	-	-	-	0.18	34	72	3.5

In Lake Mburo Ephemeroptera contributed ($\geq 10\%$) and ($\geq 20\%$) to the diets of *Astatoreochromis alluaudii* and *Astatotilapia aneocolor*, respectively; however ephemeropterans were absent from the diet of these two species in Lake Kachera. Fish eggs/embryos formed another important dietary component of *A. aneocolor* ($\geq 34\%$) in Lake Mburo but were not encountered in any of the fish examined in Lake Kachera. In both lakes there was generally a larger proportion of fishes with empty stomachs (2118) compared to those that contained food material (654), however this was more pronounced in Lake Kachera than in Lake Mburo (Table 3.2).

3.2.2 Nabugabo drainage lakes

In the three Nabugabo lakes (Kayugi, Kayanja and Nabugabo), examination of 18 fish species, or size groups for *Lates niloticus*, gave rise to 30 different prey or food resources (Table 3.3). In all the lakes examined, insects formed the most important primary prey (50%) in most fishes with the exception of *Oreochromis esculentus* that fed mainly on algae ($\geq 34\%$) and detritus (25%), however, *O. esculentus* still included at least ($\geq 13\%$) insects in its diet (Table 3.3). *Oreochromis leucostictus* in Lake Nabugabo was the only fish that did not include any insects in its diet and mainly fed on detritus (48%), macrophytes (38%) and algae ($\leq 15\%$). Fish was another important food item and constituted the major prey for the commercially important *L. niloticus* throughout its life history. Both size classes *L. niloticus*, <20 cm TL, 20-60 cm TL, mainly depended on fish for their dietary requirements ($\geq 74\%$), however, still included insects in their diet. The proportion of insects was higher in the smaller sized *L. niloticus* ($\geq 34\%$) compared to larger sized ones ($\leq 5\%$). Cannibalism was also observed for both size classes of *L. niloticus* (Table 3.3).

drainage system from August 2001 to August 2003. Number of stomachs with food, total number of fish observed and trophic positions of fishes are presented in the final three columns.

Fish species	Lake	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Macrophytes	Seeds	Ciliate	Zooplankton	C. nilotica	Unidentified insects	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Sandgrains	Molluscs	Fish eggs/embryo	Unidentified fish	R. argentea	Haplochromines	Clarias sp.	L. niloticus	Tilapia	Brycinus sp.	Sample size (food)	Sample size (total)	Trophic position	
A. nubila	Kayugi	-	-	-	-	- 0.11	-	-	-	-	- 0.20	0.17	-	-	-	-	- 0.06	0.46	-	-	-	-	-	-	-	-	-	-	-	-	-	10	64	3.3	
	Kayanja	-	-	-	-	-	-	-	-	-	- 0.29	0.12	-	-	-	-	-	-	- 0.09	0.51	-	-	-	-	-	-	-	-	-	-	-	-	6	30	3.5
A. velifer	Kayugi	-	-	-	-	- 0.06	-	-	-	-	- 0.49	0.26	-	-	-	-	- 0.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	67	3.4
	Kayanja	0.04	-	-	-	- 0.04	-	-	-	-	- 0.11	0.22	-	-	-	-	- 0.16	0.10	-	-	-	-	-	-	- 0.32	-	-	-	-	-	-	-	27	188	3.7
B. sadleri	Nabugabo	0.08	-	-	-	-	-	-	-	-	- 0.16	0.04	-	-	-	-	- 0.21	-	- 0.51	-	-	-	-	-	-	-	-	-	-	-	-	-	21	319	3.4
	Nabugabo	-	-	-	-	- 0.16	-	-	-	-	- 0.05	0.10	-	-	-	- 0.28	0.16	0.13	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	39	108	3.2
C. alluaudi	Kayanja	-	-	-	-	-	-	-	-	-	- 0.19	-	-	-	-	- 0.51	0.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	9	3.2
C. gariepinus	Kayanja	-	-	-	-	- 0.02	-	-	-	-	- 0.33	- 0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 0.20	-	-	-	-	-	3	17	3.5
G. simpsoni	Kayanja	-	-	-	-	-	-	-	-	-	- 0.50	-	-	-	-	-	-	-	-	-	-	-	-	- 0.50	-	-	-	-	-	-	-	-	3	4	4.0
G. victoriae	Nabugabo	0.71	-	-	-	-	-	-	-	-	- 0.18	-	-	-	-	-	- 0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	37	2.4
	Kayugi	-	-	-	-	- 0.02	-	-	-	-	- 0.08	0.08	-	-	-	-	- 0.12	0.05	0.17	0.12	-	-	-	-	- 0.05	0.03	0.02	0.06	-	-	-	- 0.18	50	60	3.8
L. niloticus-M	Kayanja	-	-	-	-	- 0.02	-	-	-	-	- 0.05	0.14	-	-	-	- 0.19	0.11	-	- 0.24	-	-	-	-	-	-	- 0.25	-	-	-	-	-	-	33	99	3.6
	Nabugabo	0.05	-	-	-	- 0.01	-	-	-	-	-	-	-	-	-	-	- 0.05	-	-	-	-	-	-	-	- 0.13	0.19	0.24	-	-	-	-	- 0.15	133	435	4.3
L. niloticus-S	Nabugabo	-	-	-	-	-	-	-	-	-	- 0.04	0.03	-	-	-	-	- 0.10	- 0.07	-	-	-	-	-	-	- 0.01	- 0.08	0.12	0.19	-	-	-	- 0.12	117	352	4.0
O. esculentus	Kayugi	0.25	0.14	0.07	0.13	0.02	0.14	-	-	-	- 0.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	58	2.4
	Kayanja	0.25	0.16	0.22	0.07	0.03	0.10	- 0.03	-	-	- 0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	164	339	2.2
O. leucostictus	Nabugabo	0.48	0.04	0.08	0.02	0.01	0.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	56	2.0
O. niloticus	Nabugabo	0.16	0.01	0.01	0.01	- 0.09	-	-	- 0.15	-	- 0.11	0.04	-	-	-	-	- 0.07	0.05	0.19	-	-	-	-	-	- 0.06	0.04	-	-	-	-	-	-	73	253	3.3
P. aethiopicus	Kayugi	0.04	-	-	-	- 0.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 0.41	-	-	-	-	-	-	-	4	4	3.3
P. beadle	Kayanja	0.15	-	-	-	- 0.51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 0.33	-	-	-	-	-	-	-	5	16	2.8
	Nabugabo	-	-	-	-	- 0.33	-	-	-	-	-	-	-	-	-	-	-	-	- 0.25	-	-	-	-	-	-	-	-	-	-	-	-	3	4	2.9	
P. catostoma	Nabugabo	0.03	-	-	-	- 0.04	-	-	-	-	- 0.06	0.05	-	-	-	-	- 0.09	0.25	0.15	0.03	0.22	-	-	-	- 0.08	-	-	-	-	-	-	-	38	286	3.7
	Kayugi	-	-	-	-	-	-	-	-	-	- 0.10	0.12	-	-	-	-	- 0.31	0.04	0.24	0.19	-	-	-	-	-	-	-	-	-	-	-	-	75	160	3.6

Fish species	Lake	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Macrophytes	Seeds	Ciliate	Zooplankton	<i>C. nilotica</i>	Unidentified insect	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Sandgrains	Molluscs	Fish eggs/embryo	Unidentified fish	<i>R. argentea</i>	Haplochromines	<i>Ciaras</i> sp.	<i>L. niloticus</i>	Tilapia	<i>Brycinus</i> sp.	Sample size (food)	Sample size (total)	Trophic position
<i>P. venator</i>	Kayanja	-	-	-	-	-	-	-	-	-	-	0.29	-	-	-	-	0.71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	5	3.5
	Kayugi	-	-	-	-	-	-	-	-	0.02	0.05	0.11	-	-	-	-	-	0.21	0.10	0.06	-	-	0.03	-	0.16	-	0.26	-	-	-	-	17	61	4.0
	Kayanja	-	-	-	-	-	0.07	-	-	-	-	0.07	0.12	-	-	-	-	-	-	-	-	-	0.07	-	0.28	-	0.22	-	0.07	-	-	29	105	3.9
<i>S. afroischeri</i>	Nabugabo	-	-	-	-	-	0.03	-	-	-	0.10	0.03	0.08	-	-	0.13	0.14	0.03	0.05	0.20	0.16	-	0.01	-	-	-	-	-	-	-	0.05	86	183	3.5
<i>S. intermedius</i>	Nabugabo	-	-	-	-	-	-	-	-	-	0.02	0.04	0.07	-	0.03	0.06	0.04	0.08	0.06	0.22	0.15	-	-	-	0.04	0.17	-	0.03	-	-	-	58	133	3.8
<i>T. zillii</i>	Kayugi	0.06	0.06	0.14	0.18	0.01	0.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	6	2.0
	Kayanja	0.03	-	-	-	-	0.12	-	-	-	-	0.11	0.05	0.23	-	-	0.02	-	-	-	-	-	-	-	0.42	-	-	-	-	-	-	25	69	3.7
	Nabugabo	0.08	0.01	-	-	-	0.08	-	-	-	-	0.19	0.03	-	-	-	0.17	-	0.42	-	-	-	0.01	-	-	-	-	-	-	-	-	11	24	3.4

It is also important to note that *C. nilotica* was not recorded as one of the food items for *L. niloticus* in Lake Nabugabo, as it is absent from this system. Fish were important in the diet of other fish species: *Prognathochromis venator* ($\geq 42\%$), *P. aethiopicus* ($\geq 33\%$), *Astatotilapia verifer* ($\geq 32\%$), *T. zillii* (24%), *C. gariepinus* ($\geq 20\%$) and *O. niloticus* ($\geq 10\%$) (Table 3.3). Oligochaetes were an important food item, especially for *A. nubila* and *A. verifer* ($\geq 51\%$), *Synodontis afrofisheri* and *Schilbe intermedius* ($\geq 20\%$), *Petrocephalus catastoma* ($\geq 19\%$), and *Gnathonemus victoriae* ($\geq 12\%$). Hirudinea (leeches) also formed an important component in the diets of *Paralabidochromis beadlei* ($\geq 22\%$), *S. afrofisheri*, and *S. intermedius* ($\geq 15\%$) (Table 3.2). In all the three, lakes there were generally a larger proportion of fishes with empty stomachs (2463) compared to those that contained food material (1088), however this was more pronounced in Lake Nabugabo compared to lakes Kayugi and Kanyanja (Table 3.3).

3.2.3 Kyoga drainage system lakes

In the four Kyoga lakes (Nawampasa, Nakuwa, Bisina and Kyoga), 35 fish species examined consumed 31 different prey or food resources (Table 3.4). Overall, insects formed the most important primary prey ($\geq 50\%$) in most fishes with the exception of almost all the tilapiine species, which were herbivores and mainly fed on algae ($\geq 22\%$), detritus ($\geq 8\%$), and macrophytes ($\geq 4\%$) in lakes Nawampasa and Bisina. However, *O. niloticus* and *T. zillii* in Lake Bisina tended to incorporate more macrophytes (62%) in their diet, which are abundant in the lake. *Oreochromis niloticus* in lakes Nakuwa and Kyoga (Bukungu and Iyingo areas) depended mainly on an insect diet i.e. Diptera ($\geq 44\%$) and Ephemeroptera ($\geq 46\%$), respectively. Oligochaetes formed another important dietary item for *O. niloticus* (40%) in the main Lake Kyoga (Iyingo area) (Table 3.4). Fish formed another important component of diet and constituted the major prey for the commercially important *L. niloticus* through its life history based on the sampled size classes. The largest obtained fish size of *L. niloticus* (60 -100 cm TL) from Lake Kyoga (Iyingo area) mainly depended on a fish diet ($\geq 96\%$). In both lakes Kyoga and Nakuwa the medium-sized *L. niloticus*, mainly depended on fish ($\geq 84\%$), but included a relatively large proportion of insects (36%) in Lake Nakuwa.

The medium-sized *L. niloticus* in Lake Nakuwa exhibited higher cannibalism (28%) compared to that of the main Lake Kyoga (< 15%). In Lake Nakuwa, small *L. niloticus* (< 20 cm TL) mainly fed on insects (67%) and fish (19%) but fed on mainly fish in the main Lake Kyoga. However, terrestrial millipedes, which were completely absent in the diet of other fishes, contributed 19% to their small sized *L. niloticus* (Table 3.4). It is also important to note that *C. nilotica* contributed $\geq 10\%$ to the diet of *L. niloticus* and *S. afrofisheri*. Fish also formed an important dietary component to other fish species: *Pyxichromis orthostoma* (100%), *Prognathochromis pellegrin* (80%), *Harpagochromis. micheali* (63%), *Astatotilapia latifasciata* (40%), *Harpagochromis squamulatus* (39%), *Bagrus docmac* (39%), *Prognathochromis argenteus* ($\geq 38\%$), *P. aethiopicus* ($\geq 29\%$), *C. gariepinus* ($\geq 27\%$), *Haplochromis lividus* (25%), *Xystichromis phytophagus* (20%) and *S. intermedius* ($\geq 10\%$) (Table 3.4). Molluscs were an important diet item for *P. aethiopicus* in all lakes ($\geq 13\%$), and for *S. victoriae* and *S. afrofisheri* ($\geq 10\%$) (Table 3.4). In all lakes examined in the Kyoga drainage system, out of 5575 fishes only 2031 contained food material (Table 3.4)

Table 3.4. Fish stomach contents (proportion of volume) in diets of fishes pooled from all sampled sites within lakes in the Kyoga drainage system from August 2001 to May 2004. Number of stomachs with food, total number of fish observed and trophic positions of fishes re presented in the final three columns.

Fish species	Lake/Site	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Vascular plants	Seeds	Ostracods	C. nilotica	unidentified insects	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Trichoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Molluscs	Fish eggs/embryo	Millipedes	Unidentified fish	R. argentea	Haplochromines	Clarias sp.	L. niloticus	Tilapia	Barbus sp.	A. frenatus	Sample size (food)	Sample size (total)	Trophic position
A. "fattooth"	Nawampasa	0.20	-	-	-	-	0.34	-	-	-	-	-	-	-	-	-	0.46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	66	2.7	
A. "kyogaastato"	Iyungu	0.09	-	-	-	-	-	-	-	0.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	74	3.4	
A. latifasciata	Nawampasa	-	-	-	-	-	-	-	-	0.14	-	-	-	-	-	-	-	-	-	-	-	0.16	0.56	0.07	-	-	-	-	0.07	-	-	9	19	3.5	
	Bisina	-	-	-	-	-	-	-	-	0.07	-	-	-	-	-	-	-	-	-	-	-	0.53	-	0.40	-	-	-	-	-	-	-	5	45	3.6	
A. nubila	Iyungu	-	-	-	-	-	-	-	-	0.38	-	-	-	-	-	-	0.05	-	0.38	-	-	-	-	0.19	-	-	-	-	-	-	-	6	28	3.7	
B. allianalis	Bukungu	-	-	-	-	-	-	-	-	0.55	-	-	-	-	-	-	-	-	0.45	-	-	-	-	-	-	-	-	-	-	-	-	4	41	3.7	
B. docmac	Bisina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.24	-	-	-	-	0.39	0.38	-	-	-	-	-	-	7	10	4.4	
B. sadleri	Nawampasa	-	-	-	-	-	-	-	-	0.18	0.05	-	-	0.19	-	0.15	-	-	0.42	-	-	-	-	-	-	-	-	-	-	-	-	68	167	3.6	
	Bisina	-	-	-	-	-	0.13	0.10	-	-	0.07	0.04	0.07	-	0.07	-	0.12	-	0.20	0.07	-	-	0.04	0.07	-	-	-	-	-	-	-	63	244	3.3	
	Iyungu	-	-	-	-	-	-	-	-	-	0.43	-	-	0.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	10	3.2	
	Bukungu	-	-	-	-	-	-	-	-	-	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	37	3.5	
C. garepinus	Nawampasa	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-	0.31	-	0.13	-	-	-	-	-	-	0.47	-	-	-	-	-	-	5	13	4.0	
	Nakuwa	-	-	-	-	-	0.09	-	-	0.01	0.07	-	-	0.48	-	0.05	0.01	0.16	-	-	0.04	-	-	0.09	-	-	-	-	-	-	-	10	20	3.3	
	Bisina	-	-	-	-	-	0.17	-	-	0.01	-	-	-	-	-	0.21	-	0.15	-	-	0.13	-	-	0.33	-	-	-	-	-	-	-	17	32	3.6	
	Iyungu	-	-	-	-	-	0.06	-	-	0.18	-	0.10	0.15	-	-	0.06	-	0.15	-	-	0.04	-	-	0.06	0.21	-	-	-	-	-	-	15	25	3.6	
H. lividus	Nawampasa	0.05	-	-	-	-	0.22	-	-	-	0.28	0.35	-	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	268	3.1	
	Bisina	0.17	-	-	-	-	0.08	-	-	-	0.23	-	-	-	-	0.11	-	0.15	-	-	-	-	-	0.25	-	-	-	-	-	-	-	81	267	3.5	
H. micheali	Bisina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.38	-	-	-	0.63	-	-	-	-	-	-	-	3	15	4.3	
H. squamulatus	Bisina	0.31	0.01	0.02	0.01	0.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.39	-	-	-	-	-	-	-	3	25	3.0	
L. cryptodon	Nawampasa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00	-	-	-	-	-	-	-	-	-	4	15	3.5	
L. maxillaris	Nawampasa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.35	-	0.65	-	-	-	-	-	-	-	4	25	4.1	
L. niloticus-L	Iyungu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-	0.72	0.20	0.04	-	-	-	-	-	3	8	4.4	

Fish species	Lake/Site	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Vascular plants	Seeds	Ostracods	C. nilotica	unidentified insects	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Trichoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Molluscs	Fish eggs/embryo	Millipedes	Unidentified fish	R. argentea	Haplochromines	Clarias sp.	L. niloticus	Tilapia	Barbus sp.	A. frenatus	Sample size (food)	Sample size (total)	Trophic position	
L. niloticus-M	Nakuwa	-	-	-	-	-	-	-	-	0.13	0.18	-	-	-	-	-	-	0.04	0.14	-	-	-	-	-	0.10	0.14	-	0.28	-	-	-	-	103	130	4.0	
	Iyungu	-	-	-	-	0.03	-	-	-	0.03	-	-	-	-	-	-	-	-	0.04	0.04	-	0.04	0.01	-	0.09	0.15	0.16	-	0.11	0.19	0.14	-	196	314	4.1	
	Bukungu	-	-	-	-	-	-	-	-	0.01	0.03	0.03	-	-	-	-	-	-	-	0.06	-	-	-	-	0.06	0.11	0.13	0.09	0.14	-	0.23	0.10	81	139	4.4	
L. niloticus-S	Nakuwa	-	-	-	-	-	-	-	-	0.14	0.08	-	-	-	-	-	0.06	0.29	0.24	-	-	-	-	-	0.19	-	-	-	-	-	-	-	69	101	3.7	
	Iyungu	-	-	-	-	-	-	-	-	0.10	0.08	-	-	-	-	-	0.12	-	0.08	-	-	-	-	-	0.19	0.12	0.18	0.12	-	-	-	-	373	637	3.8	
	Bukungu	-	-	-	-	-	-	-	-	0.05	0.04	-	-	-	-	-	-	-	0.08	-	-	-	-	-	-	0.12	0.20	0.23	0.08	-	0.20	-	61	129	4.3	
O. esculentus	Nawampasa	0.16	0.24	0.44	0.06	0.06	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	41	2.0	
	Bisina	0.20	0.19	0.34	0.07	0.02	0.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	16	2.0	
	Nawampasa	0.31	0.24	0.29	0.06	0.01	0.09	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	21	2.0	
O. leucostictus	Nawampasa	0.09	0.29	0.39	0.04	0.02	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	23	2.0	
	Nakuwa	0.08	0.07	0.13	0.05	-	0.17	0.01	-	-	-	-	-	-	-	0.02	0.28	0.16	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	42	104	2.8	
	Bisina	0.16	0.09	0.09	0.03	0.01	0.62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	31	2.0	
O. niloticus	Iyungu	0.03	0.01	0.02	-	-	0.09	-	-	-	0.46	-	-	-	-	-	-	-	-	-	0.40	-	-	-	-	-	-	-	-	-	-	-	-	26	183	3.3
	Bukungu	-	-	-	-	-	-	-	-	-	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	20	3.5	
	Nawampasa	0.16	0.24	0.27	0.10	0.03	0.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	32	2.0	
P. "blackpara"	Bisina	0.45	0.12	0.16	0.12	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	15	2.0	
	Bukungu	-	-	-	-	-	-	-	-	0.14	-	-	-	-	-	-	-	-	0.86	-	-	-	-	-	-	-	-	-	-	-	-	-	5	42	3.9	
	P. "shovelmouth" Bisina	-	-	-	-	-	0.26	-	-	0.23	-	-	-	-	-	-	-	-	0.51	-	-	-	-	-	-	-	-	-	-	-	-	-	8	37	3.4	
P. aethiopicus	Nawampasa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.87	-	-	-	-	-	-	-	7	13	4.3	
	Nakuwa	0.03	-	-	-	-	0.21	-	-	-	-	-	-	-	-	-	-	-	0.39	-	-	0.16	-	-	0.20	-	-	-	-	-	-	-	18	37	3.4	
	Bisina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.35	-	-	0.35	-	-	0.29	-	-	-	-	-	-	-	12	32	3.8	
P. argenteus	Iyungu	-	-	-	-	-	0.28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.37	-	-	0.35	-	-	-	-	-	-	-	-	10	18	3.3
	Bukungu	-	-	-	-	-	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	12	2.0	
	Nawampasa	-	-	-	-	-	-	-	-	0.17	-	-	-	-	-	-	-	-	0.28	-	-	-	-	-	0.55	-	-	-	-	-	-	-	30	70	4.2	
P. catostoma	Bisina	-	-	-	-	-	-	-	-	0.13	-	-	-	-	-	-	-	-	0.50	-	-	-	-	-	0.38	-	-	-	-	-	-	-	18	85	4.1	
	Bisina	-	-	-	-	-	-	-	-	-	0.63	-	-	-	-	-	-	0.37	-	-	-	-	-	-	-	-	-	-	-	-	-	4	16	3.5		

Fish species	Lake/Site	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Vascular plants	Seeds	Ostracods	C. nilotica	unidentified insects	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Trichoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Molluscs	Fish eggs/embryo	Millipedes	Unidentified fish	R. argentea	Haplochromines	Clarias sp.	L. niloticus	Tilapia	Barbus sp.	A. frenatus	Sample size (food)	Sample size (total)	Trophic position
P. orthostoma	Nawampasa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00	-	-	-	-	-	-	-	3	16	4.5
	Bisina	-	-	-	-	-	-	-	-	-	0.20	-	-	-	-	-	-	-	-	-	-	-	-	0.80	-	-	-	-	-	-	-	8	39	4.3	
	Nakuwa	-	-	-	-	-	0.05	-	-	0.13	0.07	0.18	0.08	-	-	-	0.15	0.02	0.14	0.06	-	-	-	-	-	-	-	-	-	-	-	-	59	304	3.4
S. afrofisheri	Bisina	0.07	-	-	-	-	0.16	-	-	0.09	0.20	-	-	-	-	-	0.24	0.04	-	0.11	-	0.09	-	-	-	-	-	-	-	-	-	-	78	507	3.1
	Iyungu	-	-	-	-	-	0.03	-	-	0.16	0.04	0.29	-	-	-	-	0.11	-	0.10	-	-	0.11	0.15	-	-	-	-	-	-	-	-	31	131	3.4	
	Bukungu	-	-	-	-	-	-	-	-	0.15	-	0.15	-	-	-	-	-	-	0.69	-	-	-	-	-	-	-	-	-	-	-	-	-	3	36	3.8
S. intermedius	Nakuwa	-	-	-	-	-	-	-	-	0.05	0.03	0.27	0.05	-	0.17	-	0.18	-	0.16	-	-	-	-	-	0.10	-	-	-	-	-	-	-	49	113	3.6
	Iyungu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00	-	-	-	-	-	-	-	-	-	-	-	-	3	9	4.0	
	Bukungu	-	-	-	-	-	-	-	-	-	-	0.44	-	-	-	-	-	-	0.43	-	-	-	-	-	0.13	-	-	-	-	-	-	7	8	3.8	
S. victorianus	Nawampasa	-	-	-	-	-	0.28	-	-	-	0.14	-	-	-	-	0.22	0.16	-	0.16	-	-	-	0.04	-	-	-	-	-	-	-	-	-	30	73	3.1
	Nakuwa	-	-	-	-	-	0.12	-	-	0.04	0.08	0.19	-	-	-	-	0.09	0.20	0.12	-	-	0.14	-	-	-	-	-	-	-	-	-	64	160	3.3	
	Bisina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.41	-	-	-	-	0.59	-	-	-	-	-	-	-	-	-	4	14	3.2	
T. zillii	Iyungu	-	-	-	-	-	0.08	-	-	0.06	0.08	0.08	-	-	0.04	-	0.12	0.05	0.12	-	-	0.12	-	-	0.06	0.19	-	-	-	-	-	-	156	296	3.6
	Bukungu	-	-	-	-	-	-	-	-	-	0.24	0.76	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	11	3.5	
	Bisina	0.06	0.12	0.16	0.03	0.01	0.62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	18	2.0	
X. phytophagus	Nawampasa	0.03	-	-	-	-	0.24	-	-	-	0.18	-	-	-	-	-	-	-	-	-	-	-	0.35	0.20	-	-	-	-	-	-	-	9	53	3.3	
	Bisina	0.11	-	-	-	-	0.21	-	-	-	0.29	-	-	-	-	-	-	-	0.38	-	-	-	-	-	-	-	-	-	-	-	-	9	35	3.2	

3.2.4 Inshore areas of the northern portion of Lake Victoria

From Napoleon Gulf, Thruston, and Hannington Bays, on the northern portion of Lake Victoria, 22 fish species examined consumed 29 different prey or food resources (Table 3.5). As in all the other lakes examined, insects formed the most important primary prey ($\geq 50\%$) in most fishes with the exception of *O. leucostictus* and *Oreochromis variabilis* in Napoleon Gulf, and *Afromastacembelus frenatus* in Thruston Bay. In these fishes, insects were completely absent from the diet and they mainly fed on detritus ($\geq 59\%$), algae ($\geq 30\%$) or molluscs (100%), respectively. *Oreochromis niloticus* in all the areas tended to be omnivorous, but in Napoleon Gulf its diet was more similar to that of *O. leucostictus* and *O. variabilis*, i.e detritus ($\geq 16\%$) with macrophytes (31%) and insects such as chironomids (23%). The diets of *O. niloticus* in Thruston and Hannington Bays were similar and included mainly insects, i.e. ephemeroptera and chironomids ($\geq 33\%$) and algae ($<17\%$). Fish formed another important component of diet and constituted the major prey for the most commercially important *L. niloticus* throughout its life history. In all the sites, *L. niloticus* 20-60 cm mainly depended on fish for their dietary requirements ($\geq 65\%$) but included a relatively large proportion of insects in their diet ($\geq 25\%$) in Napoleon Gulf and Thruston Bay compared to Hannington Bay (9%). The small-sized Nile perch, (<20 cm TL) depended on a fish diet ($\geq 47\%$) but included large proportions of millipedes (25%) and Hirudinea (7%) in Hannington and Thruston Bays, respectively. It is also important to note that *C. nilotica* contributed to the diet of *L. niloticus* (5-15%), *O. niloticus* (33%), *S. afrofischeri* (13%) in Thruston Bay, and *S. victoriae* (12%) in Napoleon Gulf. Fish formed an important dietary component to other fish species: *Astatotilapia* sp. (30%), *P. aethiopicus* (26%), *O. niloticus* (15%) in Thruston Bay, *P. raponianus* (24%), *H. guarti* (52%) in Napoleon Gulf and *P. crassilabris* ($\geq 17\%$) in both Thruston and Hannington Bays. Molluscs were an important diet item for *P. aethiopicus* ($\geq 30\%$), *A. alluaudi* ($\geq 20\%$), *P. raponianus* ($\geq 12\%$) and *B. jacksoni* ($\geq 10\%$). In all areas of Lake Victoria, out of 5621 fishes only 1679 contained food material (Table 3.4)

Table 3.5. Fish stomach contents (proportion of volume) in diets of fishes pooled from all sampled sites in inshore areas of northern portion of Lake Victoria from August 2001 to August 2003. Number of stomachs with food, total number of fish observed and trophic positions of fishes given in right most columns.

Fish species	Site	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Vascular plants	<i>C. nilotica</i>	Unidentified insects	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Trichoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Sandgrains	Molluscs	Fish eggs/embryo	Millipedes	Un identified fish	<i>R. argentea</i>	Haplochromines	<i>Synodontis</i> sp.	<i>Clarias</i> sp.	<i>L. niloticus</i>	Tilapia	Sample size (food)	Sample size (total)	Trophic position		
<i>A. alluaudi</i>	Thruston	-	-	-	-	-	- 0.12	- 0.03	-	-	-	-	-	- 0.18	- 0.15	-	-	-	-	-	- 0.19	0.13	- 0.07	- 0.13	-	-	-	-	-	-	- 49	149	3.5		
	Hannington	-	-	-	-	-	-	0.11	-	-	-	-	-	-	0.05	-	-	0.02	-	-	- 0.82	-	-	-	-	-	-	-	-	-	- 13	63	3.1		
<i>A. frenatus</i>	Thruston	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 1.00	-	-	-	-	-	-	-	-	-	-	- 3	10	3.0	
	<i>Asiatotilapia</i> sp.	-	-	-	-	-	-	- 0.50	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 3	46	3.5	
<i>B. jacksonii</i>	Thruston	-	-	-	-	-	- 0.04	- 0.35	-	-	-	-	-	- 0.09	- 0.14	-	-	-	-	-	- 0.07	-	- 0.30	-	-	-	-	-	-	-	-	- 11	166	3.8	
	Hannington	-	-	-	-	-	-	- 0.38	-	-	-	-	-	-	-	-	- 0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 4	65	3.8	
	Thruston	-	-	-	-	-	-	- 0.22	-	-	-	-	-	-	- 0.33	- 0.23	-	-	-	-	- 0.22	-	-	-	-	-	-	-	-	-	-	- 10	28	3.5	
	Hannington	-	-	-	-	-	-	-	-	-	-	-	-	-	- 0.40	- 0.50	-	-	-	-	-	- 0.10	-	-	-	-	-	-	-	-	-	- 5	11	3.7	
<i>B. sadleri</i>	Napoleon	-	-	-	-	-	-	- 0.03	-	-	-	-	-	- 0.39	- 0.58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 18	49	3.8	
	Thruston	-	-	-	-	-	- 0.07	0.19	0.10	-	-	- 0.20	-	-	- 0.26	- 0.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 68	225	3.5	
<i>L. niloticus</i> -M	Hannington	-	-	-	-	-	-	- 0.07	0.21	-	-	-	-	-	- 0.44	- 0.27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 13	94	3.6	
	Napoleon	-	-	-	-	-	- 0.07	-	-	-	-	-	-	-	- 0.18	- 0.09	-	-	-	-	- 0.01	-	- 0.15	0.21	0.19	- 0.10	-	-	-	-	-	- 36	101	4.2	
<i>L. niloticus</i> -S	Thruston	-	-	-	-	-	- 0.14	- 0.04	-	-	-	-	-	- 0.12	- 0.09	-	-	-	- 0.02	-	- 0.01	-	- 0.12	0.15	0.25	0.04	-	-	-	-	-	- 0.03	199	461	4.0
	Hannington	-	-	-	-	-	- 0.05	-	-	-	-	-	-	-	-	- 0.09	-	-	-	-	- 0.02	-	- 0.23	0.33	0.28	-	-	-	-	-	-	- 61	131	4.3	
	Napoleon	-	-	-	-	-	- 0.05	0.15	-	-	-	-	-	-	- 0.13	- 0.05	-	-	-	-	- 0.07	-	- 0.11	0.11	0.24	- 0.09	-	-	-	-	-	- 60	212	3.9	
	Thruston	-	-	-	-	-	-	- 0.11	- 0.03	-	-	-	-	-	- 0.10	- 0.07	0.01	0.07	-	-	- 0.05	-	- 0.10	0.20	0.17	-	-	-	-	-	-	- 331	947	4.1	
<i>M. kannume</i>	Hannington	-	-	-	-	-	- 0.03	0.07	0.05	-	-	-	-	-	-	- 0.08	-	-	-	-	- 0.02	-	- 0.25	0.09	0.20	0.20	-	-	-	-	-	-	- 118	282	3.8
	Napoleon	0.01	-	-	-	-	-	- 0.10	0.21	0.06	-	-	-	- 0.10	0.29	0.17	0.02	-	-	-	- 0.02	0.02	-	-	-	-	-	-	-	-	-	- 23	78	3.3	
<i>O. leucostictus</i>	Napoleon	0.59	0.14	0.21	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 4	32	2.0	
<i>O. niloticus</i>	Napoleon	0.16	0.05	0.18	0.07	-	- 0.31	-	-	-	-	-	-	-	- 0.23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- 55	244	2.3	
	Thruston	0.06	0.01	0.04	0.01	-	- 0.05	0.33	- 0.07	-	-	-	-	-	- 0.12	0.14	-	-	-	-	- 0.03	-	-	-	- 0.15	-	-	-	-	-	- 15	103	3.2		
Hannington	0.09	0.02	0.05	0.01	-	- 0.07	-	-	- 0.35	-	-	-	-	-	- 0.29	-	-	-	-	-	- 0.10	0.02	-	-	-	-	-	-	-	-	-	- 17	64	3.0	

Fish species	Site	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Vascular plants	<i>C. nilotica</i>	Unidentified insects	Ephemeroptera	Coleoptera	Hemiptera	Isoptera	Trichoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Hirudinea	Sandgrains	Molluscs	Fish eggs/embryo	Millipedes	Un identified fish	<i>R. argentea</i>	Haplochromines	<i>Synodontis</i> sp.	<i>Clarias</i> sp.	<i>L. niloticus</i>	Tilapia	Sample size (food)	Sample size (total)	Trophic position	
<i>O. variabilis</i>	Napoleon	0.69	0.09	0.15	0.05	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	82	2.0	
<i>P. aethiopicus</i>	Napoleon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00	-	-	-	-	-	-	-	-	-	7	30	3.0	
	Thruston	-	-	-	-	-	-0.26	-0.14	-	-	-	-	-	-	-0.01	-0.29	-	-	-	-	-0.30	-	-	-	-	-	-	-	-	-	57	109	3.1	
	Hannington	-	-	-	-	-	-0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.63	-	-	-0.26	-	-	-	-	-	-	-	5	25	3.3
<i>P. "big eye"</i>	Thruston	-	-	-	-	-	-	-0.20	-	-	-	-	-	-	-0.26	-0.54	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	33	3.8
<i>P. crassilabris</i>	Napoleon	-	-	-	-	-	-0.12	-	-0.25	-	-	-	-	-	-0.16	-0.47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	29	3.6
	Thruston	-	-	-	-	-	-	-0.16	0.12	-	-0.15	-	-	-	-0.08	0.13	0.16	-	-	-	-0.04	-	-	-0.17	-	-	-	-	-	-	-	100	248	3.7
	Hannington	-	-	-	-	-	-	-0.28	-	-	-	-	-	-	-0.23	-0.31	-	-	-	-	-	-	-	-0.18	-	-	-	-	-	-	-	20	109	3.8
<i>H. guiarfi</i>	Napoleon	-	-	-	-	-	-	-0.27	-	-	-	-	-	-	-	-0.10	0.11	-	-	-	-	-	-	-0.52	-	-	-	-	-	-	-	6	22	4.1
	Thruston	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-0.31	-0.58	-	-	-	-	-	-	-	-0.07	-	-	-	-	-	-	-	6	29	3.8
<i>P. "redfin"</i>	Napoleon	-	-	-	-	-	-	-0.26	0.25	-	-	-	-	-	-0.10	-0.33	-	-	-	-	-0.06	-	-	-	-	-	-	-	-	-	-	20	71	3.6
	Thruston	0.07	-	-	-	-	-0.04	0.09	0.07	0.10	-	-	-	-	-0.09	0.01	0.11	-	-	-	-0.04	0.03	-	-0.06	-	-	-	-	-	-	-0.28	38	195	3.4
	Hannington	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	20	4.0
<i>P. riponianus</i>	Napoleon	0.01	-	-	-	-	-0.04	-0.10	0.10	-	-	-	-	-0.06	0.08	0.04	0.14	0.04	-	-	0.03	0.05	0.07	-0.24	-	-	-	-	-	-	-	32	136	3.7
	Thruston	0.04	-	-	-	-	-0.33	0.09	0.02	-	-	-	-	-	-0.14	0.08	0.18	-	-	-	-0.12	-	-	-	-	-	-	-	-	-	-	59	215	2.9
	Hannington	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.80	-	-	-	-0.20	-	-	-	-	-	-	-	-	-	-	5	28	3.8
<i>P. rockribensis</i>	Thruston	-	-	-	-	-	-	-	-0.48	-	-	-	-	-	-0.20	-0.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	26	3.7
<i>P. sauegai</i>	Napoleon	-	-	-	-	-	-	-	-0.17	-	-	-	-	-	-0.67	-	-0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	25	3.5
<i>P. "sheller"</i>	Napoleon	-	-	-	-	-	-	-0.32	0.10	-	-	-	-	-	-0.07	-0.31	-	-	-	-	-	-0.19	-	-0.02	-	-	-	-	-	-	-	9	34	3.7
<i>S. afrofisheri</i>	Napoleon	0.01	-	-	-	-	-0.17	0.05	0.04	0.07	-	-0.18	-	-	-0.12	-0.09	0.03	0.09	0.06	0.07	-	-	-	-	-	-	-	-	-	-	-	79	224	3.1
	Thruston	-	-	-	-	-	-	-0.13	0.32	0.08	-	-	-	-	-0.13	0.01	0.32	-	-	-	-	-	-	-0.03	-	-	-	-	-	-	-	21	75	3.6
<i>S. victorfae</i>	Napoleon	-	-	-	-	-	-	-0.12	-	-	-	-0.09	-	-	-0.12	0.33	0.18	-0.06	-0.09	-	-	-	-	-	-	-	-	-	-	-	-	5	14	3.5
	Thruston	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-0.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	15	3.3
<i>T. zillii</i>	Napoleon	0.01	-	-	-	-	-	-	-0.46	-	-	-	-	-	-0.08	-0.39	-	-	-	-	-0.06	-	-	-	-	-	-	-	-	-	-	6	16	3.6
	Thruston	0.02	-	-	-	-	-0.06	-0.06	0.20	-	-	-	-	-0.01	0.16	-0.30	-	-	-	-0.14	0.04	-	-	-	-	-	-	-	-	-	-	40	203	3.3
	Hannington	0.09	-	-	-	-	-0.02	-	-	-	-	-	-	-	-0.42	-0.47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	47	3.6

3.3 Trophic groups of fishes

Trophic groups in the different drainage systems were established in two ways using relative abundance dietary data. The UPGMA clustering technique (unweighed pair-group method with arithmetic averages, using the measure of community distance followed by Detrended Correspondence Analysis (DCA) to simultaneously display the factor scores of the fishes and food sources in the same multivariate space. In the resulting dendrogram, species utilizing similar diets are grouped together while in the DCA scatter plots, the proximity of each taxon indicates the similarity of their diet. The relationship of diet items to the derived factors can be inferred to reflect similarity in their consumers.

Generally, the fishes that grouped together in the cluster analysis were in close proximity to one another in the DCA scatter plots, indicating that both methods gave similar results. Some fish species not identified by cluster analysis grouped together in the DCA scatter plots, indicating similarity in their diets. After examination of which food sources in the scatter plot were associated with each of the clusters, it was possible to label the trophic groups and include those formerly unclassified by cluster analysis.

The simultaneous use of UPGMA cluster analysis and DCA established seven trophic groups from all the studied lakes all of which were present in the Kyoga drainage system, four in either Lake Victoria or the Nabugabo drainage system, and two for the Koki drainage system (Figs 3.1 to 3.2 A and B).

3.3.1 Koki drainage system lakes

The UPGMA cluster analysis based on 17 prey groups or food sources in the overall Koki lakes, illustrated that, there were three tight clusters at distance or dissimilarity ≤ 0.60 and $P < 0.05$), with two and three from lakes Kachera and Mburo respectively (Fig. 3.1A). Cluster 1 comprised *O. esculentus* and *O. niloticus* from both lakes; Cluster 2 *A. alluaudi* and *O. leucostictus* from Lake Mburo. Cluster 3 comprised *P. aethiopicus*, *H. squamipinus* from both lakes and *A. aneocolor* from

Lake Kachera. The remaining fish species *C. liocephalus*, *A. aneocolor* and *C. gariepinus* remained ungrouped at a distance of ≤ 0.60 .

The scores for fish species on the first two DCA axes generated from the same data as used in cluster analysis explained 18.6% variation in these data. These scores and the factor scores of the prey groups or food sources were plotted (Fig. 3.1B). The fishes with high scores on DCA 1 were carnivorous and depended on such benthic food sources as Hemiptera, oligochaetes, Coleoptera, Ephemeroptera, fish eggs, unidentified fish, and Odonata (Fig. 3.1B and Table 3.2). These fishes were mainly insectivores. The low scores on DCA 1 were associated with herbivores, which mainly depended on herbivorous diet dominated, by phytoplankton, ciliates, detritus and macrophytes. Fishes with high scores on DCA 2 tended to plot closest to prey with either hard shells or with well developed avoidance behaviors including benthic molluscs, crustaceans (crabs), leeches, oligochaetes and millipedes, and fishes. Low scores were associated with easily captured prey, but not including hard-shelled items.

The first obvious trophic group in the DCA scatter plot comprised the generalist herbivorous fishes and was associated with low and intermediate scores on DCA1 and DCA2 respectively, plotting close to plant food sources (Fig. 3.1B). The fishes in cluster 1 with the exception of *O. leucostictus* from Lake Kachera, comprised this trophic group. These fishes fed primarily on phytoplankton, detritus and macrophytes, but ciliates, chaoborus and chironomid were also important in their diet, as indicated in the scatter plot (Fig. 3.1B and Table 3.2). *Oreochromis leucostictus* from Lake Kachera was excluded from the group despite including high proportions of plant material (38%) in its diet because the proportion of insects was more (62%) than that of plants (Table 3.2), thus placing this species between the two food sources (Fig. 3.1B).

The second trophic group was the insectivorous; clusters 2 and 3; *O. leucostictus* from Lake Kachera (cluster 1) and the remaining fish species (*C. liocephalus* from Lake Kachera, *A. aneocolor* and *C. gariepinus* from Lake Mburo) that were not grouped at a distance of ≤ 0.6 in cluster analysis comprised this group. These fishes had DCA 1 scores associated with insect diet. The insects included

Odonata, Isoptera, Ephemeroptera, Coleoptera, Hemiptera, chironomid, Chaoborus and Trichoptera.

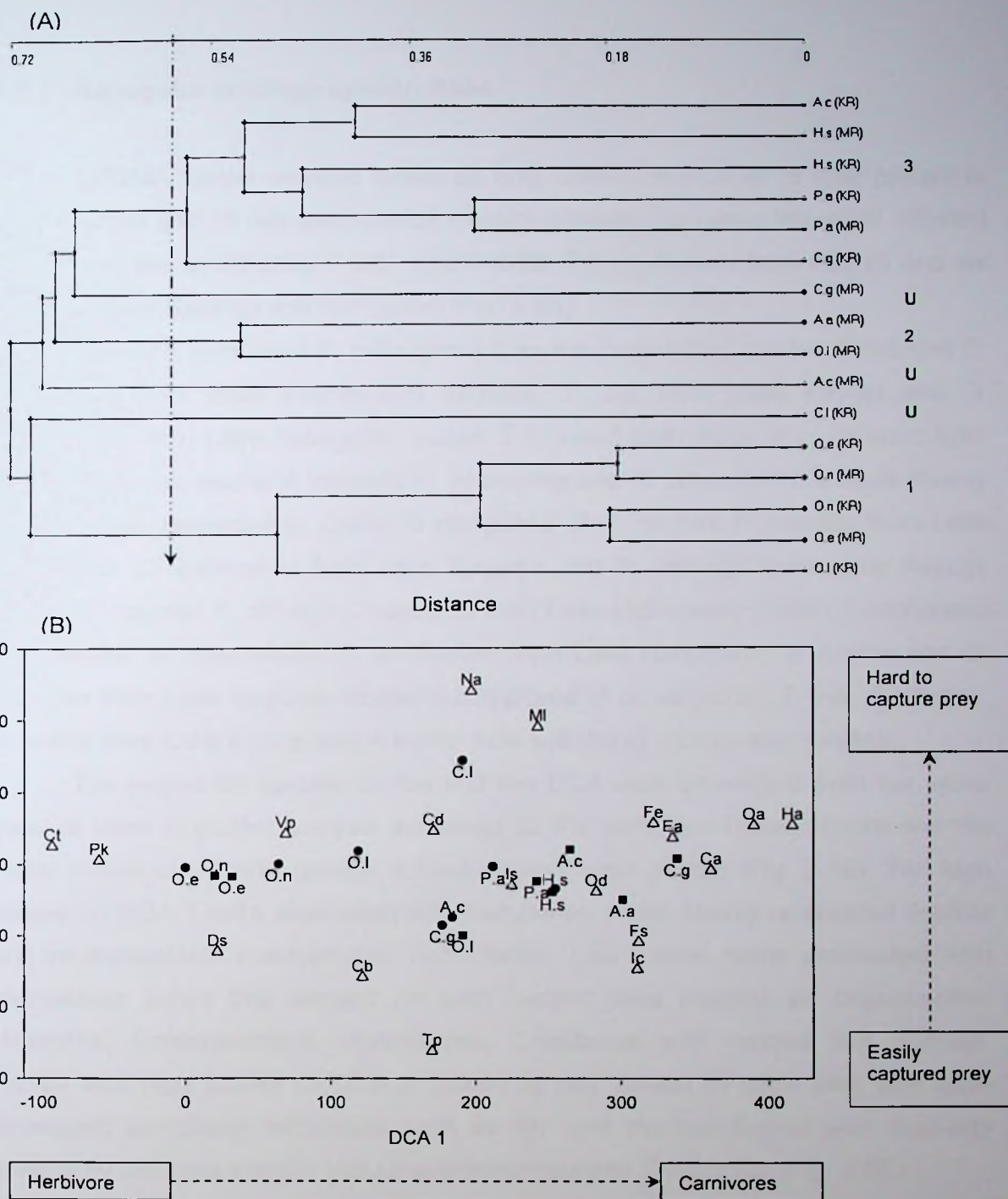


Figure 3.1 (A). UPGMA cluster diagram showing the similarity in diets of fishes using the Bray-Curtis distance measure. At ≤ 0.60 diet similarity three cluster groups of fishes were possible at ≤ 0.05 ; U indicates location of ungrouped fishes; Lake Kachera = KR and Lake Mburo = MR. (B). A DCA scatter plot showing the spatial patterns between 18 food sources (Δ) and nine fish species from Koki drainage system lakes (eigen values: 0.58 and 0.38 for DCA 1 and DCA 2 respectively; fishes are indicated by ($\bullet$) from Lake Kachera, ($\blacksquare$) from Lake Mburo and all text codes Table 3.1)

3.3.2 Nabugabo drainage system lakes

UPGMA cluster analysis based on Bray Curtis distance of 16 prey groups or food sources and 19 fish species/size classes grouped the fishes into eight different trophic clusters at distance ≤ 0.67 and $P < 0.05$. Three clusters from Kayugi and six each for lakes Kayanja and Nabugabo (Fig. 3.2A).

Cluster 1 comprised *P. aethiopicus* from the three lakes; cluster 2 included *O. esculentus* from lakes Kayugi and Kayanja, *T. zillii* from Lake Kayugi and *O. leucostictus* from Lake Nabugabo; cluster 3 included both sizes of *L. niloticus* from Lake Nabugabo; cluster 4 included *P. catostoma* and *C. alluaudii* from lakes Kayugi and Kayanja, respectively; cluster 5 comprised of *B. sadleri*, *P. beadlei* from Lake Nabugabo, *C. gariepinus* from Lake Kayanja and *P. venator* from Lake Kayugi; cluster 6 included *T. zilli* and *O. niloticus* from Lake Nabugabo; cluster 7 comprised of *A. velifer*, *S. intermedius*, *S. afrofishcheri* from Lake Nabugabo, *A. nubila*, and *G. victoriae* from Lake Kayanja; cluster 8 comprised of *G. simpsoni*, *T. zilli*, *P. venator*, *A. nubila* from Lake Kayugi and *A. velifer* from both lakes Kayugi and Kayanja.

The scores for species on the first two DCA axes generated from the same data as used in cluster analysis explained 22.6% variation. These scores and the factor scores of the prey groups or food sources were plotted (Fig. 3.3B). The high scores on DCA 1 were associated with herbivores, which mainly consumed detritus and phytoplankton, macrophytes, and ciliates. Low scores were associated with carnivorous fishes that depend on such benthic food sources as oligochaetes, Hirudinea, Ephemeroptera, chironomids, *Chaoborus* and various fish species. Fishes with high scores on DCA 2 tended to plot closest to large prey with well-developed avoidance techniques such as fish and the low scores with relatively small prey with less mobility including chironomids and *Chaoborus* (Fig. 3.2B).

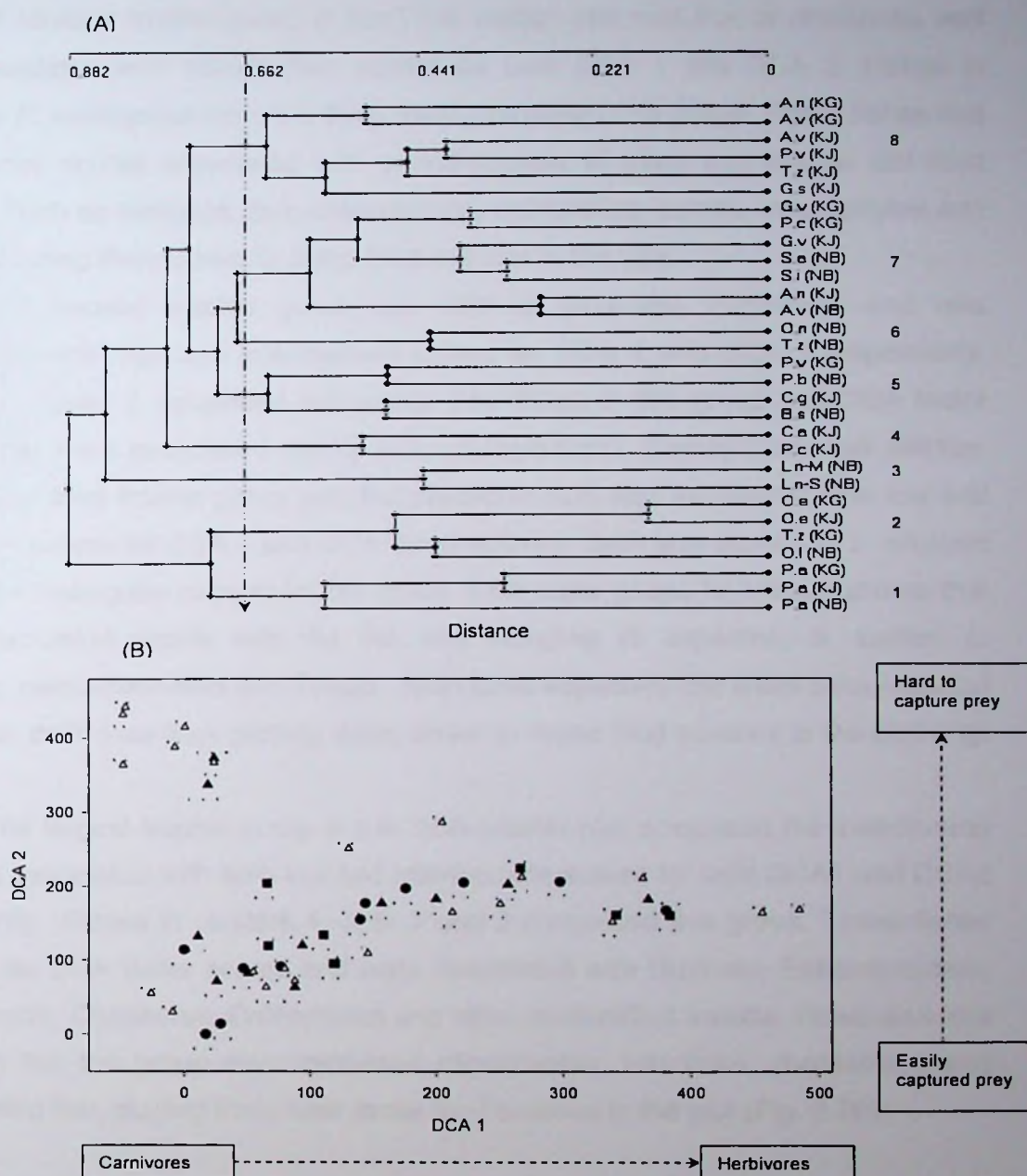


Figure 3.2(A). UPGMA cluster diagram showing the similarity in diets of fishes using the Bray Curtis-distance measure. At ≤ 0.67 diet similarity 7 cluster groups of fishes were possible, Lake Kayugi = KG, Lake Kyanja = KJ and Lake Nabugabo = NB. (B) A DCA scatter plot showing the spatial patterns between 25 food sources (Δ) and 19 fish species from Nabugabo drainage system lakes (eigen values: 0.67 and 0.47 for DCA 1 and DCA 2 respectively; fishes are indicated by ($\blacksquare$) from Lake Kayugi, ($\bullet$) from Lake Kyanja, ($\blacktriangle$) from Lake Nabugabo and all text codes Table 3.1).

The first obvious trophic group in the DCA scatter plot was that of omnivores and was associated with intermediate scores for both DCA 1 and DCA 2. Fishes in cluster 1 *P. aethiopicus* from the three lakes comprised this group. These fishes had DCA factor scores associated with a combination of plant and animal diet food sources such as molluscs, fish, coleopterans, unidentified insects, macrophytes and detritus placing them closer to those food sources in the plot.

The second trophic group was that of generalist herbivores and was associated with high and intermediate scores for DCA 1 and DCA 2 respectively. Fishes in cluster 2 comprised this group. The fishes in this group had DCA factor scores that were associated mainly with phytoplankton, macrophytes and detritus.

The third trophic group was the piscivores and was associated with low and high DCA scores for DCA 1 and DCA 2 respectively. Both size groups of *L. niloticus* from Lake Nabugabo comprised this group. Both sizes groups had factor scores that were associated mainly with the fish diet including *R. argentea*, *B. sadleri*, *L. niloticus*, Haplochromines and Tilapia. Both sizes especially the small ones included insects in their diets thus plotting them closer to those food sources in the plot (Fig. 3.2B)

The largest trophic group in the DCA scatter plot comprised the insectivores and was associated with both low and intermediate scores for both DCA1 and DCA2 (Fig. 3.2B). Fishes in clusters 4, 5, 6, 7 and 8 comprised this group. These fishes had similar DCA factor scores and were associated with Odonata, Ephemeroptera, chironomids, *Chaoborus*, Coleopteran and other unidentified insects. However some fishes in this the group also consumed oligochaetes, Hirudinea, zooplankton and unidentified fish, placing them near those food sources in the plot (Fig. 3.2B).

3.3.3 Kyoga drainage system lakes

UPGMA cluster analysis based on Bray Curtis distance of 26 prey groups or food sources and 30 fish species/size classes grouped the fishes into 16 different clusters at distance or dissimilarity ≤ 0.52 and $P < 0.05$, with seven, five, nine, eight and five

clusters from lakes Nawampasa, Nakuwa, Bisina, Lake Kyoga-Iyingo and Kyoga-Bukungu respectively (Fig. 3.3A).

Cluster 1 was comprised of *O. nilotictus* from Lake Kyoga Bukungu area and *S. victoriae* from the same lake, Iyingo area; cluster 2 included *L. niloticus* 20-60 cm from both areas of Lake Kyoga and *L. niloticus* <20 cm from the same lake, Iyingo area; Cluster 3 included *S. intermedius*, *S. victoriae* from Lake Nakuwa and *S. afrofischeri* from the same lake and Lake Kyoga Iyingo area; cluster 4 was comprised of *L. niloticus* <20 cm, *S. victoriae* and *C. gariepinus* from Lake Kyoga Iyingo area and *L. niloticus* 20-60 cm from Lake Nakuwa; cluster 5 included *B. sadleri* from Lake Bisina and *C. gariepinus* from Lake Nakuwa; cluster 6 was comprised of *L. niloticus* 60-100 cm from Lake Kyoga Iyingo area, *P. aethiopicus* from Lake Nawampasa and haplochromine cichlids, *H. micheali*, *P. pellegrin* from Lake Bisina, *P. orthostoma* and *L. maxillaris*; cluster 7 included *P. aethiopicus* from lakes Kyoga Iyingo area, Nakuwa and Bisina, and *A. latifasciata* from Lake Bisina; cluster 8 was comprised of *B. docmak*, *H. lividus* from Lake Bisina, *P. argenteus* and *C. gariepinus* from the same lake and Lake Nawampasa; cluster 9 *B. sadleri* and *P. catastoma* from Lake Bisina and *A. "kyogastato"* from Lake Kyoga Iyingo area; cluster 10 included *S. afrofischeri*, *P. "blackpara"* from Lake Kyoga Bukungu area and *S. intermedius* from the same lake Iyingo area; cluster 11 included *B. altianalis*, from Lake Kyoga Bukungu area, *A. nubila* from the same lake, Iyingo area, *X. phytophagus*, *P. "shovelmouth"* from Lake Bisina and *B. sadleri* from Lake Nawampasa; cluster 12 was comprised of *L. cryptodon* and *A. latifasciata* from Lake Nawampasa; cluster 13 included *P. aethiopicus* from Lake Kyoga, Bukungu area as well as *T. zilli* and *O. niloticus* from Lake Bisina; cluster 14 included *O. niloticus* and *O. leucostictus* from Lake Nawampasa, *O. variabilis* and *O. esculentus* from both lakes Nawampasa and Bisina; cluster 15 was comprised of *S. afrofischeri* from Lake Bisina and *H. lividus* from Lake Nawampasa; finally cluster 16 included *O. niloticus* from Lake Nakuwa and *A. "fattooth"* from Lake Nawampasa.

The scores for species on the first two axes generated from the same data as used in cluster analysis explained 33.7% variation in these data. These scores and the factor scores of the prey groups or food sources were plotted (Fig. 3.4B). The

high scores on DCA 1 were associated with herbivores, which mainly consumed detritus, phytoplankton and macrophytes. The low scores were associated with carnivorous fishes that depended food sources such as various fish *R. argentea*, haplochromines, *Clarias* sp., *L. niloticus*, Tilapia, *Barbus* sp. and unidentified fishes. The fishes with low scores on DCA 2 tended to plot closest to either hard shells or with well developed avoidance behaviors including benthic molluscs and fish and high scores with easily captured prey such as the fish eggs (Fig. 3.3B).

The first obvious trophic group in the DCA scatter plot comprised the phytoplanktivores and was associated with high and intermediate scores for DCA 1 and DCA 2 respectively (Fig. 3.3B). These fishes had DCA factor scores that were associated with phytoplankton. Some fishes in this group included detritus and macrophytes in their diet, placing them close to those food sources (Fig. 3.3B and Table 3.4). The fishes in cluster 14 comprised this group.

The next trophic group was that of the macrophyte eaters. Fishes in cluster 13 comprised this group. These fishes had factor scores that were associated with the macrophytes and detritus food sources but mainly depended on macrophytes (Fig. 3.3B and Table 3.4).

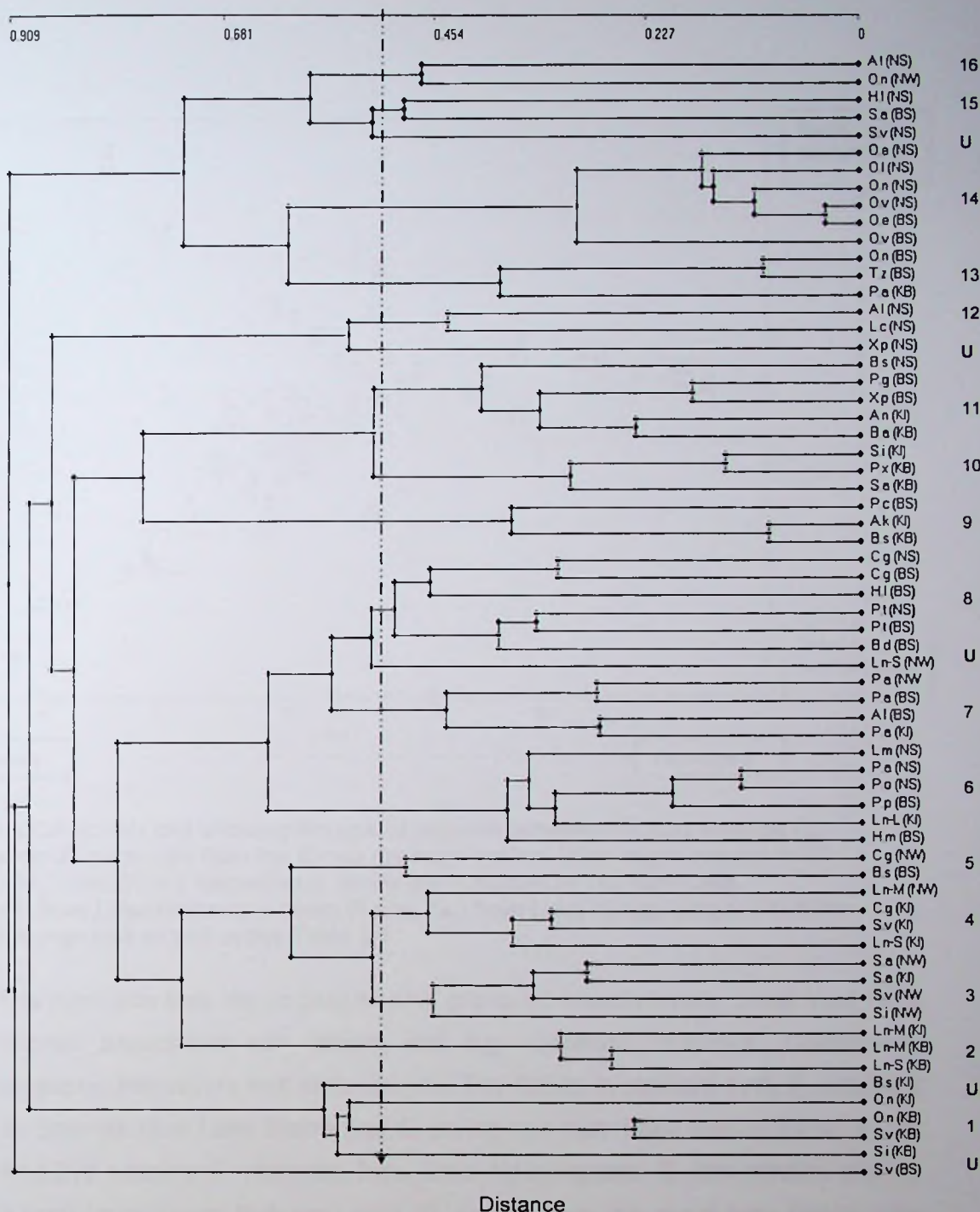


Figure 3.3A. UPGMA cluster diagram showing the similarity in diets among 35 fish species using Bray- Curtis distance measure from the Kyoga drainage system. At ≤ 0.52 diet similarity 16 cluster groups of fishes were possible and U indicates location of the ungrouped fish species. (Nawampasa = NS, Nakuwa = NW, Bisina = BS, Kyoga-Iyingo = KI, Kyoga-Bukungu = KB and other text codes Table 3.1).

The next trophic group was that of molluscivores, which had DCA scores that were associated with molluscs, food source. The fishes in clusters 7 and one species *S. victoriae* from Lake Bisina, not grouped at a distance ≤ 0.52 and $P < 0.05$ in the cluster analysis comprised this group. Some fishes in this group also fed on fish, Odonata, chironomids, Ephemeroptera and macrophytes placing them close to those food sources in the plot.

Another visible trophic group was that of piscivores, which had DCA factor scores associated with the fish diet: *R. argentea*, haplochromines, *Clarias*, *L. niloticus*, *Barbus* sp. and other fish as food sources. The group comprised of fishes in clusters 2 except *S. victoriae* from Lake Kyoga Iyingo area, *B. docmak* from Lake Bisina and *C. gariepinus* from Lake Nawampasa from cluster 8 as already indicated in insectivorous trophic group above. Some fishes in this group consumed *Caridina*, Isoptera, and Ephemeroptera, placing them close to those food sources in the scatter plot.

Another clear trophic group in the plot was that of the pedophage fishes, that had DCA scores that were associated with fish eggs/embryo food source. The fishes in cluster 12 comprised this group. Some of these fishes fed on unidentified insects, unidentified fish and molluscs placing them close to those fish sources (Table 3.3). This trophic group was only recorded in Lake Nawampasa, however similar species were encountered in Lake Bisina but had empty stomachs.

The last trophic group was the omnivores, which comprised cluster 16 and the remaining fishes not grouped by UPGMA cluster analysis at a distance ≤ 0.52 and $P < 0.05$. These included *O. niloticus* from lakes Nakuwa and Kyoga Iyingo area, and *X. phytophagus* from Lake Nawampasa. The fishes in this group had scores that were associated with a mixed diet of plants and animals. They fed on oligochaetes, macrophytes, molluscs, fish eggs, fish, ostracods, Diptera larvae and pupae.

3.3.4 Inshore areas of northern portion of Lake Victoria

UPGMA cluster analysis illustrated that based Bray-Curtis distance of 29 prey groups or food sources and 23 fish species/size classes grouped fishes into 7

different clusters at distance ≤ 0.60 and $P < 0.05$, with six in both Napoleon Gulf and Thruston Bay; and four in Hannington Bay. Fig.3.4A).

Cluster 1 was comprised of *O. variabilis*, *O. leucostictus* and *O. niloticus* all from Napoleon Gulf; cluster 2 was comprised of *A. frenatus* from Thruston Bay, *A. alluaudi* from Hannington Bay and *P. aethiopicus* from Hannington Bay and Napoleon Gulf. Cluster 3 consisted of *P. "redfin"*, *P. crassilabris*, and *Astatotilapia* sp. from Thruston Bay, as well as *P. riponius* and *H. guiarti* from Napoleon Gulf; cluster 4 included both sizes of *L. niloticus* from all sampled areas of the lake; cluster 5 was comprised of *P. riponius*, *P. aethiopicus* and *A. alluaudi* from Thruston Bay, and *S. Victoriae* and *S. afrofisheri* from Napoleon Gulf; cluster 6 consisted of *P. "sheller"* from Napoleon Gulf, *H. guiarti*, *P. "big eye"*, *P. rockcribensis*, and *S. afrofisheri* from Thruston Bay, *P. riponius* and *Astatotilapia* sp. from Hannington Bay, *P. "red fin"* and *P. crassilabris* from both Napoleon Gulf and Hannington Bay, *B. jacksoni* from Thruston and Hannington Bays, *T. zillii* and *B. sadleri* from all sampled areas of the lake; lastly cluster 7 included *S. victoriae* from Thruston, *O. niloticus* from Hannington Bay, *P. sauvegi*, *M. kannume* and *Astatotilapia* sp. from Napoleon Gulf.

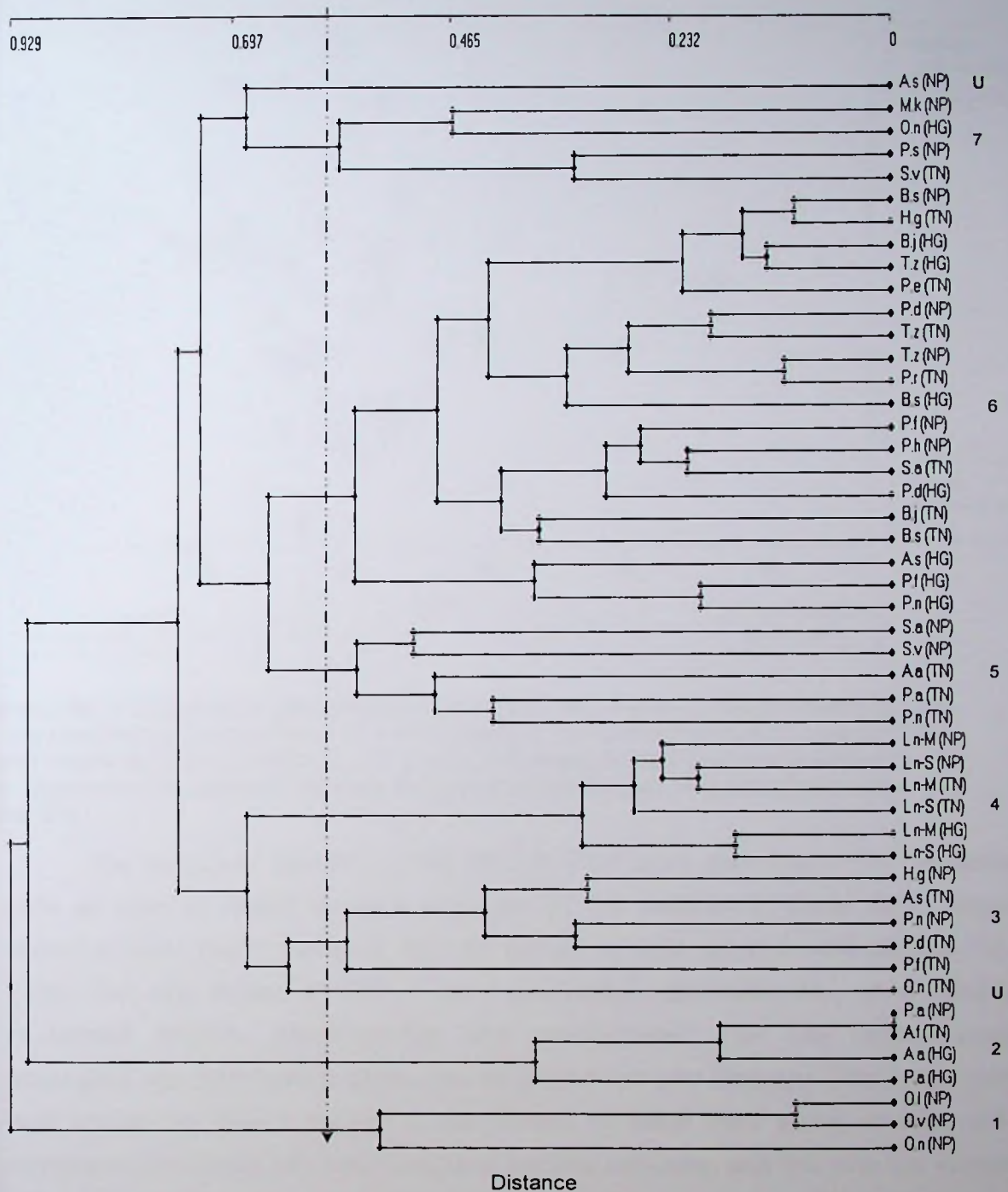


Figure 3.4 A. UPGMA cluster diagram showing the similarity in diets of 23 fish species/size groups using Bray-Curtis distance measure from the northern portion of Lake Victoria. At ≤ 0.60 diet similarity 7 cluster groups were possible and U indicates location of the ungrouped fish species (Napoleon Gulf = NP, Thruston Bay = TN, Hannington Bay = HG and other text codes Table 3.1)

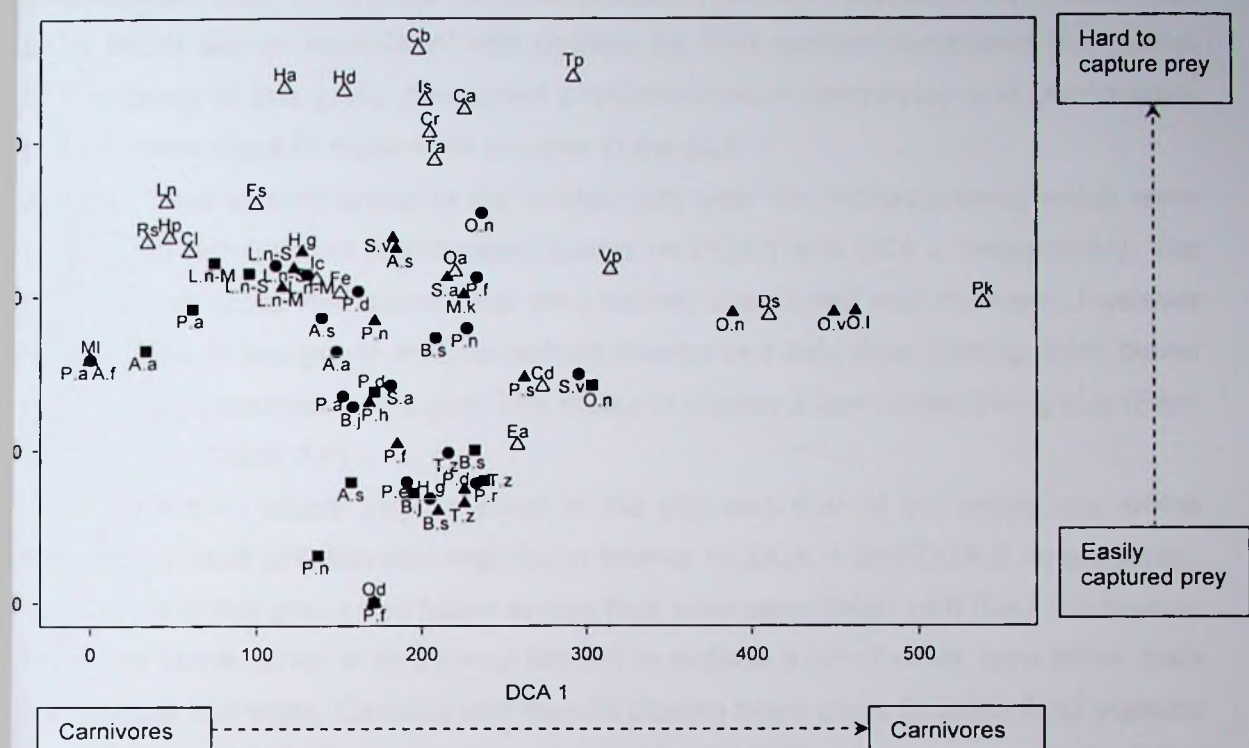


Figure 3.4B. A DCA scatter plot showing spatial patterns between 23 food sources (Δ) and fish species/size groups from the inshore areas of the northern portion of Lake Victoria. Eigen values: 0.72 and 0.33 for DCA 1 and DCA 2 respectively, fishes are indicated by ($\blacktriangle$) from Napoleon Gulf, ($\blacksquare$) from Thruston Bay, ($\bullet$) from Hannington Bay and all text codes (Table 3.1)

The scores for species on the first two DCA axes generated from the same data as used in cluster analysis explained 27.7% variation in these data. These scores and the factor scores of the prey groups or food sources were plotted (Fig. 3.4B). The high scores on DCA 1 were associated with herbivores, which mainly consumed detritus, phytoplankton and macrophytes. The low scores were associated with carnivorous fishes that depended fish and Molluscs. The fishes with high scores on DCA 2 tended to plot closest to either hard shells or with well-developed avoidance behaviors including benthic molluscs, and fish and low scores with easily captured prey such as the Odonata and Ephemeroptera (Fig. 3.4B). The first obvious fish trophic group in the scatter plot comprised the detritivores, which was associated with high and intermediate scores for DCA 1 and DCA 2,

respectively (Fig. 3.4B). The fishes in cluster 1, all from Napoleon Gulf, which had DCA factor scores associated with detritus as food source, comprised this group. Some fishes in this group consumed phytoplankton, macrophytes and chironomids placing them close to those food sources in the plot.

Another clear trophic group in the scatter plot was the molluscivores, which were associated with low and intermediate scores on DCA 1 and DCA 2, respectively. The fishes in this group had scores that were closely associated with molluscs. However some fishes in this group also consumed insects and fish, thus placing them closer to those food sources in the plot. The fishes in cluster 2 comprised this group (Figs. 3.4 A and B; Table 3.4).

The third visible trophic group in the plot was that of the piscivores, which were associated with low and high factor scores on DCA 1 and DCA 2, respectively. The fishes in this group had factor scores that were associated with fish food source. However some fishes in this group tended to include a lot of other food items such as molluscs, fish eggs, *Caridina* and insects placing them close to those food sources on the DCA plot. Fishes in clusters 4 and *H. guarti* from cluster 3 comprised this group; however, *H. guarti* also consumed a large proportion of insects (48%) (Figs. 3.4A and B; Table 3.5).

Insectivorous fishes comprised the largest trophic group, which had relatively low and intermediate factor scores on DCA 1 and DCA 2, respectively (Fig. 3.4B). Fishes in clusters 4 except *H. guarti* as already mentioned above in piscivores, 5, 6, 7 and the only ungrouped *O. niloticus* from Thruston Bay, at a distance of ≤ 0.60 in cluster analysis comprised this group. Fishes in this group were associated with the insect food sources e.g., Odonata, Ephemeroptera, chironomids, Trichoptera, Coleoptera, Hemiptera, and Isoptera. However some fishes in this group tended to feed on oligochaetes, fish eggs, Hirudinea and *Caridina*, placing them closer to those food sources in the DCA plot.

The detritivores were only recorded in Napoleon Gulf throughout the whole study (Fig. 3.4A and B).

3.5 Fish species and spatial trophic diversities

In general fish species occupied similar trophic groups in the different lakes examined (Table 3.5) but were not specialized for only those trophic groups, and occasionally fed across other trophic levels (Tables 3.1 to 3.4). Exceptions included the tilapiines, *A. alluaudi*, *P. aethiopicus* and *L. niloticus*. *Oreochromis niloticus* exhibited the highest feeding plasticity, being a detritivore in Napoleon Gulf Lake Victoria, a phytoplanktivore in Lake Nawampasa, a macrophyte eater in Lake Bisina, a generalist herbivore in lakes Kachera and Mburo; an omnivore in lakes Nakuwa and Kyoga, Iyingo area; and an insectivore in lakes Nabugabo, Kyoga, Bukungu area and in both Thruston and Hannington Bays Lake Victoria. The least feeding plasticity was observed in *O. variabilis*, which was only a detritivore in Napoleon Gulf and phytoplanktivore in lakes Nawampasa and Bisina and this fish species tended to overlap strictly only between these two trophic groups (Tables 3.5 and 3.4).

Table 3.6 Trophic groups of the dominant fish species/size groups encountered in the Victoria and Kyoga basin lakes from August 2001 to May 2004 (Kachera = KR, Mburo = MR, Kayugi = KG, Kanyanja = KJ, Nabugabo = NB, Nawampasa = NS, Nakuwa = NW, Bisina = BS, Kyoga-Iyungu = KI, Kyoga-Bukungu = KB, Napoleon = NP, Thruston Bay = TN and Hannington Bay = HG)

Species	Trophic groups							
	Detritivores	Pytoplantivores	Macrophyte eaters	Herbivores	Omnivores	Insectivores	Molluscivores	Piscivores
<i>Jacksonii</i>	-	-	-	-	-	HG	-	-
<i>dleri</i>	-	-	-	-	-	NB, NS, BS, KI, KB, NP, TN, HG	-	-
<i>cmac</i>	-	-	-	-	-	-	-	BS
<i>oticus-L</i>	-	-	-	-	-	-	-	KI
<i>oticus-M</i>	-	-	-	-	-	-	-	NB, NW, KI, KB, NP, TN, HG
<i>oticus-S</i>	-	-	-	-	-	NW	-	NB, KI, KB, NP, TN, HG
<i>atlooth"</i>	-	-	-	-	NS	-	-	-
<i>yogaastato"</i>	-	-	-	-	-	KI,	-	-
<i>luaudii</i>	-	-	-	-	-	MR, TN	HG	-
<i>neocolor</i>	-	-	-	-	-	KR, MR	-	-
<i>ifasciata</i>	-	-	-	-	-	-	-	NS, -
<i>abila</i>	-	-	-	-	-	KG, KJ, KI,	-	-
<i>elifer</i>	-	-	-	-	-	KG, KJ, NB	-	-
<i>totilapia sp.</i>	-	-	-	-	-	NP, TN, HG	-	-
<i>mpsoni</i>	-	-	-	-	-	KJ	-	-
<i>idus</i>	-	-	-	-	-	NS, BS	-	-
<i>icheali</i>	-	-	-	-	-	-	-	BS
<i>tuamipinnis</i>	-	-	-	-	-	KR, MR	-	-
<i>tylodon</i>	-	-	-	-	-	-	-	NS -
<i>axillaris</i>	-	-	-	-	-	-	-	NS
<i>eculentus</i>	-	NS, BS, -	-	KR, MR, KG, KJ,	-	-	-	-
<i>ucostictus</i>	NP -	-	-	NB,	-	KR, MR	-	-
<i>oticus</i>	NP -	-	BS	KR, MR	NW, KI	NB, KB	-	-
<i>ariabilis</i>	NP NS, BS	-	-	-	-	-	-	-
<i>Jackpara"</i>	-	-	-	-	-	KB	-	-
<i>hovelmouth"</i>	-	-	-	-	-	BS	-	-
<i>genteus</i>	-	-	-	-	-	NS, BS	-	-
<i>adlei</i>	-	-	-	-	-	NB	-	-
<i>eye"</i>	-	-	-	-	-	TN	-	-
<i>ssilabris</i>	-	-	-	-	-	NP, TN, HG	-	-
<i>iariti</i>	-	-	-	-	-	TN	-	NP
<i>hostoma</i>	-	-	-	-	-	-	-	NS
<i>llegrin</i>	-	-	-	-	-	-	-	BS
<i>fin</i>	-	-	-	-	-	NP, TN, HG	-	-

Species	Trophic groups									
	Detritivores	Pytoplantivores	Macrophyte eaters	Herbivores	Omnivores	Insectivores	Molluscivores	Peadophages	Piscivores	
<i>onianus</i>	-	-	-	-	-	NP, TN, HG	-	-	-	
<i>ckcribensis</i>	-	-	-	-	-	TN	-	-	-	
<i>uvegai</i>	-	-	-	-	-	NP	-	-	-	
<i>eller</i>	-	-	-	-	-	NP	-	-	-	
<i>nator</i>	-	-	-	-	-	KG, KJ	-	-	-	
<i>lli</i>	-	-	BS	KG,	-	KJ, NB, NP, TN, HG	-	-	-	
<i>pytophagus</i>	-	-	-	-	-	NS, BS	-	-	-	
<i>luaudi</i>	-	-	-	-	-	KJ,	-	-	-	
<i>riepinus</i>	-	-	-	-	-	KR, MR, NS, NW, BS, KI	-	-	-	
<i>cephalus</i>	-	-	-	-	-	KR	-	-	-	
<i>ianalis</i>	-	-	-	-	-	KB	-	-	-	
<i>enatus</i>	-	-	-	-	-	-	TN	-	-	
<i>rofischeri</i>	-	-	-	-	-	NB, NS, NW, BS, KI, KB, NP, TN	-	-	-	
<i>ctorianus</i>	-	-	-	-	-	NB, NS, NW, BS, KI, KB, NP, HG	-	-	-	
<i>ctoriae</i>	-	-	-	-	-	KG, KJ	-	-	-	
<i>annume</i>	-	-	-	-	-	NP	-	-	-	
<i>stoma</i>	-	-	-	-	-	KG, KJ, BS	-	-	-	
<i>thiopicus</i>	-	-	KB,	-	-	KR, MR, NW, BS, KI, TN	KG, KJ, NB, NP	-	NS	
<i>ermedius</i>	-	-	-	-	-	NB, NW, KI, KB	-	-	-	

Trophic diversity also varied within and across the studied lakes (Fig. 3.5). Insectivores, piscivores, and molluscivores were the most widely distributed trophic groups and were present in most of the lakes or areas. Detritivores and peadophages were the rarest trophic groups, and were only recorded in Napoleon Gulf Lake Victoria and Lake Nawampasa, respectively. The highest number of trophic groups was recorded in Lake Bisina (6) and the least was in the two Koki lakes (Kachera and Mburo) (6) (Fig. 3.5). Many factors synergistically explain the restructuring of the Lake Victoria food web of which Nile perch is one. I compared the current results from the studied lakes with the pre-perch boom trophic structure of Lake Victoria based on only haplochromine cichlids get a rough picture on the role of Nile perch in restructuring the food web (Fig. 3.5B)

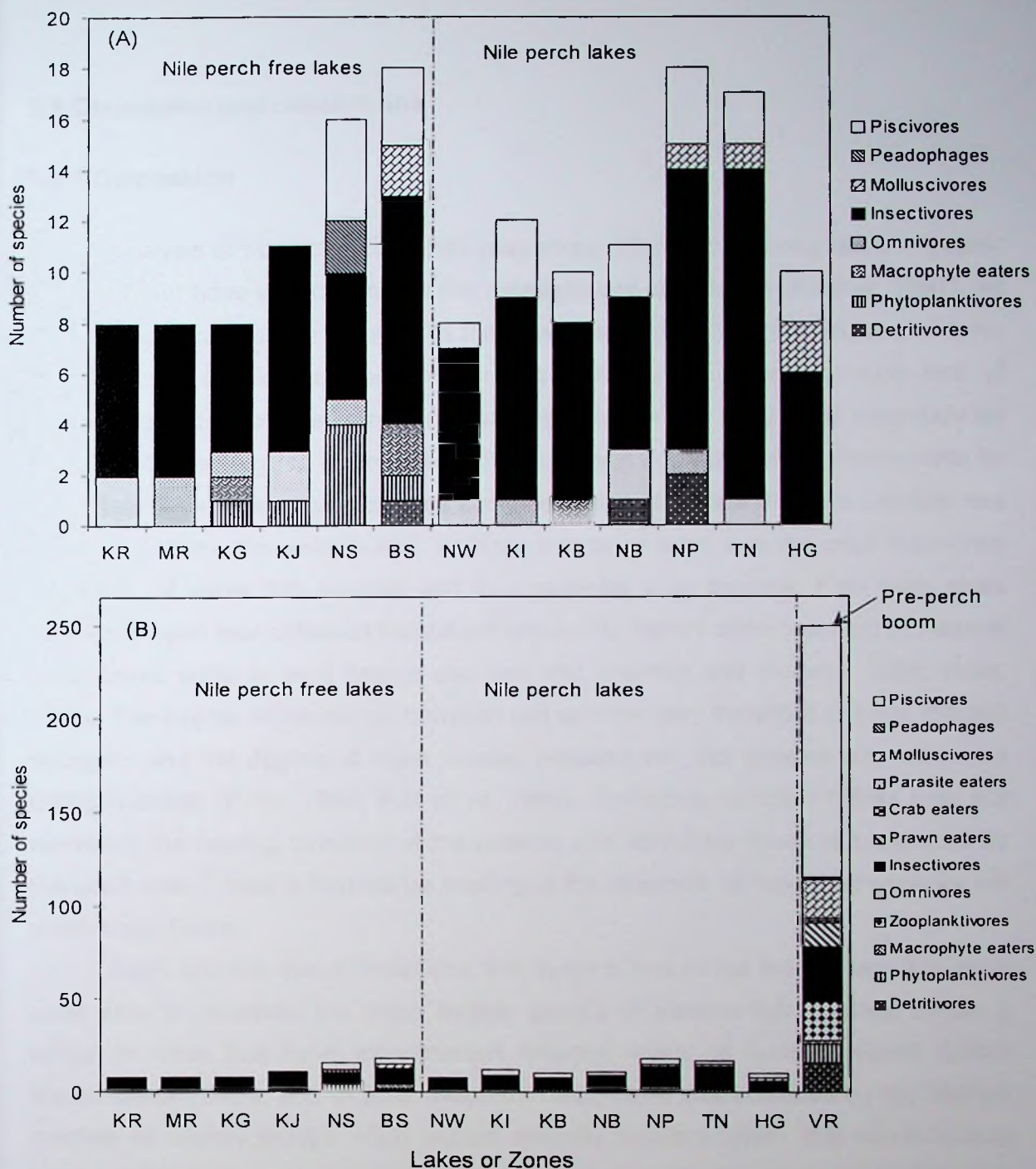


Fig. 3.5 (A) Trophic diversity of species by number from the studied lakes in the Victoria and Kyoga basin lakes (August 2001 to May 2004) and (B) comparison of the current data with pre-perch Lake Victoria situation (KR =Kachera, MR = Mburo, KG = Kayugi, KJ = Kayanja, NS = Nawampasa, BS = Bisina, NW = Nakuwa, KI = Kyoga-Iyingo, KB = Kyoga-Bukungu, NP = Napoleon gulf, TN = Thruston bay, HG = Hannington Bay and VR = Pre-perch Lake Victoria. Data on pre-perch boom is only on haplochromines 1984 and are from (Goldschmidt, 1996).

3.6 Discussion and conclusions

3.6.1 Discussion

Analysis of trophic relationships may show differences among lakes in trophic structure that have implications for the management of fisheries (Koslow, 1997). As with various previous diet studies in fish, there are many inherent sources of error that must be considered when interpreting these results. These include lack of sufficient diet data on prey sizes and over the range of fish body sizes especially for larger predators (e.g., *C. gariepinus* and *P. aethiopicus*). Much of the dietary data for the different species or size classes has been lumped for the different habitats and seasons to raise the sample size. Another source of error was the poor taxonomic resolution of some fish species and their potential prey species. Fish body sizes frequently span four orders of magnitude across life history often resulting in discrete ontogenetic shifts in both habitat use and diet (Werner and William, 1984; Ross, 1986). The trophic relationships between two species may therefore change through ontogeny and the degree of niche overlap between the two species may also vary ontogenetically (Polis, 1984; Piet *et al.* 1999). Therefore sampled fishes may not represent the feeding behavior of the juvenile and immature fishes not captured by the used nets. These in turn will be missing in the analyses as food resources for the piscivorous fishes.

Even with the above limitations, this study is one of the few studies that have been able to elucidate the major trophic groups of various fish species across a range of lakes that have experienced different levels of human impact. Lakes Nawampasa, Bisina, and Victoria (Napoleon Gulf) were characterized by the highest number of trophic groups. High habitat diversity (macrophytes) that characterizes most satellite lakes and absence of Nile perch may explain the observed high trophic diversity in lakes Nawampasa and Bisina (Mbabazi *et al.*, 2004). In Napoleon Gulf, the high habitat diversity (macrophytes, rocky crevices) and the high transparency (secchi depth 1.35 m Silsbe, 2004) provide best refuge for fish preyed upon by Nile perch in those lakes/areas (Seehausen *et al.*, 1997; Seehausen *et al.*, 2003). Habitat complexity also reduces the foraging efficiency of the piscivorous predators and thus

minimizes the predation risk for prey fish (Werner and Hall, 1988; Persson and Eklov, 1995; Lewin *et al.*, 2004). Generally fish diets relate to prey density and availability all of which are abundant in the near shore areas of larger and the generally shallow lakes, which directly applies to most of the sampled lakes. The Koki lakes (Kachera and Mburo) and Lake Nakuwa from the Kyoga drainage system exhibited the lowest number of trophic groups mainly due to the low species diversity associated with them. Similar observations in Lake Naivasha indicated that a community with very few species can not fully exploit all potential food resources (Moreau, 1997; Hickley *et al.*, 2002) basing on Mavuti *et al.* (1996) using ECOPATH (Christensen and Pauly, 1992).

In general, the fish trophic groups in the lakes only reflect broad patterns in diet preferences. Members of these groups consume similar prey at broad taxonomic levels, e.g fish or insects, and within similar habit types but feed upon a variety specific food items on a local scale which reflects resource partitioning at a more detailed scale as has been shown by earlier studies (Garrison, 2000). Such differences may be partly related to habitat differences or geographic variations, such as differences in food availability at different localities (Nakamura *et al.*, 2003). The relative isolation of lake ecosystems can also contribute to among-lake differences in the composition of fish communities (Magnuson *et al.*, 1998) resulting from differences among lakes in biotic conditions (prey communities, presence or absence of competitors or predators) that promote dietary variation among populations (Lacasse and Magnan, 1992). Most of the Victoria and Kyoga basin satellite lakes were originally part of a large swamp whose topography allowed isolated lakes and associated biological communities to form (Kendall, 1969). Fishes fed on a range of food items including detritus, algae, macrophytes, zooplankton, insect larvae and pupae, adult insects, *Caridina* sp., oligochaetes, leeches, millipedes, crabs and various fish such as haplochromines, *Rastrineobola* sp., *Brycinus* sp., *Barbus* sp., *Clarias* sp. Tilapia and *Lates* sp. Most of my observations of diets of the various fishes were in agreement with earlier diet studies on single species or a groups of fish species in Lakes Victoria (Corbet, 1961; Okedi, 1972, Greenwood, 1981; Mwebaza-Ndawula, 1984; Ogutu-Ohwayo, 1990b; Goudswaard

and Witte, 1997; Balirwa, 1998); Nabugabo (Ogutu-Ohwayo, 1993; Olowo and Chapman, 1999; Schofield and Chapman, 1999; Chapman *et al.*, 2003); Kyoga basin lakes (Ogutu-Ohwayo, 1994; Mbabazi *et al.*, 2004), Naivasaha (Muchiri *et al.*, 1995; Hickley *et al.*, 2002). However, there were a few notable differences in diets relative to earlier studies. For example, *O. niloticus* exhibited a high degree of dietary variability spanning four trophic groups across the studied lakes. Earlier studies on tilapiines indicated that *O. niloticus* had food habits similar to those of indigenous tilapiine species (*O. esculentus* and *O. variabilis*), which it replaced i.e feeding mainly on phytoplankton (Lowe-McConnel, 1958; Welcomme, 1967; Getabu, 1994). Later studies in littoral areas of northern Lake Victoria by Balirwa (1998) indicated that *O. niloticus* had become omnivorous. Results from this study indicated *O. niloticus* to exhibit some level of omnivory in most of the sampled lakes with the exception of lakes Nawampasa and Bisina where it still depended on similar food items to the native *O. esculentus* and *O. variabilis*.

Observations from this study on *O. leucostictus* from lakes Nabugabo and Victoria (Napoleon Gulf) were supported by earlier studies in Lake Naivasha, which found that detritus was a major diet component but chironomid larvae and oligochaetes were also important (Malvestuto, 1974; Siddiqui, 1977; Muchuri *et al.*, 1995; Hickley *et al.*, 2002). However, *O. leucostictus* was phytoplanktivorous, omnivorous, and insectivorous in lakes Nawampasa, Kachera and Mburo respectively.

The study indicated that *T. zillii* was a macrophyte eater in both lakes Kayugi and Bisina, an omnivore in Lake Kanyanja, and an insectivore in Lake Nabugabo and all the three areas of Lake Victoria. Earlier studies on Lake Naivasha indicated that macrophytes constituted 67.7% of its diet (Siddiqui, 1977) and these were mainly dominated by *Najas* sp and *Potamogeton* sp) (Hickley *et al.*, 2002). In other tropical waters, *T. zillii* above 8 cm total length has been observed to depend on a herbivorous diet readily feeding on *Hydrilla* sp. (Pieterse, 1981) but preferring *Najas* sp. to *Lemna* sp. and *Potamogeton* sp. (Buddington, 1979) however, recent studies in Lake Naivasha indicated that *T. zillii* was omnivorous (Muchiri *et al.* 1995). Most of the aquatic macrophytes common in the diet of *T. zillii* are abundant in most Kyoga

drainage lakes, especially Bisina, but are currently rare in the main Lake Kyoga. The reduction in macrophyte cover could be explained by the decreased water transparency as a result of increased algal biomass. In similar shallow lakes water transparency has been found to be the main factor controlling the biomass of submerged macrophytes (Sand-Jensen and Sondergaard, 1981; Ramlal *et al.*, 1991; Squires *et al.*, 2002). Extensive use of seine nets since the Nile perch boom, could have contributed to the reduction in macrophyte cover. The general reduction in macrophyte cover has been associated with the decline in stocks of *T. zilli* and competition for nursery grounds with other tilapias (Petr, 2000). Boosting stocks of *T. zillii* in Lake Bisina could help in reducing the abundant macrophytes present in the lake through consumption, followed by detailed studies to assess the impact. However, herbivorous fish being efficient grazers and inefficient assimilators can play a significant role as a nutrient source or in accelerating their recirculation (Prejs, 1984). With eutrophication and increased macrophyte consumption due to increased herbivores, a new part of their biomass may be finally converted into additional algal biomass, the main threat in lakes e.g Grass carp partially digest their food and the feces are a large source of nutrients that are readily utilized by phytoplankton, resulting in elevated algal biomass and in some cases algal blooms (Bettoli *et al.*, 1993; Petr, 2000).

The results also indicate that in all sizes Nile perch were the sole piscivores in lakes where they have been introduced except in Lake Nakuwa where the small sized Nile perch (< 20 cm) were insectivorous and in Napoleon Gulf of Lake Victoria where one haplochromine cichlid *H. guiarti*, was a piscivore. In the lakes Bisina and Nawampasa, *B. docmak* and *P. aethiopicus* were piscivores, respectively. Piscivorous haplochromine cichlids were also recorded in both lakes. The piscivorous haplochromine cichlids included *H. micheali* and *P. pellegrin* in Lake Bisina and *L. maxilaris*, *P. argenteus* and *P. orthostoma* in Lake Nawampasa. The remaining lakes lacked obligate piscivores but most fish included fish in their diets. Nile perch (<20 cm) in Lake Nabugabo were found to be strongly piscivorous ($\geq 66\%$ fish diet) compared to earlier studies where they were piscivorous at about ≥ 30 cm (Chapman *et al.*, 2003). Nile perch are characterized by a strong dietary flexibility as

evidenced by dietary change over a time scale in Lake Victoria. Between 1968 and 1977, Nile perch (20-60cm) consumed mainly haplochromines (92% frequency of occurrence Ogutu-Ohwayo, 1994); 1988 and 1992 haplochromines became rare (4%) and *C. nilotica*, *R. argentea* and juvenile *L. niloticus* were more frequent (Mkumbo and Ligtvoet, 1992; Ogutu-Ohwayo, 1994; Schofield and Chapman, 1999). Nile perch in Lake Nakuwa ate mainly benthic invertebrates, dominated by insects. This may reflect the low species richness of especially of haplochromines and other smaller fishes such *Barbus species* that are present in the main Lake Kyoga (Namulemo *et al.*, 2003). Lake Nakuwa is instead dominated by *S. afrofischeri* (Chapter 2), which is difficult to capture by Nile perch, because of its defensive structural morphology. The observed high rates of cannibalism in the medium-sized Nile perch (20-60 cm) in Lake Nakuwa, 28% in contrast to 14% in the main Lake Kyoga, and the increased consumption of invertebrate prey 48% in contrast to 13% in the main Lake Kyoga support the rareness of the other preferred prey. In lakes Victoria and Kyoga, Nile perch began feeding on its young ones only when the haplochromines had been depleted (Ogutu-Ohwayo, 1993). The above observations in Lakes Bisina and Nawampasa are supported by earlier studies on Lake Victoria where *B. docmac* and piscivores haplochromines were the top predators before Nile perch boom (Corbet, 1961; Greenwood, 1981; Witte and Van Oijen, 1990) and recent studies on haplochromines on Kyoga basin lakes (Mbabazi *et al.*, 2004). However, in this study I identified *L. maxillaris* as a piscivorous in Lake Bisina as opposed to peadophages in the recent study on Kyoga basin lakes (Mbabazi *et al.*, 2004), but it still included large proportions of fish eggs. This could have arisen from the small sample size analyzed (4) or the high flexibility generally observed in feeding behavior of most cichlid fishes (Keast, 1977; Karel, 1884; Balirwa, 1998).

A comparison of the trophic diversity in lakes with and without Nile perch provides insight into how predation and competition from a top predator such as Nile perch may structure fish communities and corresponding food web complexity as has been reported in earlier studies (Ogutu-Ohwayo, 1990c; Kaufman, 1992; Lowe-McConnell, 1994). However the food web of Nile perch lakes is further complicated by human exploitation of *R. argentea* especially in lakes Victoria and Kyoga.

Exploitation captures juvenile Nile perch as bycatch (Muhoozi, 2002). Exploitation of *R. argentea* is likely to intensify in lakes Nakuwa and Nabugabo (Ogutu-Ohwayo, 1998). Although *R. argentea* is often common in stomach contents of Nile perch, the high values of $\delta^{15}\text{N}$ signatures compared to those of Nile perch indicate that *R. argentea* does not contribute much to the somatic growth of the Nile perch.

This study recorded only two species that were peadophage (*L. cryptodon* and *A. latifasciata*). Earlier studies agreed with observations on *L. cryptodon* but not on *A. latifasciata* that was generally an algal eater in Lake Nawampasa (Mbabazi *et al.*, 2004. This current study classified *A. latifasciata* as a molluscivore in Lake Bisina providing evidence of dietary flexibility in this cichlid.

Detritivores were only encountered in Lakes Victoria (Napoleon Gulf) and Bisina, and these were *O. variabilis* and *O. leucostictus*. However, these same species were found to be mainly phytoplanktivorus in Lake Nawampasa supporting earlier studies on these tilapiines in Lake Victoria (Lowe-McConnel, 1958; Welcomme, 1967; Getabu, 1994).

Omnivores were common in most studied lakes but still comprised of mainly cichlids and *P. aethiopicus*.

The foraging behavior and feeding ecology of fish are generally characterized by adaptive flexibility and trophic adaptability (Dill, 1983; Gerking, 1994). More than for many other groups of animals, many fishes can feed on a variety of prey and shift among prey types as circumstances change (Beudoin and Tonn, 1999). The observed high versatility in cichlid fishes has been documented and is known to increase tolerance to changing environmental conditions especially help them cope with fluctuations in food (Keast, 1977; Karel, 1984).

The increasing abundance of omnivorous and detritivorous fishes in shallow lakes is commonly associated with changes related to eutrophication (Horppila and Kairesalo, 1990; Karjalainen *et al.*, 1999). Specifically this study has indicated that most fish species exhibited some varying degrees of omnivory and detritivory which is indicative of varying trophic states for these lakes.

Trophic diversity and food web complexity in Lake Victoria was high relative to other Nile perch lakes. This may reflect the high habitat diversity in Lake Victoria

that includes various types of wetland ecotones and rocky crevices that provide refuge from the predatory Nile perch (Seehausen *et al.*, 1997; Chapman *et al.*, 2003). Despite the relatively high trophic diversity associated with the inshore areas of Lake Victoria, the other large portion of the open lake remains underutilized by the fishes, most likely a reflection of high predation pressure by Nile perch. Thus, the observed trophic diversity that currently characterizes the lake is much less than was observed before Nile perch boom. In addition to Nile perch predation, eutrophication contributed to the simplification of the Lake Victoria food web (Seehausen *et al.*, 1997; Verschuren *et al.*, 2002). Generally, predatory fishes that overlap in habitat differ in behavior and have specialized prey species or sizes, reducing competition for prey. Decreased visibility reduces the encounter rates with prey, which results in incorporation of more prey types of low quality to the prey spectrum (Rodriguez and Lewis, 1997). The resulting decrease in niche segregation and increased competition may lead to extinction of the less efficient predators when population sizes are resource limited (Tokeshi, 1999). The dramatic decrease in water transparency in Lake Victoria over the past 20 years or more (Seehausen *et al.*, 1997; Witte *et al.*, 1999) is likely to have increased competition among the piscivores in the lake. The increase in Nile perch, a generalized predator that can feed efficiently on small prey types, may have added competitive pressure on the then abundant piscivorous cichlids that were forced to converge with each other and Nile perch on a generalized prey spectrum (Seehausen *et al.*, 2003). These findings were supported by this study which indicated a high dietary overlap among the few piscivores encountered in most sampled lakes

In lakes without Nile perch, high food web complexity was mainly due to the high habitat diversity comprising mainly submerged macrophytes and absence of Nile perch (Mbabazi *et al.*, 2004). Fish use macrophytes for shelter and refuge, as a food source either directly or indirectly, in form of epiphyton (periphyton) and associated invertebrates, and as spawning, nesting and nursery sites (Petr, 2000). Several previous studies have found out that many fish species associate with either the water surface immediately above the plants, the periphery of the dense stands, "holes" formed in the plant beds, or the bottom directly below dense canopy

formations to use both open and structurally complex areas for foraging and predator avoidance (Killgore *et al.* 1989). The current thick merged/submerged aquatic macrophytes in Lake Bisina could therefore explain the disappearance of the once established introduced Nile perch (Personal communication with elders) in the lake resulting from predator avoidance.

Other studies have indicated that submerged aquatic macrophytes provide cover for young fish, which grow better in intermediate plant densities and edge areas, than in areas of uninterrupted high-density plants or without plants (Morrow *et al.*, 1991). Large densities of aquatic macrophytes have been found to reduce fish condition factor resulting in stunted fish populations (Colle and Shireman, 1980). Several other studies have shown that the growth rate of prey fish is retarded when they are confined to the vegetation due to predation risk (Mittlebach, 1988; Persson and Eklov, 1995). The maximum foraging rate decreases when the fish shift from pelagic to vegetated habitat (Person and Crowder, 1997). Slower growth results from an increase in competition among the prey fish in the refuge (Petr, 2000). The piscivorous predators can also change from an active pursuit foraging mode to an ambush sit and wait foraging mode with an increase in vegetation density as has been observed in other aquatic ecosystems (Savino and Stein, 1982; Eklov and Diehl, 1994). The predation risk leads to competition among prey fish in the refuge and may explain the smaller sizes of the tilapiine fish species that are caught in most of the vegetated satellite lakes around the Victoria and Kyoga Basins.

3.6.2 Conclusions

This study has identified the spatial differences in trophic structure of the fish communities in studied lakes that are at different levels of anthropogenic impact. Associated with these patterns were differences in complexity of food webs and strength of species interactions especially for aquatic systems located in different watersheds. Generally the captured fishes and or sizes consumed a wide range of prey taxa or food items but exhibited a high dietary overlap. This study has moved a long way from a single species or restricted group approach comprising one or two

trophic levels towards ecosystem approach with numerous fish species. Future fish dietary studies should emphasize ecosystem analysis including human activities affecting water quality and especially by excessive pressure caused by introduced species or intensive fisheries. Further studies on patterns of food resources and habitat use at finer scales of taxonomic, spatial and temporal resolution should be done. Greater understanding of ecological attributes and relationships including diet and habitat requirements will be critical for the future management of the fisheries.

CHAPTER FOUR

4.0 Stable isotopes of carbon and nitrogen as indicators of trophic structure and food sources of the fish communities in the Victoria and Kyoga basin lakes

4.1 Introduction

Animals regulate the flows of energy and nutrients in ecosystems through consumption, digestion, metabolism, behavior and thereby indirectly control the population dynamics of other organisms with which they interact (Schindler *et al.*, 2003). Ecosystem based fisheries management recognizes that target fish stocks are part of a complex food web, that non-human predators of stocks are competitors with fishing and that the rest of the biotic community is part of the environment in which the fish live and fishing occurs (Mangel, 2000).

An understanding of the factors responsible for fisheries production is of crucial importance for effective fishery management as its knowledge permits predictions of fish production. Fish can be viewed as the final step in a series of carbon (or energy) transformations beginning with carbon dioxide fixation by plants (Forsberg, *et al.*, 1993). Fish production in natural aquatic systems originates from phytoplankton, benthic algae, aquatic and/or terrestrial plants, and their relative importance to fish is system dependent (Gu *et al.*, 1996; Benedito-Cecilio *et al.*, 2000).

Trophic relationships have long been studied using stomach content analysis, direct observations or collection of prey remains. These techniques enable monitoring of short-term dietary intake. However unless samples are regularly collected, they are unable to indicate long-term feeding history and can be difficult to employ when some species eat only infrequently (Beaudoin *et al.*, 1999), or rapidly digest soft-bodied prey (Hobson *et al.*, 1994). Stomach contents are sometimes not identifiable and different components of the diet may not necessarily be assimilated or incorporated into the fish tissue (Gu *et al.*, 1996) and therefore stomach contents may fail to show actual energy flows in aquatic systems (Rounick and Winterbourne,

1986). The ability to define trophic relationships accurately is key to understanding of ecosystem processes (Paine, 1988) and this presents a challenge in aquatic systems where trophic interactions cannot be directly observed and traditional methods have limitations.

Stable isotope analysis offers an alternative technique in trophic relationship studies in that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of a consumer provide a time-integrated measure of assimilated prey, rather than a list of prey items encountered by chance in the diet (Michener and Schell, 1994; Gu *et al.*, 1996; Herdwig *et al.*, 2004). Accuracy in time integration of utilized prey is gained but with loss of precision as to the identity of individual prey items. According to isotopic composition of the consumers' tissues, the relative assimilation among a range of items ingested is recorded (Fry and Arnold, 1982; Manetta *et al.*, 2003).

This chapter examines feeding relationships among the consumers fish and their potential invertebrate or plant food sources to determine the ultimate sources (producers) from which fish consumers derive their energy using stable carbon and nitrogen isotopes as source and trophic level indicators respectively. Unlike stomach content analysis used in Chapter 3 that depended on direct observation of what the fishes had recently ingested, the isotopic composition of fish consumers reflect their assimilated diets over an extended period determined by the turnover rate of their tissues. The length of the dietary time integration in the muscle of fish is estimated to be one year or greater (Hesslein *et al.*, 1991). Unidentifiable dietary items also bias stomach content analysis, underestimation of the importance of quickly digested food items like zooplankton and some polychaete species that did not appear in the stomach contents. It was assumed that unlike stomach content analysis (Chapter 3), results from stable isotope analysis in trophic interactions; would generate data that can be directly input into ecosystem models, which require knowledge of trophic pathways from primary production and interactions for predicting aquatic ecosystem functioning. The detailed materials and methods of stable isotope analysis used by this study are fully described (Chapter 2).

Table 4.1 A list of fish species or their length size classes and potential food sources included in stable isotope analysis (August 2001 - May 2004), text code and former taxonomic genera. Note the absence of a dot in text codes for food items.

Family	Species (author)	Former Genera	Text Code
Characidae	<i>Brycinus jacksonii</i> (Boulenger, 1912)	<i>Alestes</i>	B.j
	<i>Brycinus sadleri</i> (Boulenger, 1906)	<i>Alestes</i>	B.s
Bagridae	<i>Bagrus docmak</i> (Forsskål, 1775)		B.d
Centropomidae	<i>Lates niloticus</i> (Linneas, 1758)		L.n
Cichlidae	<i>Oreochromis esculentus</i> (Graham, 1928)		O.e
	<i>Oreochromis leucostictus</i> (Trewavas, 1933)		O.l
	<i>Oreochromis niloticus</i> (Linneas, 1758)		O.n
	<i>Oreochromis variabilis</i> (Boulenger, 1906)		O.c
	<i>Tilapia zillii</i> (Gervas, 1848)		T.z
	<i>Astatotilapia "kyogaastato"</i>	<i>Haplochromis</i>	A.k
	<i>Astatorechromis alluaudi</i> (Pellegrin,	"	A.a
	<i>Astatotilapia aneocolor</i> (Greenwood, 1973)	"	A.c
	<i>Astatotilapia latifasciata</i> (Regan, 1829)	"	A.l
	<i>Astatotilapia "miniblack"</i>	"	N.m
	<i>Astatotilapia nubila</i> (Boulenger, 1908)	"	A.n
	<i>Astatotilapia velifer</i> (Trewavas, 1933)	"	A.v
	<i>Astatotilapia</i> sp.	"	A.s
	<i>Gaurochromis simpsoni</i> (Greenwood, 1965)	"	G.s
	<i>Haplochromis lividus</i>	"	H.l
	<i>Harpagochromis squamipinnis</i> (Regan, 1921)	"	H.s
	<i>Harpagochromis squamulatus</i>	<i>Haplochromis</i>	H.q
	<i>Lipochromis cryptodon</i> (Greenwood, 1959)	"	L.c
	<i>Lipochromis maxillaris</i> (Trewavas, 1928)	<i>Haplochromis</i>	L.m
	<i>Lipochromis obesus</i> (Boulenger, 1908)	"	L.o
	<i>Lipochromis parvidens</i> (Boulenger, 1911)	"	L.p
	<i>Paralabidochromis "redfin"</i>	"	P.f
	<i>Paralabidochromis "blackpara"</i>	"	P.x
	<i>Prognathochromis "shovelmouth"</i>	"	P.g
	<i>Prognathochromis argenteus</i> (Regan, 1922)	"	P.t
	<i>Paralabidochromis beadlei</i>	"	P.d
	<i>Paralabidochromis crassilabris</i> (Boulenger, 1906)	"	P.d
	<i>Paralabidochromis chilotes</i> (Boulenger, 1911)	"	P.i
	<i>Harpagochromis guarti</i> (Pellegrin, 1913)	"	H.g
	<i>Pyxichromis orthostoma</i> (Regan, 1922)		P.o
	<i>Psammochromis riponians</i> (Boulenger, 1914)	<i>Haplochromis</i>	P.n
	<i>Paralabidochromis rockribensis</i>	"	P.r
	<i>Ptyochromis sauvegai</i> (Pfeffer, 1896)	"	P.s
	<i>Paralabidochromis "sheller"</i>		P.h
	<i>Prognathochromis stilleto</i>	"	P.l
	<i>Prognathochromis venator</i> (Greenwood, 1965)	"	P.v
	<i>Ptyochromis</i> sp		Py

Family	Species (author)	Former Genera	Text Code
	<i>Xystichromis phytophagus</i> (Greenwood, 1966)	<i>Haplochromis</i>	X.p
Clariidae	<i>Clarias gariepinus</i> (Burchell, 1822)		C.g
	<i>Clarias liocephalus</i> (Boulenger, 1898)		C.l
	<i>Barbus altianalis</i> (Boulenger, 1900)		B.a
Cyprinidae	<i>Barbus kerstenii</i> (Peters, 1868)		B.k
	<i>Barbus trispodopluera</i> (Boulenger, 1902)		B.t
	<i>Rastrineobola argentea</i> (4.5 cm) (Pellegrin, 1904)		Ra1
	<i>Rastrineobola argentea</i> (5.5 cm)		Ra2
	<i>caecomstacembelus frenatus</i> (Gosse, 1986)	<i>Mastacembelus</i>	A.f
Mastacembelidae	<i>Synodontis afrofisheri</i> (Hilgendorff, 1888)		S.a
Mochokidae	<i>Synodontis victoriae</i> (Boulenger, 1906)		S.v
	<i>Gnathonemus victoriae</i> (Ruppell, 1832)		G.v
Momyridae	<i>Mormyrus kannume</i> (Forsskål, 1775)		M.k
	<i>Mormyrus macrocephalus</i> (Worthington, 1929)		M.m
	<i>Petrocephalus catostoma</i> (Steindacher, 1914)		P.c
Propteridae	<i>Protopterus aethiopicus</i> (Heckel, 1851)		P.a
Schilbeidae	<i>Schilbe intermedius</i> (Ruppell, 1832)		S.i

Food sources	Text Code
Plants (1 ⁰ producers)	
Detritus	Ds
Phytoplankton	Pk
<i>C. papyrus</i>	Cp
<i>Cylosorus</i> sp	Cs
<i>F. congensis</i>	Fc
<i>M. violacea</i>	Md
<i>Lymnophyton</i> sp	Lt
<i>Nymphaea</i> sp	Na
<i>V. cussipata</i>	Vc
<i>Typha</i> sp	Ty
<i>H. verlicilata</i>	Hv
<i>E. crassipes</i>	Ec
<i>N. horrida</i>	Nj
<i>C. submersum</i>	Cm
Phragmites	Ph
Invertebrates (1 ⁰ consumers)	
Chironomids	Cd
Chaoborus	Cb
Ephemeroptera	Ea
Oligochaetes	Os
Molluscs	MI
Big bivalves	Bb
Small bivalves	Sb
Hirudinea (Leech)	Hd
<i>C. nilotica</i>	Cn

4.2 Carbon sources

The use of carbon stable isotopes as indicative of energy sources depends on the fact that consumers have an isotopic composition similar to their diets. There is little fractionation from prey to predator and different energy sources can have distinct $\delta^{13}\text{C}$ signatures (Hecky and Hesslein, 1995). Since $\delta^{13}\text{C}$ signatures are conserved up the food chain, but can vary at the base of the food chain, the $\delta^{13}\text{C}$ of aquatic consumers provide information about sources of energy to higher consumers (Vander Zanden and Rasmussen, 1999). The minor stepwise trophic enrichment of $\delta^{13}\text{C}$ signatures of 1‰ per trophic transfer described fully in chapters 1 and 2, enhanced its utility for tracking energy sources of the food webs of the examined lakes.

4.2.1 Koki drainage system lakes

Chapter 3 indicated that invertebrates were the most important food items in most fish species. Fish also formed another important food source especially in the large predatory species and haplochromine cichlids. Among the primary producers phytoplankton was more common in stomach contents of most primary consumers, than macrophytes, despite the abundance of macrophytes in most of the examined lakes or areas. Macrophytes provided a direct food source to only one fish species (*T. zillii*) in Lake Bisina. Chapter 3 further indicated that fishes were generalistic feeders and exhibited a high level of omnivory. Results from this chapter support those from Chapter 3.

In both Lakes Mburo and Kachera, there was a clear separation in carbon isotope ratios for primary producers (Fig. 4.1). Plankton, *Vossia cuspidata* and *Cyperus papyrus* showed similar isotopic signatures, being ^{13}C enriched compared to the other primary producers; however, plankton were more ^{13}C depleted ($\geq 5\text{‰}$) in Lake Kachera relative to Lake Mburo. The nitrogen isotope ratios for primary producers showed little separation except for the C_3 tree *Euclea schemperi* in Lake Mburo and *C. papyrus* in both lakes that exhibited high $\delta^{15}\text{N}$ signatures. The *E.*

schemperi and *C. papyrus* have higher $\delta^{15}\text{N}$ than that of fish and invertebrates respectively which rules them out as contributing significantly to upper food web diets.

In both lakes, *Oreochromis esculentus* occupied similar position in isotopic space suggesting a direct dependence on the aquatic macrophytes, which also did not differ in their isotopic signatures between the lakes. However, other fishes and plankton were more enriched in Lake Mburo than in Lake Kachera ($\sim 5\text{‰}$). This suggests that most of the food web in both lakes may be tracking plankton (Fig. 4.1). Stable isotope analysis indicated that *O. esculentus* and *Oreochromis niloticus* did not depend directly on *Cyperus papyrus* in these lakes but could depend on it indirectly through detritus (Tables 3.2 and Figs 3.1 B and 4.1). Plankton and *C. papyrus* were the major sources of photosynthetic energy and contributed significantly to the diets of most consumers especially fish in the two lakes. The fish had highly variable $\delta^{13}\text{C}$ ratios (-22‰ to -8‰) and (-12.2‰ to -2.1‰) for lakes Kachera and Mburo respectively. There was variation both within and among taxa, suggesting that these fishes had broad diets deriving energy from a range of C_4 and C_3 plants, including phytoplankton whose $\delta^{13}\text{C}$ can vary in time if CO_2 is variable and sometimes low causing variation in isotopic fractionation by photosynthesis (Hecky and Hesslein, 1995). In general, as algal biomass increases, algae will have heavier $\delta^{13}\text{C}$. It is unlikely that C_3 plants (i.e. *Aeschynomene eraphroxylon*, *Pistia stratiotes*, *Cyclosorus sp* and *E. schemperi*) were significant contributors of carbon to the aquatic consumer food web, whose carbon was much heavier than that of these C_3 plants. The $\delta^{13}\text{C}$ of animal food web was more similar to the littoral C_4 higher plants (*V. cuspidata* and *C. papyrus*) and the C_3 phytoplankton. In Lake Mburo, hippopotamus probably introduce significant quantities of C_4 grass remains because of their habit of grazing grasses on land at night and defecating undigested organic materials during their residence in the water during the day. The nutrient enrichment provided by the hippos can also cause denser phytoplankton populations resulting in a heavier $\delta^{13}\text{C}$ as well as directly introducing enriched $\delta^{13}\text{C}$ undigested plant debris directly into the lake (Table 3.2 and Fig. 3.1B)

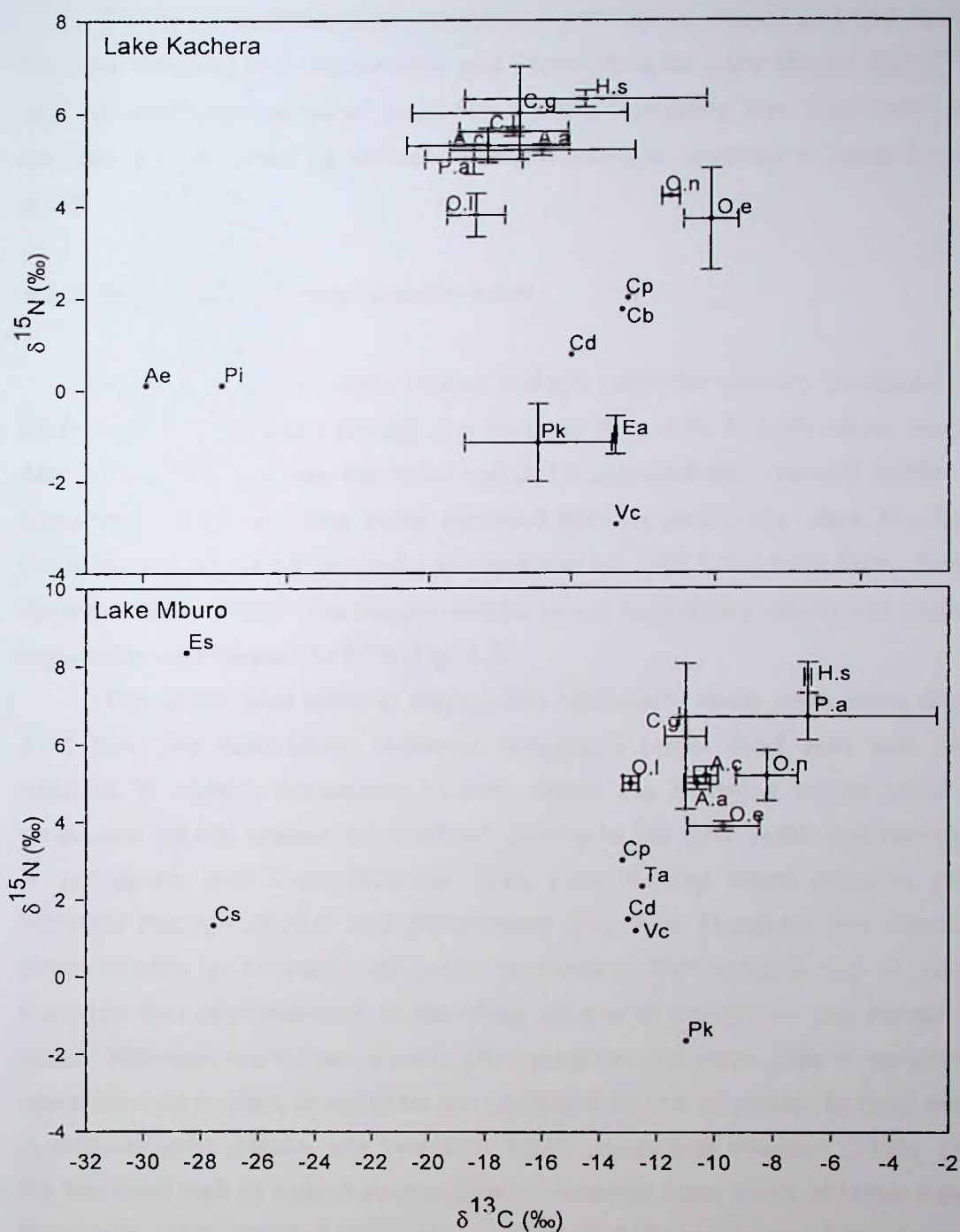


Figure 4.1. The mean $\pm$ SD of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for nine fish species and 10 potential food sources from Koki lakes. Note the lighter and high variation in $\delta^{13}\text{C}$ of food web structure of L. Kachera compared to Lake Mburo. Overlapping SD in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and SD were only calculated for organisms that raised three individuals (See Table 4.1 for a key to labels).

The three invertebrates examined in both lakes, *Chaoborus* and chironomids for Lake Kachera and chironomids and Trichoptera for Lake Mburo, had $\delta^{13}\text{C}$ ratios that fell within the range of most fish species indicating that they were also food sources, as confirmed by stomach content analysis (Chapter 3 Table 3.2 and Fig. 3.1B).

4.2.2 Nabugabo drainage system lakes

As in Koki lakes stable carbon isotope ratios for primary producers showed clear separation in lakes Kayugi and Kayanja (Fig. 4.2). In both lakes, the C_4 plant *Miscanthus violacea* was the least carbon13 depleted and showed similar isotopic signatures (-12.6 ‰). The more depleted primary producers were the C_3 plants, *Ficus congensis* (-28.5 ‰) and *Lymnophyton* sp. (-27.5 ‰) from lakes Kayugi and Kayanja, respectively. The stable isotope ratios for primary producers showed little separation with respect to $\delta^{15}\text{N}$ (Fig. 4.2).

The upper food webs in Kayugi and Nabugabo lakes were more depleted in $\delta^{13}\text{C}$ than the Koki lakes. However, Kayanja's upper food web was similar to Kachera in carbon signatures. In both lakes, the sampled higher plant primary producers did not appear to contribute directly to the food webs of those lakes, but *F. congensis* and *Cyclosorus* sp. from Lake Kayugi could possibly contribute indirectly through detritus and chironomids (Fig. 4.2). However, the dominance of phytoplankton in stomachs of some herbivorous fish species e.g *O. esculentus* indicates that phytoplankton is the likely source of energy for the fishes in these lakes. Although did not sampled it, phytoplankton can have quite a variable carbon signature and is often found to be the dominant source of carbon to food webs even in shallow lakes (Hecky and Hesslein, 1995; Jones and Wadron, 2003). However, the fish food web of Lake Kayanja differed distinctly from those of lakes Kayugi and Nabugabo, probably due to a wide variation in $\delta^{13}\text{C}$ signature of the base of food webs as observed in Koki lakes (Fig. 4.1) supported by earlier studies (Fry and Sherr, 1984; Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999; France and Peters, 1997; Leggett *et al.*, 1999).

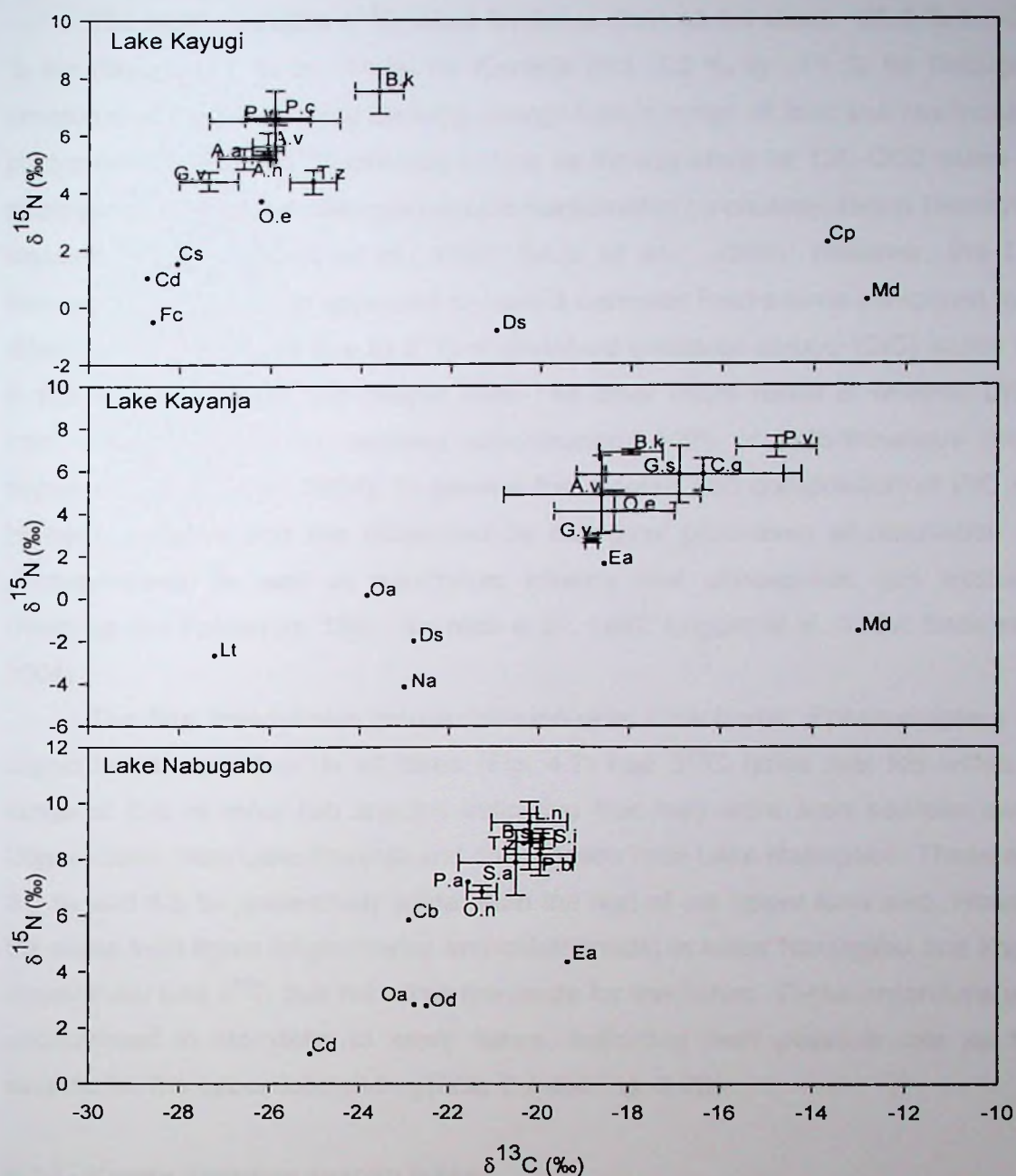


Figure 4.2 The Mean $\pm$ SD of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the 18 fish species and 12 food sources from Nabugabo lakes. Note the lighter and heavier $\delta^{13}\text{C}$ of the fish food webs of Kayugi and Kanyanja respectively. Overlapping S.D in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and S.D were only calculated for organisms that raised three individuals (See Table 4.1 for a key to labels).

The highly variable $\delta^{13}\text{C}$ ratios for fishes from all the lakes, -28.3 ‰ to -24.0 ‰ for Kayugi, -21 ‰ to -14 ‰ for Kanyanja and -22 ‰ to -19 ‰ for Nabugabo, indicate that the fishes were deriving energy from a range of food sources including phytoplankton whose $\delta^{13}\text{C}$ can vary in time as the signature for ^{13}C -CO₂ varies and photosynthetic demand changes isotopic fractionation by photosynthesis (Hecky and Hesslein, 1995; Leggett *et al.*, 1999; Bade *et al.*, 2004). However, the Lake Nabugabo fish food web appeared to have a narrower food source compared to the other two lakes may be due to $\delta^{13}\text{C}$ of dissolved inorganic carbon (DIC) varies less in this relatively larger and deeper lake. The other major factor is whether DIC is from atmosphere (~ -4), respired allochthonous (-28) or autochthonous (highly depleted) (Bade *et al.*, 2004). In general the amount and composition of DIC vary between systems and are influenced by biological processes of respiration and photosynthesis as well as equilibrium kinetics and atmospheric gas exchange (Herczeg and Fairbanks, 1987; Aravena *et al.*, 1992; Leggett *et al.*, 1999; Bade *et al.*, 2004)

The four invertebrate groups (chironomids, Chaoborus, Ephemeroptera and oligochaetes) examined in all lakes (Fig. 4.2) had $\delta^{13}\text{C}$ ratios that fell within the range of that of most fish species indicating that they were food sources except Oligochaetes from Lake Kanyanja and chironomids from Lake Nabugabo. These were 3.3 ‰ and 3.5 ‰ respectively lighter than the rest of the upper food web. However the same food items (oligochaetes and chironomids) in lakes Nabugabo and Kayugi respectively had $\delta^{13}\text{C}$ that fell within the range for the fishes. These organisms were encountered in stomachs of some fishes, indicating their possible role as food sources for the upper food webs (Table 3.2 and Fig. 3.2B).

4.2.3 Kyoga drainage system lakes

With respect to stable carbon isotope ratios for primary producers, all the lakes showed clear separation (except in Lake Nawampasa where the samples for primary producers yielded insufficient quantities for analysis). The primary producers

varied across the lakes examined depending on the abundance (phytoplankton) and availability (macrophytes) (Fig. 4.3).

In all the lakes where phytoplankton and detritus were sampled, the two items formed the major potential carbon source due to their relatively low $\delta^{15}\text{N}$ signatures (0-2‰) and $\delta^{13}\text{C}$ signatures that fell within the range of those for the upper fish food webs (Fig. 4.3).

In Lake Bisina, *Ceratophyllum submersum* and detritus had $\delta^{13}\text{C}$ ratios that fell within the range of the main fish food web and formed another direct carbon source. In the same lake, the ^{13}C enriched *Hydrilla verticillata* had $\delta^{13}\text{C}$ carbon ratio that differed by 1.0 ‰ from that of *Tilapia zilli* ruling out the possibility of direct contribution to its diet. Although stomach content analysis by both this study (Chapter 3) and earlier studies (Siddiqui, 1977; Pieterse, 1981), found this fish to feed mainly on macrophytes. The other primary producers (*Najas* sp., *Typha* sp., *Nymphaea* sp and *V. cuspidata*) could not contribute directly to the fish food web because of their highly negative $\delta^{15}\text{N}$ values (Fig. 4.3). However these primary producers may contribute to the fish food web through detritus that was found abundant in stomach of tilapiine species as microbes derived from them would have enriched ^{15}N e.g. *O. variabilis* and *O. leucostictus* from lakes Bisina and Nawampasa respectively (Chapter 3).

In Lake Kyoga, it is unlikely that *E. crassipes* contributed to the fish food web due to its lighter carbon compared to the fish food web and *C. papyrus* could not be a direct food source due the highly negative $\delta^{15}\text{N}$ value (Fig. 4.3).

Based on results from the other lakes, $\delta^{13}\text{C}$ for the fishes and stomach content analysis (Chapter 3), the main carbon source for Lake Nawampasa fish was likely to be phytoplankton. However, looking at depleted carbon signatures for the fish, the phytoplankton in this lake would have to be more $\delta^{13}\text{C}$ depleted than the other three lakes.

Despite all these lakes having the same source of carbon, i.e mainly phytoplankton, their $\delta^{13}\text{C}$ values varied, with Lake Nawampasa having the most depleted carbon (-27 ‰ to -22 ‰), followed by Nakuwa (-23 ‰ to -16.8 ‰), and Kyoga-Iyingo and Bisina (-25 ‰ to -13‰). This variation is explained by the variation

in $\delta^{13}\text{C}$ signatures in DIC at the base of the food webs in the different lakes (Fig. 4.3) and as observed for Koki lakes. Similar variations in $\delta^{13}\text{C}$ carbon signatures of primary producers among lakes have been documented in freshwater ecosystems (Vander Zanden and Rasmussen, 1999; France and Peters, 1997). The five invertebrate groups (*C. nilotica*, Ephemeroptera, chironomids, *Chaoborus* and Trichoptera) examined had $\delta^{13}\text{C}$ ratios that fell within the $\delta^{13}\text{C}$ range of most fish species indicating that they were food sources, which was also confirmed by stomach content analysis (Chapter 3; Table 3.4 and Fig. 3.3B).

The $\delta^{15}\text{N}$ signatures for primary producers showed little separation with except for *Nymphaea* sp, *Typha* sp, *V. cuspidata* in Lake Bisina and *C. papyrus* in Lake Kyoga that exhibited highly negative values. This is partly due the large variation in $\delta^{15}\text{N}$ signatures at different soil horizons and the systematic enrichment of deeper-rooted plants over those with shallow roots (Virginia *et al.*, 1989, Hecky and Hesslein, 1995). Similarly the dense root mats such as in papyrus often contain anoxic waters where denitrification can produce enriched NO_3 in contrast to algae, which are always drawing from a well-mixed epilimnion (Hecky and Hesslein, 1995). The range of $\delta^{15}\text{N}$ signatures in all the phytoplankton and detritus were low (0-2‰) and their $\delta^{13}\text{C}$ signatures were within the range of the upper fish food web suggesting them as the main source of energy for the upper fish food webs in the lakes (Fig. 4.3).

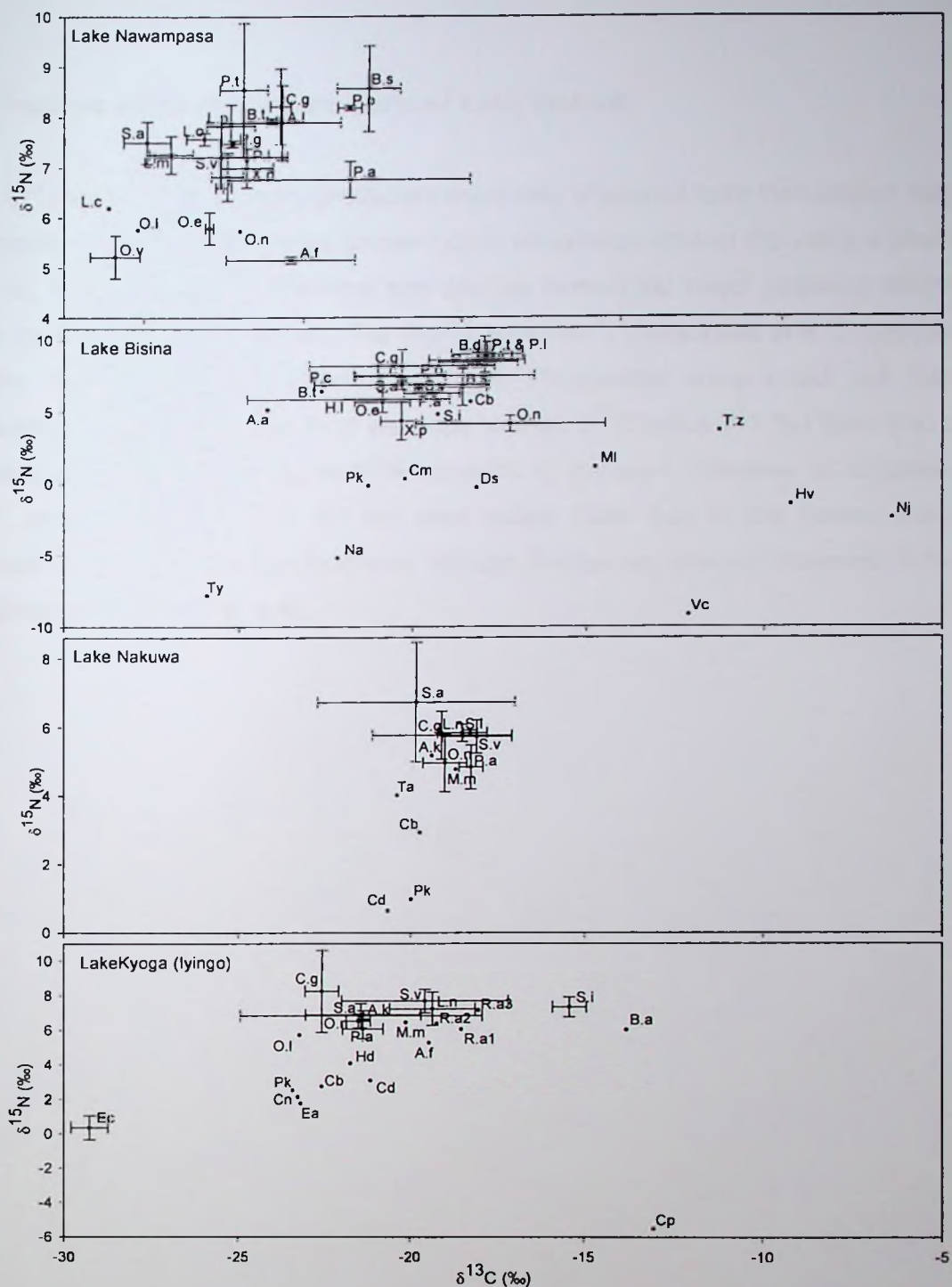


Figure 4.3. The Mean $\pm$ S.D of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the 32 fish species and 18 food sources from Kyoga lakes. Note the lighter $\delta^{13}\text{C}$ of the fish food webs of Nawampasa compared to the rest of the lakes. Overlapping S.D in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicate overlap in diet and their sources respectively. Fish and potential food sources were based on one to three individuals per species per lake or area and S.D were only calculated for organisms that raised three individuals (See Table 4.1 for a key to labels).

4.2.4 Inshore areas of northern parts of Lake Victoria

In Lake Victoria, primary producers were only analyzed from Hannington Bay. Their stable carbon isotope ratios showed clear separation among the various plants (Fig. 4.4). In this Bay, phytoplankton and detritus formed the major potential carbon source for the food of the fishes. The highly enriched *V. cuspidata* and *C. papyrus* and the highly depleted *Cylosorus* sp. and Phragmites were ruled out from contributing directly to the fish food web due to their $\delta^{13}\text{C}$ ratios ($>1\text{‰}$) from that of the fishes and the highly negative $\delta^{15}\text{N}$ value for *C. papyrus*. However *V. cuspidata* and *C. papyrus*, whose $\delta^{13}\text{C}$ did not vary widely from that of the fishes, could contribute indirectly to the fish food web through detritus as already observed in the other lakes examined (Fig. 4.4).

Based on results on primary producers from Hannington Bay and the other lakes examined and the $\delta^{13}\text{C}$ ratios for the fishes and invertebrates, the main carbon source for the other areas of Lake Victoria (Napoleon Gulf and Thruston Bay) examined was extrapolated to be phytoplankton. However, looking at the depleted carbon signatures for the fish and invertebrates, it is clear that the phytoplankton in Napoleon Gulf and Thruston Bay must be more enriched in ^{13}C than phytoplankton in Hannington ($\geq 3.0\text{‰}$). The fish of Napoleon and Thruston appeared to be similar, but the carbon signatures of *O. leucostictus* in the two areas differed by approximately (3.6 ‰) indicating differences in carbon sources within the lake (Fig. 4.4). The five invertebrates groups (chironomids, Oligochaeta, molluscs, *C. nilotica* and Ephemeroptera) examined in all bays had $\delta^{13}\text{C}$ ratios that fell within the range of that of the most fish species indicating that they were possible food sources which was also confirmed by stomach content analysis (Table 3.4 and Fig. 3.4B).

Despite all these lakes having the same source of carbon, i.e mainly phytoplankton, their carbon signatures varied somewhat. The variable $\delta^{13}\text{C}$ ratios for fishes from the different areas of the lake indicate that the fishes were deriving energy from a range of food sources which may vary within the lake. This variation is mainly due to differences $\delta^{13}\text{C}$ signatures of DIC at the base of the food web, as already mentioned for different aquatic systems.

4.3 Trophic positions, relationships and $\delta^{15}\text{N}$ signatures among fishes

In contrast to the simple food chains and discrete trophic categories found in pelagic areas of most lakes, stable isotope analyses of fishes in the more complex littoral areas and shallow lakes examined here, indicated that assigning fishes and invertebrates to specific or discrete trophic levels with simple trophic relations among predatory fish and their prey fish based on only $\delta^{15}\text{N}$ was not possible. This is because the observed enrichment values for $\delta^{15}\text{N}$ were considerably lower than 3.4‰ typically assumed for a trophic transfer in stable isotope studies (DeNiro and Epstein, 1978; Cabana and Rasmussen, 1994). This was likely a consequence of dietary overlap and omnivory (feeding at more than one trophic level), but variable

fractionation coefficient of nitrogen in each trophic transfer may also play a significant role (Jones and Waldron, 2003). Nonetheless, clear separation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of primary producers in most lakes or areas helped in the identification of main carbon and nitrogen source of consumers.

The $\delta^{15}\text{N}$ signatures alone could not be used to estimate the trophic position, because the $\delta^{15}\text{N}$ signatures of the primary producers were highly variable among and within systems (Fig. 4.5). This is supported by other studies (Toda and Wada, 1990; Kling *et al.*, 1992; Kline *et al.*, 1993; Gu *et al.*, 1994; Cabana and Rasmussen, 1996) that have shown similar $\delta^{15}\text{N}$ variability. Based on the energy-weighted mean number of trophic transfers between the basal resources and the consumer by Vander Zanden and Rasmussen (1999), interpreting the $\delta^{15}\text{N}$ signature of the fish consumers relative to appropriate baseline $\delta^{15}\text{N}$ values among lakes or areas, provided a continuous measure of the fishes' trophic positions (Table 4.2). The baseline $\delta^{15}\text{N}$ determined for selected tilapiine species (*O. esculentus*, *O. variabilis*, *O. leucostictus* and *O. niloticus*) using the $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ relationship (Vander Zanden and Rasmussen, 1999) for each of the study lakes or areas described fully in Chapter 2 were used. The selected tilapiine species were the most appropriate because they are large and long-lived primary consumers and integrate temporal variability in primary producer $\delta^{15}\text{N}$ compared to planktonic primary consumers.

A continuous measure of trophic position (TP) was thereafter determined for each fish species using the formula.

$$\text{TP}_{\text{fish}} = (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}})/3.4 + 2 \quad (1)$$

where TP_{fish} = fish trophic position; $\delta^{15}\text{N}_{\text{fish}}$ = $\delta^{15}\text{N}$ of fish; 3.4 = one trophic level increment in $\delta^{15}\text{N}$, $\delta^{15}\text{N}_{\text{baseline}}$ = $\delta^{15}\text{N}$ of tilapiine species from ($\delta^{15}\text{N}$ - $\delta^{13}\text{C}$) and 2 = the assumed trophic level position of primary consumers (tilapiine species) used to estimate $\delta^{15}\text{N}_{\text{baseline}}$ signatures.

The trophic positions of the different fish species examined in the different examined lakes (Table 4.2)

Table 4.2. The trophic position of the dominant fish species encountered in the Victoria and Kyoga basin lakes (August 2001 to August 2003) determined using the primary consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relationship according to Vander Zanden and Rasmussen (1999).

	Nile perch free lakes						Nile perch lakes					
Fish/Taxa	Kachera	Mburo	Kayugi	Kayanja	Nawampasa	Bisina	Nakuwa	Kyoga-Iyogo	Nabugabo	Napoleon gulf	Thruston Bay	Hannington Bay
<i>A. alluaudii</i>	2.4	2.1	2.4			1.6				2.7	2.6	2.1
<i>A. aneocolor</i>	2.4	2.1										
<i>A. frenatus</i>					2.1			1.9		2.9	2.1	2.0
<i>A. kyogaastato</i>							2.0					
<i>A. latifasciata</i>					2.9	3.0						
<i>A. "miniblack"</i>					2.6	2.1						
<i>A. nubila</i>			2.5									
<i>A. velifer</i>			2.6	2.2								
<i>Astatotilapia sp</i>										2.7		
<i>B. altianalis</i>								2.2				
<i>B. docmak</i>						3.1						
<i>B. jacksonii</i>											3.1	2.9
<i>B. kerstenii</i>			3.5	2.8								
<i>B. sadleri</i>					3.2	2.4			2.6	3.3	3.1	2.8
<i>B. trispidopleura</i>					2.9	2.3						2.5
<i>C. gariepinus</i>	2.6	2.4		2.5	3.0	2.8	2.2	2.6		2.6	3.0	
<i>C. liocephalus</i>	2.5											
<i>G. simpsonii</i>				2.5					2.7			
<i>G. victoriae</i>			2.0	1.6								
<i>H. guiarti</i>										3.1	3.3	
<i>H. lividus</i>					2.5	2.0						
<i>H. squamipinus</i>	2.7	2.9										
<i>P. venator</i>			2.9									
<i>L. cryptodon</i>					2.1	2.6						
<i>L. maxillaris</i>					2.5							
<i>L. niloticus</i>							2.5	2.5	2.8	2.9	3.3	2.1
<i>L. obesus</i>					2.7							
<i>L. pervidens</i>					2.8	2.2						
<i>M. kannume</i>										3.0	3.0	
<i>M. macrocephalus</i>							2.0	2.2				
<i>O. esculentus</i>	2.0	1.8	2.0		2.2	2.0						
<i>O. leucostictus</i>	1.9	2.1			1.8			1.8		1.8	1.6	
<i>O. niloticus</i>	2.1	2.1			2.2	1.7	2.0	2.2	2.0	2.2	2.4	2.0
<i>O. variabilis</i>					1.8					2.0		
<i>P. "shovelmouth"</i>					2.7	3.0					2.6	

Fish/Taxa	Nile perch free lakes						Nile perch lakes					
	Kachera	Mburo	Kayugi	Kayanja	Nawampasa	Bisina	Nakuwa	Kyoga-Iyogo	Nabugabo	Napoleon gulf	Thruston Bay	Hannington Bay
<i>P. aethiopicus</i>	2.3	2.6		2.4	2.7	2.3	2.0	2.0	2.1	2.4		2.0
<i>P. argenteus</i>					3.0	3.1						
<i>P. beadleri</i>									2.5			
<i>P. catastoma</i>			2.9			2.1						
<i>P. chilotes</i>											3.0	
<i>P. crassilabris</i>										2.7	2.8	2.4
<i>P. orthostoma</i>					3.1	2.7						
<i>P. red fin</i>										2.5	3.0	2.4
<i>P. riponians</i>										3.1	3.0	2.6
<i>P. rockcribensis</i>											2.9	
<i>P. savegei</i>												2.5
<i>P. sheller</i>										2.8		
<i>P. stilleto</i>					2.6	3.1						
<i>Ptyochromis</i> sp.					2.6							
<i>P. victorae</i>						2.2						
<i>R. argentea</i> (4.5 cm)												2.5
<i>R. argentea</i> (5.5 cm)												2.6
<i>S. afrofischeri</i>					2.5	2.4	2.3	2.3		3.1	3.0	
<i>S. intermedius</i>						1.9	2.3	2.6	2.4			
<i>S. victoriae</i>					2.5	2.4	2.2	2.6		3.1	3.0	
<i>H. squamulatus</i>						2.8						
<i>T. zillii</i>			2.4			1.6			2.6	2.5	2.8	2.2
<i>X. phytophagus</i>					2.6	1.7						
<i>Y. "lemwazooplanktivore"</i>					3.0							

4.3.1 Koki drainage systems lakes

In the Koki system lakes $\delta^{15}\text{N}$ signatures and trophic positions placed fish at the top of the lakes' food webs, with the haplochromine cichlid *Harpagochromis squamipinus* occupying the topmost trophic positions (2.7 and 2.9) for Kachera and Mburo, respectively, reflecting a stronger tendency to carnivory (Fig. 4.1). The stomach content analysis (Chapter 3) supported this, indicating that *H. squamipinus* mainly fed on Odonata, chironomids and fishes. Note that odonates are carnivores,

as are some chironomids (Brewer, 1994). *O. leucostictus* and *O. esculentus* exhibited the lowest trophic levels, 1.9 and 1.8 for Kachera and Mburo, among the fishes reflecting their tendency towards herbivorous diet. The other fishes (Table 4.2) exhibited trophic positions that varied between the above and low trophic positions reflecting mixed diet.

The above observations were all confirmed from stomach content analysis (Chapter 3; Table 3.1). However, it was clear that none of the fish were functioning as obligate piscivores because there is little separation in their $\delta^{15}\text{N}$ trophic level signatures (Fig. 4.1 and Table 4.2). Omnivory was common among the fishes, with a potentially high degree of dietary overlap. Only habitat separation within the lakes would prevent strong trophic competition among these trophic generalists.

At the base of the food webs were *V. cuspidata* and plankton for lakes Kachera and Mburo, respectively. In both lakes invertebrates had $\delta^{15}\text{N}$ that were intermediate between those of the fishes and papyrus and the plankton, possibly indicating their dependence on the plankton and their predation by fish. However, *C. papyrus* and *E. schemperi* exhibited a higher $\delta^{15}\text{N}$ than all invertebrates sampled in both lakes and can be excluded as direct dietary inputs to those invertebrates, but a mixed diet of papyrus debris and plankton could account for the $\delta^{15}\text{N}$ signatures of all the fish (Fig. 3.1 and Table 3.1). The two *Oreochromis* spp. had non-overlapping isotopic signatures in the two lakes and were most similar to *C. papyrus* among the plants and plankton in Lake Mburo. Despite broad similarity in their diets based on stomach analyses, the isotopic results indicate some trophic or habitat separation that would reduce direct competition and could partly explain why *O. niloticus* has been able to co-exist with *O. esculentus* in these lakes and may not support the hypothesis that *O. esculentus* was eliminated from lakes Victoria and Kyoga mainly through competition with *O. niloticus*.

4.3.2 Nabugabo drainage system lakes

In these lakes trophic positions estimated from $\delta^{15}\text{N}$ signatures placed fish at the top of the lakes' food webs, with the haplochromine cichlid *P. venator* at 2.9, the

cyprinid *B. kerstenii* at 3.5 and *L. niloticus* at 2.8 in lakes Kayugi, Kanyanja and Nabugabo, respectively (Fig. 4.2). Stomach content analysis showed that *P. venator* from both lakes Kayugi and Kanyanja and *L. niloticus* from Lake Nabugabo were dominantly piscivorous. Stomach content analysis did not yield any support to the diet of *B. kertenii* as all the 52 fishes examined from all the three lakes had empty stomachs. However other studies have indicated that it feeds on large proportions of the easily digested zooplankton and insects (Baliwa, 1984). Zooplankton tends to be part of complex food webs involving microbial trophic levels (Azam *et al.*, 1983), which are rarely appreciated from gut content analysis studies (Pinnegar *et al.*, 2002). *O. esculentus* (2.0), *G. victoriae* (1.6) and *O. niloticus* (2.0) in lakes Kayugi, Kanyanja and Nabugabo, respectively, occupied the lowest trophic positions among the fishes reflecting a strong tendency towards a herbivorous diet. However, *O. esculentus* appeared to have the same trophic level in lakes Kayugi and Kanyanja. Stomach content analysis supported herbivory in *O. esculentus*, but indicated *O. niloticus* and *G. victoriae*, to be omnivorous (Chapter 3; Table 3.2 and Fig. 3.2B). However, *G. victoriae* occupied a higher trophic level in Lake Kayugi than in Lake Kanyanja (Table 4.2) possibly due to the dependence on ephemeroptera in Kanyanja, and on chironomids in Lake Kayugi. Ephemeroptera are known to be purely detritivore while chironomids are omnivorous (Brewer, 1994). This was supported by earlier studies on Lake Victoria and on the Victoria Nile, which indicated that *G. victoriae* fed primarily on chironomids and ephemeropteran larvae (Corbet, 1961; Greenwood, 1966; Okedi, 1972). The other fishes had intermediate $\delta^{15}\text{N}$ signature and trophic positions (Fig. 4.2 and Table 4.2) reflecting omnivory. The above observations were all confirmed from stomach content analysis (Chapter 3; Table 3.2). Omnivory was common among the fishes with a potentially high degree of dietary overlap. Plankton was probably at the base of the food webs in all the lakes. In all lakes invertebrates had $\delta^{15}\text{N}$ signatures lower than that of the fishes indicating predation by fish (Fig. 4.2).

4.3.3 Kyoga drainage system lakes

In these lakes the $\delta^{15}\text{N}$ signatures and trophic positions placed fish at the top of the lakes' food webs, with *B. sadleri* (3.2) in Lake Nawampasa and *B. docmak* (3.1), *P. argenteus* (3.1) and *P. stilleto* (3.1) in Lake Bisina being the topmost predators, reflecting a stronger tendency of carnivory. The other top predators were *P. orthostoma* (3.1), *C. gariepinus* (3.0) and *P. argenteus* (3.0) in Lake Nawampasa and *P. "shovelmouth"* (3.0) and *A. latifasciata* (3.0) from Lake Bisina (Fig. 4.3 and Table 4.2). Stomach content analysis showed that *P. argenteus* from both lakes, *C. gariepinus* and *B. docmak* from Lake Bisina were mainly piscivores but included insects in their diets; *B. sadleri* and *P. "shovelmouth"* were insectivorous, mainly depending on predatory insects like Odonata (Chapter 3). However, *B. sadleri* is more likely to include the easily digested zooplankton (therefore not observed in stomachs) like *R. argentea*. The $\delta^{15}\text{N}$ signatures (Fig. 4.3) and trophic positions of *L. niloticus* (2.5) in Lake Nakuwa and *C. gariepinus* (2.6), *S. victoriae* (2.6), *S. intermedius* (2.6) in Lake Kyoga placed them as the top most trophic positions in those lakes even though they were not true piscivorous predators. Stomach content analysis showed that *L. niloticus* mainly depended on fish, but included insects in their diet; *C. gariepinus* and *S. intermedius* mainly fed on insects but included relatively large proportions of fish in their diets and *S. victoriae* ate mainly insects and *C. nilotica* (Chapter 3).

In both lakes Nawampasa and Bisina, tilapiine species occupied the lowest trophic positions among the fishes reflecting a tendency towards a herbivorous diet, with *O. variabilis* (1.8) and *O. leucostictus* (1.8) in Lakes Nawampasa and *T. zillii* (1.6) in Lake Bisina all having estimated trophic positions < 2. However *O. niloticus* (1.7) and *X. phytophagus* (1.7) from Lake Bisina occupied even lower trophic positions than those of Lake Nawampasa, reflecting differences in the $\delta^{15}\text{N}$ signatures of the basal food webs among lakes. Stomach analyses supported these observations, indicating *O. variabilis* and *O. leucostictus* from both lakes to feed mainly on phytoplankton; *T. zillii* and *O. niloticus* fed on macrophytes. However *X. phytophagus* from Lake Bisina fed mainly on herbivorous molluscs but also

consumed large proportions of higher plant material and fish (Table 3.3), indicating that this fish mainly fed on macrophytes but did feed on fish opportunistically. Earlier studies based on stomach contents on Lake Nawampasa found *X. phytophagus* to feed mainly on macrophytes (Mbabazi *et al.*, 2004).

O. niloticus (2.0), *M. macrocephalus* (2.0) and *P. aethiopicus* (2.0) in Lake Nakuwa and *O. leucostictus* (1.8) and *A. frenatus* (1.9) in Kyoga, formed the base of the fish food web. However, stomach content analysis indicated that *O. niloticus* was mainly feeding on insects when the samples were taken. *P. aethiopicus* was feeding on insects, molluscs, macrophytes and fish, while no stomach content analysis evidence was obtained for *O. leucostictus* and *A. frenatus* due to insufficient numbers (Chapter 3; Table 3.3 and Fig. 3.3B). The trophic levels of < 2 indicate the precision of a continuous measure of trophic position that weighs the connections according to their relative energetic importance (Vander Zanden and Rasmussen, 1996). The other fishes had intermediate $\delta^{15}\text{N}$ signatures and trophic positions reflecting an omnivorous diet with heavy dependence on insects. The above observations were all confirmed from stomach content analysis (Chapter 3). Omnivory was common among the fishes with a potentially high degree of dietary overlap. The base of the food webs appeared to be mainly plankton in all the lakes. In most lakes, invertebrates had $\delta^{15}\text{N}$ lower than that of the fishes indicating they are consumed by fish.

4.2.4 Inshore areas of northern parts of Lake Victoria

In all areas of the lake that I sampled, $\delta^{15}\text{N}$ signatures and trophic positions placed fish at the top of the lakes' food webs but the highest trophic position varied across the areas, with *B. sadleri* (3.3) in Napoleon Gulf, both *H. guiarti* (3.3) and *L. niloticus* (3.3) in Thruston Bay and *B. jacksoni* (2.9) in Hannington Bay, being the topmost trophic position (Fig. 4.4 and Table 4.2). The trophic positions of these fishes suggest that most of these fishes are not prominent in the diets of other fishes at least for the sizes sampled. Stomach content analysis supported stable isotope analysis, indicating that *B. sadleri*, *B. jacksoni* and *H. guiarti* fed on predatory insects

mainly Odonata and chironomids, but *H. guiarti* frequently included fish in its diet. *L. niloticus* was mainly dependent on fish but also included insects depending on size (Table 3.4). In all areas of the lake sampled, the above fish species generally occupied relatively higher trophic positions except *L. niloticus* (2.1) in Hannington Bay, which might be due to ontogenetic changes with smaller fish feeding lower in the food web (Ogutu-Ohwayo, 1993; 1994, Schofield and Chapman, 1999; Chapman *et al.*, 2003).

In all Lake Victoria sites, the tilapiine species exhibited the lowest $\delta^{15}\text{N}$ enrichment and trophic positions among the fishes, reflecting a strong tendency to herbivorous diet (Fig. 4.4), with *O. leucostictus* in Napoleon Gulf (1.8) and Thruston Bay (1.6), and *O. niloticus* (2.0) in Hannington Bay, occupying the lowest trophic positions. Stomach content analysis on *O. leucostictus*, in Napoleon Gulf, where the minimum sample requirement was realized, indicated that it mainly fed on detritus and phytoplankton. Despite *O. niloticus* having the least enriched $\delta^{15}\text{N}$ signature ($\sim 6.0\text{‰}$) and trophic level in Hannington Bay, it occupied slightly higher trophic levels in Napoleon (2.2) and Thruston (2.4). The *O. niloticus* $\delta^{15}\text{N}$ signatures and trophic levels tended to overlap with those of other fishes in the same sampled area, e.g. *P. aethiopicus* (2.0) and *A. frenatus* (2.0), reflecting an omnivorous and insectivorous diet. Stomach content analysis supported this, indicating *O. niloticus* to be mainly omnivorous in Napoleon Gulf and insectivorous in Thruston and Hannington Bays, and *P. aethiopicus* to feed mainly on molluscs but also fish and macrophytes. There was no stomach content data for *A. frenatus* in Hannington Bay but it also mainly fed on molluscs in Thruston Bay. Molluscs frequently (e.g. Hecky and Hesslein, 1995) have lower $\delta^{15}\text{N}$ signatures than expected for an algal grazer (Fig. 4.4) which could partly explain the lower trophic position of *P. aethiopicus* (2.0) and *A. frenatus* (2.0). The other fishes had intermediate $\delta^{15}\text{N}$ signatures and trophic positions reflecting a mixed diet (Fig. 4.4 and Table 3.4). Omnivory was common among the fishes with potentially high degree of dietary overlap. The base of the food webs appeared to be mainly phytoplankton in all the areas of the lake. In all areas examined invertebrates had $\delta^{15}\text{N}$ lower than that of the fishes indicating consumption by fish (Fig. 4.4).

4.2.5 Spatial variability in the basal $\delta^{15}\text{N}$ signatures among lakes

The relationship between the $\delta^{15}\text{N}$ signatures of *O. niloticus* and phytoplankton accounted for 52% variance and were closely correlated (Fig. 4.5). The ranges of $\delta^{15}\text{N}$ signatures for *O. niloticus* and phytoplankton in five study lakes or areas where both taxa were samples varied from 3.99‰ to 6.70‰ across lakes. However, the observed $\delta^{15}\text{N}$ ranges were generally lower than the assumed 3-4 ‰ per trophic level (Minagawa and Wada, 1984; Peterson and Fry, 1987; Cabana and Rasmussen, 1994) and this was supported by stomach content analysis where *O. niloticus* fed across different discrete trophic levels across lakes ranging from being purely phytoplanktivorous through omnivorous to mainly insectivorous (Chapter 3; Table 3.5). In aquatic systems, the $\delta^{15}\text{N}$ signatures of primary producers and consumers may vary spatially and temporally within and between systems (Yashioka *et al.*, 1994; Gu *et al.*, 1996). The $\delta^{15}\text{N}$ signatures of primary producers is a function of the signature of inorganic or organic nitrogen utilized by algae and the level of isotopic discrimination expressed in the process of nutrient uptake (Gaoericke *et al.*, 1994; Legget *et al.*, 2000). The dissolved inorganic nitrogen varies considerably across systems and may also fluctuate on a seasonal basis within a system (Legget *et al.*, 2000). The observed changes in the basal $\delta^{15}\text{N}$ signatures could be associated with the changes in the lakes especially those related to anthropogenic impacts as has been observed in other aquatic ecosystems (Cabana and Rasmussen, 1996). Variability in the $\delta^{15}\text{N}$ signatures of the forage base will have implications for assessment of relative trophic position of organisms higher in the food web.

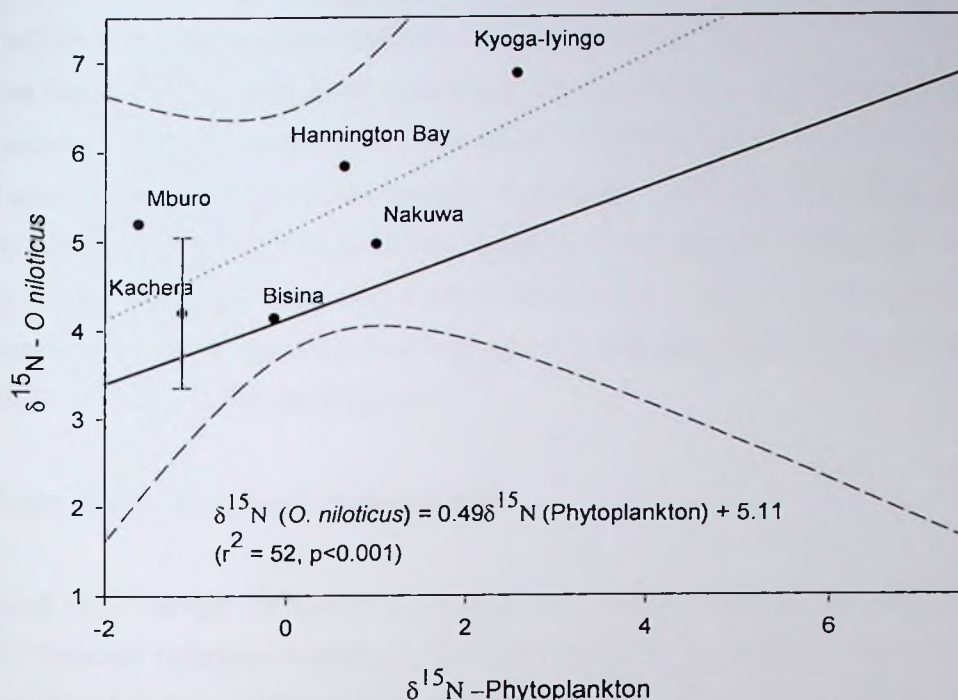


Figure 4.5. Relationships between $\delta^{15}\text{N}$ signatures of *O. niloticus* and phytoplankton across the examined lakes in the Victoria and Kyoga basin lakes (August 2001 to September 2003). Error bar represent 1SD. Note the high variation in $\delta^{15}\text{N}$ signatures in phytoplankton compared to *O. niloticus*. The thick continuous line represents the 3.4‰ fractionation line.

4.4 Food chain length

Based on food chain length values calculated from stable isotope analysis, food chain lengths from primary consumers ranged from 0.5 to 1.7 across the thirteen study lakes or areas. This among-lake or area variation provided an opportunity to examine some relationships and lake or food web characteristics that are pertinent to hypotheses of food chain length. This study examined the relationships between food chain length, species richness and water transparency (Secchi depth).

Trophic position estimates of the fish species in the different lakes indicated a variation in food chain length within and across the sampled lakes and drainage

systems. However, there is a general increase in $\delta^{15}\text{N}$ with increase in trophic position within and across lakes (Table 4.2 and Figs 4.1 to 4.4)

The lakes without Nile perch generally exhibited longer food chain lengths at lower species richness compared to the lakes with Nile perch. However Thruston Bay of Lake Victoria recorded the longest food chain among the studied systems, and Lake Nakuwa from the Kyoga drainage system recorded the shortest. The other relatively long food chains were recorded in lakes Bisina and Nawampasa from the Kyoga drainage system, Kayanja and Kayugi from Nabugabo drainage system, and Napoleon Gulf of Lake Victoria (Fig. 4.6).

4.4.1 Factors affecting food chain length

Food chain length generally increased with increasing fish species richness (Fig. 4.6). Species richness explained 35% and 97% of the among-lake variation in food chain length in lakes without Nile perch ($r^2 = 0.35$, $p < 0.001$) and those with Nile perch ($r^2 = 0.97$, $P < 0.001$) respectively (Figs. 4.6A and B). Generally addition of species in Nile perch free lakes and Nile perch lakes has a small effect and significantly increases food chain length respectively.

Food chain length also generally increased with increasing water transparency measured as secchi depth (m) (Fig. 4.7). Water transparency (secchi depth) explained 55% and 31% of the among-lake variation in food chain length in the lakes without Nile perch ($r^2 = 0.55$, $p < 0.001$) and in those with Nile perch ($r^2 = 0.31$, $P < 0.001$) (Figs. 4.7A and B). Generally increase in water transparency in lakes without Nile perch increases food chain length but has a small effect on food chain length in lakes with Nile perch.

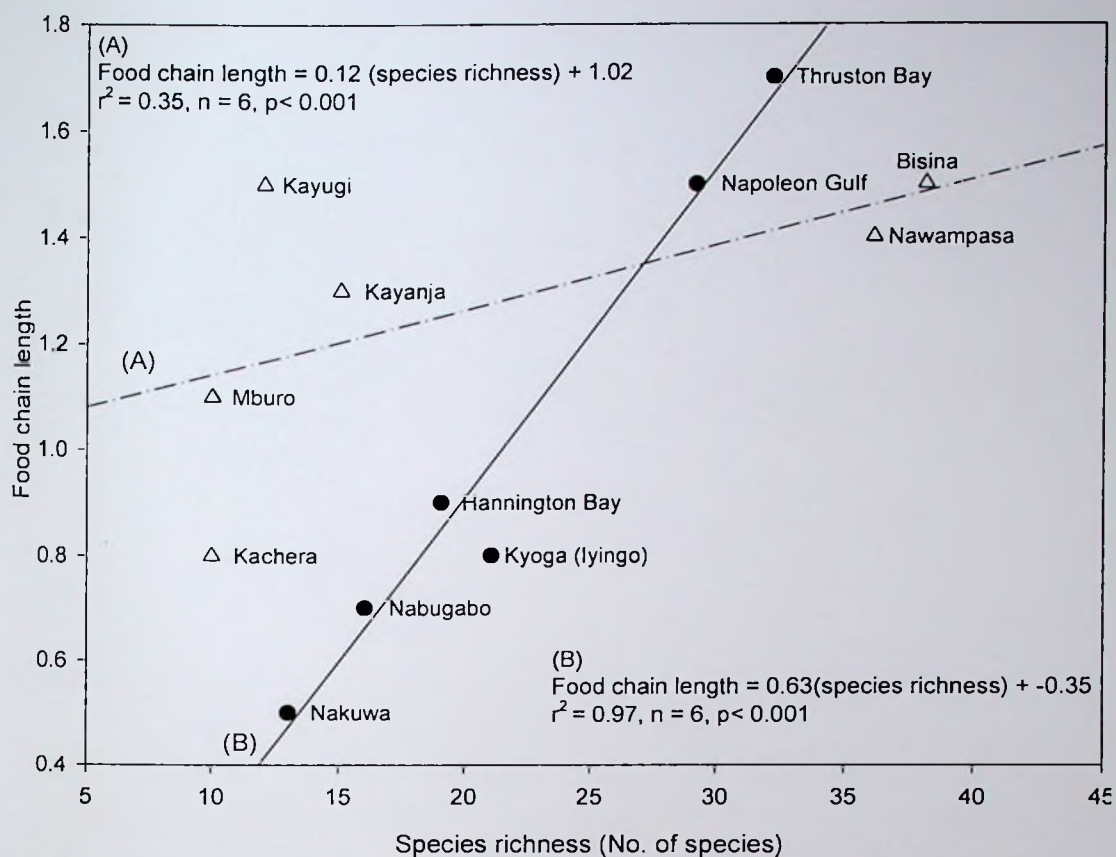


Figure 4.6. Relationships between food chain length and species richness (No. of species) in lakes (A) without and (B) with Nile perch in the examined Victoria and Kyoga basin lakes (August 2001 to August 2003).

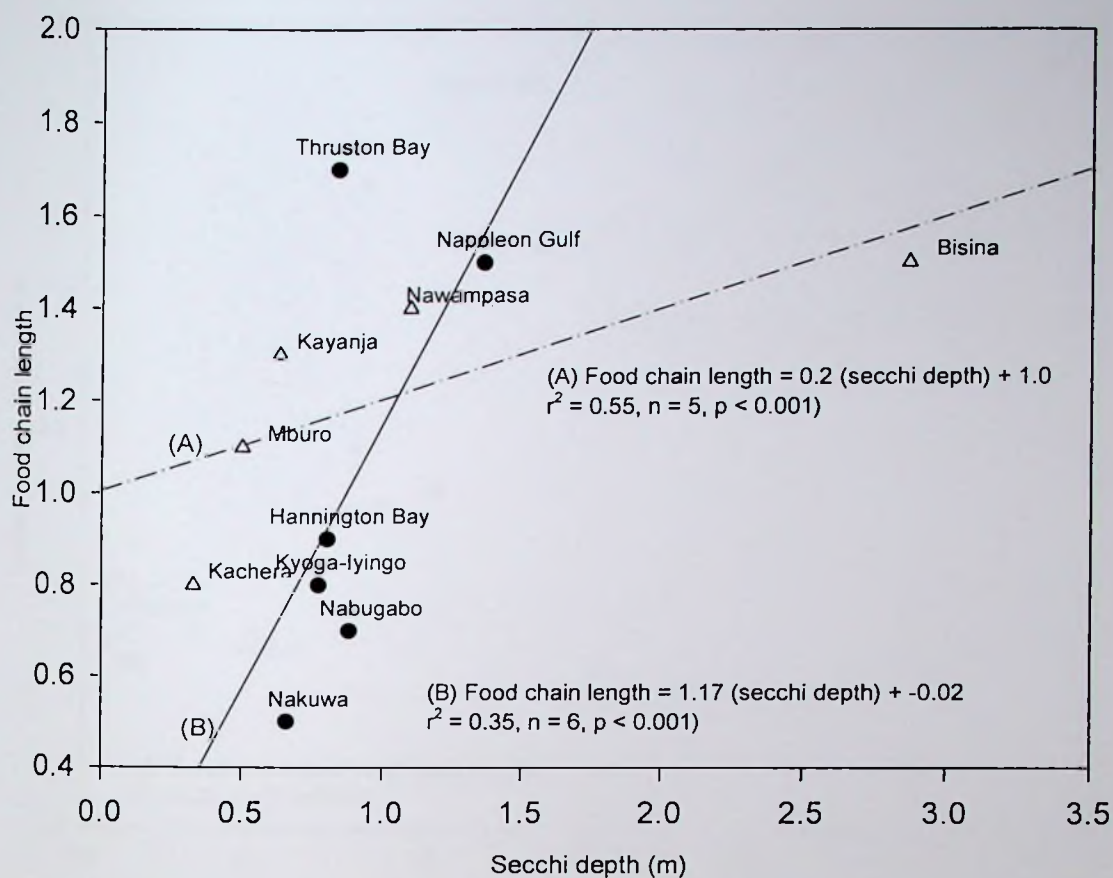


Figure 4.7. Relationships between food chain length and water transparency (secchi depth) in lakes (A) without and (B) with Nile perch in the examined Victoria and Kyoga basin lakes (August 2001 to August 2003).

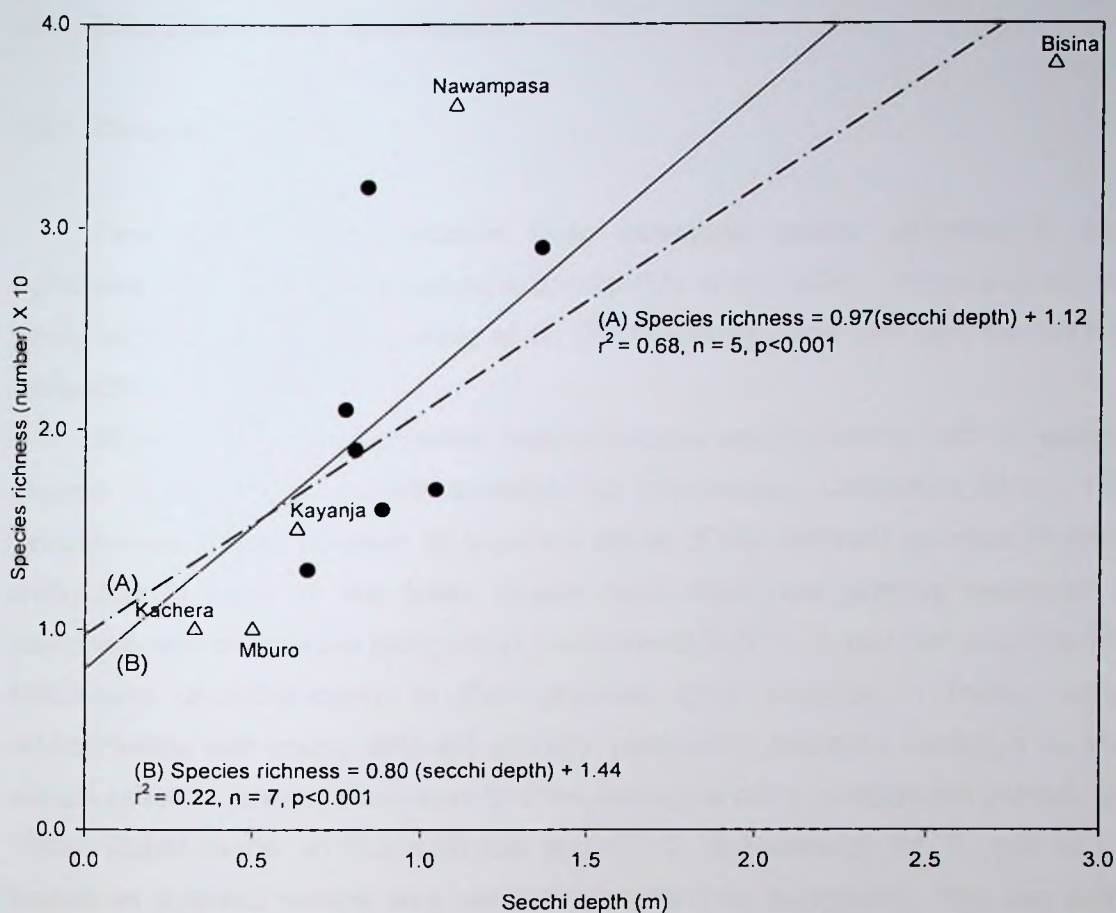


Figure 4.8. The relationship between species richness and water transparency (secchi depth) in (A) Nile perch free and (B) Nile perch lakes examined in the Victoria and Kyoga basin lakes (August 2001 to August 2003). Note the small and large effect of water transparency in the Nile perch free and Nile perch lakes respectively on species richness. The least-square regression line is shown ($P < 0.001$)

4.5 Discussion and Conclusions

4.5.1 Discussion

Few stable isotope studies have assessed spatial variation in source signatures or food web structure concurrently (Gu *et al.*, 1994; Yoshioka *et al.*, 1994; Hecky and Hesslien, 1995; Herwig *et al.*, 2004) among lakes with very similar faunal composition.

Shallow lakes are complex heterogeneous environments with a variety of sources of primary production available for exploitation (Jeppesen *et al.*, 1998). Nevertheless, it was possible to separate some of the different sources of primary production in most of the lakes where more than one primary producer was examined, with separation being most pronounced in $\delta^{13}\text{C}$. It was not possible to link consumers unambiguously to their putative food sources in these complex environments with many different primary producers, because variation in stable isotope ratios of primary producers is often averaged out in consumers (Kiriluk *et al.*, 1995). Dependence on macrophytes (except *C. submersum* for *T. zillii* in Lake Bisina) as a direct source was not indicated for any consumer. The low nutrient content, high content of indigestible organic matter and allelopathic chemicals limit the use of terrestrial and higher aquatic plants despite their abundance in the studied lakes (Hecky and Hesslein, 1995). When most of the lakes sampled were considered, it became clear that the upper food web of fishes demonstrated a dependence on mainly plankton in most lakes because their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values fell in the range of that observed for most fish consumers.

Data from this study supports other recent stable isotope studies which have shown that macrophytes contribute very little direct carbon to aquatic food webs despite their abundance (Bunn and Boon, 1993; Keough *et al.*, 1996; Herwig *et al.*, 2004). Macrophytes, however, may enter the aquatic food web as detritus, undergoing complex chemical and isotopic fractionations as microbes assimilate them, which further make it difficult to detect macrophytes as indirect sources (Keough *et al.* 1996). Most primary production by macrophytes is not consumed by

herbivores, but is rather returned to the environment as detritus to play critical roles in organizing and sustaining ecosystems (Wetzel, 1983; Crawley, 1997). Indirectly detritus has the potential to support species diversity and contributes to larger predator biomass (Hairston and Hairston, 1993; Moore *et al.*, 2004).

Recent isotopic evidence in freshwater food webs, suggests that benthic algae and terrestrial riparian vegetation can play important roles in supporting invertebrate consumers and fish in lakes (Hecky and Hesslein, 1995; France, 1997) and our results indicate similar relationships for the studied lakes. This study found little evidence that fishes assimilated much zooplankton, but instead they fed primarily on benthic invertebrates, which consume a broad diversity of both detrital and autochthonous sources (Herwig *et al.*, 2004). Low depths may limit the trophic role of zooplankton for larger fish in these systems; however juvenile fish that are more likely to depend on zooplankton were not captured by the sampling methods. Fish had a varied diet, which in part was influenced by their species and size, but in general displayed a lack of specialization. The presence of vegetation has been shown to influence the diet of fish (Diel, 1992), inducing a shift to benthic/epiphytic invertebrate prey and fish at an earlier age (Svanbäck and Eklov, 2002). In these shallow lakes and bays the distinction between littoral (vegetated) and pelagic (open water) is less distinct than in deeper lakes and such clear segregation of habitats and organisms is unlikely (Jones and Waldron, 2003; Beaudoin *et al.*, 2001). In almost all lakes, nearly all the fishes consumed benthic /epiphytic invertebrates (Tables 3.1 to 3.4; 4.1; Figures 3.1B to 3.4B; 4.1 to 4.4).

Among the Koki lakes, it was apparent that the food web of Lake Mburo had fish species and plankton with more enriched carbon signatures than in Lake Kachera ($\geq 5\text{‰}$). This is likely due to nutrients that arise directly from the dung from large population of hippopotamuses with no major return pathways known (Laws, 1968; Grey and Harper, 2002). Hippopotamuses graze selectively on short grass species C_4 plants (Lock, 1972; Grey and Harper, 2002) with a daily intake of about 18Kg of dry matter (Laws, 1968). The ingested grasses use the C_4 photosynthetic pathway and exhibit distinct highly ^{13}C enriched signatures compared to aquatic basal resources. As the beast grazes on land and usually defecates in the water,

there is transfer of nutrients to the lakes. Fecal return by ungulates is positively and linearly linked to both primary production and consumption (Douglas and McNaughton, 1992). Ungulates excrete >90% and 65-95% phosphorus and nitrogen they ingest respectively (Ruess, 1987) and these nutrients will enrich lakes because they are in forms readily available to plants and soil microbes (Floate, 1981). This nutrient enrichment will stimulate algal growth and high phytoplankton biomass.

Although this study did not examine the importance of external carbon to the aquatic food webs, there was an indication of this in the Nabugabo lakes, especially Lake Kayanja whose fish food web consisted of heavier $\delta^{13}\text{C}$ signatures compared to the other two lakes. This observation could be explained by characteristics of the lakes and their catchments described fully in Chapter 2. Many factors may be involved in establishing the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values at a given site, but studies have related increases in $\delta^{15}\text{N}$ to the extent of anthropogenic activity in watersheds and input of waste water (Cabana and Rasmussen, 1996; Lake *et al.*, 2001) reflecting the nutrient enrichment associated with human activities. Lake characteristics (Chapter 2) could be another factor associated with nutrient inputs (Beaudoin *et al.*, 2001; Schindler and Scheuerell, 2002).

It was apparent that the trophic enrichments for $\delta^{15}\text{N}$ (Fig.s 4.1 to 4.4) were considerably lower than a typical assumed shift of (3.4‰) per trophic level predicted from a synthesis of previous stable isotope studies (DeNitro and Epstein, 1978; Post, 2002) and was likely due differences in fractionation (Adams and Sterner, 2000; Ben-David and Schell, 2001) or a consequence of omnivory (Jepsen and Winemiller, 2002; Jones and Waldron, 2003), which was evident in stomach contents of the fishes. Feeding at two trophic levels can reduce the expected 3.4‰ enrichment in ^{15}N of a single trophic transfer because integration of a lighter resource is mixed with heavier ^{15}N resource with the result that the differential can be less than expected if the consumer were only feeding on the heavier food resource. Results from other studies indicated that trophic enrichments for $\delta^{15}\text{N}$ can vary depending on the trophic level, animal diet system or ecosystem under consideration and lower than expected (i.e. < 3.4‰) enrichments often occur

(Pinnegar *et al.* 2001; Vander Zanden and Rasmussen, 2001; Zah *et al.*, 2001; Herwig *et al.*, 2004).

Among lake differences in the $\delta^{15}\text{N}$ signatures of fishes may not only be due to diet differences, but also to differences in the basal $\delta^{15}\text{N}$ of primary producers (Cabana and Rasmussen, 1996). Variation in basal signals of $\delta^{15}\text{N}$ in aquatic systems can vary due to differences in fractionation (Minagawa and Wada, 1984, Campbell *et al.*, 2003), fertilizer (Peterson *et al.*, 1993) or sewage (Estep and Vigg, 1985; Cabana and Rasmussen, 1996) or differences in the isotopic composition of dissolved inorganic nitrogen (DIN) available to primary producers (Kline *et al.*, 1990). Nutritional stress has also been associated with enriched $\delta^{15}\text{N}$ signatures e.i. catabolism of the body's proteins during periods of starvation may enrich $\delta^{15}\text{N}$ signatures (Hobson and Clark, 1992b; Ambrose, 1993). There was a high variation in the $\delta^{15}\text{N}$ signatures of macrophytes across the lakes ranging from *V. cuspidata* (–9.18 ‰) in Lake Bisina to *E. schemperi* (8.4‰) in Lake Mburo (Figs 4.1 and 4.3). This is particularly true of terrestrial plants due to the large variation in their source of $\delta^{15}\text{N}$ (Shearer *et al.*, 1978; Shearer and Kohl, 1989) and the systematic enrichment of deep-rooted plants over those with shallow roots (Virginia *et al.*, 1989). Among terrestrial macrophytes, the variation in $\delta^{15}\text{N}$ signatures could also be explained by the differences in whether they are nitrogen fixing and non-nitrogen fixing plants; usually nitrogen-fixing plants are depleted by 2‰ relative to non-nitrogen fixing plants (Virginia *et al.*, 1998; Lajtha and Marshall, 1994).

It is interesting to note that the Nile perch lakes had food chain lengths substantially shorter than Nile perch free lakes (Figs 4.1 to 4.5 and Table 4.2). Comparing the Nile perch lakes food chain lengths with those of the Nile perch free lakes show how the predatory Nile perch has shortened the food webs of the lakes where it is found. In part, this was through selective predation on the large obligate piscivorous haplochromines, whose removal and replacement by the more omnivorous Nile perch could have shortened the food chain length. However, competition of the introduced Nile perch and tilapiine species with both the native piscivores and phytoplanktivores haplochromines (Seehausen *et al.*, 1997) could have contributed to the shortening of the food chain lengths. Earlier studies have

indicated that the variety, size and numbers of prey changed since the predatory Nile perch was introduced and became established. After depletion of the highly diversified haplochromines it shifted to the prawn *Caridina nilotica* (Roux), anisopteran nymphs, *R. argentea*, *O. niloticus* and its own juveniles (Hamblyn, 1966; Ogutu-Ohwayo, 1985, 1990b; Hughes, 1986; Ogari and Dadzie, 1988; Ligtvoet and Mkumbo, 1990; Ogutu-Ohwayo, 1998). Despite the presence of *R. argentea* in stomachs of Nile perch (Chapter 3), their relatively high $\delta^{15}\text{N}$ signatures and trophic positions in comparison to those of *L. niloticus* (Fig. 4.4), does not support *R. argentea* to be among the major diets contributing to somatic growth of Nile perch and this is supported by a recent study on Lake Victoria (Campbell *et al.*, 2003). Fishing also alters the species composition within spatial assemblages and thereby alters interactions. The shift in species interactions associated with spatial distribution is a potentially indirect impact of exploitation (Garrisson and Link, 2000).

The longer food chain length observed in Napoleon Gulf and Thruston Bay could be explained simply by more intensive sampling in a variety of habitats in these areas compared to the Hannington Bay. However, the observed longer food chain and associated food web complexity in the littoral areas of Lake Victoria is likely because of the high fish species and habitat diversity and also the better refuge for fishes preyed upon by the Nile perch (Seehausen *et al.*, 1997).

This study has also indicated that trophic status especially in shallow lakes and littoral areas of Lake Victoria, can affect food chain length, as found in earlier studies (Seehausen *et al.*, 1997). Eutrophication results in increased turbidity, which generally affects fish interactions, including feeding and predator avoidance (Milinski, 1993). Predation threat is perceived to be higher in mesotrophic, clear water lakes (Persson *et al.*, 1988) because clear waters are usually associated with piscivorous fishes, in addition to favoring hunting efficiencies of most piscivores including fishes and birds (Seehausen *et al.*, 1997; Jacobsen *et al.*, 2004). Predation pressure can induce changes in prey fish behavior, such as habitat shift or reduced activity. This study has shown that turbid waters are characterized by shorter food chains because they tend to exclude obligate piscivores.

The generally high variation in $\delta^{15}\text{N}$ signatures and trophic positions of larger top predators (*L. niloticus*, *C. gariepinus*, *P. aethiopicus*, *Synodontis* sp., and *S. intermedius*) within and across lakes is explained by shifts in both habitat use and diet (Ogutu-Ohwayo, 1985; 1994; Hughes, 1986; Mwebaza-Ndawula, 1984; Witte *et al.*, 1995; Olowo and Chapman, 1999; Nakamura *et al.*, 2003). Different size classes within a species may therefore be considered functionally different in terms of trophic dynamics (Ross, 1986; Garrison and Link, 2000; Liao *et al.*, 2002). Differences in the diet of various life history stages in fish may be the result of extrinsic factors such as temporal variations in abundance of certain prey taxa or intrinsic factors, including the ingestion of additional/different larger prey taxa or increases in mouth gape size with body size (Pusey and Bradshaw, 1996; Herne, 1998; Lukoschek and McCormik, 2001; Nakamura *et al.*, 2003). Prey available for fish could be a function of both prey abundance and developmental constraints imposed on the fish (Gill and Morgan, 2003; Nakamura *et al.*, 2003). The ontogenetic difference could also be due to other factors, including differences in catching ability (Juanes, 1994) and habitat utilization, which decreases intra-specific competition (Holbrook and Schmitt, 1992). Trophic relationships of the same fish species may therefore span across trophic levels through its life history. This study could not fully explore these possibilities as it focused on larger fishes and not juveniles.

For most tilapiines, their $\delta^{15}\text{N}$ signatures and trophic positions differed slightly with the exception of *O. niloticus* (Figs 4.1 to 4.5 and Table 4.2) e.g trophic position 1.7 in Nile perch free lakes to 2.4 in Nile perch lakes. This observation was supported by stomach content analysis, where *O. niloticus* spanned across trophic levels Chapter 3 and earlier stomach content studies (e.g Getabu, 1994; Baliwa, 1998). The generalist feeding behavior of *O. niloticus* partly explains why it has been successful in colonizing and stabilizing in new habitats (Baliwa, 1998).

Clearly, lakes that are similar in terms of community composition can differ in trophic structure when energy flow is taken into account (Vander Zanden *et al.*, 1999). The fact that most populations do not conform to discrete trophic levels provides further direct evidence that omnivory is common in the studied systems, suggesting that the fishes were generalist feeders capitalizing on available

resources. The high omnivory observed among the fishes also support the recent microcosm, observational and modeling studies showing that omnivory is common (Polis, 1991; Lawler and Morin, 1993; McCann *et al.*, 1998). The flexibility in functional feeding mode observed in this study has been reported from other field studies (Palmer *et al.*, 1993; Miller *et al.*, 1998).

The longer food chain length in the Nile perch free lakes is explained by high species diversity and high habitat complexity associated with shallow lakes described in Chapter 2 and supported by earlier studies (Diehl and Kornijów, 1998; Jeppesen *et al.*, 1998, Mbabazi *et al.*, 2004).

4.5.2 Conclusions

The stable isotopes of carbon and nitrogen have been used to help elucidate trophic structure and energy sources among most fishes, and have indicated that the food web of shallow relatively pristine to eutrophic lakes and shallow littoral areas of a deeper lake are complex, characterized by limited food chain length, omnivory and generalism. The Nile perch free lakes and littoral areas of Lake Victoria exhibited relatively longer food chains compared to the other Nile perch lakes. Analysis of isotopic variability among individual taxa has also indicated the usefulness of SIA in evaluating changes in the feeding patterns and niche breadth of species. Comparison of results from the present and previous studies clearly indicate a need for the fine-scale analyses of stable isotopes among taxa to consider intra-specific size-related variation caused by ontogenetic dietary switches (Genner *et al.*, 2003). Stable isotope analysis is a rapid means of determining trophic specialization or generalization in fish stocks and can provide information on primary energy sources. Survey of isotopic food web structure can provide essential information for fisheries management. A more detailed study to include the microbial food web of these aquatic systems is required to get a complete understanding of trophic interactions and energy flow especially the contribution of detritus as a heterogeneous resource and habitat for many species in the aquatic food web.

CHAPTER FIVE

5.0 Trophic relationships as the basis for fisheries ecosystem management in the Victoria and Kyoga basin lakes

5.1 Introduction

Although it is widely recognized that both the commercial and non commercial fish species and other taxa play an important role in the transfer of energy to higher trophic levels in aquatic systems little attention has been paid to their overall environmental dependencies and interactions especially in disrupted systems. This inattention is a major knowledge gap as environmental stress accompanying wetland alteration and overexploitation of fisheries increase, particularly with the shift towards ecosystem-based fisheries management of inland waters (FAO, 1995; 2003; Langton and Haedrich, 1997; NMFS 1998; Okey and Harrington, 1999).

Human impacts and natural perturbations on fish populations often take the form of food web alterations and can include the addition or removal of species. The alterations impact fish populations by changing one or more parameters that govern their growth rate (Vitousek *et al.*, 1997; Bodini, 2000; Sala *et al.*, 2001). Human activities shift the balance among fish species through extirpation of many indigenous fish species and dominance of usually fewer introduced fish species, which can withstand exploitation and degraded habitats (Bairwa *et al.*, 2003).

During most of the 20th century, multispecies fisheries on diverse lake ecosystems characterized Lakes Victoria, Kyoga, Nabugabo and other smaller lakes. After indigenous fishes in these lakes were initially fished down, the lakes became dominated by a number of introduced species such as Nile perch (Ogutu-Ohwayo, 1990b; Bairwa *et al.*, 2003). The lakes ended the century with much more fish production based on few (three) species and dependent on the introduced species (Bairwa *et al.*, 2003). The intensive exploitation of fish communities often leads to substantial reduction in abundance of target species and in the overall changes in species composition (Greenstreet and Hall, 1996; Bairwa *et al.*, 2003),

other impacts result into significant alterations in interactions among fish species, competing species or predators and prey that overlap in time and space (Garrison and Link, 2000) and the geographic ranges of overexploited species typically decline. The fisheries of Lake Victoria are characterized by intensive exploitation using different fishing gear types aiming at three dominant target species, but these fisheries are also impacted by human interferences altering habitats and fish assemblages (Muhoozi, 2002). All these factors lead to changes in food web structure and complexity (Hecky *et al.*, 1994). The recent expansion of the Lake Victoria fisheries based on three species has prompted concerns about the state of current and future fish stocks (Ogutu-Ohwayo, 1985; 1994; Muhoozi, 2002; Balirwa *et al.*, 2003) especially as exploitation has been accompanied by eutrophication altering critical habitats.

The ability to predict the effects of trophic relationships is crucial for the management and conservation of ecosystems and accurate representation and description are essential to a wide range of ecological studies (Paine, 1988; Vander Zanden *et al.*, 1997). Despite the importance of trophic relationships, attempts to understand and quantify feeding relationships are often confounded by high levels of food web complexity and/or spatial and temporal variation at a number of scales.

In order to understand key factors that structure fish assemblages and associated food web complexity, this Chapter synthesizes results from previous chapters and earlier studies on changes on fish assemblages in the Victoria and Kyoga basin lakes and other freshwater ecosystems elsewhere. In general terms the study re-examines quantification of feeding relationships, dietary groups and/or food sources, dietary shifts, trophic relationships and possible factors that explain the observed changes in food web complexity.

5.1.1 Quantification of trophic relationships

Earlier studies on trophic relationships on the fishes in Victoria and Kyoga basins were diet descriptions of single species or a taxonomic group of fishes and were based on lists of prey items recovered and quantified from fish stomachs. The

number of stomachs with a specific prey (frequency of occurrence method), the total number or weight or volume of a specific prey found in stomachs (e.g. Corbet, 1961; Okedi, 1972; Balirwa 1984; 1998; Ogutu-Ohwayo, 1985; 1993; 1994; Mwebaza-Ndawula, 1984; Namulemo, 1997; Olowo and Chapman, 1999; Schofield and Chapman, 1999; Chapman *et al.*, 2003; Mbabazi, 1999; Mbabazi *et al.*, 2004) were the main approaches used to make inferences on trophic relationships. These data have further been used for estimation of trophic positions of most fishes from dietary data (Froese and Pauly, 2000) using ECOPATH (Christensen and Pauly, 1992). Each of these techniques however has shortcomings for accurately expressing the amount of various preys that constitute the diet of a consumer (Bowen, 1996; Gu *et al.*, 1996; Liao *et al.*, 2001; Vander Zanden *et al.*, 2001). Expression of stomach contents with counts may give an impression that specific prey item that occurs more frequently represents one of the most important prey items; but if these are small prey items they may comprise a small proportion of the total food consumed. Similarly, in the use of weight or volume, consumption of one large prey item would imply that this prey is a major component of the diet, when actually very few individuals have consumed it (Bowen, 1996). Furthermore, stomach contents tend to provide snapshots of diets in time and space and can suffer when some species only eat infrequently (Beaudoin, *et al.*, 1999) or rapidly digest soft-bodied prey leaving little evidence of the importance of such prey (Hobson *et al.*, 1994). Some species that feed intermittently and frequently also regurgitate food upon capture. Stomach content analysis also does not quantify certain dietary items that are hard to identify e.g. macerated fish and insects that are important in diets of fish. Trophic relationships in fish can vary seasonally and spatially within taxonomic groups and thus the use of default values of trophic level one for any prey item (Froese and Pauly, 2000) using ECOPATH (Christensen and Pauly, 1992) as similar trophic simulations may lead to unrealistic trophic position estimates.

To overcome such limitations and considering the multivariate nature of diet e.g. the habitat characteristics being either continuous or discrete and prey type being discrete, this study used non-parametric multivariate techniques (Hill and Gauch, 1980; Gauch, 1982; Legendre and Legendre, 1998) and a continuous

measure of an organism's trophic position (Winemiller, 1990; Vander Zanden and Rasmussen, 1996; Vander Zanden *et al.*, 1997) to analyze stomach contents described in (Chapter 2).

An alternative approach is to use naturally occurring stable isotope ratios of tissue as dietary tracers (e.g. DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Peterson and Fry, 1987; Hecky and Hesslein, 1995; Cabana and Rasmussen, 1996; Gu *et al.*, 1996; Vander Zanden and Rasmussen, 1999; Vander Zanden *et al.*, 1999; Beaudoin *et al.*, 2001; Vander Zanden and Vadeboncoeur, 2002; Jones and Waldron, 2003; Herwig *et al.*, 2004). Stable isotope analysis would be of little importance for ecologists if it did not provide unique information. Stable isotope solves the difficulty of getting unbiased and complete observations through foraging behavior of fishes, which may prove difficult especially in aquatic ecosystems or under dense vegetations (Kelly, 2000). Stable isotope analysis differs from stomach content analysis in that they reflect materials assimilated, not merely ingested, and give time integrated trophic information for a year or more in fish species (Hesslein *et al.*, 1993) and thus they are less subject to spatial, temporal and behavioral variation in trophic systems. Unlike stomach contents, stable isotope analysis does not provide specific information on resource utilization e.g. the taxonomic composition of the ingested food items. Many prey items are similar in their isotopic composition, making it difficult to determine if a fish feeds strictly on one prey such as Ephemeroptera or a combination of the prey that averages to the same $\delta^{15}\text{N}$ as Ephemeroptera. These problems however could be overcome to some extent by using multiple isotopes (Hesslein *et al.*, 1991). This limits some applications e.g. selection of diet items for candidate fish species for aquaculture, and it cannot discriminate between planktonic or profundal (deep water) zoobenthos because they both have $\delta^{13}\text{C}$ of settling phytoplankton (Vander Zanden and Rasmussen, 1999; Vander Zanden and Vadeboncoeur, 2002). However stomach content studies are costly and labor-intensive, and adequately characterizing diets requires examination of large numbers of stomachs. While stable isotopes do not provide taxonomic resolution of diet, relatively few specimens (generally fewer than 10 individuals of a

species) are needed to infer trophic relationships and energy flow pathways (Vander Zanden and Rasmussen, 2002).

The application of stable isotopes to study trophic relationships in the wild has become increasingly common in recent years; however concern remains for the validity of a number of assumptions inherent in the technique (Gannes *et al.*, 1997; Adams and Sterner, 2000). Without available data on specific enrichment factors for organism diet combinations in the Victoria and Kyoga basin basins, the study was unable to resolve the trophic position of fish species based on $\delta^{15}\text{N}$ signatures as the only indicator and the assumed shift (3-4‰) per trophic level (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Post, 2002). The basal $\delta^{15}\text{N}$ signatures of primary producers vary widely among lakes (Chapter 3) supported by earlier studies (Cabana and Rasmussen, 1996) and habitats within a lake (Vander Zanden and Rasmussen, 1999). However this study overcame this problem by measuring an organism's $\delta^{15}\text{N}$ relative to the lake specific $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of commonly occurring primary consumers such as tilapiine species (*O. esculentus*, *O. variabilis*, *O. leucosticus* and *O. niloticus*) commonly referred to as baseline $\delta^{15}\text{N}$ according to Vander Zanden and Rasmussen, 1999. Considering the consistent enrichment in $\delta^{15}\text{N}$, this value can be indicative of consumer's relative trophic level but not trophic position, because trophic position is a continuous (rather than discrete) variable that represents the potentially diverse energetic pathways that link a given consumer to the base of the food web (Levine, 1980; Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999; 2002).

Despite the many advantages of stable isotope approach over stomach content analysis, stable isotopes do not replace stomach content information and there is increasing recognition that these two approaches provide complementary information and robust analysis. Direct analysis of diets provides immediate and direct evidence for specific feeding relationships and is critical for evaluating stable isotope model outputs. This study used the two independent methods on various fish species simultaneously from a diverse array of lakes that are at different levels of human interference to characterize their trophic relationships.

5.1.2 Dietary groups and food sources

From both stomach contents analysis (Chapter 3) and $\delta^{13}\text{C}$ isotope signatures (Chapter 4) invertebrates constituted an important dietary component of most fish species in the studied lakes or areas. As stated, the diverse invertebrate species have not been isotopically segregated. Limitations still remain and we should be cautious when making inferences on trophic positions versus levels. Both terrestrial and aquatic insects dominated as important invertebrate food for fish. The invertebrates included, *C. nilotica*, molluscs, oligochaetes and leeches. Invertebrates were particularly important because almost all the fish species including piscivorous and herbivorous fish included insects (dipteran larvae/pupae and Ephemeroptera) in their diets. Another important food item was fish, especially for the predatory Nile perch the basis of the current fishery in those lakes where it is found; and in a number of other fish species across the studied lakes (Chapter 3) which was supported by earlier studies identifying piscivory as common (e.g Corbet, 1961; Okedi, 1972; Greenwood 1981; Ogutu-Ohwayo, 1984; 1990c; 1994; Olowo and Chapman, 1999; Chapman, *et. al.*, 2003). Both stomach contents and $\delta^{13}\text{C}$ signature indicated phytoplankton and detritus were the most important food sources at the bottom of the food web for all fish communities across the examined lakes or areas. Traditional approaches to the study of food webs however, emphasize the transfer of local primary productivity in the form of living plant organic matter across trophic levels and forget that the dead organic matter or detritus, a common feature of most ecosystems can play a frequently overlooked role as a dynamic heterogeneous resource and habitat for many species (Moore *et al.*, 2004).

In pelagic aquatic systems, particulate and dissolved forms of detritus as well as phytoplankton may act as physical barriers that affect penetration of light and temperature within the water column. The attenuation of light by particulate or dissolved detritus in the water column reduces photosynthetic rates and reduces the feeding efficiencies of visually-oriented predators, which in turn is reflected in the fish species composition (Rodriguez and Lewis, 1997; Seehausen *et al.*, 2003). The dissolved form of detritus (DOC) decreases photosynthetic radiation and primary

production, selectively attenuates infrared light (the main source of heat), reduces ultraviolet (UV) light and in small lakes alters the depths of the thermocline, altering the structure and functioning of communities in aquatic ecosystems (Schindler *et al.*, 1996; Williamson *et al.*, 2001). The particulate items as potential food sources become unavailable to the fish and most of the invertebrates encountered in fish stomachs also use detritus as a food source and as habitat (Brewer, 1994; Lake *et al.*, 2000). This has further indicated that invertebrates are an important link in the transfer of energy from lower energy levels to higher trophic consumers especially fish and contribute both directly and indirectly to fish production.

Despite the dominance of aquatic macrophytes in most of these lakes both stomach contents and $\delta^{13}\text{C}$ signatures did not indicate direct contribution of macrophytes to the aquatic food webs in most examined lakes except in Lake Bisina where *C. submersum* appeared to contribute directly to *T. zilli*. *T. zilli* has been observed to feed on aquatic macrophytes in dams and Lake Albert (Greenwood, 1966), Kyoga basin lakes (Twongo, 1988) and other aquatic ecosystems (Buddington, 1979; Pieterse, 1981). Macrophytes, however, also contribute to the detritus and provide energy to higher trophic levels (Keough *et al.* 1996; Herwig *et al.*, 2004). $\delta^{13}\text{C}$ stable isotope studies have indicated macrophytes, especially C_3 plants or their detritus to contribute significantly to the carbon supply of the fish communities (Manneta *et al.*, 2003) and as can C_4 plants to a smaller extent (Forsberg *et al.*, 1993; Vaz *et al.*, 1999). Carbon fixed by emergent macrophytes and other terrestrial macrophytes in the riparian vegetation can be easily distinguished based on their photosynthetic pathways and water demand (Hecky and Hesslein, 1995). The C_3 plants such as *Pistia stratiotes*, *Aeschynomene eraphiroxyon*, *Cyclosorus* sp., *Euclea schempri*, *Ficus congensis*, and *Eichhornia crassipes* discriminate strongly against ^{13}C isotopes by the primary CO_2 -fixing enzyme (RuBP), resulting in lighter $\delta^{13}\text{C}$ signatures (-31.2 to -27.6‰). The C_4 plants such as *Cyperus papyrus*, *Vossia cuspidata* and *Miscanthus violacea* discriminate less against ^{13}C isotopes, which was also, reflected in their $\delta^{13}\text{C}$ signatures (-13.7 to -12.0‰). Results from this study on macrophytes were in agreement with those of earlier studies in the Lake Victoria basin (Gichuki *et al.*, 2001; Campbell *et al.*, 2003) and

Kyoga (Hecky and Hesslein, 1995). While most submerged aquatic macrophytes and phytoplankton use the C_3 photosynthetic pathway, their carbon signatures were significantly heavier than that of terrestrial and emergent C_3 plants. There is some uncertainty as to the cause of this difference but, probable explanation is the use of bicarbonate as a source of carbon and the slow diffusion of CO_2 in water, which might reduce enzymatic discrimination (O'Leary, 1988; Boutton, 1991; Hecky and Hesslein, 1995). The observed minor step-wise enrichments in $\delta^{13}C$ signatures during trophic transfer ($\sim 1\text{‰}$) limits its use in assessing trophic levels, however this characteristic enhances the utility of carbon of $\delta^{13}C$ ratios for tracking carbon sources through a food chain (Peterson and Fry, 1987; Michener and Schell, 1994; Hecky and Hesslein, 1995) and may be used to quantify the contribution of benthic and pelagic to secondary consumers (Fry and Sherr, 1984; Boutton, 1991; Hobson *et al.*, 1994; Hecky and Hesslein, 1995; Vander Zanden and Vadeboncoeur, 2002). However, distinguishing between C_4 plants and plants that use a third photosynthetic pathway, crassulacean acid metabolism (CAM), is difficult with carbon isotopes only, but can be done in combination with hydrogen isotopes (Sternberg, 1989; Lajtha and Marshall, 1994). This is though a relatively uncommon pathway in aquatic plants.

5.1.3 Trophic or dietary shifts

Adequate representation of diet of many fish species is complicated by differences in diet that occur within species among individuals of different sizes, geographical locations, and during different seasons. Ontogenetic change in feeding habits is an almost universal phenomenon in fishes. As many large predators increase in size, they change habitat, movement patterns, size of jaws, teeth and stomach, energy requirement, experience with prey, vulnerability to predation and other factors that result from variable exposure to prey or improved ability of larger predators to capture different prey items and this is no exception for fish (Ogutu-Ohwayo, 1985; 1993; 1994; 1999; Chivers and Smith, 1998; Juanes, 1994; Liao *et al.*, 2002; Gill and Morgan, 2003; Chapman *et al.*, 2003). Ontogenetic development of fish dictates the type and size of ingested prey within a time of years. Fish body

sizes increase across life history, often resulting in discrete ontogenetic shifts in both habitat use and diet (Werner and Gilliam, 1984; Ross, 1986; France *et al.*, 1998). The trophic relationship between species may therefore vary ontogenetically (Polis, 1984; Piet *et al.*, 1999). An explicit incorporation of these size-based differences in resource use is essential to evaluating the spatial and trophic structure of fish assemblages.

In this current study only larger specimens of the sampled fish community were collected because of the selectivity of fishing techniques. In general the lack of small juvenile fish will result in under representation of zooplankton in the trophic analysis and will also limit the perceived importance of juvenile fish as prey items. Despite the limitations, ontogenetic dietary shift was clearly shown for *L. niloticus* from stomach contents which mainly contained invertebrates at total length < 20 cm and dominantly fish between 20 and < 60cm, but even neither of these size groups were pure invertebrate eaters or piscivores. This was supported by earlier studies based on stomach contents (Ogutu-Ohwayo, 1985; 1994; Schofield and Chapman *et al.*, 1999; Chapman *et al.*, 2003) and recently by stable isotope isotopes in Lake Victoria (Campbell *et al.*, 2003). The other predators such as *B. docmak*, *C. gariepinus*, *S. intermedius*, *P. aethiopicus* and the piscivorous haplochromines were too few or infrequent to permit ontogenetic assessment but are even more likely to undergo this dietary shift from their observed few stomach contents where they were either full of insects or fish. With reduced availability of fish prey the large predators in these systems incorporated a broad range of prey into their diets e.g. larger Nile perch in lake Nakuwa included a lot of invertebrates in its diet and exhibited a lot of cannibalism. Nile perch in Lake Victoria is known to feed on its own young when the haplochromines are reduced (Ogutu-Ohwayo, 1985; 1990b; Hughes, 1986; Ogari and Dadzie, 1988; Ligtvoet and Mkumbo, 1990). The predatory birds still remain among the top predators in aquatic food webs of the studied lakes as had been recorded by earlier studies on lake Victoria (Wanink and Goudswaard 1994); however birds and humans are always thought about last in quantification of trophic relationship in aquatic systems.

This study indicated that there were dietary shifts due to geographical differences among fish species across studied lakes based on both stomach content analysis (Chapter 3) and stable isotope analysis (Chapter 4). Earlier studies by Olowo and Chapman (1999) based on stomach content analyses also indicated that *B. domak* mainly fed on haplochromines in Lake Edward but fed on mainly invertebrates in Lake Victoria after the Nile perch boom. Such differences may be partly related to habitat differences or geographic variations, such as differences in food availability at different localities (Nakamura *et al.*, 2003). The relative isolation of lake ecosystems can also contribute to among-lake differences in the composition of fish communities (Magnuson *et al.*, 1998; Olden and Jackson, 2001) resulting in lake to lake differences in biotic conditions (prey communities, presence or absence of competitors or predators) and should promote diet flexibility and variability among populations (Lacasse and Magnan, 1992). The high flexibility in diet and habitat exhibited by *B. docmak* could partly explain its persistence in low numbers in Lake Victoria (Olowo and Chapman, 1999). The high food plasticity that fishes from tropical regions exhibit (Lowe McConnell, 1975) explains how individuals from the same populations can ingest food from different sources, widely varying in isotopic composition (Gu *et al.*, 1997). The power of stable isotope approach stems from the capacity to provide time integrated trophic information at the level of individual consumers. This allows examination of intra-population or individual-level diet specialization in ways not possible using traditional stomach content techniques.

Variation in feeding of fish species is further demonstrated by seasonal differences in diet that have been reported within species. For example in shallow habitats of northern Lake Victoria Nile tilapia exhibited a dietary shift from mollusks and *Caridina* in the short dry, cool season to more chironomids (numbers per fish) during the long dry season than any other time even though the biomass ingested may have been less than that of detrital material based on stomach content analysis Figure 5.1 (Balinwa, 1998).

To date, no studies have quantified the effects of seasonal changes on trophic relationships among fishes in the Victoria and Kyoga basin lakes based on stable isotope analysis. However studies done in other freshwater aquatic systems

have indicated changes in isotopic signatures with seasonal patterns especially with $\delta^{13}\text{C}$ signatures (Toda and Wada, 1990; Gu *et al.*, 1994; Yoshioka *et al.*, 1994; Cabana and Rasmussen, 1996; Herwig *et al.*, 2004) and $\delta^{15}\text{N}$ signatures of the forage base (Goericke and Fry, 1994). Seasonal variation in diets may reflect seasonal migratory movements among fish species and/or their prey, associated with changing environmental factors (Horpilla and Kairesalo, 1990; Garrison, 2000;).

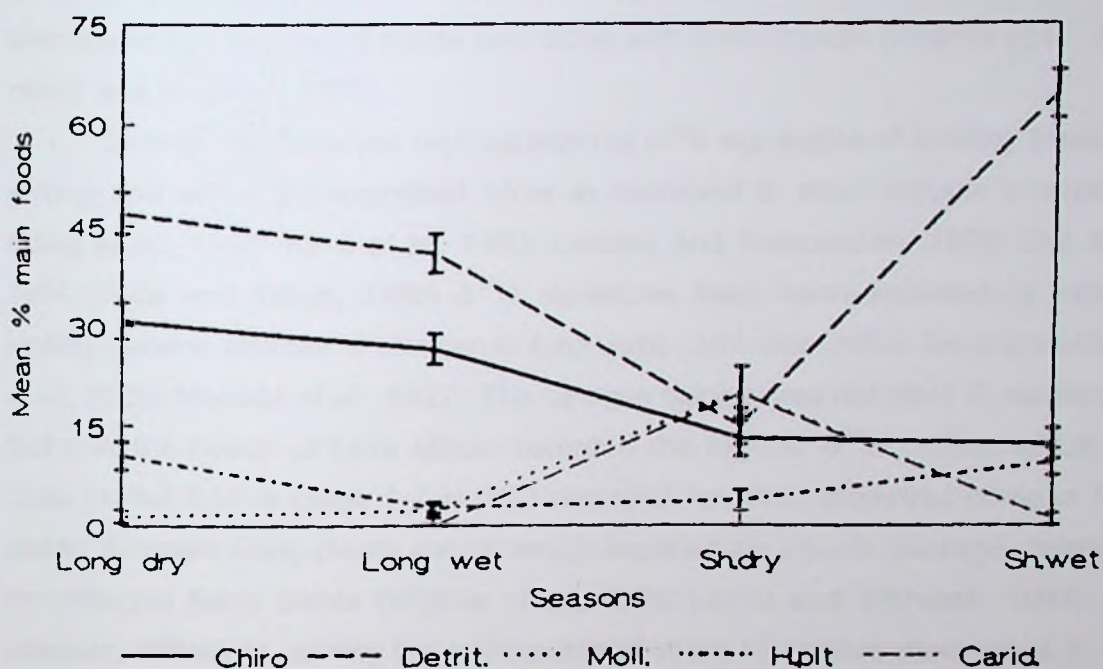


Figure 5.1. Seasonal variation (volumetric mean % SE) in the relative importance of main food items in stomachs of *O. niloticus* (pooled across size classes) from the littoral zone of northern Lake Victoria between 1995 and 1996 (Bairwa, 1998).

5.1.4 Trophic relationships

There have been relatively few investigations comparing diets of sympatric populations of fish species on a spatial scale across water bodies in the Victoria and Kyoga basin lakes. Several studies have looked at populations of one to three species on a spatial scale (Ogutu-Ohwayo, 1994; Olowo and Chapman, 1999; Nagayi, 1999) or one to three species on a spatial and temporal scale within the

same water body (Baliirwa, 1998). As was the case for $\delta^{13}\text{C}$ ratios, the utility of $\delta^{15}\text{N}$ ratios in animal ecology relies on their distribution in foods and how they are incorporated into the tissues of the consumer; however unlike $\delta^{13}\text{C}$ there is no single process, like photosynthesis, that creates a large isotopic fractionation of $\delta^{15}\text{N}$ in plants that can be traced through food webs (Kelly, 2000). Comparison of $\delta^{15}\text{N}$ signatures for emergent macrophytes and terrestrial plants was problematic due partly to the large variation in the $\delta^{15}\text{N}$ signatures of soils and the systematic enrichment of deep-rooted plants over those with shallow roots (Virginia *et al.*, 1989; Hecky and Hesslein, 1995).

Despite the observed high variation of $\delta^{15}\text{N}$ signatures of primary producers among and within the examined lakes as observed in other aquatic ecosystems (Kling *et al.*, 1992; Kline *et al.*, 1993; Cabana and Rasmussen, 1996; Gut *et al.*, 1994; Toda and Wada, 1990) $\delta^{15}\text{N}$ signatures have been successfully used to identify general sources of nitrogen to food webs (Ambrose, 1993; Benedicto-Cecilio *et al.*, 2000; Manetta *et al.*, 2003). The nitrogen fixing terrestrial plant *E. eschschperi* found at the beach of Lake Mburo recorded the highest $\delta^{15}\text{N}$ (+8‰), which was close (+1‰) from a range (−7 to 7‰) recorded for other terrestrial nitrogen fixing plants. Nitrogen-fixing plants are generally depleted by 2‰ on average, relative to non-nitrogen fixing plants (Virginia *et al.*, 1989; Lajtha and Marshall, 1994). It is however, difficult to identify the relative contributions of various plant types to food webs based on $\delta^{15}\text{N}$ signatures alone, but their use in combination with $\delta^{13}\text{C}$ can often rule out the possible food sources (Chapter 4).

The use of $\delta^{15}\text{N}$ signatures for animal ecology lies in their relationship with trophic level. The average enrichment of 3 ‰ (range 3-10‰) in $\delta^{15}\text{N}$ signatures for whole-body samples over the diet was first experimentally documented by (DeNiro and Epstein, 1978). Later studies supported 3 ‰ enrichments of whole bodies over diet (e.g. Minagawa and Wada, 1984; Peterson and Fry, 1987) and thereafter $\delta^{15}\text{N}$ signatures have been successfully used to describe trophic relationships in a number of food web studies (Rau *et al.*, 1992; Vander Zanden *et al.*, 1997; Vander Zanden and Rasmussen, 1999; 2001; 2002; Post, 2002) which were primarily simple pelagic food webs with high diet selection or specialization (Hecky personal

communication). In combination, these results and those from laboratory experiments support the generalization that, on average, a 3-4‰ enrichment in $\delta^{15}\text{N}$ signatures accompanies each trophic transfer (Peterson and Fry, 1987; Tieszen *et al.*, 1983; Ambrose, 1993; Michener and Schell, 1994). The applicability of $\delta^{15}\text{N}$ as an absolute measure of trophic position or food chain length for comparative studies, therefore, is limited by the variability in $\delta^{15}\text{N}$ of the forage base such as phytoplankton and can be mistakenly interpreted as a variation in trophic structure if the basal signature is not sampled (Kidd *et al.*, 1995; Vander Zanden *et al.*, 1997; Legget *et al.*, 2000).

In the current study however, from both $\delta^{15}\text{N}$ signatures and stomach contents it was apparent that the food webs of these lakes and lake areas were not structured in a simple linear fashion, but rather they indicated omnivory (feeding at more than one trophic level. Hence, the $\delta^{15}\text{N}$ did not exhibit a typical assumed shift of 3-4 ‰ per trophic level (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Post, 2002). We cannot discount possible differences in fractionation factors (Adams & Sterner, 2000; Ben-David and Schell, 2001). However the observed high dietary overlap among fish species within lakes or areas could be cited as evidence for potential competitive interaction between these groups as have been found in other aquatic systems (Fogarty and Murawski, 1998). Stable isotope can be used to resolve such intra and among-population feeding variations and has been used successfully in many freshwater ecosystems (Vander Zanden *et al.*, 2000; Vander Zanden and Rasmussen, 2002). The range $\delta^{15}\text{N}$ of most fishes in the study lakes/areas (Chapter 4) generally agreed with their generalized feeding habits from stomach content analysis (Chapter 3).

Slight discrepancies between feeding habits and measured $\delta^{15}\text{N}$ were found in the top predators of these lakes. In particular Nile perch in almost all the lakes where it was found had relatively lower $\delta^{15}\text{N}$ values than expected and its signature was overlapping with the other fishes some of which were its expected prey, suggesting that those fishes are not prominent in the diet of Nile perch at least for the sizes sampled. The other contrary expectations were that sometimes fishes which were observed to feed on fish from stomach contents had lower $\delta^{15}\text{N}$

signatures than those that fed on invertebrates and in some cases omnivorous fishes having the lowest $\delta^{15}\text{N}$ signature compared to herbivores. Generally the observed among or within lake differences in dietary overlap (Chapter 3) and the $\delta^{15}\text{N}$ signatures (Chapter 4) of the fishes may be partly due to differences in diet but also due to differences in the basal $\delta^{15}\text{N}$ of primary producers (Cabana and Rasmussen, 1996). Fresh water systems can have variable basal signals of $\delta^{15}\text{N}$ signatures due to differences in trophic status (Minagawa and Wada, 1984), additions of fertilizer (Peterson *et al.*, 1993 or sewage (Estep and Vigg, 1985; Cabana and Rasmussen, 1996) or due to differences in the trophic composition of the inorganic nitrogen or organic nitrogen utilized by primary producers (Kline *et al.*, 1990; Goerliche *et al.*, 1994; Legget *et al.*, 2000). Recent studies have found $\delta^{15}\text{N}$ signatures of primary producers from densely populated areas to be (8‰) greater than same organisms from relatively uninhabited systems and that this signal was reflected in the fish muscle $\delta^{15}\text{N}$ (Cabana and Rasmussen, 1996; Lake *et al.*, 2001). Human and animal waste will increase the $\delta^{15}\text{N}$ of recipient waters and their dependent food webs. Although this study concentrated on mainly night catches and may have missed peak feeding periods for some species, the large number of empty stomachs in the fishes could also reflect nutritional stress. Nutritional stress has been associated with enriched $\delta^{15}\text{N}$ signatures as catabolism of the body's proteins during periods of starvation may enrich $\delta^{15}\text{N}$ signatures of remaining tissues (Hobson and Clark, 1992; Ambrose, 1993). The fishes generally had a varied diet, which in part was influenced by species, sizes and geographical location, but in general displayed a lack of specialization. Both methods stomach content and stable isotope analyses indicated the tilapiine species from the relatively less disturbed Nile perch free lakes Nawampasa and Bisina exhibited a greater degree of dietary specialization.

5.1.5 Trophic/feeding patterns

To date, no studies have extensively studied the trophic patterns among fishes in the Victoria and Kyoga basin lakes. Understanding of fish consumer's

trophic patterns and positions requires more than knowledge of the prey items that make up its diet but also the dynamics of the feeding process. Understanding ecological interaction between consumers and prey therefore requires knowledge of the amount of food ingested, availability of different foods and the feeding frequency of the predator. Analysis of stomach contents allows inference of feeding patterns through reconstruction of meal sizes, ingestion times, feeding duration, and feeding frequency. The frequency of occurrence of empty stomachs, the number, weight, and stage of each food item, all give insight into the feeding patterns of a consumer.

Among these aspects, this study only recorded a high proportion of empty stomachs in fish diets, which is common for commercial fisheries operations (Wetherbee *et al.*, 1990). The use of long lines and active methods that involve beating of the water may attract fishes with empty stomachs, however this is unlikely when using passive gear such as gill nets or active gear such as trawls. This study dominantly employed experimental passive gill nets but fishes from commercial catches operations augmented experimental samples.

The high frequency of occurrence of empty stomachs together with the observation of often only few food items, many of them in advanced stages of digestion in many predatory fishes lends support to the notion that many predatory fishes are intermittent rather than continuous feeders, otherwise one would expect to regularly find multiple food items at different stages of digestion and few empty stomachs as been observed in other freshwater ecosystems (Medved *et al.*, 1985; Cortés and Gruber, 1990). Data on the proportion of empty stomachs in a sample together with total time required to complete gastric evacuation (not captured in this study) are important in estimating the feeding frequency of fish species (Diana, 1979). An area that would help aquaculture i.e. knowing how much to feed and the frequency.

Individual-level trophic variation and diet consistency is poorly understood and difficult to detect source of trophic variation. Yet, the differences in foraging patterns of individual fishes from a population can have major ecological implications. For example, trophic specialization is thought to reduce intra-specific competition (Van Buskirk and Smith, 1989; Schindler *et al.*, 1997) and can have

profound consequences for overall population dynamics (Partridge and Green, 1985;). Trophic differences among individuals in a population may be responsible for the within-population variation in growth and life history patterns (Vander Zanden *et al.*, 2000). The complexity of food webs from shallow lakes and littoral areas and the lack of presence/absence data for potential prey items make it impossible to follow a similar approach in the exploration of these food webs. The variability in trophic positions among populations as shown by both the dietary data (Chapter 3) and $\delta^{15}\text{N}$ signatures (Chapter 4) indicate that knowledge of the trophic position of a given population may not be extrapolated to represent that of the other population of the same species in a different ecosystem. This is clearly shown by trophic position values from $\delta^{15}\text{N}$ signatures where species can switch their trophic position from lake to lake (Table 4.1). Only direct sampling of food web structure within a lake/wetland of interest will provide essential data on trophic relationships within the lake.

3.1.5 Trophic positions

The observed prevalence of omnivory and the complexity of natural food webs in shallow lakes and littoral areas of relatively deeper lake suggest that neither discrete food chain nor connectance food web approaches will adequately represent the pathways of energy flow and mass transfer in aquatic ecosystems (Vander Zanden and Rasmussen, 1996). This problem was overcome by use of a continuous measure of trophic position of fishes based on both dietary data (Chapter 3) and $\delta^{15}\text{N}$ signatures (Chapter 4) to strike a balance between the food web approaches, which fail to weigh trophic connections according to energetic importance and the food chain approaches that ignore omnivory and complexity that characterize ecosystems (Vander Zanden and Rasmussen, 1996).

During the pre-perch era, *B. docmak*, *C. gariepinus* and *S. intermedius* (Fryer, 1960; Corbet, 1961; Olowo and Chapman, 1999) and post-perch *L. niloticus* (Gee, 1964; 1969; Ogutu-Ohwayo, 1985; 1990a,b; Hughes, 1986; Ogari and Dadzie, 1988; Ligtvoet and Mkumbo, 1990) it was and is still commonly accepted these are the top

predators in Lake Victoria and most likely in the other lakes of the Victoria and Kyoga basins where they were and/or are still found. However, until recently virtually no quantitative estimates of trophic levels existed for most fishes in the two basins. Froese and Pauly (2000) estimated trophic positions of most fishes from Lake Victoria including the pre-perch data from dietary data using ECOPATH (Christensen and Pauly, 1992). Campbell *et al.*, 2003 has attempted a more comprehensive assessment based on stable isotope and historical dietary analyses and estimates the trophic levels for fishes in two bays of Lake Victoria based on $\delta^{15}\text{N}$ signatures.

$\delta^{15}\text{N}$ signatures evidence indicates that all fish species examined from the studied lakes or areas spanned one trophic level based on the assumed trophic transfer of 3-4‰ per trophic level (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Post, 2002). However based on continuous measure trophic positions calculated from both diet and $\delta^{15}\text{N}$ signatures, trophic positions varied greatly among populations of given species. The range in trophic position for a given species was about one trophic level for each of the examined fish species. Comparison of trophic positions calculated from dietary and $\delta^{15}\text{N}$ signatures, explained 57% variation and was characterized by a high degree of overlap especially among the top predators, however the trophic positions calculated from dietary data were generally higher than those from $\delta^{15}\text{N}$ signatures (Figure 5.2; $r^2 = 0.57$, $p < 0.001$, $n = 15$, $\delta^{15}\text{N} = 0.45 \cdot \text{Diet} + 0.97$)

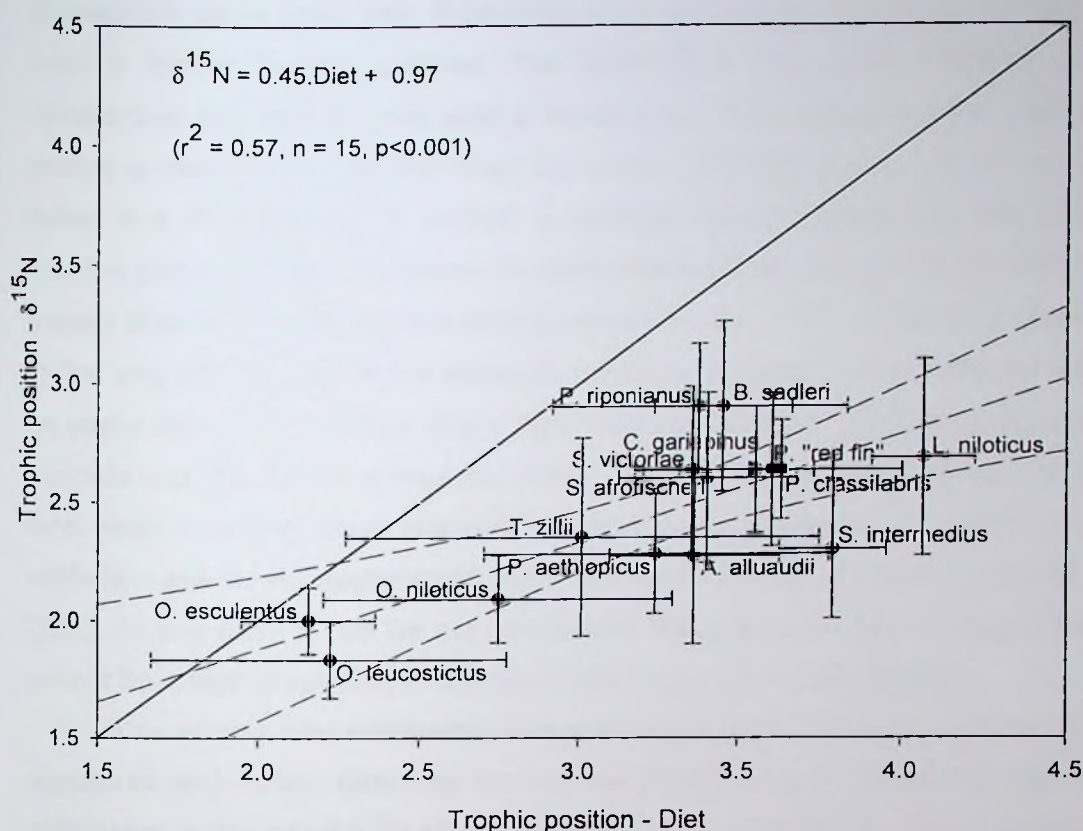


Figure 5.2. Comparison of mean trophic estimates of fifteen fish species common to at least three study sites, calculated using dietary and $\delta^{15}\text{N}$ methods. Error bars represent 1 SD. The solid diagonal line represents the 1:1 line.

Trophic position estimates based on $\delta^{15}\text{N}$ signatures for the individual fishes provided evidence that it is not necessarily the larger predators that occupy higher trophic positions in ecosystems as has always been assumed from stomach content analysis Chapter 3 and (Figure 5.2). From most of the studied lakes or areas both with and without Nile perch, small fishes were the top predators and occupied highest trophic positions (Chapter 4). In particular Nile perch in almost all the lakes occupied intermediate trophic position and its $\delta^{15}\text{N}$ values tended to even overlap with some of its expected fish prey if not lower, however the reason for this has already been explained in ontogenetic shifts above (5.1.3). However it should be noted that dietary increase in body size might not necessarily increase with trophic position (Vander Zanden *et al.*, 2000). A predatory fish may not consume

increasingly large prey with increasing size and larger prey may not necessarily have a higher trophic position. For example a Nile perch feeding on large herbivorous tilapiine species and a small piscivorous haplochromine species, will occupy a lower trophic position than the latter. Secondly most of those small sized fishes (e.g. *R. argentea*, *B. sadleri*, *B. kerstenii* and *P. catostoma*) are associated with the zooplankton or predatory invertebrates such as odonata and choaborus that heavily depend on zooplankton diet (Luecke and Litt, 1987). This study was unable to find any zooplankton in the stomach contents of these fishes, because they tend to be easily digested (Pinnegar *et al.*, 2002) but found predatory invertebrates such as odonata and chaoborus to mention a few. Zooplankton tends to be part of complex food webs involving many microbial trophic levels (Azam *et al.*, 1983) and these subtleties are rarely appreciated from stomach content analysis (Pinnegar *et al.*, 2002). In any case it can be concluded that these small fishes with enriched $\delta^{15}\text{N}$ cannot be a high proportion of the diet of the larger piscivorous fishes.

The among lake differences in trophic positions of fishes based on both $\delta^{15}\text{N}$ signatures and dietary data may not only be attributed to differences in diet but also differences in the basal $\delta^{15}\text{N}$ of primary producers. Systems can have variable basal signals of $\delta^{15}\text{N}$ due to differences in trophic status (Minagawa and Wada, 1984), additions of fertilizer (Peterson *et al.*, 1993), sewage (Estep and Vigg, 1985; Cabana and Rasmussen, 1996) or to differences in the isotopic composition of the inorganic nitrogen available to primary producers (Kline *et al.*, 1990). A recent study has shown that the $\delta^{15}\text{N}$ signal of primary consumers from lakes with heavily populated watersheds was an average of 8‰ greater than the same organisms from relatively uninhabited systems (Cabana and Rasmussen, 1996), and that the signal in these organisms was correlated with fish muscle $\delta^{15}\text{N}$. So from lake to lake variance in the $\delta^{15}\text{N}$ of the top trophic level may vary only because of different basal $\delta^{15}\text{N}$ signatures (Chapter 4).

The range in trophic position values is approximately one trophic level ($\sim 3.5\text{‰}$ $\delta^{15}\text{N}$) among populations of each of the studied fish species. This within-species variability in trophic positions can be attributed partly to highly flexible and opportunistic feeding of these fish species (Dill, 1983) or variation in trophic positions

of prey organisms. Determining the definite sources of variation from the two possibilities would require measurement of the trophic position of most organisms in the lower food web. Furthermore the estimates from this study accompanying dietary trophic positions values are conservative since the study is unable to account for the unknown variation in the trophic positions of the prey items.

5.2 Factors that influence trophic structure and food web complexity

Little is known about patterns and processes that structure communities in shallow lakes and littoral areas of deeper lakes in the Victoria and Kyoga basin lakes compared to the pelagic areas of lake Victoria as has been observed in other fresh water ecosystems (Schindler and Scheuerell, 2002; Vander Zanden and Vadeboncoeur, 2002).

The shallow lakes and littoral areas of deeper lakes comprise heterogeneous areas with a varying degree of structural complexity, thus forming a mosaic of different microhabitats (Chick and McIvor, 1994). Shallow lakes and littoral habitats examined by this study vary substantially in water depth, temperature, bottom type, density of emerged or submersed macrophytes, and the presence or absence of other natural or artificial structures such as trees, rocks and landing sites (chapter 2). Therefore it is not surprising that attempts to classify and find determinants structuring fish communities in similar ecosystems often do not have a single unique solution (Pierce *et al.*, 1994; Fischer and Ekmann, 1997). It is however known that like, in other types of ecosystems, fish tend to react to stresses in certain predictable ways irrespective of the stress applied, be it fishing, general physical degradation of the environment, diffuse pollution or eutrophication (Welcomme, 1999). Using outputs from this study and other information from elsewhere, the following factors that work simultaneously have been identified to explain the observed food web complexities in the studied lakes or areas.

5.2.1 Fishing

In Africa, overfishing is a recurrent problem closely associated with environmental conditions. Africa has suffered food crises for decades, exacerbated in the Sahelian areas by prolonged drought through the late 1970s and the 1980s. When severe drought compromises production of livestock and crops, rural communities turn to hunting and fishing to satisfy their protein needs (Baliwa *et al.*, 2003)

Fishing pressure has induced significant changes in the fish assemblages of the Victoria and Kyoga basin lakes over through out the 20th Century e.g. by 1960s there was evidence of overexploitation of most of the larger species in Lake Victoria (Graham, 1929; Jackson, 1971; Ogutu-Ohwayo, 1990 a,b; Baliwa *et al.*, 2003).

The formerly multi-species nature of these fisheries was often extremely complex in both fishing gears and methods, besides the socio-economics of the fishery (Welcomme, 1999; Muhoozi, 2002). The changes in the complexity in the fisheries of these lakes over time are associated with changes in trophic structure and food web complexities among the fish communities. The changes include direct removal of the target species (Pope and Macer, 1996; Garrison and Link, 2000; Laurans *et al.*, 2004) and the indirect effects on unexploited species through alterations in trophic interactions such as predatory or competitive release. Large or slow-growing species with late maturity decline in abundance more rapidly than their smaller, faster-growing, counterparts (Jennings *et al.*, 1999; Welcomme, 1999; 2003; Baliwa *et al.*, 2003; Laurans *et al.*, 2004) under fishing pressure. Examples of direct removal in Lake Victoria were the declines in large fish species such native tilapiines (Graham, 1929; Ogutu-Ohwayo, 1990a;b), river vulnerable, the migratory fish species *L. victorinus* (Cadwalladr, 1969) and the catfishes (Goudswaard and Witte *et al.*, 1997; Baliwa *et al.*, 2003); and the indirect effects of reductions in these fishes could have been the predation release of haplochromines and reduced competitive release for piscivorous and phytoplanktivorous haplochromines which were not quantified. The recent over fishing of the predatory Nile perch in lakes Victoria and Kyoga has also coincided with partial recovery of some haplochromine

species (Ogutu-Ohwayo; 1994; Schindler *et al.*, 1997; Seehausen *et al.*, 1997b; Witte *et al.*, 2000). The current human high exploitation of *R. argentea* further complicates the food web and threatens the sustainability of the Nile perch fishery because harvesting of *R. argentea* is associated with large quantities of by catch juveniles of Nile perch and other important ecological and or commercial species (Muhoozi, 2002). Similar observations were reported for the demersal fish communities of marine ecosystems of West Africa where increased fishing pressure resulted in the reduction of biomass of higher trophic levels and increase in biomass of lower trophic levels. This was associated with a release of predation pressure in the demersal fish community (Laurans *et al.*, 2004)

The multi-species fishery in most the studied lakes is associated with a array of fishing gear and methods some which have some impacts on the food web complexity and these include the popular beach seine, cast nets, and boat seines, angling which involves digging for bait under soft stratum and of recent, an increased creation of microhabitats through manipulation of floating islands (sudds) by anchoring with heavy stones and strong ropes on Lake Kyoga. The multi fishing gears and methods results into habitat alteration and unobserved mortality, destruction of nursery functions (Blaber *et al.*, 2000) and rich feeding areas (Costa and Eliot, 1991) all of which are associated with changes in associated biota and food web complexity.

In Lakes Victoria and Kyoga, however, intense fishing of the Nile perch in the 1990s also coincided with selected faunal resurgence especially of haplochromines species (Ogutu-Ohwayo, 1994; Seehausen *et al.*, 1997b; Witte *et al.*, 2000). However fishery removals have been associated with considerable removal of nutrients (phosphorus and nitrogen) from fresh waters (Sarvala *et al.*, 1984) and marine systems (Hjerne and Hansson, 2002). In Lake Victoria the fishery removes a small amount of P just equivalent to that removed by River Nile annually (Hecky personal communication). In The Black Sea, the fishery removes approximately 18% of the estimated anthropogenic loads especially phosphorus that reaches the sea, hence reduces society costs for nutrient reduction and regulates eutrophication to some level (Hjerne and Hansson, 2002). Changes followed by fish removals, are

accompanied by changes in species composition which are associated with changes in the food web complexity and finally nutrient dynamics, therefore changes in food web complexity can provide an understanding of one of our major environmental problems; eutrophication common to most of our aquatic systems.

5.2.2 Direct additions or losses of biota

While loss of species by human exploitation from freshwater ecosystems has occurred (Graham, 1929; Ogutu-Ohwayo, 1990b; Welcomme, 1999; Garrison and Link, 2000; Pinnegar *et al.*, 2002), it is a relatively minor threat to biodiversity and food web complexity in comparison with the impacts of introduced species (Zaret, 1973; Witte *et al.*, 1992a; b; Ogutu-Ohwayo, 1990c; Kaufman, 1992; Kaufman *et al.*, 1997; Richter *et al.*, 1997; Marchetti *et al.*, 2004). Introduced species may deplete, if not eliminate, native species by predation, competition, habitat alteration and hybridization (Barel *et al.*, 1985; Ogutu-Ohwayo, 1985; 1990a; b; 1994; Richter *et al.*, 1997; Ricciardi and Rasmussen, 1998; Seehausen *et al.*, 1997a;b; Seehausen *et al.*, 2003). Addition or loss of species may also act on fish populations by changing one or more parameters that govern their growth rates (Bodini, 2000).

Predation of Nile perch has partly contributed to the decline of haplochromines in Lakes Victoria and Kyoga (Barel *et al.*, 1985; Ogutu-Ohwayo, 1985; 1990b; Witte *et al.*, 1992) and in Lake Nabugabo (Ogutu-Ohwayo, 1993; Chapman *et al.*, 2003). These haplochromines were ecologically so diverse that they utilized almost all resources available to freshwater fishes and therefore played an important role in transfer of energy to higher trophic levels (Fyrs and Iles, 1972; Mbabazi *et al.*, 2004). The reduction and disappearance of over 200 haplochromine species is hypothesized to have contributed to disruption of the food web complexity in these lakes in that their diverse trophic roles were taken over by insects which are believed to be less efficient at utilization of food resources and much of the organic matter is not channeled efficiently through the food and remains unconsumed; accumulation of which cause deoxygenation (Hecky 1993) however there is no

documented evidence to support the hypothesis and therefore remains a knowledge gap.

Besides predation, competition for habitat and food by the Nile perch with the native predators like the catfishes and haplochromines cichlids could have contributed to the current simplification and re-structuring in the fish assemblages and food web complexity (Goudswaard and Witte, 1997; Kaufman, 1992).

Apart from Nile perch, several other tilapiines were introduced into most of the examined lakes (Garrod, 1961, Welcomme, 1988) and particularly *O. niloticus* is likely to have competed with the native tilapiines *O. esculentus* and *O. variabilis*, and the phytoplanktivorous haplochromines for food resources and habitat (Seehausen *et al.*, 1997b; Balirwa, 1998).

5.2.3 Eutrophication

Although terrestrial ecosystems are vulnerable to the global nitrogen glut, aquatic ecosystems have probably suffered most thus far, being ultimate receptacle of much of the nutrient load (nitrogen and/or phosphorus) from point or non-point sources generated as a result of anthropogenic changes in the catchments (Lake *et al.*, 2000). In Lake Victoria over the last century, excess nutrients have doubled primary production and increased algal biomass from 8 to 10 fold (Mugidde, 1993). Accompanied by a shift from a dominance of pre-eutrophication diatoms mainly *Alucoseira* sp. to the current Cyanobacteria (Hecky, 1994). When the un consumed or utilized algae dies and decays it robs water of its dissolved oxygen, suffocating aquatic organism which explains the observed fish kills (Ochumba and Kibaara, 1989; Kaufman and Ochumba, 1993; Hecky, 1993). The increasing turbidity and eutrophication explains the simplification of the formerly complex balanced food web through a combination of demersal haplochromine displacement and increased invertebrate abundances (Hecky, 1993). Increased abundances of insect larvae and especially the atyid shrimp *C. nilotica* (Witte *et al.*, 1992a) and cyprinid *R. argentea* (Wanink *et al.*, 2001) favored survival of the juvenile Nile perch, which fed on largely invertebrates (Ogutu-Ohwayo, 1990c). Increased survivorship of juvenile perch led

to explosion of the adult perch population that decimated the haplochromines (Hecky, 1993). Despite their ability to utilize almost all resources available in fresh waters (Fryer and Iles, 1872), they had a limited ability to adjust to the rapidly increasing food resources as a result of excess nutrients. Eutrophication only favored the r-selected life cycle species i.e. invertebrates and Nile perch (Hecky, 1993) to K-selected haplochromine (Witte *et al.*, 1992b) species because they had the ability to respond to rapid increase in food supply (Odum, 1985).

This study has indicated that in addition to predation by Nile perch food chain length generally increased with increased transparency measured as secchi depth (m) (Chapter 4), which was supported by earlier studies that eutrophication contributed to the simplification of the Lake Victoria food web (Seehausen *et al.*, 1997a; Verschuren *et al.*, 2002). Generally predatory fishes differ in performance and have specialized prey species or sizes to minimize competition. Decreased visibility reduces the visual field and the encounter rates with preferred prey, which results in incorporation of more less preferred prey types of low quality to the prey spectrum and affects fish species composition with associated food web complexity (Rodriguez and Lewis, 1997). Reduction in transparency leads to convergence in prey spectra of predator species that are specialized for different types of high quality prey (Seehausen *et al.*, 2003). The resulting niche desegregation and increased competition would lead to extinction of the less efficient predators when population sizes are resource limited (Tokeshi, 1999). The dramatic decrease in water transparency in Lake Victoria over the past 20 years or more (Seehausen *et al.*, 1997; Witte *et al.*, 1999; Seehausen *et al.*, 2003) is likely to have increased competition among the visual piscivorous fishes in the lake. The increase in Nile perch a generalized predator that can efficiently utilize small prey types may have added competitive pressure on the then abundant piscivorous cichlids that were forced to converge with each other and Nile perch on a generalized prey spectrum (Seehausen *et al.*, 2003).

Eutrophication also has been found out to influence sexual selection among some cichlids haplochromines. Increased turbidity as a result of eutrophication reduces the diversity of the color signals on both sides of the spectrum which causes

relaxation of sexual selection for color and loss of male nuptial coloration leading to erosion of species due the breakdown of reproductive barriers (Seehausen *et al.*, 1997).

Generally eutrophication, results in reduction in the visual range, visual resolution and visual dimensionality that leads to loss of species diversity (Seehausen *et al.*, 2003) and associated food web complexity. Therefore eutrophication and turbidity may explain the observed food web complexity among the examined lakes, which are at different levels of anthropogenic impacts and trophic states.

5.2.4 Habitat diversity and fish food webs

5.2.4.1 Aquatic macrophytes

Despite the critical role of aquatic macrophytes in the ecological integrity of fresh water ecosystems, to date few studies comprising of single species or a group a taxonomic group of fishes have characterized a few ecological or behavioral aspects of fish and macrophyte interactions in the Victoria and Kyoga basin lakes (Kaufman and Ochumba, 1993; Chapman *et al.*, 1995, Balirwa, 1998) and instead eradication of aquatic macrophytes remains a recommended component of fisheries management programmes in most inland waters (Petr, 2000).

Results from this study indicate an association of lakes with high aquatic macrophyte abundance with high species diversity and longer food chain lengths (Chapter 4), which is supported by earlier studies in other fresh water ecosystems. Aquatic macrophytes harbor among other organisms, a fish fauna characterized by small fish species or juveniles of many species that grow to large sizes as adults and offer them shelter and foraging places as well as providing spawning sites to most fish species (Glinsky, 1984; Delariva *et al.*, 1994; Lauridsen and Buenk, 1996; Lewin *et al.*, 2004). Fish communities associated with aquatic macrophytes take advantage of the food availability in this microhabitat (Gilinsky, 1984; Rozas and Odum, 1988), since macrophytes provide a substratum where algae and bacteria may develop,

and detritus may deposit, contributing to the abundance of invertebrates (Dihel and Kornijow, 1998). Aquatic macrophytes also provide protection from predators (Gilinsky, 1984; Chapman *et al.*, 1995; Lewin *et al.*, 2004) and are direct and indirect source of food for fish and aquatic birds (Petr, 2000).

However, large densities of aquatic macrophytes have been associated with a reduction fish condition factor resulting in stunted fish populations (Colle and Shireman, 1980). Several other studies have shown that the growth rate of prey fish is retarded when they are confined to the vegetation due to predation risk (Persson and Eklov, 1995) and increase in competition among the prey fish in the refuge (Petr, 2000). The maximum foraging rate decreases when the fish shifts from the pelagic to the vegetated habitat (Person and Crowder, 1997). However piscivorous predators have reduced foraging efficiency with an increase in vegetation density and thus minimize the predation risk of the prey (Savino *et al.*, 1992; Werner and Hall, 1988; Eklov and Diehl, 1994; Persson and Eklov, 1995). The predation risk can explain the smaller sizes of the tilapiine fish species that are caught in most of the vegetated satellite lakes around the Victoria and Kyoga Basins and the disappearance of the once introduced Nile perch in Lake Bisina can be explained by the reduction in foraging efficiency due to increased macrophyte densities (Personal communication with elders).

The reason advanced for proliferation of both the floating and submerged nuisance aquatic macrophytes has been favorable nutrient environment and human impacts through eutrophication, especially in smaller shallow aquatic systems (Petr, 2000), which I presume is no exception to the studied lakes. However like the other biota, aquatic macrophytes are also threatened by increased eutrophication through reduction of water transparency (Ramlal *et al.*, 1991; Squires *et al.*, 2002). Illumination of the lake bed is a fundamental requirement for the development of littoral vegetation (Hutchinson, 1975; Squires *et al.* 2002).

In Lake Kyoga the invasion and spread of Water hyacinth coincided with resurgence of haplochromines which would have not only provided refugia against predatory Nile perch (Ogutu-Ohwayo, 1994; Mbabazi 1999) but also provided foraging places because like any other aquatic macrophytes they Water hyacinth was

associated with a high diversity of invertebrates (Wanda *et al.*, 2001) and could have provided crucial links in the littoral fish food web (Balirwa, 1995). Despite the intensive fishing pressure on Nile perch in lakes Victoria, Kyoga and Nabugabo (Ogutu-Ohwayo, 1994) which possibly contributed to the resurgence of native fishes, the current rareness of haplochromines in this study, along with the recent high reduction in water hyacinth and the almost constant fishing intensity on Nile perch suggests that the role Water hyacinth played as ecotonal refugium and foraging area is necessary for the resurgence of haplochromines.

5.2.4.2 Rocky habitats

Rocky habitats are usually associated with littoral areas, the interface of land and water, and support a diverse biota ranging from algae, invertebrates, juvenile fish and adult fish that are adapted to survive in this habitat's unique conditions (Alin *et al.*, 1999; Seehausen *et al.*, 1997b). Rocky shores not only provide refuge for fishes, but also food, fish nurseries and roosting and feeding grounds for birds and their associated food web complexity and help in stabilization of the inshore sediments (Alin *et al.*, 1999). Currently the highest fish species diversity in Lake Victoria has been associated with rocky habitats and most of these species (mainly haplochromines), with the exception of some few catfishes and cyprinids (Greenwood, 1965; Trewavas, 1933; Witte and van Densen, 1995) had never been recorded in other habitats (Seehausen *et al.*, 1997b). Certain rocky habitats however have lost a major part of their fauna (Seehausen *et al.*, 1997a) due to changes in water transparency.

The rock-dwelling fishes especially cichlids are threatened by fishing through collection as baits for the Nile perch long line fishery using a line and hook (Ligtvoet *et al.*, 1995). The highly complex food web associated with rock shores is further threatened by eutrophication described in 5.2.3 and sedimentation. In coming sediment loads that are carried by influent water masses can alter rocky benthic habitats in several ways (Cohen *et al.*, 1993). Increased turbidity may reduce light penetration and result in decreasing levels and maximum depths of benthic primary

productivity in the littoral zone (Hecky and Hesslein, 1995). Secondly incoming sediments may also bind or release nutrients or toxins, altering energy flows through associated biotic communities. Cracks and crevices fill with sediments, reducing habitat heterogeneity, the range of potential habitats and predation refuges for many highly specialized fish and invertebrate species. Covered rocky substrate also decreases the surface area available for epilithic algal growth and invertebrate colonization (Alin *et al.*, 1999).

5.2.5 Catchments' disturbances

Conversion of land to agriculture is proceeding at a considerable pace in many developing countries, and the United Nations Environment Programme (UNEP) predicts that agricultural land could nearly double in Africa by 2050 (WRI, 1998). In Uganda, the human population growth in the watersheds is 3-4% per annum (Hecky and Bugenyi 1992; Hecky, 1993; Ogutu-Ohwayo *et al.*, 1997). The rapid increase in the rural population around these lake catchments has increased demand for livestock, agriculture and fuel wood accelerating the rates of deforestation and deforestation, resulting into soil erosion, sedimentation, siltation and nutrient loading of the lakes (Hecky, 1993; Boostma and Hecky, 1993; Ogutu-Ohwayo *et al.*, 1997; Alin *et al.*, 1999).

The large population densities of wild animals in some watersheds of lakes that are located in protected areas, especially the grazers such hippopotamuses (Laws, 1968; Lock, 1972; Grey and Harper, 2002) and ungulates (Douglas and Naughton, 1992), also add high nutrient loads through the dung with no major return pathways (Laws, 1968). Ungulates excrete >90% of the phosphorus they ingest, ~ 99% of which is fecal, and 65-95% of their ingested nitrogen, ~ 85% of which is urinary (Ruess, 1987). Excretal phosphorus and nitrogen are in forms readily available to plants and soil microbes (Wilkinson and Lowery, 1973; Floate, 1981).

Sedimentation from catchment disturbances alters the abundance or composition of the above sediment biota, the soils, which leads to the deposition of fine particles on freshwater sediment particles, thus reducing the interstitial spaces

REFERENCES

- Abrams, P.A., 1993. Effect of increased productivity on the abundance of trophic levels. *American Naturalist* 141: 351-371.
- Adams, S.M., B.L. Kimmel & G.R. Plosky, 1983. Sources of organic matter for reservoir fish production: a trophic dynamics analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1480-1495.
- Adams, T.S. & R.W. Sterner, 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. *Limnol. Oceanogr.* 45: 601-607.
- Alin, S., R., A.S. Cohen, R. Bills, M.M. Gashagaza, E. Micheal, J.J. Tiercelin, K. Martens, P. Couveliers, S.K. Mboko, K. West, M. Soregham, S. Kimbali & G. Ntakimazi, 1999. Effects of landscape disturbance on animal communities in Lake Tanganyika, East Africa. *Conservation Biology* 13 (5): 1017-1033.
- Ambrose, S.H., 1993. Isotopic analysis of paleodiets: methodological and interpretive considerations. In Sanford, M.K. (Ed.), *Investigations of Ancient Human Tissue*. Gordon and Breach, Langhorne, PA, pp. 59-130.
- Aravena, R., Schiff, S.L., Trumbore, S.E., Dillion, P.J. and Elgood, R. (1992). "Evaluating dissolved inorganic carbon cycling in a forested lake watershed using carbon isotopes", *Radiocarbon*, 34(3), 636-645.
- Arrington, D.A., K.O. Winemiller, W.F. Loftus & S. Akin, 2002. How often do fishes "run on empty"? *Ecology*, 83 (8) 2145-2151.
- Atlas of Uganda, 1967. 2nd Edition, Uganda Government. The Department of Lands and Surveys. 29 p.
- Auster, P.J., R.J. Malatesta, R.W. Langton, L. Watling, P.C. Valentine, C.L.S. Donaldson, E.W. Langton, A.N. Shepard & I.G. Babb, 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (northwest Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science* 4: 185-202.
- Auster, P.J. & R.W. Langton, 1999. The effects of fishing on fish habitat. In: Lenaka, L.R. (Ed). *Fish habitat: Essential fish habitat and rehabilitation*. American Fisheries Society, Symposium 22, Bethesda, MD.
- Azam, F.T., T. Fencel, J.G. Field, J.S. Gray, L.A. Meyer-Reil & T.F. Thingstad, 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10: 257-263.
- Bade, D.L., S.R. Carpenter, J.J. Cole, P.C. Hanson & R.H. Hesslein, 2004. Controls of $\delta^{13}\text{C}$ -DIC in lakes: Geochemistry, metabolism and morphometry. *Limnology and Oceanography* 49 (4): 1660-1172.
- Bagenal, 1978. *Methods for assessment of fish production in fresh waters*. 365 p. Blackwell Scientific Publications.
- Balirwa, 1984. Ecological separation in *Barbus* species in Lake Victoria. MSc. thesis, University of Dar es Salaam.
- Balirwa, J.S., 1995. The Lake Victoria environment: its fisheries and wetlands – a review. *Wetlands Ecology & Management* 3: 209-224.

- Balirwa, J.S., 1998. Lake Victoria Wetlands and Ecology of the Nile tilapia, *Oreochromis niloticus* Linne. Ph.D Thesis. 247 pp. Wageningen Agricultural Univ., Wageningen, NL.
- Balirwa, J.S., C.A. Chapman, L.J. Chapman, I.G. Cowx, K. Geheb, L. Kaufman, R.H. Lowe-McConnell, O. Seehausen, J.H. Wanink, R.L. Welcomme & F. Witte, 2003. Biodiversity and Fishery Sustainability in the Lake Victoria Basin: An Unexpected Marriage? *Bioscience* 53:703-715.
- Barel C.N.D., R. Dorit, P.H. Greenwood, G. Fryer, N. Hughes, P.B.N. Jackson, H. Kawanabe, R.H. Lowe-McConnell, M. Nagoshi, A.J. Ribbink, E. Trewavas, F. Witte & K. Yamaoka., 1985. Destruction of fisheries in Africa's lakes. *Nature* 315 (6014): 19-20.
- Bartell, S.M & J.K. Kitchell, 1978. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. *Marine Ecology Progress Series* 96: 125-137.
- Basaguren, A. & J. Pozo, 1994. Leaf litter processing of Older eucalyptus in the Aurra Stream system (Northern Spain) II. Macroinvertebrates associated. *Archiv fuer -Hydrobiologie* 132: 57-68.
- Bax, N.J., 1991. A comparison of the fish biomass flow to fish, fisheries and mammals in six marine ecosystems. *ICES Marine Science Symposia* 193: 217-224.
- Beadle, L.C., 1981. Inland waters of tropical Africa. 2nd edition: 475p Longman, London.
- Beamish, R.J & C. Mahnken., 1999. Taking the next step in fisheries management. approaches for fisheries management. University of Alaska Sea Grant, AK-SG-99-01, Fairbanks, 1-21.
- Beaudoin C.P & W.M Tonn, 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia* 120: 386-396.
- Beaudoin C.P., W.M. Tonn, V. Prepas & B.K. Kotok, 2001. A stable carbon and nitrogen isotope study of lake food webs in Canada's Borel Plain. *Freshwater Biology* 46: 465-477.
- Ben-David, M. & D.M. Schell, 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. *Oecologia* 27: 180-184.
- Benedito-Cecilio, E. C.A.R.M. Araujo-Lima, B.R. Forsber, M.M. Bittencourt & L.C. Martinell, 2000. Carbon sources of Amazonian fisheries. *Fisheries Management Ecology* 7: 305-315.
- Benson B.J. & J.J. Magnuson, 1992. Spatial heterogeneity of littoral fish assemblages in lakes: relation to species diversity and habitat structure. *Canadian Journal of Fisheries and aquatic Science* 49: 1493-1500.
- Bettoli, P.W., M.J. Maceina, R.L. Noble & R.K. Betsill, 1993. Response of a reservoir fish community to aquatic vegetation removal. *N. Amer. J. Fish. Manage.* 12:509-16.
- Beukema, J.J., 1995. The long-term effects of mechanical harvesting of lugworms on the zoo-benthos community of a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research*. 33(2): 219-227.
- Bilby, R.E & P.E. Bisson, 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Canadian journal of Fisheries and Aquatic sciences* 49: 540-551.
- Blaber, S.J.M., D. P. Cyrus, J-J. Albret, Chong Ving Ching, J.W. Day, M. Elliot, M.S. Fonseca, D.E. Hoss, J. Oresanz, I.C. Potter & W. Silvert, 2000. Effects of fishing on the

- structure and functioning of estuarine and nearshore ecosystems. *ICES Journal of Marine Science* 57: 590-602.
- Blumenshine, S.C., Y. Vadeboncoeur, D. M. Lodge, K.L. Cottingham & S.E. Knight, 1997. Benthic-pelagic links: responses of benthos to water-column nutrient enrichment. *Journal of the North American Benthological Society* 16: 466-479.
- Blumenshine, S.C., D.M. Lodge & J.R. Hodgson, 2000. Gradient of fish predation alters body size distributions of lake benthos, *Ecology* 81: 374-386.
- Bodini, A. 2000. Reconstructing trophic interactions as a tool for understanding and managing ecosystems: application to a shallow eutrophic lake. *Canadian Journal of Fisheries and Aquatic sciences* 57: 1999-2009.
- Bootsma, H.A & R.E. Hecky, 1993. Conservation of the African Great lakes: A limnological perspective. *Conservation Biology* 7 (30): 644-656.
- Bootsma, H.A., R.E Hecky, R.H. Hesslein & G.F. Turner., 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analyses. *Ecology* 77:1286-290.
- Boulton, A.J., 1999. The role of subsurface biological filters in gravel-bed river rehabilitation strategies, pp. 81-86 In: I. rutherford, & R. bartley (Eds). Second Australian stream Mangement Conference: The Challenge of Rehabilitating Australia's Streams, Vol I. Clayton (Australia): CRC for Catchment Hydrology, Monash University.
- Boutton, T.W., 1991. Stable carbon isotope ratios of natural materials. II. Atmospheric, terrestrial, marine and freshwater environments. *In: Carbon isotopes techniques*. Coleman, D.C. and B. Fry (Eds). Academic Press, san diego, Calif.
- Bowen, S.H. 1996. Ouatitative description of the diet pp. 513-532. In: Murphy B.R. & D.W. Willis (ed). *Fisheries Techniques*, 2nd edition, American Fisheries Society, Bethesda.
- Brewer, M.J., 1994. *Insect Biology and Management Resource Manual*. pp. 23, MP-76. University of Wyoming.
- Briand, F. J. & E. Cohen, 1984. Community food webs have scale invariant structure. *Nature* 307: 264-266.
- Bruton M., 1990. The Conservation of the fishes of Lake Victoria. Africa: an ecological perspective. *Environmental Biology of Fishes*. 27: 161-175.
- Brunke, M. & T. Gonser, 1997. The ecological significance of exchange processes between rivers and ground water. *Freshwater Biology* 37: 1-133.
- Bunn S.E. & P.I. Boon, 1993. What sources of organic carbon drive food webs in billabongs: a study based on multiple stable isotopes *Oecologia* 96: 85-94.
- Buddington, R.K., 1979. Digestion of an aquatic macrophyte by *Tilapia zillii* (Gervais). *Journal of Fish Biology*. 15: 449-55.
- Bugenyi, F.W.B. & J.S. Baliirwa. Human intervention in natural processes of the Lake Victoria ecosystem: The problem. *In: Solanki & S. Herodek (Eds.)*. Conservation and management of lakes. Syp. Biol. Hung., 38: 311-339. Academiai Kiado, Budapest.
- Burgis, M.J., K.M. Mavuti, J. Moreau & I. Moreau, 1987. The Central Plateau, p.359-388; In: *African Wetlands and Shallow Water bodies (Zones humides et lacs peu profonds d'Afrique)*. Directory (Répertoire). Burgis M.J. & J>J. Symoens (Eds) ORSTOM, Coll. Travaux et Documents No. 211, Paris 1987. 650p.

- Cabana, G. & J.B. Rasmussen., 1994. Modelling food chain structure and contaminant bioaccumulation using stable isotope nitrogen isotopes. *Nature* 372: 255-373.
- Cabana, G., & J.B Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proc. Nat. Acad. of Sci.* 93: 10844-10847.
- Cadwalladr, D.A., 1969. A discussion of possible mangement measures to revive the Labeo victorinus fishery of Lake Victoria with specific reference to Nzoia River, Kenya. Uganda Fisheries Department. Occassional paper 2: 1-6.
- Campbell. L.M., R.E Hecky & S.B. Wandera, 2003. Stable isotope analyses of food web structure and Fish diet in Napoleon and Winam gulfs, Lake Victoria, East Africa. *J. Great Lakes Res.* 29 (2): 243-257.
- Carpenter, S.R., J.F. Kitchell, & J.R. Hodgson, 1985. Cascading trophic interactions and lake productivity. *BioScience*, 35: 634-639.
- Carpenter S.R & J.F Kitchell., 1988. Consumer control of lake productivity. Large scale experimental manipulations reveal complex interactions among lake organisms. *BioScience* Vol. 38 No. 11: 764-769.
- Carpenter, S.R., & J.F. Kitchell, 1993. The Trophic cascade in Lakes. Cambridge University Press, London.
- Carpenter S.R., C.E. Kraft & R.A. Wrioth, 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. *American Natularist* 140: 781-798.
- Carpenter, S.R., K.L. Cottingham, & D.E. Schindler, 1992. Biotic feed backs in lake phosphorous cycles. *TRENDS in Ecology and Evolution.* 7: 332-336.
- Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N. & Smith, V.H. (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications*, 8, 559-568.
- Cartes, J.E. & F. Maynou, 2001. Trophodynamics of Boreomysis artica, a deep-water dominant mysid from the suprabenthic community of the Catalan Sea (western Mediterranean) *Mar. Ecol. Prog. Ser.*, 221: 225-234.
- Casatti, L., H.F. Mendes & K.M. Ferreira, 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana Reservoir, Paranapanema River, southeastern Brazil. *Braz. J. Biol.* 63 (2): 213-222.
- Chapin III, F.S., B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala & D. Tilman, 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500-504.
- Chapman, L.J., L.S. Kaufman, C.A. Chapman & E. Mackenzie, 1995. Hypoxia tolerance in East African cichlids: Potential for low oxygen refugia in Lake Victoria. *Conservation Biology* 9: 1-15.
- Chapman, L.J & C.A. Chapman, 1998. Hypoxia tolerance of the Mormyrid Petrocephalus catstoma: Implications for persistence in swamp refugia. *Copeia* 1998, 762-768.
- Chapman, L.J & K. Hulen. 2001. Implications of hypoxia for the brain size and gill surface area of mormyrid fishes. *Journal of Zoology* 254:461-472.
- Chapman, L., C.A. Chapman, P.J. Schofield, J.P. Olowo, L. Kaufman, O. Seehausen, & R. Ogutu-Ohwayo, 2003. Fish Faunal Resurgence in Lake Nabugabo, East Africa. *Conservation Biology* 17 (2): 500-511.

- Chick, J.H. & C.C. McIvor, 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing the littoral zone as a landscape. *Canadian Journal of Fisheries and Aquatic Science*, 51: 2873-2882.
- Christensen, V. & D. Pauly. 1992. A guide to ECOPATH II Software System. Version 2.1. ICLARM Software, 6.
- Christensen, V., 1995. A model of trophic interactions in the North Sea in 1981, the year of stomach. *Dana* 11: 1-28.
- Christensen, N.L. & 12 others., Woodmansee., 1996. The report of Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6: 665-691.
- Christian, L., 1995. Role and consequences of fish diversity in the functioning of African freshwater ecosystems: a review. *Aquatic Living Resources* 8: 59-79.
- Chippis, S.R. & J.E. Garvey in press. Assessment of food habits and feeding patterns. In (C. Guy and M. Brown, eds) *Analysis and Interpretation of Freshwater Fisheries data*. American Fisheries Society, Bethesda, Maryland. Chapter 11.
- Coleman F.C., & S.L. Williams, 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *TRENDS in Ecology & Evolution* 17 (1): 40-44.
- Colle, D.E. & J.V. Shireman, 1980. Coefficients of condition for largemouth bass, bluegill, and redear sunfish in hydrilla-infested lakes. *Trans. Amer. Fish. Soc.* 109: 521-31.
- Collie, J.S., G.A. Escanero, & P.C. Valentine, 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. *Marine Ecology Progress Series* 155: 159-172.
- Cohen, J.E. & F. Briand, 1984. trophic links of community food webs. *Proceedings of the National Academy of Sciences (USA)* 81: 4105-4109.
- Cohen, J.E, F. Briand, & C.M. Newman, 1990. *Community food webs: data and theory*-Springer- Verlag.
- Cohen, A.S., R.Bills, C.Z. Cocquyt & A.G. Galjon, 1993. The impact of sediment pollution on biodiversity in Lake Tanganyika. *Conservation Biology*, 7: 667-677.
- Corbet, P.S., 1961. The food of non-cichlid fishes in the Lake Victoria basin, with remarks on their evolution and adaptation to lacustrine conditions. *Proc. Zool. Society. London* 136: 1-101.
- Cortés, E. & S.H. Gruber, 1990. Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris*. *Journal of Fish Biology* 44: 331-341.
- Costa, m.J. & M. Elliott, 1991. Fish usage and feeding in two industrialized estuaries – the Tagus, Portugal, and the Forth, Scotland. *In Coasts and estuaries: Spatial and Temporal Comparisons*, pp. 289-297. Ed. By M. Elliot, and J.P Ducrotoy. Olsen and Olsen, Fredensborg, Denmark.
- Craig, H., 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochimica Cosmochimica Acta* 12: 133-149.
- Crawley, M.J., 1997. *Plant ecology*. Blachwell Science, University Press, Cambridge.
- Crul, R.C.M., 1995. Limnology and hydrology of Lake Victoria, comprehensive and comparative study of Great Lakes. UNESCO/IHP-IV Project M-5.1 UNESCO Publishing, Paris, 79p.

- Crul, R.C.M., 1998. Management and conservation of the African Great Lakes. *Lakes Victoria, Tanganyika and Malawi*. Comparative and comprehensive study of Great Lakes. UNESCO/ IHP-IV PROJECT M-51. ISBN 92-3-103593-2. pp. 58-59.
- Dahl, K., T. Borchardt, N. Dankers, & H. Farke, 1994. Status, trends, regulation and ecological effects of the Wadden Sea fishery. *Ophelia*, supplement, 6: 87-97.
- Daily, G.C. (Ed.), 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC, 392 pp.
- Dayton, P., S. Thrush, T. Agardy, & R. Hofman, 1995. Environmental effects of marine fishing. *Aquat. Cons. Mar. Fresh. Ecosys.* 5: 1-28.
- Darwin, C., 1859. *The Origin of Species by means of Natural Selection or the Preservation of Favored Races in the struggle for Life* pp 247. Down, Bromley, Kent.
- Davenport S.R. & N.J. Bax, 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries and Aquatic Science*. 59: 514-530.
- Delariva, R.L., A.A. Agostinho, K. Nakatani & G. Baumgartner, 1994. Ichthyofauna associated to aquatic macrophytes in the upper Parana River floodplain. *Rev. Unimar* 16: 41-60.
- del Giorgio, P.A., & R.L. France., 1996. Ecosystem-specific patterns in the relationship between zooplankton and POM or microplankton $\delta^{13}\text{C}$. *Limnology and Oceanography* 41: 359-365.
- DeNitro & S. Epstein, 1978. Influence of diet on the distribution of carbon isotope on the distribution of carbon isotopes in animals. *Geochim. Cosmoch. Acta* 42: 495-506.
- DeNitro & S. Epstein, 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* 45: 341-351
- Diana, J., 1979. The feeding pattern and daily ration of top carnivore, the northern pike, *Esox lucius*. *Canadian Journal of Fisheries and Aquatic Science* 57: 977-991.
- Diana, J., 1994. *Biology and ecology of fishes*. Cooper, Carmel, Indiana, USA.
- Diehl, S. & R. Kornijów, 1998. Influence of submerged macrophytes on trophic interactions among fish and macro-invertebrates. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., and Christoffersen, K. (eds). *The structuring role of submerged macrophytes in lakes*. Springer Verlag, New York, pp 24-46.
- Dill, L. M., 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 398-408.
- Douglas A. F. & S. J. McNaughton, 1992. The ecology of plants, large mammalian herbivores and grout in Yellowstone National Park. *Ecology* 73: 2043-2058.
- Draper, N. & H. Smith, 1981. *Applied regression analysis*. 2nd edition. Wiley, New York. 709pp.
- Dunne, J.A., R.J. Williams & N.D. Martinez, 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5: 558-567.
- Duque, A.B., & K.O. Winemiller, 2003. Dietary segregation among large catfishes of the Apure and Arauca Rivers, Venezuela. *Journal of Fish Biology* 63: 410-427.
- Ehleringer, J.R. & P.W. Rundel, 1989. Stable Isotopes, history, units, and instrumentation. In *Stable isotopes in ecological research*. P.W. Rundel, J.R. Rundel & K.A. Nagy (eds). Springer-Verlag, New York. pp. 1-6.

- Eklov, P. and S. Diehl, 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98: 344-53.
- Eklov, P. & S.F. Hamrin, 1989. Predator efficiency prey selection: interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd *Scardinius erythrophthalmus*. *Oikos* 56: 149-56.
- Emerton, L., 1997. Economic Assessment of Sechelles Biodiversity. Conservation and national Parks Section, Division of Environment, Ministry of Foreign Affairs, Planning and environment, Republic of sechelles, Mahé.
- Emerton, L., 1999. Balancing the opportunity costs of wild life conservation for communities around Lake Mburo National park, Uganda pp27, ISBN 1843690047.
- Estep, M.L.F & Vigg, S., 1985. Stable carbon and nitrogen isotope tracers of trophic dynamics in natural populations and fisheries of the Lahontan lake system, Nevada. *Canadian Journal of Fisheries and Aquatic sciences* 42: 1712-1719.
- FAO, 1995. FAO Code of Conduct for responsible Fisheries. FAO, Rome. Pp 12.
- FAO, 1996. Precautionary approach to capture fisheries and species introductions. FAO Technical Guidelines for Responsible Fisheries. 2, 3-27.
- FAO, 1996. Fisheries and Aquaculture in Europe: Situation and Outlook in 1996. FAO, Fisheries Department, Rome.
<http://www.fao.org/fi%2A/publ/circular/c911/c911%2D2.htm>
- FAO, 2000. The state of world fisheries and aquaculture 2000. FAO, Rome.
- Fischer, P. & R. Eckmann, 1997. Spatial distribution of littoral fish species in large European lake, Lake Constance, Germany. *Archiv für Hydrobiologie*, 140: 91-116.
- Floate, M.J.S., 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In F.E. Clark and T. Rosswall, editors. Terrestrial nitrogen cycles; processes, ecosystem strategies and management impacts. *Ecological Bulletins-NFR* 33: 585-601.
- Forbes, S.A., 1925. The lake as a microsom. *Bullen of the Illinois Natural History Survey* 15: 537-550.
- Fogarty, M.T.J. & S.A Murawski, 1998. Large scale disturbance and the structure of Marine systems: Fishery impacts on Georges Bank. *Ecological Applications*, 6-22.
- Forsberg, B.R., C.A.R.M. Araujo, L.A. Martinelli, R.L. Victoria & J.A. Bonassi, 1993. Autotrophic carbon sources for fish of Central Amazon. *Ecology* 74: 643-652.
- France, R.L., 1995 a. Carbon -13 enrichment in benthic compred to planktonic algae: food web implications. *Marine Ecology Progress Series* 124: 307-312.
- France, R.L., 1995 b. Differentiation between littoral and pelagic food webs in lakes using carbon isotopes. *Limnology and Oceanography* 40: 1310-1313.
- France, R.L. In press. Comparing $\delta^{13}\text{C}$ among littoral food webs using lake DOC. *Aquatic Ecology*.
- France, R.L., 1997. Stable carbon and nitrogen isotopeic evidence for ecotonal coupling between boreal forests and fishes. *Ecol. Freshwater. Fish* . 6: 78-83.
- France, R.L. & R.H. Peters, 1997. Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. *Canadian Journal of Fisheries and Aquatic Science*. 54: 1255-1258.

- France, R.L., R. Peters & L. McCabe, 1998. Spatial relationships among boreal riparian trees, litterfall and soil erosion potential with reference to buffer strip management and cold water fisheries. *Ann. Bot. Fennici* 35: 1-9.
- France, R.L., 1999. Relationship between DOC concentration and epilithon stable isotopes in boreal lakes. *Freshwater Biology* 41: 101-105.
- Froese, R. & D. Pauly, 2000. Fish base 2000: concepts, design and data source (Eds). ICLARM, Los Baños, Laguna, Philippines 344pp.
- Fry, B. & P.L. Parker, 1979. Animal diet in Texas sea grass meadows; ^{13}C evidence for the importance of benthic plants. *Estuarine and Coastal Marine Science* 8: 499-509.
- Fry, B. & C. Arnold, 1982. Rapid $^{13}\text{C}/^{12}\text{C}$ turnover during growth of brown shrimp (*Penaeus aztecus*). *Oecologia* 54: 200-204.
- Fry, B. & E.B. Sherr, 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sc.* 27: 13-47.
- Fry, B., 1988. Food web structure on Georges Bank from C, N and S isotopic compositions. *Limnology and Oceanography* 33: 1182-1190.
- Fryer, G., 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. *E. Afr. Agric. J.* 25: 267-270.
- Fryer, G. & T.D. Iles, 1972. The Cichlid Fishes of the Great Lakes of Africa: their biology and evolution. Oliver and Boyd, Edinburgh, UK.
- Gaedke, U., D. Straile & C. Pahl-Wostl, 1996. Trophic structure and carbon flow dynamics in the pelagic community of a large lake, p. 60-71. In: G.A. Polis and K.O. Winemuller (eds.), Food webs, integration of patterns and dynamics. Chapman and Hall.
- Gannes, L.Z., D.M. O'Brien & C. Martinez del Rio, 1997. Stable isotopes in animal ecology: assumptions, caveats and a call for more laboratory experiments. *Ecology*, 78: 1271-1276.
- Garcia, M.A. & C. Newton, 1997. Current situation, trends and prospects in world capture fisheries. *American Fisheries Society Symposium*. 2, 1-54.
- Gauch, H.G. Jr., 1982. Multivariate analysis in community ecology pp. 298: NY: Cambridge University Press.
- 2: 185-190.
- Garrison, L.P. & J.S. Link, 2000. Fishing effects on spatial distribution and trophic structure in the Georges Bank fish community. Symposium proceedings on the ecosystem effects of fishing, *ICES Journal of Marine Science* 57: 723-730.
- Garrison, L.P., 2000. Spatial and dietary overlap in Georges Bank groundfish community. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1679-1691.
- Garrod, D.J. 1961. The history of the fishing industry of Lake Victoria, East Africa, in relation to the expansion of marketing facilities. *E. Afr. Agric. For. J.* 27(2):95-99.
- Garvey, J.E., N.A. Dingledine, N.S. Donovan & R.A. Stein, 1998. Exploring spatial and temporal variation within reservoir food webs: predictions for fish assemblages. *Ecological Applications* 8: 104-120.
- Gasith, A. & A.D. Hasler, 1976. Airborne litterfall as a source of organic matter in lakes. *Limnology and Oceanography* 21: 253-258.

- Gaston, K.J., 1996. Species richness: measure and measurement. Pp. 77-113 In K.J. Gaston, editor Biodiversity: a biology of numbers and difference. Blackwell Scientific, Oxford, UK.
- Gee, J.M., 1964. Nile perch investigations. East African Freshwater Fisheries Research Organisation (EAFFRO) Annual Report 1962/63. 14-24.
- Gee, J.M., 1969. A comparison of certain aspects of the biology of *Lates niloticus* (Linne) in some East African lakes. *Rev. Zool. Bot. Afr.* 80: 244-262.
- Gearing, J.N., 1991. The study of diet and trophic relationships through natural abundance $\delta^{13}\text{C}$. In: Carbon Isotope Techniques (Eds D.C. Cleman and B. Fry), pp. 201-218. Academic press, Inc., San Diego.
- Genner, M.J., G.F. Turner, S. Barker & S.J. Hawkins., 1999. Niche segregation among Malawi Cichlid fishes? Evidence from stable isotope signatures. *Ecology Letters* 2: 185-190.
- Genner, M.J., S.J. Hawkins & G.F. Turner, 2003. Isotopic change through out the life history of a lake cichlid fish. *Journal of Fish biology* 62: 907-917.
- Gerking, S.D., 1994. Feeding ecology of fish. San Diego: Academic Press, California.
- Getabu, A., 1994. A comparative study on the feeding habits of *Oreochromis niloticus* in Nyanza Gulf, Lake Victoria and sewage ponds. In: *Proceedings of the second EEC Regional Seminar on recent trends of Research on Lake Victoria Fisheries*. Kisumu, Kenya, 25-27 September, Kenya, 1992 (Eds Okemwa E., E. Wakwabi and A. Getabu). ICIPE Press, Nairobi, Kenya.
- Gichuki, J., L. Triest & F. Dehairs, 2001. The use of stable isotopes as tracers of ecosystem functioning in contrasting wetland ecosystems of Lake Victoria Kenya. *Hydrobiologia* 458 (1-3): 91-97.
- Gill, H.S. & D.L. Morgan, 2003. Ontogenetic changes in the diet of the black-stripe minnow *Galaxiella nigrostriata* (Shipway, 1953) (Galaxiidae) and the salamwnder fish *Lepidogalaxias salamandroides* (Mees, 1961) (Lepidogalaxiidae). *Ecology of Freshwater Fish* 12: 151-158.
- Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65: 455-468.
- Gislason, H., M. Sinclair, S. Sainsbury & R. O'Boyle., 2000. Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES Journal of Marine Science*. 57 (3) 468-475.
- Goericke, R. & B. Fry, 1994. Variations of marine plankton $\delta^{13}\text{C}$ with latitude, temperature and dissolved CO_2 in the world ocean. *Global Biogeochem. Cycles* 8: 85-90.
- Goldschmidt, T., F. Witte & J. de Visser., 1990. Ecological segregation in zooplanktivorous haplochromines species (Pisces, Cichlidae) from Lake Victoria. *Oikos* 58: 343-355.
- Goldschmidt, T., F. Witte & J. wanink., 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology*. 7: 686-700.
- Goldschmidt, T., 1996. Darwin's Dreampond: Drama in Lake Victoria. 27 pp. The MIT, Cambridge, Massachusetts, USA.
- Goldwasser, L. & J. Roughgarden, 1997. Sampling effects and the estimation of food web properties. *Ecology* 78: 41-54.

- Goudswaard, K. & F. Witte, 1997. The catfish fauna of Lake Victoria after the Nile perch upsurge. *Environmental Biology of Fishes* 49: 21-43.
- Goudswaard, P.C. & J.H. Wanink, 1993. Anthropogenic perturbation in Lake Victoria: effects on fish introductions and fisheries on fish eating eagles. Proceedings of the VIII Pan-African Ornithology Congress 31-38.
- Graham, M. 1929. The Victoria Nyanza and its fisheries. A report of the survey of Lake Victoria 1927-1928 and Appendices. Crown Agents for colonies. 225pp.
- Greenstreet, S.P.R. & S.J. Hall, 1996. Fishing and groundfish assemblage structure in the northwestern North sea: an analysis of long-term and spatial trends. *J. Anim. Ecol.* 65: 577-598.
- Greenwood, P.H. 1965. The cichlid fishes of Lake Nabugabo, Uganda. *Bulletin of the British Museum of Natural History (Zoology)* 12(9): 313-357.
- Greenwood, P.H. 1966. The fishes of Uganda. 131 pp. The Uganda society (Kampala), Nairobi, Kenya.
- Greenwood, P.H., 1974. The cichlid fishes of Lake Victoria East Africa: the biology and evolution of a species flock. *Bull. Br. Mus. Nat. Hist. (Zool.)* Suppl. 6: 1-134.
- Greenwood, P.H., 1981. *The Haplochromine Fishes of the East African Lakes*. Fraus International Publications, München, pp. 1-839.
- Grey, J. & M. Harper, 2002. Using stable isotopes analyses to identify allochthonous inputs into Lake Naivasha mediated via the hippopotamus gut. *Isotopes Environ. Health Stud.* 38(4): 245-250.
- Grime, J.P., 1997. Biodiversity and ecosystem function: the debate deepens. *Science* 277: 1260-1261.
- Gu, B., D.M. Schell, V. Alexander, 1994. Stable carbon and nitrogen isotopic analysis of the plankton food web in a subarctic lake. *Canadian Journal of Fisheries and Aquatic science* 51: 1338-1344.
- Gu, B., S.L. Schelske, & M.V. Hoyer, 1996. Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake. *Journal of Fish Biology* 49: 1233-1243.
- Gu, B., C.L. Schelske & M.V. Hoyer, 1997. Intrapopulation feeding diversity in blue tilapia: Evidence from stable isotope analysis. *Ecology* 78 (7): 2263-2266.
- Hairston, N.G., F.E. Smith & L.B. Slobodkin, 1960. Community structure, population control, and competition. *American Naturalist* 94: 421-425.
- Hairston, N.G., Jr., & N.G. Hairston, Sr., 1993. Cause effect relationships in energy flow trophic structure and interspecific interactions. *American Naturalist* 142: 379-411.
- Hall, S.J. & D.G. Raffaelli, 1991. Food web patterns: lessons from a species rich web. *Journal of Animal Ecology* 60: 823-842.
- Hall, S.J. & D.G. Raffaelli, 1993. Food webs: theory and reality. *Advances in Ecological Research* 24: 187-239.
- Hansson, S., J.E. Hobbie, R. Elmgren, U. Larsson, B. Fry, & S. Johansson., 1997. The stable nitrogen isotope ratio a marker of food web interactions and fish migration. *Ecology* 78: 2249-2257.

- Hansson, L.A. & others, 1998. Biomanipulation as an application of food chain theory: Constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* 1: 558-574.
- Hardin, G., 1966. The tragedy of the commons. *Science* 162: 1243-1248.
- Harding, J.S., E.F. Benfield, P.V. Bolstad, G.S. Helfman, E.B.D. Jones III, 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Science* 95: 14843-14847.
- Harvey C.J. & J.F. Kitchell, 2000. A stable isotope evaluation of the structure and spatial heterogeneity of a Lake Superior food web. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1395-1403.
- Havelange, S., G. Lepoint, P. Dauby & J.M. Bouqueneau, 1997. Feeding of sparid fish *Sarpa salpa* in a sea grass ecosystem: diet and carbon flux *Publicazioni della Stazione Zoologica di Napoli: I: Marine Ecology* 18: 289-297.
- Hecky, R.E., 1991. The pelagic ecosystem. Pages 90-110. In G.W. Coulter, editor. *Lake Tanganyika and its life*. Oxford University Press, Oxford, United Kingdom.
- Hecky, R.E., & F.W.B. Bugenyi, 1992. Hydrology and chemistry of the African Great Lakes and water quality issues: Problems and solutions. *Mitt. Verein. Internat. Limnol.* 23: 45-54.
- Hecky, R.E., 1993. The Eutrophication of Lake Victoria. *Internat. Ver. Theor. Ang. Limnol. Ver.* 25: 39-48.
- Hecky, R.E., F.W.B. Bugenyi, P. Ochumba, J. F. Talling, R. Mugidde, M. Gophen & L. Kaufman., 1994. Deoxygenation of benthic algae to lake food webs as revealed by stable isotope analyses. *North America Journal of Benthological Society* 14: 631-653.
- Hecky, R.E., & R.H. Hesslein., 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analyses. *North America Journal of Benthological Society* 14: 631-653.
- Henderson, R.A. & R.M. Seaby, 2002. Community Analysis Package, Version 2.0. Oisces Conservation Ltd, Lymington, UK.
- Herczeg, A.L. & G. Fairbanks, 1987, Anomalous carbon isotope fractionation between atmospheric CO₂ and dissolved inorganic carbon induced by intense photosynthesis. *Geochim. Cosmochim. Acta* 51: 895-899.
- Hershey A.E., G.M. Gettel, M.E. McDonald, M.C. Miller, H. Mooers, W.J. O'Brien, J. Pastor, C. Richards & J.A. Schuldt, 1999. A geomorphic-trophic model for landscape control of arctic lake food webs. *Bioscience* 49: 887-897.
- Herwig B.R., D.A. Souk, J.M. Dettmers & D.H. Wahl., 2004. Trophic structure and energy flow in blackwater lakes of two large flood plain rivers assessed using stable isotopes. *Canadian Journal Fisheries and Aquatic Sciences* 61: 12-22.
- Hesslein, R.H., M.J. Capel, D.E. Fox, & K.A. Hallard., 1991. Stable isotopes of sulphur, carbon and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2258-2265.
- Hesslein, R.H., K.A. Hallard, & P. Ramlal., 1993. Replacement of sulphur, carbon, and nitrogen in tissue of growing broad white-fish (*Cregonus nasus*) in response to change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Science* 50: 2071-2076.

- Hickley, P., R. Bailey, D. M. Harper, R. Kundu, M. Muchiri, R. North & A. Taylor, 2002. The status and future of the Lake Naivasha fishery, Kenya. *Hydrobiologia* 488: 181-190.
- Hill, M.O. & H.G. Gauch, 1990. Detrended correspondence analysis, an improved ordination technique. *Vegetation* 42: 477-58.
- Hjerne, O & S. Hansson, 2002. The role of fish and fisheries in Baltic Sea nutrient dynamics. *Limnology and Oceanography* 47:1023-1032.
- Hobson, K.A. & R.G. Clark, 1992. Assessing avian diets using stable isotope δ ; turnover of ^{13}C in tissues. *Condor* 94: 181-188.
- Hobson, K.A., J.F. Piatt & J. Pitocchelli, 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63: 786-798.
- Holbrook, S.J. & R.J. Schmitt, 1992. Causes and consequences of dietary specialization in surf perches: patch choice and intraspecific competition. *Ecology* 73: 402-412.
- Holling, C.S., 1986. The resilience of terrestrial ecosystems: local surprise and global change. In: Clark, W.C., Munn, R.E. (Eds.), *Sustainable Development of the Biosphere*. Cambridge University Press, Cambridge, pp. 292-317.
- Holmlund C.M. & M. Hammer, 1999. Ecosystem services generated by fish populations. *Ecological Economics* 29: 253-268.
- Holyoak, M. & S. Schadev, 1998. Omnivory and stability of simple food webs. *Oecologia* (Berlin) 117: 413-419.
- Hornung M. & B. Reynolds, 1995. The effects of natural and anthropogenic environmental changes on ecosystem processes at the catchment scale. *TRENDS in Ecology and Evolution* 10: 443-449.
- Horppila, J. & Kairesalo, T. 1990: A fading recovery: the role of roach (*Rutilus rutilus* L.) in maintaining high phytoplankton productivity and biomass in Lake Vesijärvi, southern Finland. *Hydrobiologia* 200/201: 153-165.
- Howell, R., 1985. The effect of baitdigging on the bioavailability of heavy metals from surface intertidal marine sediments. *Marine Pollution Bulletin*, 16: 292-295.
- Hughes, N.F., 1986. Changes in the feeding biology of the Nile perch, *Lates niloticus* (L.) (pisces: Centropomidae), in Lake Victoria, East Africa since its introduction in 1960, and its impact on native fish community of the Nyanza Gulf. *Journal of Fish Biology* 29: 541-548.
- Hynes, H.B.N. 1950. The food of the freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in the food of fishes. *Journal of Animal Ecology* 19: 36-58.
- Hutchison, G.E., 1975. Treatise on Limnology, Vol. 1 Geography, Physics and Chemistry. In John Wiley and Sons, New York. 1015pp.
- International Lake Environment Committee (ILEC), 2001. Survey of the State of World Lakes. www.ilec.or.jp/database/afr/dafr15.html
- Jackson, P.B.N., 1971. The African Great Lakes fisheries: past, present and future. *African Journal of tropical Hydrobiology and Fisheries* 1: 45-54.

- Jacobsen, L., S. Berg, N. Jepsen & C. Skov, 2004. Does roach behaviour differ between shallow lakes of different environmental states? *Journal of Fish Biology* 65 (1): 135-147.
- Jennings, S., & M.J. Kaiser, 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 46: 28-46.
- Jennings, S., S.P.R. Greenstreet & J.D. Reynolds, 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* 68: 617-627.
- Jennings, S., & N.V.C. Polunin, 1996. Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fisheries. *Journal of Fish Biology* 46: 28-46.
- Jennings, S., O. Reñones, B. Marales-Nin, N.V.C. Polunin, J. Moranta, & J. Coll, 1997. Spatial variation in the ^{15}N and ^{13}C stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: Implications for the study of trophic pathways. *Marine Ecology-Progress series* 146: 109-116.
- Jeppesen, E., T.L. Lauridsen, T. Kairesalo & P.M. Peroow, 1997. Impact of submerged macrophytes on fish zooplankton interactions in lakes. In: Jeppesen, E., Søndergaard, M., Søndergaard, M. and Christoffersen, K. (eds), The structuring role of submerged macrophytes in lakes. Springer-Verlag, pp. 91-114.
- Jeppesen, E., J.P. Jensen, M. Søndergaard, T. Lauridsen, L. J. Pedersen, & L. Jensen, 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342/343: 151-164.
- Jeppesen, E., M. Søndergaard, M. Søndergaard, K. Christoffersen, 1998. The structuring role of submerged macrophytes in lakes. Ecological Studies series 131. New York, Springer.
- Jepsen, D.B. & K.O. Winemiller, 2002. Structure of tropical river food webs revealed by stable isotope ratios. *Oikos* 96: 46-55.
- Juanes, F., 1994. What determines prey size selectivity in piscivorous fishes? In: Stouder D.J., K.L. Fresh, R.J. Feller (Eds). Theory and application in fish feeding ecology. S. Carolina, University Press, Columbia, p. 79-1000 (Belle WE. Baruch Library in Marine Sciences No. 18).
- Juda, L., 1996. Developing international law and ecosystem-based fisheries management. In: K. Sherman, N.A. Jaworski and T.J. Smayda (eds.), The Northeast shelf ecosystem: Assessment, sustainability and management. Blackwell Science, Cambridge, 31-46 pp
- Juliano, S.A., 1998. Species introduction and replacement. among mosquitoes: interspecific resource competition or apparent competition? *Ecology* 79:255-268.
- Johnston, T.C., K. Kelts, & E. Odada, 2000. The Holocene history of Lake Victoria. *Ambio* 29: 2-11
- Jones, J.I. & S. Waldron, 2003. Combined stable isotope and gut contents analysis of food webs in plant-dominated, shallow lakes. *Freshwater Biology* 48: 1396-1407
- Kamugisha, J., Z. Ogutu & M. Ståhl, 1997. *Parks and People: Conservation and livelihoods at the Crossroads*, Regional Soil Conservation Unit/SIDA, Nairobi.

- Karel F. L., 1984. Functional Versatility, Speciation, and Niche Overlap: Are Fishes Different? In D. G. Meyers and J. R. Strickler (eds.), *Trophic Interactions within Aquatic Ecosystems*. AAS Selected Symposium 85, 269-305
- Karjalainen, J., M. Leppä, M. Rahkola & K. Tolonen, 1999. The trophic role of benthivorous and planktivorous fish in a mesotrophic lake ecosystem. *Hydrobiologia* 408/409: 73-84.
- Kaufman, L., 1992. The lessons of Lake Victoria: catastrophic changes in species-rich freshwater ecosystems. *BioScience* 42 (11): 846-858.
- Kaufman, L. & P. Ochumba, 1993. Evolutionally and conservation biology of cichlid fishes as revealed by faunal remnants in the northern Lake Victoria. *Conservation Biology* 7: 719-730.
- Kaufman, L., 1997. Asynchronous taxon cycles in haplochromine fishes of the greater Lake Victoria region. *South African Journal of Science* 93: 601-606.
- Kaufman, L.S., L.J. Chapman, C.A. Chapman, 1997. Evolution in fast forward: haplochromine fishes of the Lake Victoria region. *Endeavour*. 21: 23-29.
- Kaufman, L.S., B. Heneman, J.T. Barnes & R. Fujita, 2004. Transition from low to high data richness: an experiment in ecosystem management from California. *Bulletin of Marine Science* 74: 693-726.
- Keast, A., 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. In: M.K. Hecht, W.C. Steere, B. Wallace, (eds.) *Evolutionary Biology*, 10, pp. 333-395.
- Kendall, R.L., 1969. An ecological history of the Lake Victoria Basin. *Ecological Monographs* 39 (2): 121-176.
- Kenny, D. & C. Loehle, 1991. Are food webs randomly connected? *Ecology* 72: 1794-1799.
- Keough, J.R., M.E. Siersen, & C.A. Hargley, 1996. Analysis of Lake Superior coastal food web with stable isotope techniques. *Limnology and Oceanography* 41: 136-146.
- Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Fisheries and Aquatic Science* 63: 1-27.
- Kitchell J.F., E.A. Eby, X. He., D.E. Schindler & R.M. Wright, 1994. Predator-prey dynamics in an ecosystem context. *Journal of Fish Biology*. 45: 209-226
- Kitchell J.F., D.E. Schindler, R. Ogutu-Ohwayo, & P.N. Reinthal., 1997. The Nile perch in Lake Victoria: Interactions between predation and fisheries. *Ecological Applications*, 7 (2) 653-664.
- Kitchell, J.F., T.E. Essington, C.H. Boggs, X. He & C.J. Walters, 1999. Keystone predators in the Central Pacific. Pp 665-683. In: Proc. 12th Wakefield Symposium on Ecological Considerations in Fisheries Management, Univ. Alaska Sea Grant, Anchorage, Alaska.
- Kidd, K.A., D.W. Schindler, D.C.G. Muir, W.L. Lockhart, & R.H. Hesslein, 1995. High concentrations of toxaphene in fishes from a subarctic lake. *Science* (Washington D.C.), 269: 240-242.
- Kidd, K. A., H.A. Bootsma, R.H. Hesslein, D.C.G. Muir, & Hecky, 2001. Biomagnification of DDT through the benthic and pelagic food webs of Lake Malawi, East Africa: Importance of trophic level and carbon source. *Environmental science and Technology* 35: 14-20.

- Killgore, K.J., R.P. Morgan II & N.B. Rybicki, 1989. Distribution and abundance of fishes associated with submerged aquatic plants in the Potomac River. *N. Amer. J. Fish. Manage.* 9:101-11.
- Kline, T.C., J.J. Goering, O.A. Mathisen, P.H. Poe & P.L. Parker, 1990. Recycling of elements transported upstream by runs of pacific salmon I. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in sashin Creek, south eastern, Alaska. *Canadian Journal of Fisheries and Aquatic Science* 47: 136-144.
- Kline, T.C. Jr., J.J. Gaering, O.A. Mathisen & P.H. Poe, 1993. Recycling of elements transported upstream by runs of pacific salmon: II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in the Kvichak river watershed, Bristol Bay South western Alaska. *Canadian Journal of Fisheries and Aquatic science* 50: 2350-2365.
- Kling, G.W., Fry, B., & W.J. O'Brien., 1992. Stable isotopes and planktonic structure in arctic lakes. *Ecology*, 73: 561-566.
- Kiriluk, R.M., M.R. Servos, D.M. Whittle, G. Cabana & J.B. Rasmussen, 1995. Using ratios of stable nitrogen and carbon isotopes to characterise the biomagnification of DDE, Mirex and PCB in a Lake Ontario pelagic food web. *Canada Journal Fisheries and aquatic Science* 52: 2660-2674.
- Klump, D.W., R.K. Howard & D.W. Pollad, 1989. Trophodynamics and nutritional ecology of seagrass communities. In: Larkum A.W.D, A.J. McComb, S.A Shepherd (eds). *Biology of Seagrasses*, Elsevier, Amsterdam, pp 394-457.
- Koslow, J.A. Seamounts and the ecology of deep sea fisheries. *American Scientist* 85: 168-176
- Kudhongania, A.W & A.J. Cordone 1974. Batho-spatial distribution pattern and biomass estimate of the major demersal fishes in Lake Victoria. *African Journal of tropical Hydrobiology and Fisheries*. 3:15-31.
- Kudhongania A.W., T. Twongo & R. Ogutu-Ohwayo, 1992. Impact of the Nile perch on the fisheries of Lakes Victoria and Kyoga. *Hydrobiologia* 232: 1-10.
- Lacasse S. & P. Magnan, 1992. Biotic and abiotic determinants of diet of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. *Can. J. Fish. Aquat. Sci.* 49: 1001-1009.
- Lajtha, K. & J.D. Marshall, 1994. Sources of variation in stable isotopic composition of plants. In: *Stable isotopes in ecology and environmental science* pp. 1-21. (eds) K. Lajtha and R.H. Michener. Blackwell Scientific, London.
- Lake, P.S., M. A. Palmer, P. Biro, J. Cole, A. P. Covich, C. Dahm, J. Gilbert, W. Goedkoop, K. Martens & J. Verhoeven, 2000. Global change and the biodiversity of fresh water ecosystems: impacts on linkages between above-sediment and sediment biota. *Bioscience* 50 (12): 1099-1107.
- Lake, J.L., R.A. McKinney, F.A. Osterman, R.J. Rruell, J. Fiddon, S.A. Ryba & A.D. Libby, 2001. Stable nitrogen isotopes as indicators of anthropogenic activities in small freshwater systems. *Canadian Journal of Fisheries and Aquatic science* 58: 870-878.
- Lamarra, V.A. 1975. Digestive activities of carp as major contributor to nutrient loading of lakes. *Verh. Int. Ver. Limnol.* 19: 2461-2468.

- Amington, R.W. & R.L. Haedrich, 1997. Ecosystem-based management. In: J. Boreman, B.S. Nakashima, J.A. Wilson and R.L. Kendall (eds.). Northwest Atlantic groundfish: Perspectives on a fishery collapse. American Fisheries Society.
- Arkin, P.A., 1996. Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries* 6: 139-164.
- Aurans, M., D. Gascuel, E. Chassot & D. Thiam, 2004. Changes in the trophic structure of fish demersal communities in West Africa in the three last decades. *Aquatic Living Resources* 17: 163-173.
- Auridsen, T.L. & I. Buenk, 1996. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. *Archiv für Hydrobiologie*, 137: 161-176.
- Bawler, S.P. & P.J. Morin, 1993. Food web architecture and population dynamics in laboratory micocosms of protists. *American Naturalist* 141: 675-686.
- Baws, R.M., 1968. Interactions between elephant and hippopotamus populations and their environments. *E. Afr. agric. For. J.* 33: 140-147.
- Begendre, L. & P. Legendre, 1998. *Numerical Ecology*. Elsevier, New York, 419pp.
- Beggett, M.F., M.R. Servos, R. Hesslein, O. Johannsson, E.S. Millard & D.G. Dixon, 1999. Biogeochemical influences on the carbon isotope signatures of Lake Ontario biota. *Canadian Journal of Fisheries and Aquatic Science*. 56: 2211-2218.
- Beggett, M.F., O. Johannsson, R. Hesslein, D.G. Dixon, W.D Taylor & M.R. Servos, 2000. Influence of inorganic nitrogen cycling on the $\delta^{15}\text{N}$ of Lake Ontario. *Canadian Journal of Fisheries and Aquatic Science*. 57: 1489-1496.
- Blewin W.-C, N. Okun & T. Mehner, 2004. Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. *Freshwater Biology* 49: 410-424.
- Blevine S., 1980. Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology* 83: 195-207.
- Biao, H., C. L. Pierce, & J. G. Larscheid, 2002. Diet dynamics of the adult piscivorous fish community in Spirit Lake, Iowa, USA 1995-1997. *Ecology of Freshwater Fish* 11:178-189
- Bigtvoet, W. & O.C. Mkumbo, 1990 Effects of changes in fish populations in Lake Victoria on the food of otters in (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology* 28:322-329.
- Bigtvoet, W. & O.C. Mkumbo, 1990. Stock assessment of Nile perch in Lake Victoria. pp. 35-74. In: CIFA, Report of the 5th Session of the Sub-committee for the Development and Managent of the Fisheries in Lake Victoria, Mwanza, Tanzania, 12-14 September 1989, FAO Fisheries Report no.430.
- Bigtvoet, R.L. & F. Witte, 1991. Perturbationthrough predator introduction: Effects on the food web and fish yields in Lake Victoria (East Africa). In: Terrestrial and Aquatic Ecosystems: Perturbation and Recovery, O. Ravera, (Ed). Chichester: Ellis Horwood Ltd.
- Bigtvoet, R.L., W. P.J. Mous, O.C. Mkumbo, Y.L. Budeba, P.C. Goudswaard, E.F.B. Katunzi, M.M. Temu, J.H. Wanink & F. Witte, 1995. The Lake victoria fish stocks and fisheries. Pp 11-53 In: Witte, F. and W.L.T. van Densen (Eds). Fish stocks and fisheris of Lake Victoria: a handbook for field, observations. Samara Publishing Ltd., Dyfed, UK.

- Indeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.
- Ink, J.S., 2002. Ecological Considerations in Fisheries management: When Does It Matter? *Fisheries* 27 (4): 10-17.
- Ipatou, E., R.E. Hecky, S.J. Eisenreich, L. Lockhart, D. Muir & P. Wilkinson, 1996. Recent ecosystem changes in lake Victoria reflected in sedimentary natural and anthropogenic organic compounds, p. 523-541. In T.C. Johnson and E. O. Odada (eds.), *The Climatology and paleoclimatology of the East African lakes*. Gordon and Breach Publ.
- Jack, J.M., 1972. The effects of hippopotamus grazing on Grasslands. *The Journal of Ecology* 60(2): 445-467.
- Jacob S.C., M.R. Lennartz & R.C. Ssaro, 1998. The role of fish, wild life and plant research in ecosystem management. *Landscape and Urban Planning* 40: 131-139.
- Jewe-McConnell, R.H. 1958. Observations on the biology of *Tilapia nilotica* Linnè in Lake East African waters (Pisces: Cichlidae). *Rev. Zool. Bot. Afr.* 57 (1-2): 129-170.
- Jewe-McConnell, R.H. 1987. *Ecological studies in tropical fish communities*. University Press, Cambridge. 76pp.
- Jewe-McConnell, R.H., 1994. The changing ecosystem of Lake Victoria, East Africa. *Fresh water Forum* 4: 76-89.
- Jewe-McConnell, R.H., 1997. EAFFRO and after: a guide to key events affecting fish communities in Lake Victoria (East Africa). *South African Journal of Science*: 570-574.
- Juczkovich J.J., S.P. Borgatti, J.C. Johnson & M.G. Everetti, 2003. Defining and Measuring Trophic Role similarity in food webs using regular equivalence. *Journal of Theoretical Biology* 220: 303-321.
- Luecke, C. & A.H. Litt, 1987. Effects of predation by *Chaoborus flavicans* on crustacean zooplankton of Lake Lenore, Washington. *Freshwater Biology* 18: 185-192.
- MacLeod, N.A., & D.R. Burton 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1919-1925.
- Mace, P.M., 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish and Fisheries*. 2, 2-32.
- Mann, K.H., 1998. Production and the use of detritus in various freshwater, estuarine and coastal marine ecosystems. *Limnol. Oceanogr.* 33: 910-930.
- Manetta, G.I., E. Benedicto-Cecilio, & M.Martinelli, 2003. Carbon sources and trophic position of the main species of fishes of Baia River, Parana River flood plain, Brazil. *Brazilian Journal of Biology* 63: 283-290
- Magnusson, J.J., W.M. Tonn, A. Banerjee, J. Toivonem, O. Sanchez & M. Rash, 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. *Ecology* 79: 2942-2956.
- Magnusson, W.E., M.C. Araujo, R. Cintra, A.P. Lima, L.A. Martinelli, T.M. Sanaiotti, H.L. Vasconcelos & R.L. Victoria, 1999. Contributions of C₃ and C₄ plants to higher trophic levels in an Amazonian savanna. *Oecologia* 119: 91-96
- Magurran, A.E., 1990. The adaptive significance of schooling as antipredator defence in fish. *Ann. Zool. Fenn.* 27: 51-6.

- ako, S.A. & M.L.F. Estep, 1985. Microbial alteration of nitrogen and carbon isotope compositions of organic matter. *Organic Geochemistry* 6: 787-790.
- alakoff, D., 1997. Extinction on the high seas. *Science* 277: 486-488.
- alvestuto, S., 1974. The Fishes of Lake Naivasha: Their Biology, Exploitation and Management. Mimeographed report to the Director of Fisheries, Government of Kenya, Nairobi, Kenya: 37pp.
- ancinelli, G., L. Costantini & L. Rossi, 2002. Cascading effects of predatory fish exclusion on the detritus-based food web of a lake littoral zone (Lake Vico, Central Italy). *Oecologia* 133: 402-411.
- angel, 2000. Trade offs between fish habitat and fishing mortality and the role of reserves. *Bulletin of Marine Science* 66 (3): 663-674.
- archetti, M.P., P.B. Moyle & R. Levine, 2004. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49: 646-661.
- arquardt, M. M. Infield, & A. Namara., 1994. *Socio-Economic Survey of Communities in the Buffer Zone of Lake Mburo National Park*, Lake Mburo Community Conservation Project, Kampala.
- artin, N.V, 1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. *Transactions American Fisheries Society*. 96: 415-422.
- artin, PS 1970. Pleistocene niches for alien animals. Ecological Energetics of a Homeothermic Predator, The Short-Tailed Shrew. *Ecology* 54(5):1166-1187
- artinez, N.D, 1991. Artifacts or attributes? effects of resolution on the little Rock Lake food web. *Ecological Monographs* 61: 367-392.
- artinez, N.D, 1993. Effects of resolution on food web structure. *Oikos* 66: 403-412.
- artinez, N.D, 1994. Scale-dependent constraints on food web structure. *American Naturalist*: 144: 935-953.
- artinez, N.D, B.A. Hawkins, H.A. Dawah, & B.P. Feifarek, 1999. Effects of sampling effort on characterization of food web structure. *Ecology* 80 (3): 1044-1055.
- arrow, J.V., K.J. Killgore and J.J. Hoover, 1991. Growth of black bass in different densities of *Hydrilla*. Procs 25th Annual Meeting, Aquatic Plant Control Research Program, 26-30 November 1990, Orlando, Florida. Final Report, pp.58-63. Environmental Laboratory, Waterways Experimental Station, Corps of Engineers, Vicksburg, Miss., USA.
- avuti, K., J. Moreau, J. Munyandorero & P.D. Plisnier, 1996. Analysis of trophic relationships in two shallow equatorial lakes, Naivasha, Kenya and Lake Ihema, Rwanda. *Hydrobiologia* 321: 89-100.
- abazi D, 1999. Trophic Structure and Diversity of Haplochromines among the Kyoga Minor lakes. (MSc. Thesis Makerere University, Kampala, Uganda).
- abazi D., R. Ogutu-Ohwayo, S.B. Wandera & Y. Kiziito, 2004. Fish species and trophic diversity of haplochromine cichlids in the Kyoga satellite lakes (Uganda). *African Journal of ecology* 42: 59-68.

- McCann, K. & A. Hastings, 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London (B)* 264: 1249-1254.
- McCann, K., A. Hastings & G.R. Huxel, 1998. Weak trophic interactions and the balance of nature. *Nature (London)* 395: 794-798.
- McCann, 2000. The diversity-stability debate. *Nature* 405: 228-233.
- McClelland, J.W., and I. Valiela, 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. *Marine Ecology Progress Series* 168: 259-271.
- Meyer, A., T.D. Kocher, P. Basasibwaki, & A.C. Wilson, 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondria DNA sequences. *Nature* 347: 550-553.
- Michener, R.H. & D.M. Shell, 1994. Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha K. Michener, R.H. (Eds). *Stable isotopes in ecology and environmental sciences*. Blackwell, Oxford, pp. 138-157.
- Miller, G.L., G.E. Stratton, F.R. Miller & E.A. Hebets, 1998. Geographical variation in male courtship behaviour and sexual isolation in wolf spiders of the genus *Schizocosa*. *Anim. Behav.* 56: 937-951.
- Minnski, 1993. Predation risk and feeding behaviour. In: Pitcher Tony J. (Ed). *Behaviour of Teleost Fishes*. Chapman and Hall, London.
- Mills, E.L., J.H. Leach, J.T. Carlton & C.L. Secor., 1994. Exotic species and the integrity of the Great Lakes. *BioScience* 44: 666-676.
- Minagawa, M.H., & E. Wada., 1984. Step wise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochimica et Cosmochimica Acta* 48: 611-1140.
- Moore J.C., E.L. Berlow, D.C. Cleman, P.C. deRuiter, O. Dong, A. Hastings, N. C. Johnson, K.S. McCann, K. Melville, P.J. Morin, K. Nadelhoffer, A.D. Rosemond, D.M. Post, J.L. Sabo, K.M. Scow, M.J. Vanni & D.H. Wall, 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7: 584-600.
- Muchiri, S. Mucai, P.J.B. Hart and D.M. Harper, 1995. The persistence of two introduced tilapia species in Lake Naivasha, Kenya, in the face of environmental variability and fishing pressure. In: *The Impact of Species Changes in African Lakes* (eds T.J. Pitcher and P.J.B. Hart): 299-319. Chapman & Hall, London.
- Murdoch, W.W., 1966. Community structure, population control and competition – a critique. *American Naturalist* 100: 219-226.
- Mugidde, R., 1993. Changes in primary productivity and biomass in Lake Victoria (Uganda). *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 25: 846-849.
- Mugidde, R. 2001. Nutrient status and planktonic nitrogen fixation in Lake Victoria, Africa. Ph.D thesis, University of Waterloo, Ontario, Canada. 191 p.
- Mugisha, A.R., 2003. Fisheries in National Parks. A Case study of Lake Mburo National Park, Uganda. pp. 430-443. In T.L. Crisman, L.J. Chapman, C.A. Chapman and L.S. Kaufman (eds). *Conservation, Ecology, and Management of African Fresh Waters*. University Press of Florida.

- Obwozi, L.I., 2002. Exploitation and management of the artisanal fisheries in the Ugandan waters of Lake Victoria. 260 pp. PhD Thesis, University of Hull, UK.
- Obaza-Ndawula, L. 1984. Food and feeding habits of *Clarias mossambicus* from four areas in the Lake Victoria basin, East Africa. *Environmental Biology of Fishes* 10 (1): 69-76.
- Olwayi, K.J.F., 1999. Population characteristics of *Oreochromis esculentus* in satellite lakes of the Victoria and Kyoga lake basins. MSc. Thesis, Makerere University, Kampala, Uganda, pp. 86.
- Okamura Y., M. Horinouchi., T. Nakai & M. Sano, 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. *Ichthyol Res* 50: 15-22.
- Okano, S., H. Miyasaka, & N. Kuhara, 1999. Terrestrial aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80: 2435-2441.
- Okuma, A., & M. Infield, 1998. *The influence of a Community Conservation Programme on farmers and Pastoralist Communities, Lake Mburo National Park Uganda: Report of a Socio-Economic Survey carried out under the Community Conservation for Uganda Wildlife Authority Project*, Uganda Wildlife Authority, Makerere University Institute of Social Research and African Wildlife Foundation, Kampala
- Okumulemo G., 1997. Distribution, relative abundance, population structure and food of surviving haplochromines cichlids in the littoral areas of Napoleon Gulf (Lake Victoria). MSc. Thesis, Makerere University, Kampala, Uganda.
- Okumulemo G, R. Ogutu-Ohwayo, S.B. Wandera & D. Mbabazi, 2003. Conservation of fish species diversity in the Victoria and Kyoga lake basins. *Uganda Journal of Agricultural Sciences* 8: 231-238
- National Research Council, 1999. Sustaining Marine Fisheries, Report of committee on ecosystem management for sustainable marine fisheries, oceans studies board, 168pp
- Nelson, J.S., (Ed.), 1994. *Fishes of the World*. Wiley, New York.
- NMFS (National Marine Fisheries Service), 1999. Ecosystem-based fishery management: A report to Congress by the National Marine Fisheries Service Ecosystem Principles Advisory Panel. NMFS, Silver Spring, Maryland. 164 pp.
- NOAA (National Oceanic and Atmospheric Administration). 1996. Magnuson-Stevens Fishery Management and Conservation Act amended through 11 October 1996. NOAA Technical Memorandum NMFS-F/SPO-23.
- Northcote, T.G., 1988. Fish in the structure and function of freshwater ecosystems: a 'top-down' view. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 361-379.
- NRC (National Research Council), 1999. Sustaining marine fisheries. National Academy Press, Washington, D.C.
- Ochumba, P.B.O. & D.I. Kibara 1989. Observations on blue green algal blooms in open waters of lake Victoria, Kenya. *African Journal of Ecology* 27: 23-34.
- Odum E.P., 1985. Trends to be Expected in Stressed Ecosystems. *BioScience* 35: 419-422.
- Odum, E.P., 1989. *Ecology and Our Endangered Life-Support Systems*. Sinauer Associates, Massachusetts, 283 pp.

- airi, J. & S. Dadzie 1988. The food of the Nile perch, *Lates niloticus* (L.) after disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). *Journal Fish Biology* 32:571-577.
- ututu-Ohwayo, R., 1985. The effects of predation by the Nile perch *Lates niloticus* (Linné) introduced into Lake Kyoga and Lake Victoria. *FAO Fisheries report* 335: 18-41.
- ututu-Ohwayo, R. 1990a. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology and Fisheries*, 27: 31-96.
- ututu-Ohwayo, R. 1990b. The reduction in fish species in Lakes Victoria and Kyoga (East Africa) following human exploitation and introduction of non-native fishes. *Journal Fish Biology* 37 (Suppl.A), 207-8.
- ututu-Ohwayo, R., 1990c. Changes in the prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). *Journal of Fish Biology* 37: 55-63.
- ututu-Ohwayo, R. & R.E. Hecky 1991. Fish introductions in Africa and some of their implications. *Canadian Journal of Fisheries and Aquatic Sciences* 48 (Suppl.1):8- 12.
- ututu-Ohwayo, R., 1993. The effects of predation by the Nile perch, *Lates niloticus* L., on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. *Conservation Biology* 7: 701-711.
- ututu-Ohwayo, 1994. Adjustments in Fish stocks and in Life History Characteristics of Nile perch, *Lates niloticus* L. in Lakes Victoria, Kyoga and Nabugabo. Ph.D thesis. 213 pp. Department of Zoology. University of Manitoba, Winnipeg, Manitoba.
- ututu-Ohwayo R., 1995. Diversity and stability of fish stocks in lakes Victoria, Kyoga and Nabugabo after establishment of introduced species 59-82 pp. *The Impact of Species Changes in African Lakes*. T.J. Pitcher and P.J.B. Hart. Eds. Chapman & Hall, London, Great Britain.
- ututu-Ohwayo, R., R.E. Hecky, A.S. Cohen & L. Kaufman, 1997. Human impacts on African Great lakes. *Environmental Biology of Fishes* 50: 117-131.
- ututu-Ohwayo, R., S.B. Wandera, G. Namulemo & D. Mbabazi, 1998. Efforts towards conservation of endangered fish species in the Victoria and Kyoga lake basins. A paper presented for the International Conference for the Paradi Association and the Fisheries Society of Africa. African Fishes and Fisheries: Diversity and utilizations, Grahamstone, South Africa, 13-19 September 1998.
- ututu-Ohwayo, R. 1998. The Nile perch fishery. In FIRI: "Towards sustainable development and management of of the fishries resources of lakes Victoria and Kyoga. Proceedings of the stakeholders workshop on; the fisheries of Lake Victoria and Kyoga, 24-25 September, 1998, Jinja, Uganda.
- ututu-Ohwayo, R., 1999. Deterioration in length-weight relationships of Nile perch, *Lates niloticus* L. in Lakes, Victoria, Kyoga and Nabugabo. *Hydrobiologia* 403: 81-86.
- Okedi, J.Y., 1972. The food and feeding habits of the small mormyrid fishes of Lake Victoria, East Africa. *Afr. J. Trop. Hydriobiol. Fish.* 2: 1-11.
- Okey, T.A. & G.A. Harrington, 1999. Criteria for designing ecosystem-based, experimental management programs: Effects of bottom trawling on the Bering Sea ecosystem. In:

- Ecosystem considerations for fisheries management, University of Alaska Sea Grant, AK-SG-99-01, Fairbanks. 622 pp.
- Oksanen, I., S.D. Fretwell, J. Arruda, & P. Niemala., 1981. Exploitation ecosystems in gradients of primary productivity. *American naturalist* 118: 240-261.
- O'Connor, P.J., A.P. Covich, F.N. Scatena & L.L. Loope, 2000. Non-indigenous bamboo among headwater streams of the Luquillo Mountains, Puerto Rico: Leaf fall, aquatic leaf decay and patterns of invasion. *Journal of Tropical Ecology* 16: 499-516.
- O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. *Bioscience* 38: 328-336.
- Oden, J.D. & D.A. Jackson, 2001. Spatial isolation and fish communities in drainage lakes. *Oecologia* 127: 572-585.
- Olive, P.J.W. 1993. Management of the exploitation of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas. *Aquatic Conservation* 3, 1-24.
- Olowo, J.P., 1998. The impact of the introduced Nile perch (*Lates niloticus*) on the foraging ecology of non-cichlid predators in the Lake Victoria basin. MSc. Thesis, University of Florida, Gainesville. pp. 173
- Olowo, J.P. & L.J. Chapman, 1999. Trophic shifts in predatory catfishes following the introduction of Nile perch into Lake Victoria. *African Journal of ecology* 37: 457-470.
- O'Reilly C.M., R.E. Hecky, A.S. Cohen & P.D. Pilsner, 2002. Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. *Limnology and Oceanography* 47 (1): 306-309.
- Orbach-Meza F.L. & S.B. Saila, 1978. Application of a Polynomial Distribution Lag Model to the Maine Lobster, Fishery. *Transactions of the American Fisheries Society* 107: 402-411.
- Osenberg, C.W. & G.G. Mittlebach, 1996. The relative importance of resource limitation and predator limitation in food chains. Pp. 134-148 in G.A. Polis and K.O. Winemiller (Eds). Food webs: intergration of patterns and dynamics. Chapman and Hall, New York, New York, USA.
- Owens, N.J.P., 1987. Natural variation in ^{15}N in the marine environment. *Advances in Marine Biology* 119: 635-645.
- Pace, M.L., J.J. Cole, S.R. Carpenter & J.F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecology and Evolution* 14: 483-488.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75.
- Paine, R.T., 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of animal Ecology* 49: 667-685.
- Paine, 1988. Food webs: road maps of interactions grist for theoretical development? *Ecology* 69: 1648-1654.
- Palmer, C., J. O'Keeffe, A. Palmer, T. Dunne & S. Radloff, 1993. Macroinvertebrate functional feeding groups in the middle and the lower reaches of the Buffalo River, eastern Cape, South Africa. I. Dietary variability. *Freshwater Biology* 29: 441-453.

- Polis, T.R., 1996. The impact of industrial fisheries on the trophic structure of marine ecosystems. *In* Food webs: Intergration of Patterns and Dynamics (Polis, G.A & K.O. Winemiller, eds), pp. 352-357. New York: Chapman & Hall.
- Polunin, L. & P. Green, 1985. Intraspecific feeding specialization and population dynamics. *Behavioral Ecology* (Eds). Silbey, R.M. and R.H. Smith pp. 207-226. Blackwell Press, Oxford, UK.
- Polunin, D., V. Christensen, J. Dalsgaard, R. Froese & F. Torres Jr, 1998. Fishing down marine food webs. *Science*. 279: 860-863.
- Polunin, D., V. Christensen, S. Guénette, T.J. Pitcher, U.R. Sumaila, C.J. Walters, R. Watson & D. Zeller, 2002. Towards sustainability in world fisheries. *Nature*: 418: 689-695.
- Polunin, B.J., G.R. Martin & A.H., Arthington, 1995. The feeding ecology of freshwater fishes in two rivers of the Australian wet tropics. *Environmental Biology of Fishes* 43: 85-103.
- Polunin, O.L., P.T. McPhearson, T.M. Casey & P.J. Morin, 1999. Environmental warming alters food web structure and ecosystem functioning. *Nature* 402: 69-72.
- Polunin, L., 1991. Behavioural response to predators reverses the outcome of competition between prey species. *Behavioral Ecology and Sociobiology* 28: 101-105.
- Polunin, L., S. Diehl, L. Johansson, G. Andersson & S.F. Hamrin., 1992. Trophic interactions in temperate lake ecosystems – a test of food chain theory. *American Naturalist* 140: 59-84.
- Polunin, L., J. Bengetsson, B. Menge, & m. power, 1996. Productivity and consumer regulation – concepts, patterns and mechanisms. *In* Polis, G.A. and winemiller, K.O. (eds.), Food webs: Intergration of Patterns and Dynamics. Chapman & Hall, pp 396-434.
- Polunin, L. & P. Eklov, 1995. Prey refuges affecting interactions between piscivorous perch (*Perca fluviatilis*) and juvenile perch and roach (*Rutilus rutilus*). *Ecology* 76: 70-81.
- Polunin, L., 1999. Trophic cascades: abiding heterogeneity and trophic level concept at the end of the road. *Oikos* 85: 385-166.
- Polunin, L. & L.B. Crowder, 1997. Fish-habitat interactions mediated via ontogenetic niche shift. *In*: Jeppsen, E., Søndergaard, Ma., Søndergaard, Mo. And Christoffersen, K. (eds), The structuring role of submerged macrophytes in lakes. Springer-Verlag, pp. 3-23.
- Polunin, B.J. & B. Fry, 1987. Stable isotopes in ecosystem studies. *Annual Reviews of Ecology and Systematics*. 18: 293-320.
- Polunin, B.J. L. Deegan, J. Helfrich, J.E. Hobbie, M. Hullar, B. Moller, T.E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M.A. Lock, D.M. McKinley, M.C. Miller, J. R. Vestalo, R. Ventullo & G. Volki, 1993. Biological responses of a tundra river to fertilization. *Ecology* 74: 653-672.
- Petr, T., 2000. Interactions between fish and aquatic macrophytes in inland waters. A review. *FAO Fisheries Technical Paper*. No. 396. Rome, FAO. 185p.
- Pielou, E.C., 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley & Sons, New York.

- G.R., J.S., Pet, W.A.H.P., Guruge, J. Vijverberg & W.L.T. Van Densen, 1999. Resource partitioning along three niche dimensions in a size structured tropical fish assemblage. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1241-1254
- terse, A.H., 1981. *Hydrilla verticillata*: a review. *Abstracts on Tropical Agriculture* 7: 9-34.
- nce, C.L., J.B. Rasmussen & W.C. Leggett, 1994. Littoral fish communities in Southern Quebec Lakes: Relationships with limnological and prey resources variables, *Canadian Journal of Fisheries and Aquatic Science*, 51: 1128-1138.
- megar, J.K. & N.V.C. Polunin, 1999. Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissue: implications for the study of trophic interactions. *Functional Ecology* 13: 225-231.
- megar, J.K., N. Campbell & N.V. Polunin, 2001. Unusual trophic fractionation patterns observed for fish host parasite trophic relationships. *Journal of Fish Biology* 59: 4994-503.
- megar, J.K., S. Jennings, M. O'Brien & V.C.N. Polunin, 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Animal Ecology* 39: 377-390.
- anas, D., M. Desrosiers, S-R. Groulx, S. Paquet & R. Carignan, 2000. Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. *Canadian Journal Fisheries and Aquatic Sciences* 57(suppl.2): 136-145.
- olis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *American Naturalist* 123: 352-368
- olis, GA 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American. Naturalist* 138:123-155.
- olis, G.A., C.A. Myers & R.D. Holt, 1989. The ecology and evolution of intraguild predation: potential competitors that beat each other. *Annual Reviews of Ecology and Systematics*. 20: 297-330.
- olis, S. G.A. & S.D. Hurd, 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147: 396-423.
- olis, G.A., & D.R. Strong., 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813-846.
- olis, G.A., SD. Hurd, C.T. Jackson & F. Sanchez-Piñero, 1997. El-Niño effects on the dynamics and control of a terrestrial island ecosystem in the Gulf of California. *Ecology* 78: 1884-1897.
- olunin, N.V.C., 1984. The decomposition of emergent macrophytes in freshwater. In *Advances in ecological research*. Vol. 14 Edited by A. MacFyden and E.D. Fotd. Academic Press Inc., London pp. 115-166.
- pe, J.G. & T.C. Macer, 1996. An evaluation of the stock structure of North Sea cod, haddock and Whiting since 1920, together with a consideration of fisheries and predation effects on their biomass and recruitment. *ICES J. Mar. Sci.* 53: 1157-1169.
- st, D.M., M.L. Pace, & N.G. Hairston., 2000. Ecosystem size determines food chain length in lakes. *Nature* 405: 1047-1049.

- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83 (3): 703-718
- Post, D.M., S.R. Carpenter, D.L. Christensen, K.L. Cottingham, J.F. Kitchell & D.E. Schindler., 1997. Seasonal effects of variable recruitment of a dominant piscivore on pelagic food web structure. *Limnology and Oceanography* 42(4): 722-729.
- Postel, S., & S. R. Carpenter, 1997. Freshwater ecosystems services. In: Daily, G.C. (Ed.), *Nature's Services*. Island Press, Washington, DC, pp. 195-214.
- Powers, M.E., 1990. Effects of fish in river food webs. *Science* 250: 811-316.
- Rejs, A., 1984. Herbivory by temperate freshwater fishes and its consequences. *Environmental Biology of Fishes* 10: 181-296.
- Reinthal, P.N., & G.W. Kling., 1994. Exotic species, trophic interactions, and ecosystem dynamics: a case study of Lake Victoria. 295-313 pp in D. Stouder, K., Fresh, & R. Feller, editors. *Theory and Applications in fish feeding ecology*, University of South Carolina Press, Columbia, South Carolina, USA.
- Ramlal, P.S., C. Anema, E. cummings et al., 1991. Macrophyte and algal studies of some lakes in the Mackenzie Delta and the Toktoyaktuk Peninsula, 1985-1986. *Canadian Data Report of Fisheries and Aquatic Sciences*, 839, 87pp.
- Ramsar Convention Bureau, 2004. The Annotated Ramsar List: Uganda. www.ramsar.org/profiles_uganda.htm
- Rasmussen, J.B., D.J. Rowan, D.R.S. Lean & J.H. Carey, 1990. Food chain structure affects PCB levels in pelagic fish from Ontario lakes. *Canadian Journal of Fisheries and Aquatic sciences* 47: 2030-2038.
- Rau, G.H., 1978. Carbon-13 depletion in a subalpine lake: carbon flow implications. *Science* 201: 123-155.
- Rau, G.H., 1980. Carbon-13/carbon-12 variation in subalpine lake aquatic insects: food sources implications. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 742-746
- Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olson, H.A. Schafer, & I.R. Kaplan, 1983. Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* 64: 1314-1318.
- Rau, G.H., D.G. Ainley, J.L. Bengson, J.J. Torres, & T.L. Hopkins, 1992. $^{14}\text{N}/^{15}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals and fish: implications for diet and trophic structure. *Marine Ecology Progress Series* 84: 1-8
- Ricciardi, A. & J.B. Rasmussen, 1998. Predicting the identity and impact of future Biological invaders: a priority for aquatic resources management. *Canadian Journal of Fisheries and Aquatic Science* 55: 1759-1765.
- Richter, B.D., D.P. Braun, M.A. Mendelson & L.L. Master, 1997. Threats to imperilled freshwater fauna. *Conservation Biology* 11:1081-1093.
- Ricklefs, R.E, 1990. *Ecology*. W.H. Freeman, New York, New York, USA.
- Rodriguez, M.A. & W.M. Lewis, 1997. Structure of fish assemblages along environmental gradients in flood plain lakes of the Orinoco River. *Ecol. Monogr.* 67: 109-128.
- Rohlf, F.J., 1963. Classification of *Aedes* by numerical taxonomic methods (Diptera: Culicidae). *Ann. Entomol. Soc. Am.* 56: 798-804.

- Wass, S.T., 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986: 352-388.
- Winick, J.S. & M.J. Winterbourn, 1985. Benthic faunas and food resources of insects in small New Zealand streams subjected to different forestry practices. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 22: 2148-2152.
- Winick, J.S. & M.J. Winterbourn, 1986. Stable carbon isotopes and carbon flow in ecosystems. *Bioscience* 36: 171-177.
- Winick, J.S., & M.J. Schoeninger., 1991. Stable carbon isotopes and carbon flow in ecosystems. *Bioscience* 36: 171-177.
- Wass, R.W., 1987. The role of large herbivores in nutrient cycling of tropical savannas. In B.H. Walker, editor. *Determinants of tropical savannas*. IRL Press, Oxford, England. pp 67-91
- Wozas, L.P. & W.E. Odum, 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* 77: 101-106.
- Walla, E., E. Ballesteros & R.M. Starr, 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and Conservation needs. *Fisheries* 26: 23-30.
- Wano, M., M. Shimizu & Y. Nose, 1984. Food habits of teleostean reef fishes in Okinawa Island, southern Japan. *Univ. Mus. Univ. Tokyo Bulletin* 25: 1-128
- Wand-Jensen, K. & M. Sondergaard, 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Intera. Rev. ges. Hydrobiologie* 66: 109-119.
- Wärvala, J., K. Aulio, H. Mölsä, m. Rajasitta, J. Salo & I. Vuorinen, 1984. Factors behind the exceptionally high fish yield in the lake Pyhäjärvi, southwestern Finland-hypothesis on biological regulation of fish production. *Aqua Fennica* 14: 49-57.
- Wavino, J., E.A. Marshall & R.A. Stein, 1992. Bluegill growth as modified by plant density: an exploration of underlying mechanisms. *Oecologia* 89: 153-60.
- Waus, M.H., M.J. Vanni, T.E. Wissing, M.T. Bremigan, J.E. Garvey & R.A. Stein., 1997. Nitrogen and phosphorous excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology and Oceanography*. 42: 1386-1397.
- Schindler, D.E., 1992. Nutrient regeneration by sockeye salmon (*Oncorhynchus nerka*) fry and subsequent effects on zooplankton and phytoplankton. *Canadian Journal of Fisheries Aquatic Sciences* 49: 2498-2506.
- Schindler, D.E. & M.D. Scheuerell, 2002. Habitat coupling in lake ecosystems. *Oikos* 98: 177-189.
- Schindler, D.E., J.F. Kitchell, X. He, S.R. Carpenter, J.R. Hodgson & K.L. Cottingham, 1993. Food web structure and phosphorous cycling in lakes. *Transactions American Fisheries Society* 122: 756-772.
- Schindler, D.E., S.R. Carpenter & K.L. Cottingham 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. In: Polis, G.A. and Winemiller, K.O. (eds), *Food webs – Intergration of patterns and dynamics*. Chapman & Hall. Pp. 96-105.

- hindler, D.E., S.R. Carpenter, J.J. Cole, J.F. Kitchell & M.L. Pace, 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* 277: 248-251.
- hindler, D.E., J.R. Hodgson, & J.F. Kitchell, 1997. Density-dependent changes in individual foraging specialization of largemouth bass. *Oecologia* 110: 592-600.
- hmitz, O. J., A.P. Beckerman & K.M. O'Brien, 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78: 1388-1399.
- holz, C.A, B.R. Rosendahl, J.W. Wesfelt & N. Rach., 1990. Results of high- resolution echo-sounding of Lake Victoria. *Journal of African Earthsciences* 11: 25-32.
- hofield, P.J. & L.J. Chapman, 1999. Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. *Environmental Biology of Fishes* 55: 343-358.
- hofield, P.J. & L.J. Chapman., 2000. Hypoxia tolerance of introduced Nile perch: Implications for survival of indigenous fishes in the Lake Victoria basin. *African Zoology* 35: 35-42.
- hausen, O., 1996. *Lake Victoria Rock Cichlids: Taxonomy, Ecology and Distribution*. Verduyn Cichlids, Zevenhuizen, pp. 1-304.
- hausen, O., J.J.M. van Alphen & F. Witte, 1997a. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808-1811.
- hausen, O., F. Witte, E.F. Katunzi, J. Smits & N. Bouton, 1997b. Patterns of the remnant cichlid fauna in southern Lake Victoria. *Conservation Biology* 11: 890-904.
- hausen, O., 1999. A reconsideration of the ecological composition of the Lake Victoria cichlid species flock before and after the Nile perch upsurge. Pp 281-293 In W.L.T. van Densen and M.G. Morris, (eds). *Fish and fisheries of lakes and reservoirs in Southeast Asia and Africa*. Westbury Publishing, Otley, United Kingdom.
- hausen, O., J.J.M. van Alphen & F. Witte., 2003. Implications of eutrophication for vision, behavioral ecology, and species coexistence – a theoretical framework. Pp268-287. In: T.L. Crisman, L.J. Chapman, C.A. Chapman & L.S. Kaufman, (Eds) *Conservation, Ecology, and Management of African Freshwaters*. University of Florida.
- earer, G. & D.H. Kohl, 1989. Estimates of N_2 fixation in ecosystems: the need for and basis of the ^{15}N natural abundance method pp 342-374. In: *Stable isotopes in ecological*. (eds), P.W. Rundell, J.R. Ehleringer and K.A. Nagy. Springer-Verlag, New York.
- earer, G.B., D.H. Kohl & S.H. Chien, 1978. The nitrogen-15 abundance in a wide variety of soils. *Soil Sci. Soc. Am. J.* 42: 899-902.
- uter, B.J., M.L. Jones., R.M. Korver, & N.P. Lester., 1998. A general life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2161-2177.
- oliqui, A. Q., 1977. Lake Naivasha, Kenya, East Africa. Fishery and its management together with a note on the food habits of fish. *Biol. Conserv.* 12: 217-218.
- iberloff, D. & T. Dayan, 1991. The guild concept and the structure of ecological communities. *Annual Reviews of Ecology and Systematics* 22: 115-143.

- ... G.M., 2003. A new digital map for Lake Victoria, East Africa. *Bulletin of the International Decade for East African Lakes (IDEAL)*.
<http://www.d.umn.edu/Ilo/Ideal/Su03.pdf>.
- ... G.M., 2004. Phytoplankton production in Lake Victoria, East Africa. pp. 213. MSc. Thesis, University of Waterloo, Ontario, Canada.
- ... P.H.A. & R.R. Sokal, 1973. Numerical taxonomy – The principles and practice of numerical classification. W.H. Freeman, San Francisco. xv + 573pp
- ... W.G. & J.E. Bowerman, 1988. Omnivory and food chain length in zooplankton food webs. *Ecology* 69: 418-425.
- ... M.M., L.F.W. Lesack & D. Huebert, 2000. The influence of water transparency on the distribution and abundance of macrophytes among lakes of the Mackenzie Delta, Western Canadian Arctic. *Freshwater Biology* 47: 2123-2135.
- ... M.M. L.F.W. Lesak & D. Huebert, 2002. The influence of water transparency on the distribution and abundance of macrophytes among lakes of the Mackenzie Delta, Western Canadian Arctic. *Freshwater Biology* 47: 2123-2135.
- ... L., 1995. Taking a new look at life through the functional lens. *Science*: 316-317.
- ... J.H., & M. Schumacher, 2000. Ecosystem structure before fishing. *Fisheries Research* 44: 201-205.
- ... J.A.E., T. Bohlin, L. Henrikson, B.I. Nilsson, H.G. Nyman, H.G. Oscarsson & P. Larsson., 1978. Effects of fish removal from a small lake. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen* 20: 794-801.
- ... L.S.L., 1989. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. In: Rundel P.W., J.R. Ehleringer, K.A. Nagy (Eds). *Stable isotopes in ecological research*. Springer, New York, pp. 24-141.
- ... R.W., A. Bjpai & T. Adams, 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. *Ecology* 78: 2258-2262.
- ... H.K., T.A. Johnston, W.C. Leggett, R.A. Bodaly, R.R. Doucet & R.A. Curyak, 2003. Trophic positions and mercury bioaccumulation in rainbow smelt (*Osmerus mordax*) and native forage fishes in northwestern Ontario lakes. *Ecosystems* 6: 289-299.
- ... B.W., 1993. Effects of Streamside vegetation on macroinvertebrate communities of white lay Creek in Eastern North America: Proceedings of the Academy of Natural sciences of Philadelphia 144: 291-340.
- ... G.H., & E.B. Worthington, 1940. Notes on food of fish in Haweswater. *Journal of Animal Ecology* 9: 183-187.
- ... C.J. & L.B. Cahoon, 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology Progress Series* 95: 19-24
- ... L.L., T.W. Boutton, K.G. Tesdahl, N.A. Slade, 1983. Fractionation and turnover of stable carbon in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57: 32-37.
- ... D., J. Knops, D. Wedin, P. Reich, M. Ritchie & E. Siemann, 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302.

- Wada, H., & E. Wada, 1990. Use of $^{15}\text{N}/^{14}\text{N}$ ratios to evaluate the food source of the mysid, *Neomysis intermedia* Czerniawsky in a eutrophic lake in Japan. *Hydrobiologia* 194: 85-90.
- Yoshiyama, M., 1999. Species co-existence: Ecological and evolutionary perspectives. Oxford, Blackwell Scientific.
- Wassenaar, E., 1933. Scientific results of Cambridge expedition to the East African lakes 1930. 1-11. The cichlid fishes. *Journal of Linnaea Society of London* 38:309-341.
- Wango, T., 1988. Recent trends in the fisheries of Lake Kyoga. Pp 140-151 In: CIFA. Report of the third session of the sub-committee for the development and management of the fisheries of Lake Victoria. 4-5 October 1984. Jinja, Uganda. *FAO Fisheries report* 335. FAO, Rome
- Vadeboncoeur, Y., M.J. Vander Zanden, & D.M. Lodge, 2002. Putting the lake back together: reintegrating benthic pathways into lake food webs. *BioScience* 52: 44-54.
- Vadeboncoeur, Y., E. Jeppesen, M.J. Vander Zanden, H. Schierup, K. Christoffersen & D. M. Lodge, 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* 48 (4): 1408-1418.
- Vander Zanden, M.J., & J.B. Rasmussen., 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs* 66: 451-477.
- Vander Zanden, M.J., G. Cabana, & J.B. Rasmussen., 1997. Comparing the trophic position of littoral fish estimated using stable nitrogen isotopes ($\delta^{15}\text{N}$) and dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1142-1158.
- Vander Zanden, M.J. & J.B Rasmussen, 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology* 80: 1395-1404.
- Vander Zanden, m.J., B.J. Shuter, N.P. Lester & J.B. Rasmussen 2000. Within and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and aquatic sciences* 57: 725-731.
- Vander Zanden, M.J. & J.B. Rasmussen, 2001. Variation in ^{15}N and ^{13}C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography* 46: 2061-2066.
- Vander Zanden, M.J., and R.B. Rasmussen. 2002. Food web perspectives on studies of bass populations in north-temperate lakes. Pages 173-184 in D.P. Philipp and M.S. Ridgway, editors. *Black Bass: Ecology, Conservation and Management*. American Fisheries Society Symposium 31, Bethesda, Maryland.
- Vander zanden, M.J., Casselman J.M., & Rasmussen J.B., 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature (Lond.)*, 401: 464-467.
- Vander Zanden, M.J. & Y. Vadeboncoeur, 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83: 2152-2161.
- Wetzel, M.J. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. In: Polis, G.A. and Winemiller, K.O. (eds), *Food webs - Intergration of patterns and dynamics*. Chapman & Hall. Pp. 81-95.

- Minni, M.J., A.S. Flecker, J.M. Hood & J.I. Headworth, 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters* 5: 285-293.
- Buskirk, J. & D.C. Smith, 1989. Individual variation in winter foraging of Black-capped Chickadees. *Behav. Ecol. Sociobiol.* 24: 358-363.
- M.M., M. Pettrere Jr., L.A. Martinelli & A.A. Mozeto, 1999. The dietary regime of detritivorous fish from the River Jacaré-Pepire, Brasil. *Fish. Manag. Ecol.* 6: 121-132.
- Virginia, R.A., W.M. Jarrell, P.W. Rundell, G. shearer & D.H. Kohl, 1989. The use of variation in the natural abundance of ^{15}N to assess symbiotic nitrogen fixation by woody plants. pp 345-394. *In: Stable isotopes in ecological research* (eds), P.W. Rundel, J.R. Ehleringer and K.A. Nagy. Springer-Verlag, New York.
- Erschuren, D., T.C. Johson, H. J. Kling, D.N. Edgington, P.R. Leavitt, E.T. Brown, M.R. Talbot & R.E. Hecky, 2002. *Proceedings of the Royal Society of London (B)* 269: 289-294.
- Isser, S.A, 1964. A study in the decomposition of *Cyperus papyrus* in the swamps of Uganda, in natural peat deposits, as well as in the presence of various additives. *East Afr. agr. For. J.* 29: 268-287.
- Mitousek, P.M., C.M D'Antonio, L.L Loope & R. Westbrooks., 1996. Biological invasions as global environmental change. *American Scientist.* 84: 468-478.
- Mitousek, P.M., H.A. Mooney, J. Lubchenco & J.M. Melillo, 1997. Human domination of Earth's ecosystems. *Science*: 277: 494-499.
- Wada, E. & A. Hattori, 1978. Nitrogen isotope effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. *Geomicrobiology Journal* 1: 85-101.
- Wanda, F.M., T. Twongo & P. Denny, 2001. The impacts of Water hyacinth *Eichhornia crassipes* (Mart) Solms on the abundance and diversity of aquatic macro-invertebrates along the shores of norther Lake Victoria, Uganda. *Hydrobiologia* 452: 79-88.
- Wanda, F.M., 2003. Resurgence potential of water hyacinth (*Eichhornia crassipes* (Mart. solms) in Lake Victoria. PhD Thesis, University of Florida, USA.
- Wanink, J. H. & K. Goudswaard. 1994. Effects of Nile perch (*Lates niloticus*) introduction into Lake Victoria, East Africa, on the diet of Pied Kingfishers (*Ceryle rudis*). *Hydrobiologia* 279/280:367-376.
- Wanink, J.H., 1998. The pelagic cyprinid *Rastrineobola argentea* as a crucial link in the disrupted ecosystem of Lake Victoria. Ph.D Thesis. 288 pp. Sociale Wetenschappen. University of Leiden, NL.
- Wanink, J. H., J. J. Kashindye, P. C. Goudswaard, and F. Witte. 2001. Dwelling at the oxycline: Does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*? *Freshwater Biology* 46: 75-86.
- Waters, T.F., 1993. Dynamics in stream ecology. In Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Edited by R.J. Gibson and R.E. Cutting. Canadian Special Publication of Fisheries and Aquatic sciences No. 118. pp. 1-8.
- Waters, T.F., 1995. Sediment in streams: Sources, Biological Effects and Control. Bethesda (M.D): American Fisheries Society.

- Wetzel, J.R., J.B. Wallace & E.F. Benfield, 1995. Organic processes in streams of the eastern United States, pp 117-187 In Cushing C.E, K.W. Cummins, G.W. Minshall (Eds). Ecosystems of the world 22. River and Stream ecosystems, Amsterdam (The Netherlands): Elsevier.
- Wetzel, R.L. 1964. The habitats and habitat preference of the young of the Lake Victoria Tilapia (Pisces: Cichlidae). *Rev. Zool. Bot. Afr.* LXX 1-28.
- Wetzel, R.L., 1967. The relationship between fecundity and fertility in the mouthbrooding cichlid fish *Tilapia leucostica*. *J. Zool., Lond.* 151: 453-468.
- Wetzel, R.L., 1988. International introductions of inland aquatic species. *FAO Fisheries technical report* 249. 318p.
- Wetzel, R.L., 1999. A review of a model for qualitative valuation of exploitation levels in multi-species fisheries. *Fisheries Management and Ecology* 6: 1-19.
- Wetzel, R.L., 2003. River fisheries in Africa. Their past, present and Future, pp 145-175. In Crisman T.L., L.J. Chapman, C.A. Chapman, L. Kaufman (eds). Conservation, Ecology and Management of African Fresh waters. Gainesville, University Press of Florida.
- Werner E.E. & D.J. Hall, 1988. Ontogenetic habitat shift in bluegill: the foraging rate-predation risk trade off. *Ecology* 54: 2277-2289.
- Werner, E.E. & J.F. Gilliam, 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. ecol. Syst.* 15: 393-425.
- Wetherbee, B.M., S.H. Gruber & E. Cortés, 1990. Diet, feeding habits, digestion and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris* in Elasmobranchs as Living Resources: advances in Biology, Ecology, Systematics and the status of Fisheries. Pratt, H.L. S.H. Gruber and T. Taniuchi (eds). NOAA Tech. Rep. NMFS90, U.S. Department of Commerce, Seattle, WA, 29-47.
- Wetzel, R.G., 1983. *Limnology*. 2nd edn. Saunders College publishing, Philadelphia, PA.
- Wetzel, R.G., 1995. Death, detritus and energy flow in aquatic ecosystems. *Freshwater Biology*. 33: 83-89.
- Wetzel, D.S., D. Rothstein, J. Dubow, A. Phillips, & E. Losos, 1998. Quantifying threats to imperiled species in the United States. *Bioscience*, 48, 607-615.
- Wilkinson, S.R. & R.W. Lowery, 1973. Cycling of mineral nutrients in pasture ecosystems. Pp. 247-315 In G.W. Butler and R.W. Bailey (eds). Chemistry and bio-chemistry of herbage. Volume 2. Academic Press, New York, USA.
- Williamson, C.E., O.G. Olson, S.E. Lott, N.D. Walker, D.R. Engstrom & B.R. Hargreaves, 2001. Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology* 82: 1748-1760.
- Wilson, J.A., J.M. Acheson, M. Metcalfe & P. Kleban, 1994. Chaos, Complexity and Community management of fisheries. *Marine Pollution* 18, 291-305
- Winnemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60: 331-367
- Wetherell, D., C. Pautzke & D. Fluharty, 2000. An ecosystem-based approach for Alaska groundfish fisheries. *ICES Journal of Marine Science* 57: 771-777.

- Witte, F. & Oijen, M.J.P. van 1990. Taxonomy, ecology and fishery of haplochromine trophic groups. *Zoologische Verhandelingen*, Leiden 262: 1-47
- Witte, F., T. Goldschmidt, K. Goudswaard, W. Ligtoet, M.J.P. Oijen & J.H. Wanink. 1992a. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology* 42:214-232.
- Witte, F., Goldschmidt, K. Goudswaard, W. Ligtoet, M.J.P. Oijen & J.H. Wanink 1992b. The destruction of an endemic species flock: quantitative data on the decline of haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* 34: 1-28.
- Witte, F., T. Goldschmidt & J. Wanink, 1995. Dynamics of the haplochromine cichlid fauna and other ecological changes in Mwanza Gulf of Lake Victoria. Pp. 83-110 In: T.J. Pitcher and P.J.B. Hart (Eds). *The impact of species changes in African lakes*. Chapman and Hall, London.
- Witte, F. & W.L.T. van Densen, 1995. *Fish stocks and fisheries of Lake Victoria (a hand book for field observations)* samara Publishing Ltd. 404pp.
- Witte, F., P.C. Goudswaard, E.F.B. Katunzi, O. Mkumbo, O. Seehausen & J.H. Wanink, 1999. Lake Victoria ecological changes and their relationships with the riparian societies. In: Kawanabe, H. Coulter, G.W. & A.C. (Eds). *Ancient lakes; their cultural and biological diversity*. Kenobi production, Belgium, pp 189-202.
- Witte, F., B.S. Msuku, J.H. Wanink, O. Seehausen, E.F.B. Katunzi, P.C. Goudswaard & T. Goldschmidt, 2000. Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. *Reviews in Fish Biology and Fisheries* 10: 233-241.
- Wootton, J.T. & M.E. Power, 1993. Productivity, consumers, and the structure of a river food chain. *Proceedings of a National Academy of Science* 90: 1384-1387.
- Wootton, J.T., M.S. Parker, & M.E. Power, 1996. Effects of disturbance on river food webs. *Science* 273: 1558-1561.
- Worthington, E.B. 1929. A report on the fishing survey of lakes Albert and Kyoga. Crown Agents for the colonies. London. 136 pp.
- Worthington, E.B. 1932. A report on the fishing survey of Uganda. Crown Agents for the colonies. London. 95 pp.
- Yashioka, T., E. Wada & H. Hayashi., 1994. A stable isotope study on seasonal food web dynamics in eutrophic lake. *Ecology*, 75: 835-846.
- Zah, R., P. Burgherr, S.M. Bemasconi & Uehlinger, 2001. Stable isotope analysis of macro-invertebrates and their food sources in a glacier stream. *Freshwater Biology* 46: 871-882.
- Zaret, T.M & R.T. Paine, 1973. Species introductions in a tropical lake. *Science* 182: 449-455.
- Zohary, T., J. Erez, M. Gophen, I. Berman Frank, & M. Stiller. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. *Limnology and Oceanography* 39: 1030-1043.

APPENDICES

Appendix I. Some of the Morphometric characteristics used in Identification

Shape, size, and prominent markings such as bands, spots or bars.

Standard Length:- Distance from the rostral tip of the upper jaw to the origin of the caudal fin.

Body Depth:- The greatest vertical depth of the body, mostly found between points near the rostral origins of the dorsal fin and of the pelvic fin. It is expressed as a percentage of the standard length.

Caudal Peduncle Length:- Distance between the vertical line through the caudal point of the anal fin insertion and that through the caudal border of the hypurals. It is expressed as a percentage of the standard length.

Caudal Peduncle Depth:- The least vertical depth of the caudal peduncle. It is expressed as the ratio length/depth of the caudal peduncle and indicates the slenderness of the caudal peduncle.

Head Length:- The length from the rostral tip of the premaxilla to the caudal convex end of the gill cover. It is expressed as a percentage of the standard length.

Snout Length:- The distance from the rostral tip of the premaxillae to the rostral point of the bony border of the orbit. It is the junction of the orbit margin of the preorbital process and that side of the lachrymal which borders the eye. It is expressed as a percentage of the head length.

Snout Width:- It is the greatest width of the head area rostral to the preorbital process of the neurocranium in dorsal aspect. It is found between a point on the left and right lachrymal abduction. It is expressed as the ratio length/width of the snout.

Preorbital Depth:- Distance from the rostral corner of the bony orbit to the rostral corner of the lachrymal. It is expressed as a percentage of the head length.

Eye Diameter:- Distance from the rostral point of the orbit to the ventral of the post orbital process. It is expressed as a percentage of the head length.

Cheek Depth:- Distance from the ventral point of the bony margin of the orbit to the most ventral point along the ventral border line of the adductor muscle. It is expressed as a percentage of the head length.

Length of the Lower Jaw:- Distance from the rostral to the caudal tip of the lower jaw. It is expressed as percentage of the head length.

Width of the Lower Jaw:- Distance between a point on the left and on the right lower jaw just rostral to the rim marking its articulation with the suspensorium. It is expressed as a percentage of the head length.

Appendix II. The DCA factor scores for the first two axes for 18 food sources and nine fish species from the Koki drainage system lakes.

Lake	Fish species	X1	X2	Food items	X1	X2
Kachera	<i>A. aneocolor</i>	184	25	Detritus	22	-23
Kachera	<i>C. gariepinus</i>	177	14	Phytoplankton	-59	105
Kachera	<i>C. liocephalus</i>	191	244	Macrophytes	69	142
Kachera	<i>H. squamipinus</i>	255	65	Ciliate	-91	125
Kachera	<i>O. esculentus</i>	0	95	Insects	311	-48
Kachera	<i>O. leucostictus</i>	119	118	Ephemeroptera	335	136
Kachera	<i>O. niloticus</i>	64	100	Coleoptera	361	91
Kachera	<i>P. aethiopicus</i>	212	96	Nematocera	197	340
Mburo	<i>A. alluaudi</i>	301	50	Hemiptera	416	153
Mburo	<i>A. aneocolor</i>	265	120	Isoptera	225	70
Mburo	<i>C. gariepinus</i>	338	107	Chironomids	171	146
Mburo	<i>H. squamipinus</i>	253	61	<i>Chaoborus</i>	122	-59
Mburo	<i>O. esculentus</i>	32	83	Odonata	283	61
Mburo	<i>O. leucostictus</i>	191	0	Oligochaeta	390	153
Mburo	<i>O. niloticus</i>	20	84	Molluscs	243	290
Mburo	<i>P. aethiopicus</i>	242	76	Fish eggs/embryo	322	156
				Fish remains	312	-10
				Tilapia	170	-162

Appendix III. The DCA factor scores for the first two axes for 25 food sources and 19 fish species from the Nabugabo drainage system lakes.

Lake	Fish species	X1	X2	Food item	X1	X2
Nabugabo	<i>T. zillii</i>	157	177	Detritus	363	211
Nabugabo	<i>S. itermedius</i>	11	132	Phytoplankton	456	164
Nabugabo	<i>S. afrofischeri</i>	26	71	Macrophytes	339	152
Nabugabo	<i>P. beadleii</i>	94	120	Seeds	-77	106
Nabugabo	<i>P. aethiopicus</i>	257	202	Ciliate	485	168
Nabugabo	<i>O. niloticus</i>	200	183	Zooplankton	213	165
Nabugabo	<i>O. leucostictus</i>	367	182	Insects	146	109
Nabugabo	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	19	337	Ephemeroptera	65	63
Nabugabo	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	24	373	Coleoptera	251	176
Nabugabo	<i>B. sadleri</i>	88	63	Hemiptera	-93	52
Nabugabo	<i>A. verifer</i>	51	82	Isoptera	-50	-90
Kayanja	<i>T. zillii</i>	222	205	Chironomids	55	84
Kayanja	<i>P. venator</i>	144	177	<i>Chaoborus</i>	80	88
Kayanja	<i>P. catostoma</i>	77	91	Odonata	131	251
Kayanja	<i>P. aethiopicus</i>	298	206	Oligochaeta	-26	55
Kayanja	<i>O. esculentus</i>	381	167	Hirudinea	-9	30
Kayanja	<i>G. victoriae</i>	0	114	Molluscs	268	212
Kayanja	<i>G. simpsoni</i>	176	197	Fish eggs/embryo	24	367
Kayanja	<i>C. gariepinus</i>	29	14	Fish remains	205	286
Kayanja	<i>C. alluaudi</i>	17	0	<i>R. argentea</i>	-48	364
Kayanja	<i>A. verifer</i>	140	155	Haps	-46	442
Kayanja	<i>A. nubila</i>	47	89	<i>Clarias</i>	88	72

Kayugi	<i>T. zillii</i>	384	160	<i>Lates sp.</i>	-48	432
Kayugi	<i>P. venator</i>	111	134	Tilapia	1	415
Kayugi	<i>P. catostoma</i>	67	119	<i>Brycinus sp.</i>	-7	388
Kayugi	<i>P. aethiopicus</i>	267	224			
Kayugi	<i>O. esculentus</i>	342	161			
Kayugi	<i>G. victoriae</i>	66	204			
Kayugi	<i>A. verifer</i>	120	95			
Kayugi	<i>A. nubila</i>	119	95			

Appendix IV. The DCA factor scores for the first two axes for 26 food sources and 30 fish species from the Kyoga drainage system lakes.

Lake	Fish species	X1	X2	Food items	X1	X2
Nawampasa	<i>A. "fattooth"</i>	353	229	Detritus	447	241
Nawampasa	<i>A. latifasciata</i>	99	357	Phytoplankton	557	223
Nawampasa	<i>B. sadleri</i>	210	195	Macrophytes	385	254
Nawampasa	<i>C. gariepinus</i>	167	135	Seeds	262	220
Nawampasa	<i>H. lividus</i>	272	222	Ostracods	396	164
Nawampasa	<i>L. cryptodon</i>	52	419	<i>Caridina</i>	139	154
Nawampasa	<i>L. maxillaries</i>	74	192	Insects	250	336
Nawampasa	<i>O. esculentus</i>	533	227	Ephemeroptera	183	114
Nawampasa	<i>O. leucostictus</i>	507	231	Coleoptera	233	158
Nawampasa	<i>O. niloticus</i>	518	230	Hemiptera	116	168
Nawampasa	<i>O. variabilis</i>	506	232	Isoptera	170	84
Nawampasa	<i>P. aethiopicus</i>	101	95	Trichoptera	340	209
Nawampasa	<i>P. argenteus</i>	141	148	Chironomids	287	205
Nawampasa	<i>P. orthostoma</i>	86	69	<i>Chaoborus</i>	291	121
Nawampasa	<i>S. victoriae</i>	301	238	Odonata	185	189
Nawampasa	<i>X. phytophagus</i>	187	290	Oligochaeta	291	70
Nakuwa	<i>C. gariepinus</i>	198	147	Hirudinea	32	115
Nakuwa	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	87	87	Molluscs	202	276
Nakuwa	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	201	154	Fish		
Nakuwa	<i>O. niloticus</i>	382	200	eggs/embryo	52	419
Nakuwa	<i>P. aethiopicus</i>	218	194	Fish remains	82	71
Nakuwa				<i>R. argentea</i>	28	58
Nakuwa	<i>S. afrofischeri</i>	223	186	Haplochromines	-21	-23
Nakuwa	<i>S. intermedius</i>	193	143	<i>Clarias sp.</i>	-47	-20
Nakuwa	<i>S. victoriae</i>	246	194	<i>Lates sp.</i>	-46	2
Bisina	<i>A. latifasciata</i>	159	197	Tilapia	-44	370
Bisina	<i>B. docmak</i>	69	62	<i>Barbus sp.</i>	-89	9
Bisina	<i>B. sadleri</i>	234	191			
Bisina	<i>C. gariepinus</i>	210	175			
Bisina	<i>H. lividus</i>	248	208			
Bisina	<i>H. micheali</i>	66	0			
Bisina	<i>O. esculentus</i>	504	232			
Bisina	<i>O. niloticus</i>	433	245			
Bisina	<i>O. variabilis</i>	480	236			
Bisina	<i>P. "shovelmouth"</i>	252	239			

Lake	Fish species	X1	X2	Food items	X1	X2
Bisina	<i>P. aethiopicus</i>	162	184			
Bisina	<i>P. argenteus</i>	142	139			
Bisina	<i>P. catostoma</i>	264	288			
Bisina	<i>P. pellegrini</i>	119	122			
Bisina	<i>S. afrofischeri</i>	287	225			
Bisina	<i>S. victoriae</i>	237	247			
Bisina	<i>T. zillii</i>	444	243			
Bisina	<i>X. phytophagus</i>	276	251			
Kyoga (Iyingo)	<i>A. "kyogaastato"</i>	270	327			
Kyoga (Iyingo)	<i>A. nubila</i>	189	289			
Kyoga (Iyingo)	<i>B. sadleri</i>	176	96			
Kyoga (Iyingo)	<i>C. gariepinus</i>	147	147			
Kyoga (Iyingo)	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	15	118			
Kyoga (Iyingo)	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	113	100			
Kyoga (Iyingo)	<i>O. niloticus</i>	264	116			
Kyoga (Iyingo)	<i>P. aethiopicus</i>	212	197			
Kyoga (Iyingo)	<i>S. afrofischeri</i>	179	217			
Kyoga (Iyingo)	<i>S. intermedius</i>	185	189			
Kyoga (Iyingo)	<i>S. victoriae</i>	187	171			
Kyoga (Bukungu)	<i>B. altianalis</i>	220	269			
Kyoga (Bukungu)	<i>B. sadleri</i>	250	336			
Kyoga (Bukungu)	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	0	38			
Kyoga (Bukungu)	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	18	43			
Kyoga (Bukungu)	<i>O. niloticus</i>	183	114			
Kyoga (Bukungu)	<i>P. "blackpara"</i>	194	210			
Kyoga (Bukungu)	<i>P. aethiopicus</i>	383	256			
Kyoga (Bukungu)	<i>S. afrofischeri</i>	177	172			
Kyoga (Bukungu)	<i>S. intermedius</i>	171	140			
Kyoga (Bukungu)	<i>S. victoriae</i>	199	167			

Appendix V. The DCA factor scores for the first two axes for 23 food sources and 23 fish species from the northern portion of Lake Victoria.

Area	Fish species	X1	X2	Food items	X1	X2
Napoleon Gulf	<i>Astatotilapia sp.</i>	184	231	Detritus	410	187
Napoleon Gulf	<i>B. sadleri</i>	210	60	Phytoplankton	538	195
Napoleon Gulf	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	115	206	Macrophytes	314	217
Napoleon Gulf	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	122	218	<i>Caridina</i>	204	306
Napoleon Gulf	<i>M. kannume</i>	225	201	Insects	136	211
Napoleon Gulf	<i>O. leucostictus</i>	462	190	Ephemeroptera	258	103
Napoleon Gulf	<i>O. niloticus</i>	388	189	Coleoptera	225	321
Napoleon Gulf	<i>O. variabilis</i>	449	189	Hemiptera	116	335
Napoleon Gulf	<i>P. aethiopicus</i>	0	159	Isoptera	201	327
Napoleon Gulf	<i>P. crassilabris</i>	226	74	Trichoptera	207	288
Napoleon Gulf	<i>H. guarti</i>	127	229	Chironomids	273	141
Napoleon Gulf	<i>P. "redfin"</i>	185	104	<i>Chaoborus</i>	197	360
Napoleon Gulf	<i>P. riponians</i>	171	184	Odonata	171	0
Napoleon Gulf	<i>P. sauvegai</i>	262	147	Oligochaeta	220	216

Area	Fish species	X1	X2	Food items	X1	X2
Napoleon Gulf	<i>P. sheller</i> "	168	131	Hirudinea	152	333
Napoleon Gulf	<i>S. afrofischeri</i>	215	212	Molluscs	0	159
				Fish		
Napoleon Gulf	<i>S. victoriae</i>	182	238	eggs/embryo	150	202
Napoleon Gulf	<i>T. zillii</i>	226	65	Fish remains	99	260
Thruston Bay	<i>A. alluaudi</i>	148	164	<i>R. argentea</i>	34	235
Thruston Bay	<i>C. frenatus</i>	0	159	Haplochromines	47	238
Thruston Bay	<i>Astatotilapia</i> sp.	139	186	<i>Clarias</i> sp.	59	229
Thruston Bay	<i>B. jacksonii</i>	158	128	<i>Lates</i> sp.	45	261
Thruston Bay	<i>B. sadleri</i>	208	173	Tilapia	291	342
Thruston Bay	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	130	214			
Thruston Bay	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	111	220			
Thruston Bay	<i>O. niloticus</i>	236	254			
Thruston Bay	<i>P. aethiopicus</i>	152	135			
Thruston Bay	<i>P. "big eye"</i>	191	79			
Thruston Bay	<i>P. crassilabrs</i>	161	203			
Thruston Bay	<i>H. guarti</i>	205	68			
Thruston Bay	<i>P. "redfin"</i>	233	212			
Thruston Bay	<i>P. riponianus</i>	227	179			
Thruston Bay	<i>P. rockcribensis</i>	233	78			
Thruston Bay	<i>S. afrofischeri</i>	181	142			
Thruston Bay	<i>S. victoriae</i>	295	149			
Thruston Bay	<i>T. zillii</i>	216	98			
Hannington Bay	<i>A. alluaudi</i>	33	165			
Hannington Bay	<i>Astatotilapia</i> sp.	157	79			
Hannington Bay	<i>B. jacksonii</i>	195	72			
Hannington Bay	<i>B. sadleri</i>	232	100			
Hannington Bay	<i>L. niloticus</i> ($\geq 20 < 60$ cm)	74	222			
Hannington Bay	<i>L. niloticus</i> ($\geq 9.6 < 20$ cm)	95	215			
Hannington Bay	<i>O. niloticus</i>	303	142			
Hannington Bay	<i>P. aethiopicus</i>	61	192			
Hannington Bay	<i>P. crassilabrs</i>	171	138			
Hannington Bay	<i>P. "redfin"</i>	171	0			
Hannington Bay	<i>P. riponianus</i>	137	31			
Hannington Bay	<i>T. zillii</i>	238	80			

Appendix VI. The Mean $\pm$ sd of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the fish species or food sources from selected Victoria and Kyoga basin lakes (August 2001 to September 2003)(See Table 4.1for a key to labels).

Koti drainage lakes																																												
Lake/Area																																												
Kachera	Organism	Pi	Cp	Cs	Ae	Vc	Es	Pk	Lt	Na	Os	Ea	Gv	Oe	Tz	Av	An	Aa	Pc	Gs	Pv	Bk	Cg	On	Pa	Sa	Pb	Si	Bs	Ln														
	$\delta^{13}\text{C}$	-27.27	-13.07	-29.90	-13.45	-16.19	-15.03	-13.27	-13.48	-10.20	-18.40	-11.60	-18.50	-18.00	-16.10	-17.10	-16.90	-14.60																										
	sd $\delta^{13}\text{C}$	0.00	0.00	0.00	0.00	2.58	0.00	0.00	0.04	0.94	1.02	0.31	1.71	2.85	3.25	1.91	3.77	4.22																										
	$\delta^{15}\text{N}$	0.10	1.99	0.10	-2.95	-1.16	0.76	1.74	-0.99	3.70	3.80	4.20	5.00	5.30	5.20	5.60	6.00	6.30																										
	sd $\delta^{15}\text{N}$	0.00	0.00	0.00	0.00	0.85	0.00	0.00	0.42	1.10	0.47	0.02	0.32	0.37	0.12	0.10	1.00	0.18																										
Mburo	$\delta^{13}\text{C}$	-13.18	-27.55	-12.71	-28.48	-10.96	-12.99			-12.49	-9.70	-12.90	-8.20	-8.80	-10.30	-10.60	-11.00	-8.80																										
	SD X	0.00	0.00	0.00	0.00	0.00	0.00			0.00	1.24	0.27	1.06	4.41	0.41	0.45	0.72	0.12																										
	Y - N	3.02	1.34	1.20	8.35	-1.64	1.50			2.35	3.90	5.00	5.20	6.70	5.20	5.00	6.20	7.70																										
	$\delta^{15}\text{N}$	0.00	0.00	0.00	0.00	0.00	0.00			0.00	0.13	0.18	0.65	0.59	0.23	0.16	1.85	0.39																										
	sd $\delta^{15}\text{N}$																																											
Nabugabo drainage lakes																																												
Kayugi	Label	Cs	Fc	Md	Ds	Cd	Cb	Lt	Na	Os	Ea	Gv	Oe	Tz	Av	An	Aa	Pc	Gs	Pv	Bk	Cg	On	Pa	Sa	Pb	Si	Bs	Ln															
	$\delta^{13}\text{C}$	-13.73	-38.06	-12.89	-12.85	-20.99	-28.72		-27.22	-23.00	-23.84	-18.56	-18.84	-18.35	-18.63				-16.32	-14.81	-17.99	-16.40																						
	sd $\delta^{13}\text{C}$	0.00	0.00	0.00	0.00	0.00	0.00		0	0	0	0	0.14	1.33	2.18				2.27	0.87	0.70	2.14																						
	$\delta^{15}\text{N}$	2.20	1.51	-0.52	0.20	-0.85	1.02		-2.68	-4.15	0.14	1.59	2.70	4.07	4.85				5.79	7.07	6.84	5.79																						
	sd $\delta^{15}\text{N}$	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.11	0.97	1.83				1.34	0.50	0.13	0.75																						
Nabugabo	$\delta^{13}\text{C}$					-25.09	-22.88		-22.48	-22.75	-19.33				-20.32				-19.68				-21.25	-21.56	-20.50	-19.96	-19.89	-20.19	-20.20															
	sd $\delta^{13}\text{C}$					0.00	0.00		0.00	0.00	0.00			0.00				0.00				0.33	0.00	1.27	0.78	0.25	0.30	0.85																
	$\delta^{15}\text{N}$					1.07	5.83		2.79	2.82	4.34			8.55				9.00				6.83	7.18	7.87	8.16	8.72	8.61	9.30																
	sd $\delta^{15}\text{N}$					0.00	0.00		0.00	0.00	0.00			0.00				0.00				0.23	0.00	1.16	0.75	0.35	0.99	0.73																
	sd $\delta^{15}\text{N}$																																											
Northern portion of Lake Victoria																																												
Napoleon Gulf	Label	Ph	Cp	Cs	Vc	Pk	Ds	Cd	Cn	Cb	Os	Ea	Ml	Sb	Bh	Ci	Ov	Oi	On	Tz	Al	Aa	As	Pf	Pi	Pc	Pn	Ps	Ph	Hg	Mk	Pa	Sa	Sv	Cg	Rat	Bs	Bj	Ln					
	$\delta^{13}\text{C}$							-17.72		-16.27	-18.58	-17.72	-16.59	-13.72	-17.14	-14.64	-16.76	-17.27	-16.27	-14.97	-16.07	-17.70	-15.90		-16.78	-15.56	-16.09	-16.15	-16.07	-16.27	-17.08	-19.75	-16.06	-15.81	-16.15	-16.07	-16.27	-17.08	-19.75	-16.05	-16.39			
	sd $\delta^{13}\text{C}$							0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.154	0.18	1.58	0.00	0.94	0.25	1.26	0.27	0.50	0.59	0.12	0.95	0.00	0.14	0.12	3.00	0.59	0.12	0.95	0.00	0.14	0.12	0.28	0.94	
	$\delta^{15}\text{N}$							2.86		7.72	5.24	2.19	3.57	2.96	3.93	6.66	4.92	4.28	5.60	6.73	7.80	7.32	7.42		6.80	7.25	8.67	7.58	8.67	8.37	6.41	8.76	8.56	7.41	9.20	7.58	8.67	8.37	6.41	8.76	8.56	7.41	9.20	8.07
	sd $\delta^{15}\text{N}$							0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.164	0.62	0.21	0.00	0.06	0.78		0.64	0.57	0.18	0.33	0.35	0.14	0.00	0.29	0.31	1.34	0.33	0.35	0.14	0.00	0.29	0.31	1.34	0.41	0.76
Thurston Bay	$\delta^{13}\text{C}$							-18.09								-20.07	-15.36	-15.15	-20.19	-17.47				-15.50	-15.38	-15.36	-15.40				-15.58	-16.15	-17.93	-16.20	-16.77	-16.03	-15.42	-14.96	-20.04	-17.99	-17.88	-19.84		
	sd $\delta^{13}\text{C}$							0.00								0.30	0.16	1.45	0.00	1.74				0.23	1.36	0.30	0.34				0.00	0.00	1.25	0.78	0.11	0.00	0.36	0.32	0.00	0.18				
	$\delta^{15}\text{N}$							3.81								3.36	6.00	7.26	5.34	6.72				7.70	8.04	7.35	8.00				8.99	7.80	6.57	7.75	8.02	8.08	8.25	8.30	8.28	8.90	8.90	8.90		
	sd $\delta^{15}\text{N}$							0.00								0.28	0.08	0.34	0.00	0.98				0.14	0.71	0.38	0.20				0.19	0.00	0.36	0.26	0.18	0.00	0.29	0.55	0.00	0.13				
	sd $\delta^{15}\text{N}$																																											
Hannington Bay	$\delta^{13}\text{C}$							-25.76	-12.04	-28.29	-12.75	-19.63	-21.17	-19.41					-17.05	-17.66	-19.26	-16.99			-16.79	-16.89	-19.26	-16.99				-15.58	-16.15	-17.93	-16.20	-16.77	-16.03	-15.42	-14.96	-20.04	-17.99	-17.88	-19.84	
	sd $\delta^{13}\text{C}$							0.00	0.00	0.00	0.00	0.00	0.00	0.00				0.25	0.51	0.00	0.47				0.91	0.26	2.48	0.00				0.00	0.00	1.25	0.78	0.11	0.00	0.36	0.32	0.00	0.18			
	$\delta^{15}\text{N}$							-0.51	-4.46	3.04	0.99	0.62	-0.17	2.37	1.13				5.84	6.47	5.89	6.10				7.64	7.35	8.28	8.67	9.00	5.85	7.64	7.35	8.28	8.67	9.00	5.85	7.64	7.35	8.28	8.67	9.00	5.85	
	sd $\delta^{15}\text{N}$							0.00	0.00	0.00	0.00	0.00	0.00	0.00				0.14	0.68	0.00	0.13				0.46	0.18	0.95	0.00				0.19	0.00	0.36	0.26	0.18	0.00	0.29	0.55	0.00	0.13			
	sd $\delta^{15}\text{N}$																																											

Крыжа дренажно систем лавос

	Organism	Pk	Cp	Cs	Ec	Vc	Ty	Na	Cm	Hv	Nj	Ds	Cd	Cb	Ta	Ml	Ea	Hd	Cn	O.v	O.e	O.l	O.n	A.f	A.a	X.p	A.k	P.c	A.m
Lake/Area Nawampasa	δ ¹³ C	-20.00											-20.67	-19.75	-20.41					-26.36	-25.19	-26.08	-24.81	-24.17		-24.73	-19.40		-24.79
	sd δ ¹³ C																			0.31	0.05	0.00	0.00	0.81		0.33	0.00		0.29
	δ ¹⁵ N																			5.22	5.79	5.76	5.73	5.15		6.99	5.18		6.98
	sd δ ¹⁵ N																			0.43	0.32	0.00	0.00	0.07		0.39	0.00		0.75
Nakuwa	δ ¹³ C																												
	sd δ ¹³ C																												
	δ ¹⁵ N																												
	sd δ ¹⁵ N																												
Bisina	δ ¹³ C	-21.30																		-20.91			-17.23		-24.21	-20.36		-22.66	-22.90
	sd δ ¹³ C																			0.80			2.72	0.00	0.60		0.00	1.90	
	δ ¹⁵ N	-0.15																		5.65			4.14	5.15	4.35		6.42	6.34	
	sd δ ¹⁵ N																			0.70			0.56	0.00	1.32		0.00	0.18	
Kyoga (Iyingo)	δ ¹³ C	-23.41	-13.03	-31.15	-29.26																								
	sd δ ¹³ C																												
	δ ¹⁵ N	2.53	-5.52	-0.33	0.36																								
	sd δ ¹⁵ N																												
Nawampasa	Organism	AI	H.I	H.q	P.e	L.m	Lo	L.p	L.c	P.t	P.I	P.y	B.I	T.z	B.a	M.m	P.a	S.a	S.v	P.u	P.o	C.g	B.s	M.m	S.i	B.d	R.a.1	R.a.2	L.n
	δ ¹³ C	-24.29	-24.97			-25.67	-25.26	-24.93	-26.44	-23.53	-24.73	-25.30	-24.42																
	sd δ ¹³ C																												
	δ ¹⁵ N	7.89	6.82			7.26	7.57	7.83	6.19	7.76	7.14	7.45	7.92																
Nakuwa	sd δ ¹⁵ N																												
	δ ¹³ C																												
	sd δ ¹³ C																												
	δ ¹⁵ N																												
Bisina	sd δ ¹⁵ N																												
	δ ¹³ C	-18.19	-21.88	-17.06	-18.37																								
	sd δ ¹³ C																												
	δ ¹⁵ N	1.38	2.91	0.39	1.17																								
Kyoga (Iyingo)	sd δ ¹⁵ N																												
	δ ¹³ C	8.57	5.86	6.14	5.73																								
	sd δ ¹⁵ N																												
	sd δ ¹⁵ N	0.54	0.11	0.19	0.32																								
Nawampasa	Organism	AI	H.I	H.q	P.e	L.m	Lo	L.p	L.c	P.t	P.I	P.y	B.I	T.z	B.a	M.m	P.a	S.a	S.v	P.u	P.o	C.g	B.s	M.m	S.i	B.d	R.a.1	R.a.2	L.n
	δ ¹³ C	-24.29	-24.97			-25.67	-25.26	-24.93	-26.44	-23.53	-24.73	-25.30	-24.42																
	sd δ ¹³ C																												
	δ ¹⁵ N	7.89	6.82			7.26	7.57	7.83	6.19	7.76	7.14	7.45	7.92																
Nakuwa	sd δ ¹⁵ N																												
	δ ¹³ C																												
	sd δ ¹³ C																												
	δ ¹⁵ N																												
Bisina	sd δ ¹⁵ N																												
	δ ¹³ C	-18.19	-21.88	-17.06	-18.37																								
	sd δ ¹³ C																												
	δ ¹⁵ N	1.38	2.91	0.39	1.17																								
Kyoga (Iyingo)	sd δ ¹⁵ N																												
	δ ¹³ C	8.57	5.86	6.14	5.73																								
	sd δ ¹⁵ N																												
	sd δ ¹⁵ N	0.54	0.11	0.19	0.32																								
Nawampasa	Organism	AI	H.I	H.q	P.e	L.m	Lo	L.p	L.c	P.t	P.I	P.y	B.I	T.z	B.a	M.m	P.a	S.a	S.v	P.u	P.o	C.g	B.s	M.m	S.i	B.d	R.a.1	R.a.2	L.n
	δ ¹³ C	-24.29	-24.97			-25.67	-25.26	-24.93	-26.44	-23.53	-24.73	-25.30	-24.42																
	sd δ ¹³ C																												
	δ ¹⁵ N	7.89	6.82			7.26	7.57	7.83	6.19	7.76	7.14	7.45	7.92																
Nakuwa	sd δ ¹⁵ N																												
	δ ¹³ C																												
	sd δ ¹³ C																												
	δ ¹⁵ N																												
Bisina	sd δ ¹⁵ N																												
	δ ¹³ C	-18.19	-21.88	-17.06	-18.37																								
	sd δ ¹³ C																												
	δ ¹⁵ N	1.38	2.91	0.39	1.17																								
Kyoga (Iyingo)	sd δ ¹⁵ N																												
	δ ¹³ C	8.57	5.86	6.14	5.73																								
	sd δ ¹⁵ N																												
	sd δ ¹⁵ N	0.54	0.11	0.19	0.32																								
Nawampasa	Organism	AI	H.I	H.q	P.e	L.m	Lo	L.p	L.c	P.t	P.I	P.y	B.I	T.z	B.a	M.m	P.a	S.a	S.v	P.u	P.o	C.g	B.s	M.m	S.i	B.d	R.a.1	R.a.2	L.n
	δ ¹³ C	-24.29	-24.97			-25.67	-25.26	-24.93	-26.44	-23.53	-24.73	-25.30	-24.42																
	sd δ ¹³ C																												
	δ ¹⁵ N	7.89	6.82			7.26	7.57	7.83	6.19	7.76	7.14	7.45	7.92																
Nakuwa	sd δ ¹⁵ N																												
	δ ¹³ C																												
	sd δ ¹³ C																												
	δ ¹⁵ N																												
Bisina	sd δ ¹⁵ N																												
	δ ¹³ C	-18.19	-21.88	-17.06	-18.37																								
	sd δ ¹³ C																												
	δ ¹⁵ N	1.38	2.91	0.39	1.17																								
Kyoga (Iyingo)	sd δ ¹⁵ N																												
	δ ¹³ C	8.57	5.86	6.14	5.73																								
	sd δ ¹⁵ N																												
	sd δ ¹⁵ N	0.54	0.11	0.19	0.32																								
Nawampasa	Organism	AI	H.I	H.q	P.e	L.m	Lo	L.p	L.c	P.t	P.I	P.y	B.I	T.z	B.a	M.m	P.a	S.a	S.v	P.u	P.o	C.g	B.s	M.m	S.i				

Trophic structure and energy flow in fish communities of two lakes of the Lake Victoria basin

D. Mbabazi, F.L. Orach-Meza¹, B. Makanga², R.E. Hecky³, J.S. Balirwa, R. Ogutu-Ohwayo⁴, P. Verburg⁴, G. Namulemo, E. Muhumuza and J. Luyiga

Fisheries Resources Research Institute, P.O. Box 343, Jinja, Uganda

¹Lake Victoria Environmental Management Project, P.O. Box 5, Entebbe, Uganda

²Zoology Department, Makerere University, P.O. Box 7062, Kampala, Uganda

³Biology Department, University of Waterloo, 200 University Avenue, Waterloo, ON, N2L-3G1; Canada

⁴Lake Victoria Fisheries Organization, P.O. Box 1625, Jinja, Uganda

Abstract

Successful management of target fishery species often hinges on the ability to effectively manage prey resources; and knowledge of trophic relationships among fishes and their prey can help guide management efforts aimed at increasing and sustaining fish production. This study characterized the trophic structure and energy flow in the fish communities of two minor lakes in Uganda: lakes Kachera and Mburo. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were measured in fishes and their potential food sources (primary producers and aquatic invertebrates). These data were augmented with results obtained from stomach content analysis. The study indicated values of $\delta^{15}\text{N}$ that were often considerably lower than 3.4‰ per trophic transfer typically assumed in stable isotope studies. The low ^{15}N trophic fractionation indicted a high degree of omnivory as well as dietary overlap among the examined consumers. Hierarchical agglomerative clustering and Detrended Correspondence Analysis (DCA) indicated a degree of similarity in the diets of fish species between the two lakes, and in lakes, algae/phytoplankton, benthic, and terrestrial material were important energy sources. However, organisms from Lake Kachera were generally more ^{13}C depleted compared with Lake Mburo indicating the importance of algal production to the upper food web in Kachera while in Mburo the $\delta^{13}\text{C}$ of the dense phytoplankton is similar to terrestrial grass material that would be contributed by the large hippopotamus population.

Key words Fishes, phytoplanktons, trophic, Uganda

Introduction

In most fisheries management the main global crisis has been overexploitation of the predator and prey stocks which has resulted in calls for multi-species and (or) "ecosystems based" assessment and management of the fish stocks and assemblages (Jennings and Kaiser, 1998; National Research Council, 1999) to avoid problems associated with fishing down the food web (Pauly *et al.*, 1998).

Food webs are macro-descriptors of community feeding interactions that can be used to map the flow of energy, materials and nutrients in ecosystems (Jepsen and Winemiller, 2002). In recent years several theoretical and empirical studies have emphasized the importance of trophic interactions for structuring lacustrine, mainly pelagic food webs and the available information from shallow lakes indicates that there are far more complex food web structures (Diehl and Kornijew, 1998). Implementation of multi-species approaches will require improved understanding of the community ecology of fish

assemblages that has rarely been explicitly incorporated into fisheries management practices.

Trophic structure has traditionally been characterized using stomach content analyses (SCA), direct observations or collection of prey remains (Balirwa, 1984, 1998; Beaudoin *et al.*, 1999; Mbabazi *et al.*, 2004).

Nowadays, the combined use of stable isotopes of carbon and nitrogen contributes to identifying the original organic nutrient sources in complex food webs (Jennings *et al.*, 1997; Magnusson *et al.*, 1999; Maneta *et al.*, 2003), assessing energy flow and trophic structure in aquatic systems (Kling *et al.*, 1992; Hesslein *et al.*, 1993; Gu *et al.*, 1994; Hecky and Hesslein, 1995; France *et al.*, 1996; Campbell *et al.*, 2003) however, the diversity of systems to which it has been applied is primarily pelagic food webs. Specifically the $\delta^{13}\text{C}$ ratio of a consumer reflects (usually within 1‰) the $\delta^{13}\text{C}$ signature of its diet (Peterson and Fry, 1987; France 1995; Vander Zanden and Rasmussen, 2001) and the $\delta^{15}\text{N}$ ratio of

a consumer reflects its trophic position because there is an average enrichment of 3.4‰ per trophic transfer (Cabana and Rasmussen, 1996; Post, 2002).

Most limnologists always consider feeding pathways derived from phytoplankton to be most important for secondary consumers and fish growth or production in lakes (Yoshioka *et al.*, Gu *et al.* 1996). There has been a growing appreciation that benthic primary producers and allochthonous organic matter from riparian vegetation are also important food resources for invertebrate consumers and fish growth (Hecky and Hesslein, 1995; France, 1997; Vadeboncoeur *et al.*, 2003). Macrophytes and periphytic algae, a conspicuous and abundant source of fixed carbon in wetlands and shallow lakes, can supply carbon to these food webs (Bunn and Boon, 1993). Several stable isotope studies have however indicated that macrophytes carbon contribution to aquatic food webs is very little even when macrophytes are very abundant (Bunn and Boon, 1993; Hecky and Hesslein, 1995; Keough *et al.*, 1996). Terrestrial organic carbon also has the potential to contribute energy to aquatic food webs (Planas *et al.* 2000) especially in streams. Terrestrial plants and macrophytes can either be C_3 or C_4 plants and have relatively fixed isotopic signatures because they use atmospheric carbon with constant isotopic signature while, algae are C_3 plants and in water can have a variable signature as isotopic signature of CO_2 varies.

Further, anthropogenic disturbance in lake catchments can change the balance of allochthonous (external) and autochthonous (internal) organic carbon sources (Holopainen *et al.*, 1991) as well as affecting community structure through habitat change.

We used stable isotope and stomach content analyses to examine feeding relationships among consumers at higher trophic levels to determine the ultimate sources (producers) from which fish consumers derive their energy.

Materials and Methods

Study sites

The study focused on two minor lakes in the Lake Victoria basin namely Mburo and Kachera (Figure 1) that are at different levels of anthropogenic interference. The sizes and shapes of these lakes vary from time to time due to floating islands. The two lakes comprise of similar fish assemblages (Namulemo and Mbabazi, 2004).

Lake Mburo is within a National park. It is characterized by controlled fishing but is intensively used for watering wild game and supports high populations of hippopotamuses during the day hours. Lake Kachera unlike Lake Mburo is shared by two districts of Mbarara and Rakai besides being not protected (i.e. outside the National park). Lake Kachera is therefore exposed to more human interference and management problems than Lake Mburo. Overfishing, high populations of domesticated animals, and agricultural activities characterize Lake Kachera with most of the communities practicing mixed farming to varying degrees (Kamugisha *et al.* 1997; Namara and Infield, 1998; Emerton, 1999).

different trophic levels and potential carbon sources were collected between August 2001 and January 2003. Sampling for fish was done using experimental multifilament gillnets with mesh sizes ranging from 25.4 mm to 203.2 mm with stretched mesh in 12.7 and 25.5 mm increments from 25.4 to 139.7 mm and 152.4 mm to 203.2 mm respectively fished overnight for approximately 12 hours. Some fishes were also obtained or purchased from local fishers. Upon retrieval, fish were sorted into their taxonomic groups, to species level whenever possible. For each captured fish the total and standard lengths were recorded and stomach removed. The stomachs were preserved in 10% formaldehyde for later stomach content analysis. Dorsal skinless muscles were removed from the anterior part of each fish from a maximum of three individuals per species and dried and dried samples were kept in scintillation vials and transported to the Environmental Isotope Laboratory (University of Waterloo, Canada) for analysis.

Aquatic macro-invertebrates were collected as potential prey from same sites as for fish within each lake (two sweeps per site). Additional samples of mollusks and other epiphytic invertebrates were hand picked. Benthic invertebrates in the profundal zone were sampled with a Ponar grab (Beaudoin *et al.*, 2001; Zah *et al.*, 2001; Jones and Waldron, 2003). For invertebrates, samples from the different sites were pooled to raise enough biomass for stable isotope analysis and were sun dried and treated as for fish above. Dominant macrophytes were hand picked and thoroughly washed to obtain clean samples (Jones and Waldron, 2003).

Phytoplankton samples were obtained from vertical hauls of a 10 m mesh plankton net beginning from about 1.5 m below the water surface of the sampled lake. Samples from the different sites were pooled to ensure sufficient biomass for stable isotope analysis. Phytoplankton was filtered from lake water by use of a pre-combusted GF/F (1.2 m) filter paper that was immediately treated as above for invertebrates and fish.

Laboratory analyses

Stomach contents were identified and the percentage volume of each food item in the diet was assessed by visually estimating how much it contributed to the total contents using either a binocular or compound microscope depending on the diet of the fish species in question (Balirwa, 1984; Winemiller, 1990; Nakamura *et al.*, 2003). Subsequently every other dietary component was awarded 16, 8, 4, 1 or 0 points depending on the relative importance of the food item in the stomach (Hynes, 1950; Genner *et al.*, 1999).

For fish and invertebrates about 1 mg (± 0.005 mg) and a slightly larger quantity for macrophytes 2 mg (± 0.005 mg) were packed into tin capsules of 5 X 3.5 mm and immediately sealed for isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous VG Micromass 903E isotope ratio mass Spectrometer at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada. Stable isotope data are presented as the relative difference between ratios of the sample and standard gases.

Field Sampling

The representative dominant taxa (fish, macro-

Table 1 Fish species list of the fish communities of the studied lakes

Family/group	Species	Author	ID CODE
Cichlidae	<i>Oreochromis esculentus</i>	Graham, 1928	O.e
	<i>Oreochromis niloticus</i>	Linneus, 1758	O.n
	<i>Oreochromis leucosticus</i>	Trewavas, 1933	O.l
	<i>Tilapia zilli</i>	Gervais, 1848	T.z
	<i>Astatoreochromis alluaudii</i>		A.a
	<i>Astatotilapia aneocolor</i>	Greenwood, 1973	A.c
	<i>Harpagochromis squamipinus</i>	Regan, 1922	H.s
Clariidae	<i>Clarias gariepinus</i>	Burchell, 1822	C.g
	<i>Clarias liocephalus</i>	Boulenger, 1912	C.l
	<i>Protopterus aethiopicus</i>	Heckel, 1851	P.a
Food sources			
Detritus			Dt
Phytoplankton (C ₃)			Pk
Vascular plants			Vp
Water fern (C ₃)	<i>Cyclosorus sp</i>		Cs
Water cabbage (C ₃)	<i>Pistia stratiotes</i>		Pi
Papyrus (C ₄)	<i>Cyperus papyrus</i>		Cp
Ambachi tree (C ₃)	<i>Aeschynomene eraphroxyon</i>		Ae
C ₃ tree	<i>Euclea schemperi</i>		Es
Hippo grass (C ₃)	<i>Vossia cuspidata</i>		Vc
Protozoa (Ciliates)			Pz
Crustacean			Cr
Ephemeroptera			Ea
Coloeoptera			Ca
Nematocera			Na
Hemiptera			Ha
Isoptera			Is
Diptera			Da
Chironomid			Cd
Chaoborus			Cb
Odonata			Od
Trichoptera			Ta
Oligochaeta			Oa
Molluscs			MI
Fish eggs (embryo)			Fe
Fish			Fs

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3$$

Where X is the isotope of interest (either ¹⁵N or ¹³C) and R is the ratio of this isotope to the most abundant isotope (¹⁴N or ¹²C). δ is the measure of heavy to light isotope in the sample.

(Hill and Gauch, 1980; Gauch, 1982) were applied to diet data in order to classify the different consumers into distinct trophic groups by using Community Analysis Package -CAP version 2 (Pisces Conservation Ltd, 2002).

Data analysis

Resource use by the individual fish species was expressed as percentage composition by points of the food item and was presented in tabular form. Specimens with less than three stomachs with food were noted but excluded from further analysis. Data were pooled for each species and lake for the entire sampling period since the aim was to determine the time-averaged trophic structure and energy sources of the fish communities. Hierarchical agglomerative cluster analysis (Pielou, 1984) and Detrended Correspondence Analysis DCA

Results

Stomach dietary analyses

In the two Koki lakes nine fish species examined resulted into 23 prey or food resources (Table 2). In the both lakes studied insects formed the most important primary prey (50%) in most fishes with the exception of *Oreochromis esculentus* and *Oreochromis niloticus* whose main primary prey was algae, however these fishes still included at least (10%) insects in their diet (Tables 2).

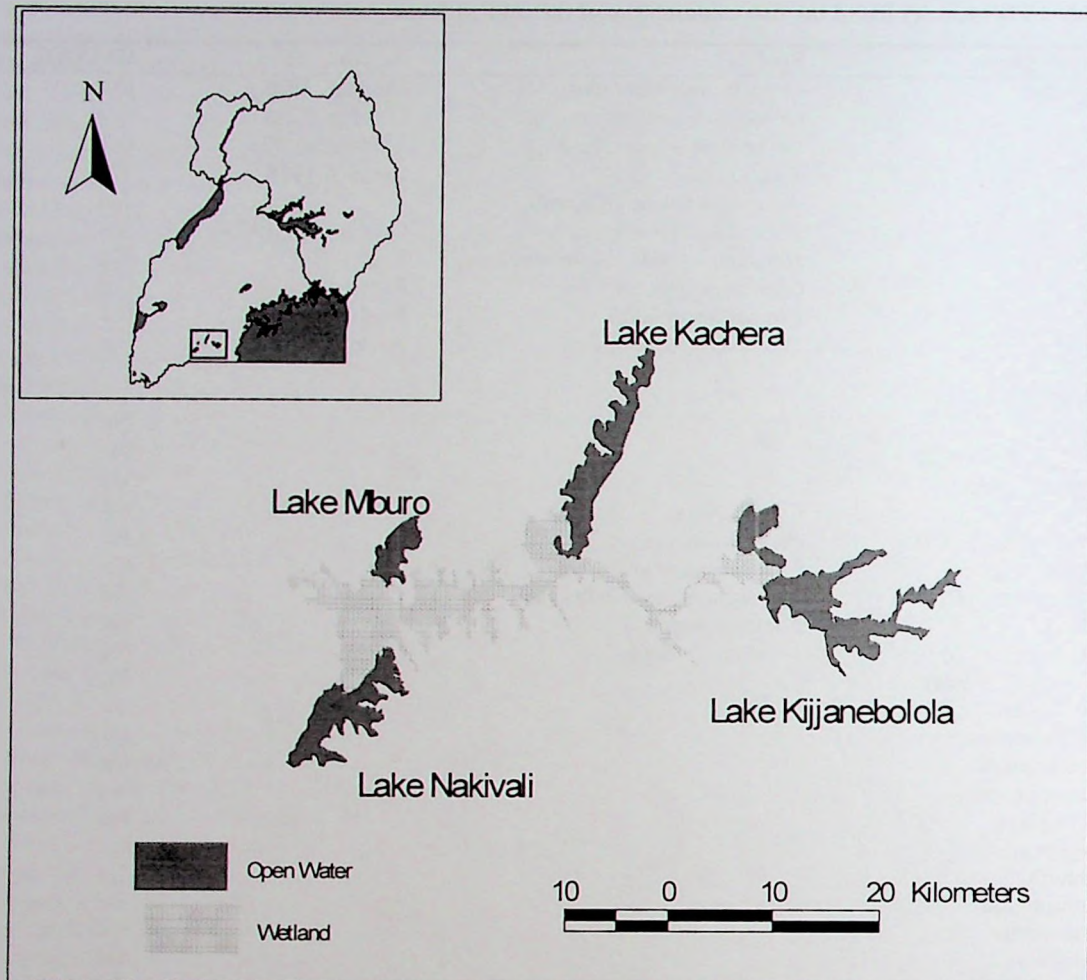


Figure. 1 A map showing the study area (lakes Mburo and Kachera) with the other associated Koki lakes, and their location in Uganda (National Biomass, 1995)

Fish also formed another important component of the diet for *H. squamipinus* (c"13%), *C. gariepinus* (c"13%) and *P. aethiopicus* (>8%). Mollusks formed an important component of diet in *P. aethiopicus* (c"10%) in both lakes and formed the largest component in the diet of *C. liocephalus* (c"35%) in Lake Kachera. Mollusks did not appear to contribute to the diet of *H. squamipinus* in Lake Kachera but contributed (c"10%) to the same fish in Lake Mburo (Table 2). Ephemeroptera contributed (c"10%) and (c"20%) in *A. alluaudii* and *A. aneocolor* respectively in Lake Mburo but was missing in the diet of the Lake Kachera fishes. Fish eggs/embryo formed another important dietary component of *A. aneocolor* (c" 34%) in lake Mburo but was not encountered in any of the fish diets for Lake Kachera. In both lakes there were generally a larger proportion of fishes with empty stomachs compared to those that contained food material, however this was more pronounced in lake Kachera than Lake Mburo (Table 2). The high percentage of fish with empty stomachs in

Lake Kachera compared to Mburo may reflect higher feeding intensity of fishes in lakes with little anthropogenic interference.

Bray-Curtis average linkage cluster analysis illustrated that based on 17 prey groups or food sources in the overall Koki lakes, the nine fish species could be grouped into two different trophic groups or clusters (at distance or dissimilarity $d''0.40$ and $P<0.05$), with all two trophic groups present in both lakes (Figure 2A). Trophic clusters were generally similar for fish species in the two but varied between their taxonomic prey (Figures. 2 B)

The DCA factor scores coded from cluster analysis above explained 26.7% variation in these data and were plotted along with the factor scores of the prey groups or food sources (Figure 3.1B). The fishes with high scores on DCA 1 were carnivorous and depended on such benthic food sources as fish eggs (Fe), ephemeroptera (Ea), coleoptera (Ca), millipedes (Md crustaceans- crabs (Cr), odonata (Od), fish (Fs) and hemiptera (Ha) (Figure 2B and Table 2).

Table 2. Fish stomach contents (% volume) in diets of fishes pooled from all sites within the individual Koki lakes from August 2001 to January 2003. Total sample size and number of fish with food in stomach are also indicated.

Fish species	Lake	Detritus	Green algae	Blue green algae	Diatoms	Other algae	Ciliate	Crabs	Un identified insects	Ephemeroptera	Coleoptera	Nematocera	Hemiptera	Isoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Sandgrains	Molluscs	Fish eggs/embryo	Millipedes	Un identified fish	Sample size (food)	Sample size (total)
<i>A. alluaudi</i>	Mburo	-	-	-	-	-	-	-	0.35	0.11	0.22	-	-	-	0.14	-	0.18	-	-	-	-	-	-	19	71
<i>A. aneocolor</i>	Kachera	0.09	-	-	-	-	0.15	-	0.05	-	-	-	-	-	0.12	0.24	-	-	-	0.03	-	-	0.31	27	233
	Mburo	-	-	-	-	-	0.14	-	0.06	0.24	-	-	-	-	0.12	0.02	-	-	-	-	0.34	-	0.06	26	501
<i>C. gariepinus</i>	Kachera	-	-	-	-	-	0.03	0.05	-	-	-	-	-	-	0.13	0.20	0.04	-	-	0.01	-	0.40	0.08	22	113
	Mburo	-	-	-	-	-	-	-	0.09	-	-	-	0.52	-	0.16	0.04	-	0.04	-	0.02	-	-	0.13	26	119
<i>C. liocephalus</i>	Kachera	-	-	-	-	-	0.11	-	-	-	0.28	-	-	-	0.22	0.04	-	-	-	0.35	-	-	-	6	24
<i>H. squamipinnis</i>	Kachera	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	0.33	-	-	-	-	-	0.33	3	44
	Mburo	-	-	-	-	-	0.12	-	0.30	-	-	-	-	-	0.15	0.02	-	0.03	-	0.12	-	-	0.25	39	285
<i>O. esculentus</i>	Kachera	0.19	0.13	0.17	0.07	0.02	0.15	0.15	-	-	-	-	-	-	0.13	-	-	-	-	-	-	-	-	55	213
	Mburo	0.10	0.09	0.14	0.05	0.02	0.27	0.08	-	-	-	-	-	-	0.11	0.15	-	-	-	-	-	-	-	138	435
<i>O. leucostictus</i>	Kachera	0.04	0.01	0.02	0.01	-	0.30	-	-	-	-	-	-	-	0.53	0.09	-	-	-	-	-	-	-	24	203
	Mburo	0.17	0.01	0.02	0.01	-	0.05	-	0.46	-	-	-	-	-	0.16	0.12	-	-	0.01	-	-	-	-	26	104
<i>O. niloticus</i>	Kachera	0.08	0.08	0.13	0.04	0.01	0.28	-	-	-	-	-	-	-	0.28	0.10	-	-	-	-	-	-	-	65	139
	Mburo	0.12	0.12	0.17	0.06	0.02	0.13	0.02	0.02	-	-	-	-	-	0.11	0.06	-	-	0.17	-	-	-	-	90	185
<i>P. aethiopicus</i>	Kachera	0.09	-	-	-	-	0.12	-	0.03	-	-	-	0.07	0.14	-	0.33	-	0.01	0.13	-	-	-	0.08	54	131
	Mburo	0.02	-	-	-	-	0.16	-	0.14	0.05	-	-	-	-	0.08	-	0.27	-	-	0.10	-	-	0.18	34	72

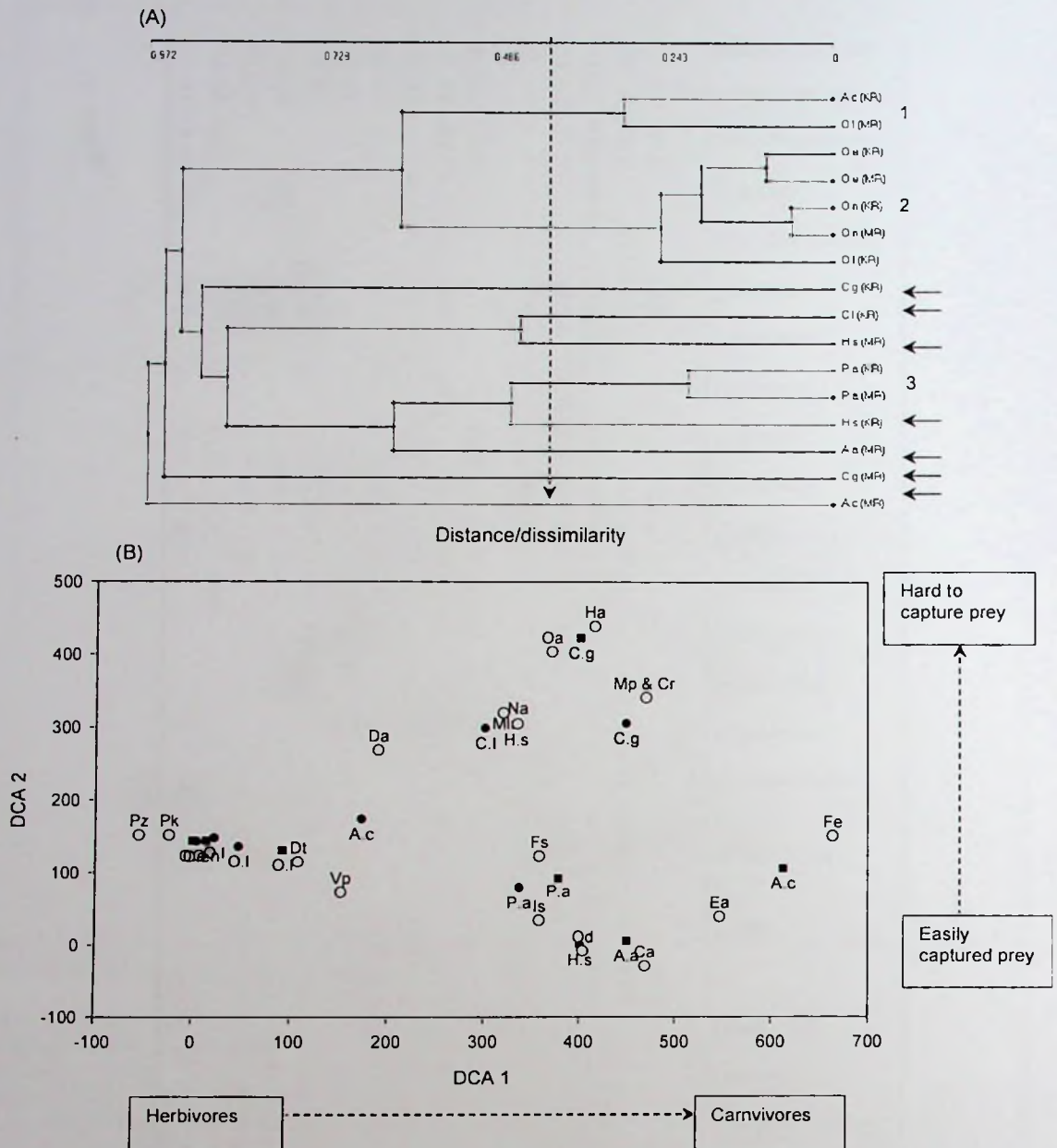


Figure 2 (A) Bray curtis average linkage cluster diagram showing the similarity in diets using the distance measure. At the ≤ 0.40 diet similarity indicates that 10 trophic groups are significant at $P < 0.05$; arrows indicate ungrouped species (B) A DCA scatter plot showing the spatial patterns between 17 food sources ($\circ$) and nine fish species from Koki lakes. DCA 1, grad. length = 6.13; eigen value (E.V) = 0.90; DCA 2 grad. length = 4.2; E.V = 0.73 (Lake Kachera (KR) or ($\bullet$); Lake Mburo (MR) or ($\blacksquare$) text codes for fish species and food sources Table 1)

These fishes were mainly the piscivores, The low scores on DCA 1 were associated with omnivores which mainly depended on planktonic diet (Pk) dominated, by phytoplankton, bacteria (Pz), detritus, vascular plants and diptera.

The first obvious trophic group in the DCA scatter plot comprised the omnivores and was associated with both low scores on both DCA1 and DCA2 plotting near plants and animal food sources (Figure 2B). The fishes in cluster 2 and 3, with similar DCA scores in the scatter plot, which comprised all tilapia species from both lakes and *A. aneocolor* (A.c (KR)) comprised this trophic group. These fishes dominantly fed on phytoplankton, detritus, vascular plants, bacteria and dipteran larvae and pupae (Figure 2B and Table 2). *A. aneocolor* (A.c (MR)) not grouped at a distance of $d''0.4$ in cluster analysis was associated with diet of ephemeroptera (Ea) and fish eggs (Fe) and vascular plants (Table 2) was conveniently included in this trophic group. The last trophic group was the piscivorous, cluster 3 and the remaining fish species (*H. squamipinnis*, H.s, (KR and MR), *A. alluaudi*, A.a (MR), *C. gariepinus*, C.g, (KR and MR) and *C. liocephalus*, C.l, (KR)) not grouped at a distance of $d''0.4$ in cluster analysis (Figure 2B).

These fishes had DCA 1 scores associated with the fish (Fs) food source. Some fishes in this group also consumed a wide range of food items such as odonata (Od), mollusks (Ml), nematocera (Na), oligochaetes (Oa), crustaceans and millipedes placing them near those food sources in the scatter plot. Finally hierarchical agglomerative cluster analysis and DCA finally established two trophic groups for the Koki lakes and were present in both sampled lakes.

Stable isotope analyses

Carbon Sources

Stable isotope ratios for primary producers generally showed a clear separation in the two studied lakes (Fig. 3). In lakes, plankton (Pk), *V. cuspidata* (Vp) and *C. papyrus* (Cp) showed similar isotopic signatures; being ^{13}C enriched compared to the other primary producers, however plankton were more ^{13}C depleted ($\delta''5\%$) in Lake Kachera relative to Lake Mburo. The stable isotope ratios for primary producers showed little separation with respect to $\delta^{15}\text{N}$ except for C3 tree *E. schimperii* (Es) in Lake Mburo and *C. papyrus* (Cp) in both lakes that exhibited exceptionally high $\delta^{15}\text{N}$ signatures.

In both lakes *O. esculentus* (O.e) and *O. niloticus* (O.n) occupied similar position in isotopic space but other fishes and plankton were more enriched in Lake Mburo than in Lake Kachera. This suggests that most of the food web in both lakes may be tracking plankton (Fig. 3), which is enriched in ^{13}C in Mburo relative to Kachera. Plankton and *C. papyrus* (Cp) came out to be the major potential food source and contributed significantly to the diets of most consumers especially fish in the two lakes. In both lakes the fish had highly variable $\delta^{13}\text{C}$ ratios both within and

among taxa, suggesting that these fishes had broad diets driving energy from a range of C_4 and C_3 plants, including phytoplankton whose $\delta^{13}\text{C}$ can vary in time if photosynthetic demand for CO_2 exceeds the supply of CO_2 and isotopic fractionation by photosynthesis is reduced (Hecky and Hesslein 1993). As algal biomass increases, algae will become enriched in ^{13}C and have a heavier $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ of the animal food web can become more similar to the C_3 higher plants (*V. cuspidata* (Vc) and *C. papyrus* (Cp)) and the C_4 phytoplankton. In Lake Mburo the nutrient enrichment provided by the hippopotamuses would cause denser phytoplankton populations resulting in a heavier $\delta^{13}\text{C}$ as well as directly introducing enriched $\delta^{13}\text{C}$ undigested C_4 grass debris from hippo defecation directly into the lake.

Trophic relationships

Assigning fishes into specific obligate trophic levels basing on their $\delta^{15}\text{N}$ was not possible because the observed enrichment values for $\delta^{15}\text{N}$ were often considerably lower than 3.4‰ typically assumed in stable isotope studies. For example *C. papyrus* (Cp) and *E. schimperii* (Es) exhibited a higher $\delta^{15}\text{N}$ than all invertebrates sampled in both lakes and can be excluded as direct dietary inputs to those invertebrates, but a mixed diet of papyrus debris and plankton could account for the $\delta^{15}\text{N}$ signatures of all the fish. Omnivory seems to be the rule among the fishes with potentially high degree of dietary overlap among the fishes. Only habitat separation within the lakes would prevent strong trophic competition among these trophic generalists.

In both lakes $\delta^{15}\text{N}$ signatures placed fish at the top of the lakes' food webs, with the haplochromine cichlid *Harpagochromis squamipinnis* being the most $\delta^{15}\text{N}$ enriched reflecting a stronger tendency to consume other fishes (Table 2). At the base of the food webs were possibly *V. cuspidata* (Vc) and more probably plankton for lakes Kachera and Mburo respectively as the upper food web appears to track the plankton as reported by Hecky and Hesslein (1995). In both lakes invertebrates had $\delta^{15}\text{N}$ that were intermediate between those of the fishes and papyrus and the plankton indicating their dependence on the plankton and their predation by fish. In both lakes the two *Oreochromis* spp. had non-overlapping isotopic signatures for the sampled fishes and were most similar to papyrus among the plants. Their isotopic signatures were the only ones among the fishes to be similar in both lakes further suggesting a dependence on papyrus detritus in both lakes.

Discussion

Analysis of trophic groups may show differences in trophic structure and ecosystem dynamics and therefore have implications for the management of fisheries (Koslow, 1997). For the same energy input of organic matter at the base of the web different trophic structures will yield different levels of secondary production and different fish

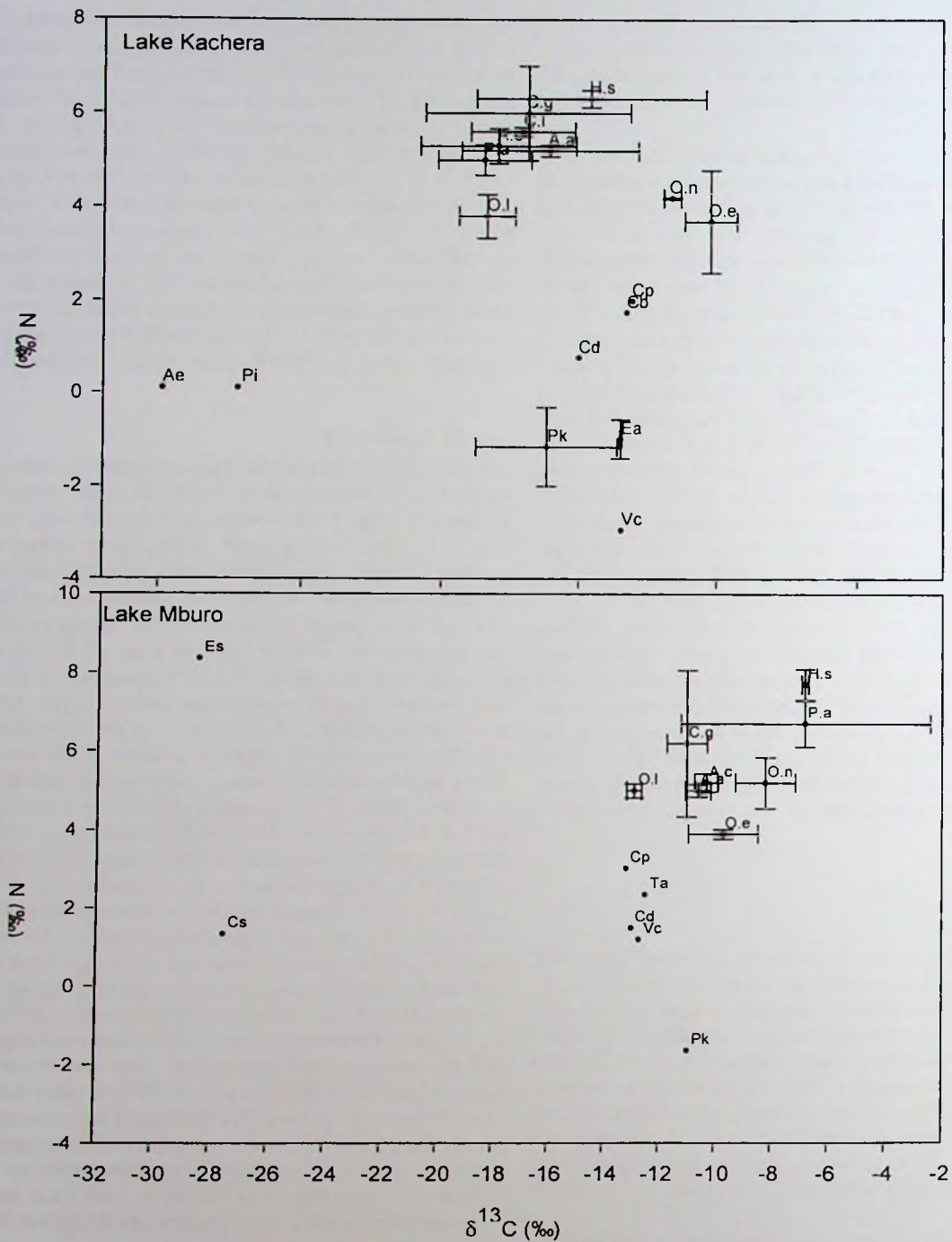


Figure 3. The Mean $\pm$ S.D of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for nine fish species fishes and 10 potential food sources from Koki lakes. Note the lighter and high variation in $\delta^{13}\text{C}$ of food web structure of Lake Kachera to Lake Mburo (text codes Table 1).

species composition that can determine the economic value of the fishery.

The trophic relationships between two species can also change through ontogeny and the degree of niche overlap between two species may also vary ontogenetically (Polis, 1984; Piet *et al.*, 1999). Therefore our fishes may not represent the feeding behavior of the juvenile and immature fishes not captured by our nets. These in turn will be missing in our analyses as food resources for the piscivorous fishes. Therefore our sampling methods can limit the interpretations possible, but our stomach analyses indicate that we have sampled most elements of the biota that occur in fish stomachs.

In general, fish species in the two studied lakes had similar diets. However, there were some few exceptions. For example in Lake Mbuho *H. squamipinnis* included molluscs and vascular plants that were not fed on at all by the same fish in Lake Kachera. In both lakes *A. alluaudii* were classified as insectivorous in contrast to molluscivores by earlier studies on Kyoga basin lakes (Mbabazi *et al.*, 2004). Such differences may be partly related to habitat differences or geographic variations, such as differences in food availability at different localities (Nakamura *et al.*, 2003). Shallow lakes are complex heterogeneous environments with a variety of sources of primary production available for exploitation (Jeppesen *et al.*, 1998).

Variation in stable isotope ratios of primary producers is often averaged out in consumers (Kirililk *et al.*, 1995) making it difficult to determine precisely which primary producers were carbon sources for a particular consumer. In these lakes overlapping carbon signatures of plankton and C_4 plants especially in Mbuho made it impossible to determine quantitatively the relative importance of these different internal carbon sources (e.g. Boudoin *et al.*, 2001) although when both lakes are considered, it is clear that the upper food web consisting of fishes demonstrates a dependence on the plankton as both the web and the plankton have heavier isotopic signatures in Mbuho.

Fish had a varied diet, which in part was influenced by their species and size, but in general displayed a lack of specialization. Omnivory is common in freshwater food webs especially among freshwater fish assemblages (Vadas, 1990) and our results (Table 2) and stable isotope analysis (Figure 3) strongly support this observation in the two studied lakes. Fish $\delta^{13}C$ signatures were typically variable and intermediate among several different prey $\delta^{13}C$ signatures and had intermediate $\delta^{15}N$ values relative to predatory and non-predatory fish or invertebrates.

There was no clear segregation between pelagic and littoral habitat organisms because within in these lakes as has been observed in other similar small lakes (Jones and Waldron, 2003; Beaudoin *et al.*, 2001), because the littoral and profundal zones are less distinct than it is in deeper lakes. However, it was apparent that the food web of Lake Mbuho was comprised of fish and plankton with more enriched carbon signatures than in Lake Kachera ($\sim 5\text{‰}$).

This is likely due to nutrients that arise directly from the dung from large population of hippopotamuses with no major return pathways known (Laws, 1968; Grey and Harper, 2002). Hippopotamuses graze selectively on short grass species C_4 plants (Lock, 1972; Grey and Harper, 2002) with a daily intake of about 18Kg of dry matter (Law, 1963). The ingested grasses use the C_4 photosynthetic pathway and exhibit distinct highly ^{13}C enriched signatures compared to aquatic basal resources. As the beast grazes on land and usually defecates in the water, there is a drain of nutrients to the lakes. Similar studies indicated that fecal return by ungulates was positively and linearly linked to both production and consumption (Douglas and McNaughton, 1992). Ungulates excrete $>90\%$ and 65-95% of the phosphorus and nitrogen they ingest respectively (Ruess, 1987) and these nutrients are in forms readily available to plants and soil microbes (Floate, 1981; Douglas and McNaughton, 1992) and will enrich lakes. Our study indicates that the fish community is dependent on energy from phytoplankton and that enrichment of this food source should produce higher fish production and yields in Lake Mbuho.

The observed trophic enrichments for $\delta^{15}N$ (Figure 3) were considerably lower than a typical assumed shift of (3.4‰) per trophic level predicted from a synthesis of previous stable isotope studies (DeNitro and Epstein, 1978; Post 2002). Results from other studies indicated that trophic enrichments for $\delta^{15}N$ can vary depending on the trophic level, animal diet system or ecosystem under consideration and lower than expected (i.e. $< 3.4\text{‰}$) enrichments often occur (Pinnegar *et al.* 2001; Vander Zanden and Rasmussen, 2001; Zah *et al.*, 2001; Herwig *et al.*, 2004), although we cannot discount differences in fractionation (Adams and Sterner, 2000; Ben-David and Schell, 2001).

Stable isotope analysis is an important tool that can be used to understand feeding ecology, food web structures and ecosystems level processes but the method should be complemented by quantitative analysis of stomach content analysis and controlled field experiments rather than as a strict substitute (Rounick and Winterbourn, 1986) if detailed information is required for fish stock management. Despite these challenges, this study indicated that the food webs of these lakes are complex, characterized by omnivory and generalism. The determination of definite food sources for the different fish species was not possible because of dietary overlap integrating primary producers signatures; however, we were able to identify that the carbon sources to fishes from the two lakes were from different origins.

Trophic structure and ecosystem management

The slight spatial differences observed in trophic structure of two similar lakes located in the same watershed drainage system may reflect differences in species membership and biomass dominance among the fish assemblages. Associated with these patterns are differences in complexity of food webs, the strength of species interactions and the resulting

energy and biomass flow especially for aquatic systems located in different watersheds. Development of ecosystem based fisheries management guidelines, should explicitly account for the spatial differences in community structure of aquatic systems located in the different watersheds. Stable isotope analysis is a rapid means of determining trophic specialization or generalization in fish stocks and can provide information on primary energy sources. Survey of isotopic food web structure can provide essential information for fisheries management.

Acknowledgements

The Lake Victoria Environmental Management Project, National Agricultural Research Organization and Uganda Government provided logistics and laboratory space. The staff and students of Biology Department, University of Waterloo provided office space, technical guidance and financial support for additional stable isotope analyzes. W. Mark assisted with stable isotope analyzes at the Environmental Isotope Laboratory, University of Waterloo and Prof. W. Taylor from the same University for guidance on multivariate statistics. The Uganda Wild life Authority permitted the research. This work was made possible with assistance from the support staff and scientists at the Fisheries Resources Research Institute, whom we sincerely acknowledge. We would end by acknowledging A. Katende without whose expertise the aquatic plants would not have been identified.

References

- Adams T.S and Sterner, R.W. , 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment *Limnology and Oceanography* 45: 601-607.
- Balirwa, 1984. Ecological separation in *Barbus* species in Lake Victoria. MSc. thesis, University of Dar es Salaam.
- Balirwa, J.S., 1998. Lake Victoria Wetlands and Ecology of the Nile tilapia, *Oreochromis niloticus* Linne. Ph.D Thesis. 247 pp. Wageningen Agricultural Univ., Wageningen, NL.
- Beaudoin C.P., Tonn W.M, Prepas V and Wassenaar L.I., 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia* 120: 386-396.
- Beaudoin C.P, Prepas. E., Tonn. W. M, Wassenaar., L.I. and B.G. Kotak, 2001. A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain *Freshwater Biology* 46: 465-477.
- Ben-David M. and Schell, D.M, 2001. Mixing models in analyses of diet using multiple stable isotopes: a response. *Oecologia* 127: 180-184.
- Bunn S.E. and . Boon, P.I, 1993. What sources of organic carbon drive food webs in billabongs: a study based on multiple stable isotopes *Oecologia* 96: 85-94.
- Cabana, G., and Rasmussen. J.B, 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proc. Nat. Acad. of Sci.* 93: 10844-10847.
- Campbell. L.M., Hecky. R.E. and Wandera, S.B., 2003. Stable isotope analyses of food web structure and Fish diet in Napoleon and Winam gulfs, Lake Victoria, East Africa. *J. Great Lakes Res.* 29 (supp. 2): 243-257.
- Diehl, S., and R. Kornijów, 1998. Influence of submerged macrophytes on trophic interactions among fish and macro-invertebrates. In: Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo., and Christoffersen. K. (eds). The structuring role of submerged macrophytes in lakes. Springer Verlag, New York, pp 24-46.
- Douglas A. F., and McNaughton, S. J. 1992. The ecology of plants, large mammalian herbivores and grout in Yellowstone National Park. *Ecology* 73: 2043-2058.
- Emerton, L., 1999. Balancing the opportunity costs of wild life conservation for communities around Lake Mburu National park, Uganda pp27, ISBN 1843690047.
- Floate, M.J.S., 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In F.E. Clark and T. Rosswall, editors. Terrestrial nitrogen cycles; processes, ecosystem strategies and management impacts. *Ecological Bulletins-NFR* 33: 585-601.
- France, R.L., 1995 a. Carbon -13 enrichment in benthic compared to planktonic algae: food web implications. *Marine Ecology Progress Series* 124: 307-312.
- France, R.L., 1996. Absence or masking of metabolic fractionation of ^{13}C in a freshwater benthic food web. *Freshwater Biology* 36: 1-6.
- France, R.L., 1997. Stable carbon and nitrogen isotope evidence for ecotonal coupling between boreal forests and fishes. *Ecol. Freshwater. Fish* . 6: 78-83.
- Gauch, H.G.: Jr., 1982. Multivariate analysis in community ecology pp. 298: NY: Cambridge University Press.
- Genner, M.J., G.F. Turner, S. Barker and S.J. Hawkins., 1999. Niche segregation among Malawi cichlid fishes? Evidence from stable isotope signatures. *Ecology Letters* 2: 185-190.
- Grey, J. and M. Harper, 2002. Using stable isotopes analyses to identify allochthonous inputs into Lake Naivasha mediated via the hippopotamus gut. *Isotopes Environ. Health Stud.* 38(4): 245-250.
- Gu, B., D.M Schell and V. Alexander, 1994. Stable carbon and nitrogen isotopic analysis of plankton food web in subarctic lake *Canadian Journal of Fisheries and Aquatic Science* 51: 1338-1344.
- Gu, B., S.L. Schelske, and M.V. Hoyer, 1996. Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake. *Journal of Fish Biology* 49: 1233-1243.

- Hecky, R.E., & R.H. Hesslein., 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analyses. *North America Journal of Benthological Society* 14: 631-653.
- Herving B.R., D.A. Souk, J.M. Dettmers & D.H. Wahl., 2004. Trophic structure and energy flow in blackwater lakes of two large flood plain rivers assessed using stable isotopes. *Canadian Journal Fisheries and Aquatic Sciences* 61: 12-22.
- Hesslein, R.H., K.A. Hallard, & P. Ramlal., 1993. Replacement of sulphur, carbon, and nitrogen in tissue of growing broad white-fish (*Coregonus nasus*) in response to change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Science* 50: 2071-2076.
- Hill, M.O. and H.G. Gauch, 1990. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 477-58.
- Holopainen, A.L., P. Huttunen & M. Ahtianen, 1991. Effects of forestry practices on water quality and primary productivity in small forest brooks. *Verh. Int. Ver. Limnol* 24: 1760-1766.
- Hynes, H.B.N. 1950. The food of the freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in the food of fishes. *Journal of Animal Ecology* 19: 36-58.
- Jennings, S., O. Reñones, B. Marales-Nin, N.V.C. Polunin, J. Moranta, & J. Coll, 1997. Spatial variation in the ^{15}N and ^{13}C stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: Implications for the study of trophic pathways. *Marine Ecology-Progress series* 146: 109-116.
- Jennings, S., & M.J. Kaiser, 1998). The effects of fishing on marine ecosystems. *Advances in Marine Biology* 46: 28-46.
- Jepsen, D.B. and K.O. Winemiller, 2002. Structure of tropical river food webs revealed by stable isotope ratios. *Oikos* 96: 46-55.
- Jones, J.I. and S. Waldron, 2003. Combined stable isotope and gut contents analysis of food webs in plant-dominated, shallow lakes. *Freshwater Biology* 48: 1396-1407.
- Kamugisha, J., Z. Ogutu & M. Ståhl, 1997. *Parks and People: Conservation and livelihoods at the Crossroads*, Regional Soil Conservation Unit/SIDA, Nairobi.
- Keough, J.R., M.E. Siersen, & C.A. Hargley, 1996. Analysis of lake Superior coastal food web with stable isotope techniques. *Limnology and Oceanography* 41: 136-146.
- Kiriluk, R. M., M. R. Servos, D. M. Whittle, G. Cabana, and J. B. Rasmussen. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, Mirex, and PCB in a Lake Ontario pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2660-2674.
- Kling, G.W., Fry, B., & W.J. O'Brien, 1992. Stable isotopes and planktonic structure in arctic lakes. *Ecology*, 73: 561-566.
- Koslow, J.A., 1997. Seamounts and the ecology of deep-sea fisheries *American Scientist* 85: 168-176.
- Larkin, P.A. 1996. Concepts and issues in marine ecosystem management. Minagawa, M.H., & E. Wada, 1984. Step wise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochimica et Cosmochimica Acta* 48: 611-1140.
- Laws, R.M., 1968. Interactions between elephant and hippopotamus populations and their environments. *E. Afr. agric. For. J.* 33: 140-147.
- Lock, J.M., 1972. The effects of hippopotamus grazing on Grasslands. *The Journal of Ecology* 60(2): 445-467.
- Magnusson, W.E., M.C. Araujo, R. Cintra, A.P. Lima, L.A. Martinelli, T.M. Sanaïotti, H.L. Vasconcelos & R.L. Victoria, 1999. Contributions of C_3 and C_4 plants to higher trophic levels in an Amazonian savanna. *Oecologia* 119: 91-96.
- Manetta, G.I., E. Benedicto-Cecilio, & M. martinelli, 2003. Carbon sources and trophic position of the main species of fishes of Baia River, Parana River flood plain, Brazil. *Brazilian Journal of Biology* 63: 283-290.
- Mbabazi D, R. Ogutu-Ohwayo, S.B Wandera & Y. kiziito, 2004 Fish species and trophic diversity of haplochromine cichlids in the Kyoga satellite lakes (Uganda). *African Journal of Ecology* 42 (1): 59-68.
- Nakamura Y., M. Horinouchi., T. Nakai and M. Sano. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. *Ichthyol Res* 50: 15-22.
- Namara, A., & M. Infield, 1998. *The influence of a Community Conservation Programme on farmers and Pastoralist Communities, Lake Mburo National Park Uganda: Report of a Socio-Economic Survey carried out under the Community Conservation for Uganda Wildlife Authority Project*, Uganda Wildlife Authority, Makerere University Institute of Social Research and African Wildlife Foundation, Kampala.
- National Research Council, 1999. Sustaining Marine Fisheries. Report of committee on ecosystem management for sustainable marine fisheries, oceans studies board, 168pp.
- Namulemo G. and D. Mbabazi. 2004. Conservation of fish species diversity in the Victoria and Kyoga basin lakes. *Ug. J. Agric. Sci* —
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese & F. Torres Jr, 1998. Fishing down marine food webs. *Science*. 279: 860-863.

- Peterson, B.J. and Fry, B., 1987. Stable isotopes in ecosystem studies. *Annual Reviews of Ecology and Systematics*. 18: 293-320.
- Pielou, E.C., 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley and Sons, New York.
- Piet G.J., Piet.J.S., Guruge, W.A.H.P, Vijverberg, J. and Van Densen, W.L.T., 1999. Resource partitioning along three niche dimensions in a size-structured tropical fish assemblage. *Canadian Journal Fisheries and Aquatic Sciences* 56: 1241-1254.
- Pinnegar, J.K., Campbell, N. and Polunin, N.V., 2001. Unusual trophic fractionation patterns observed for fish host parasite trophic relationships. *Journal of Fish Biology* 59: 4994-503.
- Planas, D., Desrosiers, M., Groulx, S-R., Paquet, S. and Carignan, V., 2000. Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. *Canadian Journal Fisheries and Aquatic Sciences* 57(suppl.2): 136—145.
- Polis, 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *American Naturalist* 123: 352-368
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83 (3): 703-718
- Rounick, J.S. and M.J. Winterbourn, 1986. Stable carbon isotopes and carbon flow in ecosystems. *Bioscience* 36: 171-177.
- Ruess, R.W., 1987. The role of large herbivores in nutrient cycling of tropical savannas. In B.H. Walker, editor. *Determinants of tropical savannas*. IRL Press, Oxford, England. pp 67-991
- Vadas, R.L., Jr. 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America *Environmental Biology of Fishes* 27: 285-302
- Vadeboncoeur, Y., Jeppesen, E., Vande Zanden, M.J. Schierup, H., Christoffersen, K. and Lodge, D.M., 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes.
- Vander Zanden, M.J. and Rasmussen, J.B., 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology* 80: 1395-1404. *Limnology and Oceanography* 48 (4): 1408-1418.
- Vander Zanden, M.J. and Rasmussen, J.B. 2001., Variation in ^{15}N and ^{13}C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography* 46: 2061-2066.
- Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60: 331-367
- Yashioka, T., E. Wada, H. Hayashi., 1994. A stable isotope study on seasonal food web dynamics in eutrophic lake. *Ecology*, 75: 835-846.
- Zah, R., P. Burgherr, S.M Bemasconi & Uehlinger, 2001. Stable isotope analysis of macro-invertebrates and their food sources in a glacier stream. *Freshw. Biol.* 46: 871-882.