

**SPATIAL – TEMPORAL DISTRIBUTION AND ABUNDANCE OF LARVAL
STAGES OF NILE PERCH (*Lates niloticus* LINNAEUS 1758) IN LAKE
VICTORIA, KENYA**

**BY
AGEMBE SIMON WERE**

**A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN
FISHERIES (FISHERIES MANAGEMENT) IN THE SCHOOL OF NATURAL
RESOURCE MANAGEMENT, UNIVERSITY OF ELDORET, KENYA**

OCTOBER, 2018

DECLARATION

Declaration by the candidate

This research thesis is my original work and has not been presented for a degree in any other University. No part of this thesis may be reproduced without the prior written permission of the authors and/or the University of Eldoret.

Signature:

Agembe Simon Were	DATE
(NRM/D.PHIL/FIS/01/2010)	

Declaration by the Supervisors

This research thesis has been submitted with our approval as University supervisors.

Dr. Frank Onderi Masese	Date
Department of Fisheries and Aquatic Sciences, University of Eldoret- Kenya.	

Prof. James M. Njiru	Date
Kenya Marine and Fisheries Research Institute Mombasa, Kenya.	

Dr. William Oweke Ojwang	Date
World Wildlife Fund, Nairobi, Kenya	

DEDICATION

This thesis is dedicated to my family members, staff and friends who provided encouragement during its preparation.

ABSTRACT

Lake Victoria is a relatively dynamic ecosystem with constant changes in both biotic and abiotic variables primarily influenced by human activities. Studies in the ecology and fisheries in Lake Victoria has mostly concentrated in the adult stages of *Lates niloticus*, the most important species in the lake. This studies have mostly attributed population decline to overfishing and pollution effects. There is little information in the contribution of larval dynamics and ecology in the fishery of the lake. This study therefore aimed to bridge this gap by providing data in the spatial – temporal distribution and abundance of larval stages of Nile perch (*Lates niloticus* Linnaeus 1758) in Lake Victoria, Kenya. Nile perch Larvae were sampled from 2011-2013 at 29 stations in the Winam Gulf of the Lake by Tows using a combination of plankton net mesh sizes. Juveniles(less than 10cm) were sampled in 2011-2013 by trawling with cod end covered with 3 mm mosquito net and gillnetting using 25 mm meshed nets. Larval abundance ranges from a low of 1 to a high of 600 with distribution in sheltered bays and river mouth stations. Peak larval abundance occurred in the month of February, August, September, November and December indicating spawning period for *L. niloticus* that coincided with full moon lunar phases. GLM analysis indicated the distribution of larvae was influenced significantly by water turbidity. Other water quality parameters had no significant effect on larval abundance. Spatially Nile perch distribution showed small sized fishes (< 5 cm) were abundant in inshore stations than open lake stations. The study generated VBGF for Nile perch in the Winam Gulf as $L_{\infty} = 169$ cm, with an exploitation rate (E) of 0.57 and mortality coefficient(Z) of 0.96 yr^{-1} . Results of food analysis indicated the fish to feed proportionately higher on *Caridina nilotica*. The ontogenetic shift in diet occurred at three different levels, larval stages fed purely on zooplankton, juveniles shifted to *Caridina* and thereafter fish dominated diets. Management measures based on the findings of this study include protection of the 200 m from the shore through legal prohibition of fishing and any other activity in the lake, further studies of near shore hydro-dynamics are required to provide insights on factors influencing the abundance and distribution of larvae and juveniles of Nile perch in the lake and the extent and nature of diel vertical migration to determine whether it is related to predator avoidance, feeding or energetics as has been observed for zooplankton.

TABLE OF CONTENTS

DECLARATION	ii
DEDICATION	iii
LIST OF TABLES	viii
LIST OF FIGURES	ix
LIST OF PLATES	xi
LIST OF ABBREVIATIONS, ACRONYMS AND SYMBOLS	xii
CHAPTER ONE	1
INTRODUCTION.....	1
1.1 Background Information	1
1.2 Statement of the Problem	6
1.3 Justification for the Study	9
1.4 Objectives.....	11
1.4.1 Overall objective.....	11
1.4.2 Specific objectives	11
1.5 Hypotheses	11
CHAPTER TWO	13
LITERATURE REVIEW	13
2.1 Genesis of Nile Perch in Lake Victoria.....	13
2.2 Biology and Ecology of Nile Perch.....	14
2.3 Nile Perch Fishery	17
2.4 Stock Assessment in Lake Victoria.....	19
2.5 Larval Ecology and Population Dynamics.....	20
2.6 Growth Parameters	22
2.7 Relationships between Environmental Parameters and Fish Distribution	23
2.7.1 Thermal and oxygen stratification.....	23
2.7.2 Changes in Secchi depth and turbidity	24
CHAPTER THREE	25
MATERIALS AND METHODS	25
3.1 Study Area.....	25
3.2 Characteristics and Selection of the Sampled Stations	29
3.3 Measurement of Physico-chemical Characteristics.....	31
3.4 Collection of Fish Samples	32
3.4.1 Larval sampling	32
3.4.2 Diel sampling.....	34

3.4.3 Trawl sampling	34
3.4.4 Gillnet sampling for juvenile and adult fishes	35
3.5 Stomach content Analysis	36
3.6 Laboratory Analysis	36
3.6.1 Water sample analysis	36
Nutrient analysis	37
3.6.2 Analysis of larval samples	38
3.6.3 Analysis of stomach contents	39
3.7 Data Analysis	39
3.7.1 Water quality assessment.....	39
3.7.2 Larval fish data analysis	40
3.7.3 Analysis of length frequency distributions	40
3.7.5 Food and feeding habits.....	46
CHAPTER FOUR.....	48
RESULTS	48
4.1 Physico-chemical Water Quality Parameters	48
4.2 Distribution of Eggs, Larvae and Prey in Relation to water quality	55
4.3 Larvae Abundance and Size structure	57
4.4 Variation in mean length of Nile Perch juveniles with depth	65
4.5 Spatio-temporal distribution of zooplankton.....	69
4.6 Spatial Distribution of Larvae	72
4.7 Population Growth Characteristics	76
4.7.1 Growth parameters	76
4.7.2 Mortality estimates and probability of capture.....	76
4.7.3 Recruitment pattern and Relative Yield Per Recruit/Biomass Per Recruit .	78
4.8 Food and Feeding Habits.....	81
4.8.1 Diel feeding	82
Objective 5: Ontogenetic shifts in structural development and food composition of <i>L. niloticus</i> in Lake Victoria, Kenya	84
4.8.2 Ontogenetic shifts in diet/ food composition.....	84
4.9 Ontogenetic Changes in food items in adult Nile Perch	86
4.9.1 Ontogenetic changes in morphological features.....	87

CHAPTER FIVE	89
DISCUSSION	89
5.1 Physico-chemical Water Quality Parameters	89
5.2 Distribution and Abundance of Larval Fish	90
5.2.1 Temporal distribution	92
5.3 Spatial distribution of Larval fish.....	94
5.4 Population Characteristics.....	95
5.5 Food and Feeding Habits.....	97
5.6 The ontogenetic shift in structural development and diet	98
CHAPTER SIX	101
CONCLUSIONS AND RECOMMENDATIONS.....	101
6.1 Conclusions	101
6.2 Recommendations	102
REFERENCES.....	103
Appendix I: Canonical Correlations of zooplankton species and the nutrients	130
Appendix II: Coefficients for Canonical Variables of water quality and zooplankton.....	131
Appendix III : Coefficients for Canonical Variables of the Second Set	132
Appendix IV: Variation in depth for the investigated stations.....	133
Appendix V: Variation in Temperature for the investigated stations	133
Appendix VI: Variation in TSS and TDS for the investigated stations	134
Appendix VII: Variation in Turbidity and Secchi depth for the investigated.....	134
stations.....	134
Appendix VIII: Length frequencies of Nile Perch caught in standard larval fish	
collected using tow nets with 500 μm mesh and nets with 750 μm mesh	135
Appendix IX: Monthly composite length frequency data of <i>L. niloticus</i>	136
representing samples collected from 2014 to 2015 pooled together.....	136

LIST OF TABLES

Table 1: Morphometry, hydrological balance and geographical features of Lake Victoria	28
Table 2: Description of sampling stations in the Kenyan waters of Lake Victoria .	30
Table 3: Depth strata areas for the allocation stations In Lake Victoria.....	31
Table 4: Mean values (and maximum values in brackets) of some of the physico-chemical parameters in the different clusters of the study area. ND denotes no data. (C1 = Inner Gulf stations, C2 = Mid Gulf stations, C3 = Offshore open Lake stations).....	50
Table 5: Nominal Logistic Regression: Parameters versus Measurements, <i>L.niloticus</i> larvae (a) response information (b) Logistic Regression Table (c) Goodness of Fit Tests. Note: TDS = Total dissolved solids	57
Table 6: Distribution of fish larvae by station sampled from September 2011 to June 2013 in Lake Victoria, Kenya (No. /m ³).	59
Table 7: Canonical Correlations of zooplankton species with the water quality parameters.....	71
Table 8: Changes in growth and population parameters of <i>L. niloticus</i> in Lake Victoria, 1991-2015.....	80
Table 9: Percentage composition of zooplankton in the diet of small Nile perch in 2012/16 and 1988/89	85
Table 10 : Larval development in <i>Lates niloticus</i> showing the approximate length (TL mm) at which the principal morphological features first appear on the fish.	88

LIST OF FIGURES

- Figure 1: Map of Lake Victoria, Kenya showing the sampled stations. (a) Number on the map denotes (1 Kisumu Bay 2 Sondu miriu , 3 Awach River mouth, 4 Off Maboko, 5 Off Gingra rock, 6 Asembeo Bay,7 Homa Bay, 8 Bala Rawi, 9 Madundu, 10 Yala River mouth, 11 Nzoia River mouth ,12 Kuja River mouth b) shows all stations by name. (Source: Author, 2018)26
- Figure 2 : Larval development in *Lates niloticus* showing the approximate length (TL mm) at which the principal morphological features first appear on the fish.33
- Figure 3: Principal coordinates projections (vector projections) of water quality parameters in Lake Victoria, Kenya53
- Figure 4: Principal Coordinates showing dimension 1 and 2 vector projections by stations in Lake Victoria, Kenya53
- Figure 5. The mosaic display to show the values (cell frequencies) in a contingency table cross-classified by one or more “factors”.54
- Figure 6: CCA of *Lates niloticus* ordination with physical chemical parameters in the Kenyan sector of Lake Victoria in 2012.....55
- Figure 7: Mean length distribution of Nile perch larvae ordered by early life history stages (Preflexion, Flexion, Postflexion and Juveniles in Lake Victoria, Kenya. Showing overlaps in lengths as they transition61
- Figure 8: Pooled tri - monthly relative abundance of *Lates niloticus* larvae for each sampling station during 2011-2013 sampling period in Lake Victoria, Kenya...62
- Figure 9: Boxplot distribution characteristics of different stages of Nile perch larvae sampled in 2013 grouped data in Lake Victoria Kenya 63
- Figure 10: Mean size distribution of Nile perch larvae sampled in 2013 grouped.....64
- Figure 11: Mean size of *Lates niloticus* larvae sampled over 24 hours in January ...65
- Figure 12: Length of Nile perch juveniles harvested at various depths using a66

Figure 13: Length-frequency distributions of Nile perch in the experimental gillnet catches set at different depth (Top 0-1m, middle 1-2m, bottom 2-3 m) in Lake Victoria, Kenya.....	67
Figure 14: Length-frequency distributions of Nile perch in the experimental	67
Figure 15: Frequency distribution of Nile perch juveniles caught in gillnets set	68
Figure 16 : Abundance of Nile perch during full and last quarter lunar phases in	69
Figure 17 : Zooplankton densities in different sampling stations in Kenyan	70
Figure 18 : Spatial distribution of Nile perch post larvae abundance by sizes of 0- ...	73
Figure 19: Spatial densities of Nile perch larvae densities and abundance from	74
Figure 20: Identified and demarcated Lates niloticus fish breeding and nursery	75
Figure 21 : The growth curves (continous lines) of cohorts of Lates niloticus, in	77
Figure 22 : Left: Values of total mortality (Z), natural mortality (M), fishing.....	77
Figure 23 : Annual percentage recruitment	78
Figure 24 : Beverton & Holt's relative yield-per-recruit and average biomass per.....	79
Figure 25 : Percent contribution by weight of major food item in overall diet of.....	81
Figure 26 : Diurnal feeding regime of L. niloticus larvae from Lake Victoria,	83
Figure 27 : Food composition in guts of larvae collected during diel sampling.....	83
Figure 28 : Food of Lates niloticus of different lengths from Lake Victoria,	85
Figure 29 : Frequency of occurrence of the main prey types of Nile perch up to	86
Figure 30: Ontogenetic shift in prey items observed in the stomach of wide length range of Nile perch larvae caught in the Kenyan waters (n = 2316). (Haps	88

LIST OF PLATES

Plate 1 : Picture of preflexion stage of <i>L. niloticus</i> larvae.....	38
Plate 2 : <i>Lates niloticus</i> larvae and eggs.....	39

LIST OF ABBREVIATIONS, ACRONYMS AND SYMBOLS

YOY	Young of the Year
MT	Metric tonnes
LVFO	Lake Victoria Fisheries Organization
USA	United States of America
TL	Total Length
ICES	International Council for Exploration of the Sea
DFO	District Fisheries Officer
IUCN	International Union for Conservation of Nature
DO	Dissolved Oxygen
USD	United States of America Dollars
LVRP	Lake Victoria Research Project
IFMP	Implementation of a Fisheries Management Plan
FiSAT	Fish Stock Assessment Tools
ITCZ	Inter tropical Convergence Zone
ENSO	El Nino/Southern Oscillation
CTD	Conductivity Temperature Dissolved Oxygen
NTU	Natural Turbidity Units
YSI	Yellow Spring Instruments
RV	Research Vessel
GPS	Global Positioning System
CAS	Catch Assessment Method
HEST	Haplochromis Ecology Survey Team
GIS	Geographical information System

ACKNOWLEDGEMENTS

This thesis was accomplished with the support of many individuals to whom I am thankful. I would like to sincerely thank my principal supervisors Dr. Frank Masese, Professor James Murithi Njiru and Dr. William Ojwang for their tireless scientific guidance and constructive criticism of the work. I am also grateful for the moral support, encouragement, scientific and technical guidance provided by Professor Julius Manyala . I further extend gratitude to my former employer Kenya Marine and Fisheries Research Institute (KMFRI) for granting me study leave then and a suitable environment to conduct my research. I also thank Alfred Achieng and Edwine Yongo who assisted with some statistical analyses. I am indebted to Joseph Onyango, Zablon Awuondo, James Achiya, Maurice Achar, David Ndere, Dismas Nyakiamo, Walter Olang, Eric Odari, Peter Allela and Caleb Ochiewo for technical assistance in the field and laboratory. This doctoral research was made possible through funding from KMFRI-GoK Seed Fund and LVEMP. Last, but not least, I would like to express my gratitude to my wife Millicent and the boys James, George and the only girl Merisa for their constant support and encouragement.

CHAPTER ONE

INTRODUCTION

1.1 Background Information

Over the years Lake Victoria has developed into a major fishery producing between 400,000 to 500,000 MT of fish in the 1980s of which about 40% is landed in Tanzania, 35% in Kenya and 25% in Uganda (LVFO, 2007). This catch had a value of between US\$ 300 - 4000 million as of the year 2007 (LVFO, 2007). Simultaneously, there was a development of a lucrative export market of processed fish products to Europe, USA and Middle East (Abila & Jansen, 1997, Ntiba *et al.*, 2001; Mkumbo & Marshall, 2015). The fishery further offered employment to thousands of people in primary and secondary industry (LVFO, 2007). Hence there was a corresponding and profound capital investment into the fishery of Lake Victoria during the period (Jansen, 1997; LVFO, 2007).

Because of the ecological changes in Lake Victoria over the years, a number of studies have questioned the sustainability of the lake's high commercial fish yields (Witte *et al.*, 2000; Hecky *et al.*, 2010; Muyodi *et al.*, 2010; Sitoki *et al.*, 2013). Prior to the 1960s, Lake Victoria had a diverse fish fauna (Graham, 1929; Worthington, 1929) and its multi-species fishery comprised about 14 major types, of which two endemic tilapiine species, *Oreochromis esculentus* and *Oreochromis variabilis*, formed a substantial fishery (Kolding *et al.*, 2008; Bugenyi *et al.*, 2010). In addition, Lake Victoria was home to small-body sized species such as *Rastrineobola argentea* and haplochromine cichlids, and the influent rivers supported fisheries of *Labeo victorianus* and *Barbus altianalis* (Bugenyi *et al.*, 2010). However, the composition of fish species has changed considerably and there are potential indicators of further

change (Mkumbo, 2002; Muhoozi, 2002; Witte *et al.*, 2000; Mkumbo & Marshall, 2015). Currently, two exotic species, Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) and the small native cyprinid (*R. argentea*) form the basis of the commercial fishery (Mkumbo & Marshall, 2015).

Despite the current decline of fish stocks in Lake Victoria, the fishery continue to support livelihoods and other extractive natural resources to millions of people within its shores and the immediate hinterland. For instance, landings of Nile perch from Lake Victoria in Kenya were estimated at 9,712 MT valued at Ksh. 3.14 billion in 2009 (Kenya Fisheries Dept., 2009). However, there has been a considerable decrease of Nile perch catches, and this has been attributed to various human related activities within the basin which include over exploitation use of wrong fishing methods, introduction of alien species, and water pollution (Verschuren *et al.*, 2002; Sitoki *et al.*, 2010; Hecky *et al.*, 2010; Masese & McClain, 2012). These phenomena have occurred against a background of knowledge gaps on species compositions, populations structure, food and feeding habits, trophic relationships, reproduction and breeding habits, growth, mortality and migrations patterns of Young of Year (YoY) and juvenile Nile perch (Kolding *et al.*, 2007).

Globally, data concerning the biology of commercially exploited fish species has been traditionally obtained from research surveys, sampling expeditions or from commercial catches (Hilborn & Walters, 1992). The two main objectives related to the collection of these data are assessmnet of trends in fish landings/ catches and producing scientific advice for resource managers. In general, most of these data are incomplete because they are only associated with the adult component of the evaluated species and often suffer from high gear selectivity during research surveys

and commercial catches (Fuiman, 2002). Many studies therefore lack information on the early stages of fish stocks. Studying the early stages of fish has significantly contributed to generating the basic concepts of stock management (Rutherford, 2002). For instance, plankton surveys have helped to describe distribution, determine the spawning period and calculate the abundance, mortality and growth of eggs, larvae and juveniles from several commercial species (Hempel, 1973). Egg and larval surveys have contributed to increasing the knowledge of the biology of several commercial species, their movements, spatial and temporal distribution, breeding/nursery grounds, spawning and feeding ecology (Rutherford, 2002).

The occurrence of fish eggs and larvae can be strongly correlated with adult abundance (Rutherford, 2002). According to Smith (1994), estimates of adult abundance can be derived from egg and larval surveys. The first abundance assessment of a commercial species was conducted according to this approach in the early 1900s by Buchanan-Wollaston (1923). Since then, fish egg and larva sampling has also been used to measure the decline or the abundance of several species such as striped bass (*Morone saxatilis*) in Chesapeake Bay (Rutherford, 2002), capelin (*Mallotus villosus*) in Barents Sea (Fossum, 1992) and Atlantic herring (*Clupea harengus harengus*) on Georges Bank (Overholtz *et al.*, 2004). In the last case, the abundance index stemming from sampling of larvae was even used for calibrating a sequential population analysis. The abundance of eggs measured at spawning sites has also been used to calculate the reproductive biomasses of mackerel (*Scomber scombrus*) in the northern Atlantic since 1977 (ICES, 2003) and the northern Gulf of St. Lawrence since 1983 (DFO, 2004).

In Lake Victoria, Nile perch, *L. niloticus* is the most commercially important fish species (Abila & Jansen, 1997). However, it currently face challenges of overexploitation and water pollution (Ogutu-Ohwayo, 2004). There has been both the creation and loss of ecological niches with reduction of haplochromines and endemic tilapiines and non-cichlids associated with anoxia and invasion by the water hyacinth and hippo grass (Ogutu-Ohwayo, 2004; Offulla *et al.*, 2004). Nile perch has been shown to respond in various ways to environmental change and is a useful candidate species to study how these changes affect the distribution, abundance, growth, reproduction, well-being and food utilization by fish species, and inter-relationships (Schofield & Chapman, 1999).

Nile perch is a piscivorous apex predator among fishes in Lake Victoria (Ogari and Dadzie, 1988). But with ecological changes occurring in the lake, it is likely that the fish has changed its feeding to utilize food items that were hitherto not on its prey list (Ogutu-Ohwayo, 1990). However, as an apex predator, Nile perch plays an important role in top-down control and biomass conversion (Ogutu-Ohwayo, 2004). Loss or reduction of this species from the lake can therefore adversely affect further ecosystem stability (Kaufman, 1992). The Nile perch population is currently dominated by young individuals (< 40 cm TL) in the Kenyan waters which suggests successful recruitment (Njiru *et al.*, 2008) but inadequate population growth (LVFO, 2007). These young fish occur mostly in waters of less than 10 m depth, which also happen to be the most heavily fished area (Ligtvoet *et al.*, 1995; Njiru *et al.*, 2008).

Overexploitation and use of illegal gears have been reported to threaten Nile perch fishery in Lake Victoria (Kitchell *et al.*, 1997). Illegal fishing gears and methods in the shallow zones of the lake has been attributed to growth over-fishing, thereby

resulting in depletion of the stock as few mature individuals are given a chance to grow and replenish to stocks (Mkumbo, 2002).

Limited data exist on the distribution of *L. niloticus* larvae and juveniles in Lake Victoria. Data on distribution and abundance of larvae and juveniles are important for identification of breeding areas and their protection. An understanding of spawning seasons, distribution of young of year (YOY) in relation to hydrographic factors is important for managing the declining Nile perch fishery in the lake. In addition, data on temporal variation in abundance and distribution of YOY is needed for identifying optimal locations for protection and conservation. Abundance and distribution of *Lates* fish larvae have direct influence on the magnitude of juvenile recruitment. However, studies on *Lates* larval dynamics are non-existent despite these data being important for decision making and fisheries management.

This study aimed at providing data on the early life stages of Nile Perch that were needed for understanding the fish's life history strategies, recruitment and sustainability in Lake Victoria. There are no comparable data on size related patterns of reproduction of Nile perch among different domains in Kenyan waters of Lake Victoria.

A clear understanding of the relationship between environmental conditions and the biology of Nile perch such as growth, size frequency distributions, reproductive biology, food and feeding habits, preferred habitat, distribution and abundance are fundamental ingredients in the management of its fishery and, most importantly, on the need to reduce the current decline in its abundance. It is only with these data that rational and sustainable utilisation of the Lake Victoria's resources can be achieved. The data can also be used directly to identify potential shifts in life history strategies

that could be indicative of overfishing, pollution and other environmental impacts that would warrant proactive management interventions. The need for updated data on Nile perch in Lake Victoria is also important because a collapse of its populations would trigger an ecological change that would reverberate throughout the entire food web. This study aimed at gathering the much needed data upon which sound management of the Nile perch fishery will be based.

Thus the objective of this study was to provide information on the early life stages of Nile perch perch, its growth, and ontogenetic shifts in food composition for comparison with existing data on the lake and elsewhere. These data are critical for reversing decline in the stocks of Nile perch in Lake Victoria.

1.2 Statement of the Problem

Lates niloticus (L) (family Latidae, common name) Nile Perch, was introduced into Lake Victoria from Lake Albert and Turkana during the 1950's and early 1960's (Anderson, 1961; Pringle, 2005). Opponents of the introduction feared that Nile perch might deplete the stocks of native fish species as well as its own numbers, through cannibalism, which would cause the fishery to collapse (Fryer, 1960). It took about two decades for Nile perch to establish itself in the lake but its numbers increased rapidly in the late 1970s, leading to a dramatic increase in fisheries productivity (Ogutu-Ohwayo, 1990). At the same time, predation by Nile perch brought about a reduction in the numbers of many native species with haplochromines falling from > 80 % of the biomass during the 1970's to < 1 % by the mid 1980's, and it was feared that many species had become extinct (Ogutu-Ohwayo, 1990; Njiru *et al.*, 2008). The growth of the fishery and increasing fishing intensity led to a decline in catches of

Nile perch creating fears that the fishery might not be sustainable without appropriate management measures (Matsuishi *et al.*, 2006; Njiru *et al.*, 2007).

While it is clear that the introduction of Nile perch *L. niloticus* into Lake Victoria has caused changes to the fisheries, it is virtually impossible to eradicate the species from the lake (cf. Barel *et al.*, 1985; Ribbink, 1987; Bwathondi, 1988). Nile perch may not be solely responsible for declining catches of certain popular fish species over the years. Over-exploitation with small-mesh nets is often cited as the principal cause (Wandera, 1986; Njiru *et al.*, 2008). Additional factors include the impacts from other anthropogenic related activities and various natural phenomena. Episodes of sudden mass fish mortalities, for instance, have been attributed to pollution, algal blooms, and/or rapid deoxygenation following the mixing of stratified water layers during violent storms (Bwathondi, 1986; cf. Ochumba, 1985; Hecky, 2010; Kolding *et al.*, 2010).

In the latter half of the twentieth century, increases in subsistence agricultural farming, deforestation, municipal and industrial effluents, and human encroachment on the shoreline led to general wetland degradation which collectively gave rise to historically unprecedented nutrient loadings into the lake (Hecky, 1993; Vershuren *et al.*, 2002). The eutrophication of Lake Victoria caused a fourfold and eightfold increase in chlorophyll-a in the offshore and inshore waters, respectively (Mugidde, 1993). These occurrences have impacted on the feeding behavior of Nile perch and in particular, on its vision as a predatory fish. The increase in algal biomass has further altered the physical, chemical, and biological environment of Lake Victoria. Secchi depth measurements declined in the offshore from a range of 5.5 to 8.2 m in the 1920s (Worthington, 1930) to a mean value less than 2.0 m in the early 1990s (Mugidde,

1993). Furthermore, increased stability of stratification, together with higher organic sedimentation to the hypolimnion, has significantly augmented the volume of seasonally anoxic water (Hecky *et al.*, 1994) and caused loss of fish habitat. As a by-product of this decomposition, the oxygen levels in the deeper layers of water are being depleted. Without oxygen, Nile perch cannot exist in the deeper portions of the lake, forcing them to exist within a narrow range of depth (Kaufman, 1992).

By early 1990s to date, the adverse effects arising from water hyacinth mats have been reported (Ofulla *et al.*, 2010). Water hyacinth mats invaded fishing grounds and blocked waterways. Twongo (1998) noted that the weed mats sealed off breeding, nursery, feeding, and fishing grounds for various inshore fish species, like tilapia and young Nile perch. The mats also had detrimental effects by blocking light, severely reducing oxygen levels, and allowing poisonous gases, such as ammonia and hydrogen sulphide, to accumulate. Thus, structural changes in the species composition of Lake Victoria's fish stocks may have been induced by the water hyacinth proliferation. However, the overall biological effect of the weed on aggregate fish stocks and catches is not well documented (Ofulla *et al.*, 2010). The purpose of this study, was therefore to explore the life history and population growth parameters of the early stages of *L. niloticus* in Lake Victoria, Kenya. Notably Nile perch is known to respond rapidly to changes in its environment (Schofield & Chapman, 1999) and therefore a good indicator of the health of aquatic ecosystem. However, despite the dynamism of Lake Victoria ecosystem, no studies have been conducted in recent years to specifically determine if environmental changes in the lake influences the biology of *L. niloticus*, including its dietary and population characteristics. There is lack of recent data on variation of food items between size classes, habitats and depth

including its population parameters by zones, depth and seasons in Nyanza Gulf which is historically a bellwether for the rest of the lake.

In spite of the aforementioned gaps in knowledge, the catches of Nile perch continues to dwindle. It is also not clear as to whether attempts to improve the sustainability of fisheries resource exploitation in the lake has been successful. It is also not known whether through ban on certain methods of fishing such as trawl and on-going enforcement of laws on other fishing illegalities, and slot size restrictions have had any effect on the biology of Nile perch.

1.3 Justification for the Study

Lake Victoria has long been famous for its rich life and in particular, as a source of high quality fisheries (Mkumbo & Marshall, 2015). These resources are believed to be overexploited (Marshall & Mkumbo, 2014) but continue to support large populations of artisanal fisheries. The extent to which decline in Kenyan portion of Lake Victoria fisheries is attributed to environmental variability and recruitment success is unknown. Larval supply to inshore and offshore fishing sites is important for fisheries replenishment. However, the pattern of larval supply to the fishing grounds has received little attention in the Kenyan waters of Lake Victoria. Yet, these data are important in fisheries management (Mkumbo & Marshall, 2015). Additionally, the extent to which recruitment variability affects fisheries production is largely unknown for the Kenya waters of Lake Victoria but may be significant. While much work has been done on the functional biology of Nile perch in Kenyan water (Ogutu-Ohwayo, 1990), there is little work on the ecology and dynamics of fish larvae. To date, no comprehensive study has been done on *L. niloticus* fish larval ecology and the extent to which Nile perch stocks may be limited by larval supply is important in

determining factors contributing to temporal and spatial variability of adult population. The quantity and composition of fish larvae replenishment is dependent on hydrographic conditions, larval ecology and spawning regimes among other factors (Leis *et al.*, 2003). A lot of work has been done on other aspects of Nile perch in Lake Victoria (Ogutu-Ohwayo, 1990). However, the pattern of *L. niloticus* larval distribution remain unknown, but may be important in understanding population dynamics and fisheries of *L. niloticus*. Compared to the pre-Nile perch introduction, the current ecosystem of Lake Victoria is unstable. Rapid changes in flora, fauna and abiotic parameters (e.g. Oxygen concentration and water transparency) are still occurring. This will have an enormous impact on fisheries and fisheries management.

Knowledge about the diurnal variation in the vertical distribution of species is essential if one wants to know what part of the stock is sampled with a particular gear at a particular time. Unfortunately, major part of the biological data concerning the fishes of Lake Victoria collected before 1980s is out of date and made useless by the recent ecological changes in the lake. The biology of the species now caught which underpinning the thriving fishery, is still poorly known. Moreover, there are indications that *L. niloticus* are subject to changes in habitat preferences, feeding habits and reproductive characteristics concomitant with the changes in the lakes ecosystem.

This is a delicate situation because this species is important to the economy of several communities in the Lake Victoria Basin (LVB) (Abila & Jansen, 1997). However, a plankton survey is conducted in order to describe the distribution and measure larva abundance for *L. niloticus* This survey covers the inshore and off-shore areas of the Kenyan waters. This region is a major spawning ground for the fish, but has never

been covered by this type of survey before. The data collected would be used to measure specific abundance of *L. niloticus* larvae and juveniles present in this study area.

1.4 Objectives

1.4.1 Overall objective

The overall objective of this study was to determine the spatial-temporal distribution and abundance of larvae and juvenile stages of Nile perch (*Lates niloticus* Linnaeus 1758) in the Kenyan waters of Lake Victoria, Kenya

1.4.2 Specific objectives

The specific objectives of the study were to determine:

- i) The effects of limnological factors on the spatial variation in abundance of larvae and juveniles of *L. niloticus* in Lake Victoria, Kenya
- ii) The distribution and abundance of larvae and juveniles of *L. niloticus* in Lake Victoria Kenya
- iii) The spatial/ bathymetric distribution, abundance and population growth characteristics of *L. niloticus* juveniles and adult stages in Lake Victoria, Kenya
- iv) Food composition of *L. niloticus* larvae and juveniles and sub-adults in Lake Victoria, Kenya
- v) Ontogenic shifts in the structural development and food composition of *L. niloticus* in Lake Victoria, Kenya

1.5 Hypotheses

The study tested the following hypotheses:

- i) H_0 There is no effects of limnological factors on distribution and abundance of larvae and juveniles of *L. niloticus* in Lake Victoria, Kenya.

- ii) H_0 There is no inshore-off-shore and depthwise differences in larval distribution and abundance of *L. niloticus* in Lake Victoria, Kenya
- iii) H_0 There is no differences in spatial vertical and horizontal distribution and abundance of *L. niloticus* larvae and juveniles in Lake Victoria, Kenya
- iv) There is no differences in food composition of *L. niloticus* larvae and juveniles and sub-adults in Lake Victoria, Kenya
- v) H_0 There is no ontogenic shifts in the diet composition of *L. niloticus* in Lake Victoria, Kenya

CHAPTER TWO

LITERATURE REVIEW

2.1 Genesis of Nile Perch in Lake Victoria

A few decades after John Speke's 'discovery' of the lake in 1858, British colonialists started to exploit the lake's watershed. They cleared the surrounding natural vegetation, denuding forests and draining swamps (Balirwa *et al.*, 2003), to start cash crop plantations which have grown in size and number over the years. Agricultural chemicals, applied on these plantations are washed into rivers during the rainy season, and end up in the lake, providing nutrients for massive algal blooms. The plantations attracted migrant workers who settled in the area. As the population grew and fishing methods advanced, overfishing became a problem and catch sizes began to drop. By the 1950s, popular species, such as “ngege” (*Oreochromis esculentus*), had diminished so severely (Witte *et al.*, 1992). At that time the lake was however still teeming with small sized bony haplochromine cichlids (Kitchell and Schindler, 1997). To remedy the situation, British officials thought of introducing new fish in the lake (Graham, 1929; Welcomme, 1967; Lowe-McConnell, 1987). Nile perch was presumed to be a solution to boost stocks as well converts the small sized cichlids into bigger attractive flesh (Witte *et al.*, 1999).

Arguments on possible impacts of new species on the ecosystem started some decades before the actual introduction (Fryer, 1966). As debate was going on, secret introductions had begun in 1954 (Goudswaard *et al.*, 2008). Subsequent official introductions followed afterwards at different sites around the lake and its catchment. At the beginning, the new species constituted only a small percentage of the lake's fish biomass, which was dominated by haplochromine cichlids (HEST, 1886; Witte *et*

al., 1992). It took over 20 years for Nile perch to establish itself as an exploitable stock (Njiru *et al.*, 2009). Up until the late 1970s, the biomass composition of the lake remained relatively constant, but in 1980, a survey of the lake revealed an abrupt and unexpected change: a total reverse in biomass composition. Cichlid numbers had fallen drastically, comprising only 1 per cent of fish weight, while those of the Nile perch had suddenly jumped to constitute 80 percent. It is thought that over 200 species of the former fish fauna had disappeared (Kitchell & Schindler, 1997, Witte *et al.*, 1992). Although not foreseen, the collapse of the haplochromine cichlids was inevitable since they were the preferred prey of the new predator. The devastation on biodiversity wrought by Nile perch has made it to be considered one of the world's 100 worst invasive species by the International Union for Conservation of Nature (IUCN) World Conservation Union Invasive Species Specialist Group (Kitchell and Schindler, 1997).

2.2 Biology and Ecology of Nile Perch

Nile perch *L. niloticus* is silver in colour with a blue tinge. It has a distinctive dark-black eye, with a bright-yellow outer ring. The fierce predator is Africa's largest freshwater fish, reaching up to 200 cm in length and weighing up to 200 kg (Kaufman, 1992). In Kenyan waters mature fish averaged 55 – 137 cm, although many fish are caught before they can grow this large (Okemwa, 1984, 1985). Nile perch occupy all habitats of the lake where dissolved oxygen (DO) of 5 mg L⁻¹ is considered sufficient (Ogutu-Ohwayo & Hecky, 1991; Kitchell & Schindler, 1997; Feroese & Pauly, 2012). It is widely distributed in Africa, occurring in the Congo, Niger, Volta and Senegal Rivers, and in Lakes Chad and Turkana, and throughout the Nile system as far as Lake Albert but was prevented from reaching Lake Victoria by the Murchison Falls (Njiru *et al.*, 2009).

The species exhibits ontogenic shift in its diet. Young perch feed on zooplankton and then shift to freshwater shrimp, *Caridina nilotica*. Adults consume fish, haplochromines being their most preferred prey (Mkumbo & Ligtoet, 1992). Size at first maturity has been changing over the years. It was estimated for males and females at 50 - 54 cm and 90 - 99 cm respectively between 1988 and 1992. Earlier studies in the Winam gulf between 1979 and 1983 estimated the sizes at 74 and 100 cm for males and females, respectively. The sizes were later observed to decrease to 55 and 85 cm for males and females respectively between 1985 and 1989 (Njiru *et al.*, 2009). Studies undertaken in Kenyan waters between 2004 and 2005 estimated size at first maturity at 54 and 62 cm for males and females, respectively (Ojwang *et al.*, 2011). In Tanzania, the size at first maturity for males and females in Mwanza Gulf (1988 - 1989) was at 60 cm and 110 cm TL, respectively (Mkumbo & Ligtoet, 1992). Later (1998/2001), the size at first maturity showed a decrease where males and females matured at 54 and 76 cm TL, respectively (Mkumbo, 2002). The decrease in maturity size has been generally attributed to increase in fishing pressure, and changes in food availability. Nile perch takes 1.6 and 2.5 years to mature for males and females, respectively. Females are extraordinarily fecund producing 1,136,000 to 17,336,000 eggs for individuals of sizes 94.5 to 153.0 cm TL (Mkumbo, 2002). Female Nile perch grow to a larger size and mature later than males and males and females reached 50% maturity at 54-64 and 62-85 cm TL respectively. The sex ratio changed with size because males were smaller than females and most fish > 80 cm were females (Njiru *et al.*, 2009) but the removal of large fish by the fishery has resulted in a more or less equal sex ratio in the 40-60 cm size range (LVFO, unpublished data).

The Lake Victoria ecosystem has undergone a series of faunal and limnological changes and alteration of the trophic dynamics by the exotic species is thought to be one of the major influences (Kaufman, 1992; Reinhart & Kling, 1994). Introduced predators generally reduce the overall ecological production in an ecosystem (Marshall, 1995), although may increase the amount of commercially harvestable fish, as is the case in Lake Victoria. The situation in the lake is still dynamic and changes in the stocks are still continuing. Nile perch is at the top of the food web in Lake Victoria and is known to have the capability of adjusting its feeding habits to take advantage of the most abundant food source (Ogari, 1988). Predator–prey interactions are known to be important determinants of yield to fisheries, thus to understand the dynamics in the Nile perch fishery, diet studies are fundamental. Seasonal fluctuations in breeding seasons, which can be triggered by environmental factors as well as food availability, the mean length at sexual maturity (L_m) and the reproductive potential or fecundity of the stock are also very important input parameters for any strategy in fishery management. These parameters vary with environmental factors as well as fishing pressure on the stocks (Pitcher & Hart, 1982).

There is considerable information on the diet of Nile perch in Lake Victoria (Hamblyn, 1966; Gee, 1969; Okedi, 1971; Hopson, 1982; Acere, 1985; Hughes, 1983; 1986; Ogari, 1985; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990; Mkumbo & Ligtoet, 1992). It is a more efficient predator than any endemic species in the lake. Since its introduction, marked changes have occurred in its feeding habits, reflecting changes in the abundance of its prey. Nile perch has shifted from feeding on haplochromine cichlids to *Caridina nilotica*, *Rastrineobola argentea*, various invertebrates and juveniles of Nile perch. More recently, *Caridina* has become the

major prey and when absent, the species has shifted to juvenile Nile perch followed by *Rastrineobola* (Ogutu-Ohwayo, 1990; Mkumbo & Ligtvoet, 1992).

The reproductive biology of Nile perch, however, is poorly documented. Information on its reproductive potential are based on observation of Worthington (1929) and Holden (1963) in Lake Albert, Kenchington (1939) in the Blue Nile, Hopson (1972; 1982) in Lake Chad and Lake Turkana, Okedi (1971) for Lakes Victoria and Kyoga and Acere (1985) for Lake Victoria and Kyoga. The last two were based on very few females. More recently Ogutu-Ohwayo (1988), examined the reproductive aspects of Nile perch, but did not consider seasonality and concentrated more on material from Lake Kyoga.

In view of the major changes that have occurred in Lake Victoria in the latter part of the 20th century, it is important to update changes in the reproductive tactics and feeding habits of Nile perch, to support formulation of management policy. This objective therefore, examines in detail these biological aspects in the Nile perch stock in the Kenyan waters of Lake Victoria. Studies on recruitment with particular reference to larval ecology among species in nursery areas

2.3 Nile Perch Fishery

At present the Nile perch fishery in Lake Victoria is largely artisanal (LVFO, 2016). The only trawlers present belong to research institutes. Small-scale fishing boats are propelled either by sails, paddles or outboard engines. One to three fishermen use a boat. The fish is caught with mainly gill nets, hand lines and long lines. Those caught by gill nets are usually dead by the time the nets are retrieved. The fish are kept in the boat sometimes with or without protection from the sun or on ice and taken to landing sites, mostly beaches, where they are weighed and purchased by processors agents

using insulated boats or vans with ice. Some of the catch is bought by local traders who are predominantly women (Reynolds *et al.*, 1988).

Nile perch bought at the beach by women is usually cut into large pieces and smoke-dried for sale in distant market across the country. Fish bought by processors is transported after one to three days to a processing plant where it is filleted. Fillets are exported either fresh by air or frozen by ship to foreign countries (Njiru *et al.*, 2012). In recent years the value of Nile perch exports from Lake Victoria reached almost 500 million USD per year (Manyala & Ojuok, 2007).

The yield of fillets from un-gutted fish is about 30 percent. The remainder is head, skin, guts, bones and fins, plus meat attached to the frame. The frames used to be smoke-dried for local consumption, while heads and skins were used as fuel under frying pans to collect oil from the guts. These days the processors use filleting remains to make fish meal. However, the swim bladder is dried and sold to traders for export to south-east Asia where it is used as food. Nile perch flesh has a high content of omega-3 fatty acids (Werimo, 1998).

The bi-annual lake-wide frame surveys that have been carried out since 2000 provide data on trends in fishing effort which has increased since 2000 but by varying degrees in each country (DFO, 2005a, 2005b; Ikwaput-Nyeko *et al.*, 2009; LVFO, 2016). From the time of its introduction until about 1980 Nile perch were of little economic importance but the Nile perch population explosion that occurred from 1980 onwards led to a huge increase in yields, which peaked at over 300,000 MT in 1990. Catches declined after that but now appear to have stabilized around 250,000 MT per annum.

Studies carried out between 1998 and 2000 suggested that the capture of fish between 50 and 85 cm TL could be permitted and slot sizes of 50 to 85 cm TL were gazetted by the countries around the lake with enforcement starting in mid-2000s (Njiru *et al.*, 2009). The slot size is based on the premise that Nile perch ≤ 50 cm TL feed predominantly on the shrimp *C. nilotica*, thus converting invertebrates into fish flesh while larger fish are predominantly piscivorous, feeding mainly on the cyprinid *R. argentea*, juvenile Nile perch, Nile tilapia, and haplochromines, which is both destructive to the lake's biodiversity and energetically wasteful. Harvesting Nile perch ≥ 50 cm TL could also lead to the recovery of the haplochromines, thus enhancing the productivity of the fisheries, especially in deep waters where only the pelagic *R. argentea* occurs (Njiru *et al.*, 2009). Thus, the slot size of 50 to 85 cm TL sought to protect immature fish, harvest mature individuals and at the same time protect the larger females, which would be expected to replenish the stocks.

2.4 Stock Assessment in Lake Victoria

Ecosystem monitoring is becoming increasingly important. However in Lake Victoria, data collection is always characterized by inconsistencies (Cowx & Knaap, 2003; Njiru *et al.*, 2012). Data collected often lacks critical components necessary for meaningful stock assessment. Reliable quantitative measures of abundance or age structure do not exist for Nile perch in Lake Victoria (Kitchell & Schindler, 1997; Cowx and Knaap, 2003). The only lake-wide fish biomass monitoring attempts were done using acoustics under the Lake Victoria Research Project, LVRP (1999-2002) and Implementation of a Fisheries Management Plan, IFMP (2005-2010) projects (Kayanda *et al.*, 2009).

2.5 Larval Ecology and Population Dynamics

The eggs of Nile perch *L. niloticus* are small, measuring 0.8 mm in diameter, with a single oil globule, enabling them to float just under the surface of water. They are only slightly heavier than water and the slightest movement in the water is enough to keep them buoyant. Spawning of *L. niloticus* takes place in relatively still waters in lakes, oxbow lakes of rivers or in flooded backwaters. The eggs hatch in 20 hours, so the larvae are at an early stage of development are hardly more than embryos in size and 1.3 mm long. When they are 7.6 mm long, the larvae begin to resemble normal fish larvae, with the yolk sac still attached. When larvae reach 13 mm long, they begin to take on the features seen in the adults, but the body is marked with irregular dark bands

Lakes are noted for their complex topography, hydrography and biota. This complexity has important implications for the biology of the fish larvae found in the waters and for attempts to study their biology (Leis, 1993). Distribution of fish larvae in any region are related to the reproductive activity of the adult population and to topographic and hydrodynamic features that affect the dispersal of larvae (Nonaka *et al.*, 2000). A study of distribution patterns of fish larvae contributes to understanding of the interrelationships among fish species during their early life history stages, as well as understanding of adult spawning patterns and reproductive strategies adopted by these fish in response to physical and geological processes (Nonaka *et al.*, 2000). Abundance of fish larvae directly influences the magnitude of juvenile recruitment (Sabate's *et al.*, 1996). This information is important for sustainable exploitation of fisheries resource and understanding the ecolocal status of the component species (Nonaka *et al.*, 2000)

In Temperate regions, the distribution and abundance pattern of larval fish have been the subject of research for decades in contrast, relatively very few studies have been done in the tropics (Sampey *et al.*, 2004). In Lakes Chad, Turkana and Albert *Lates* fry are found in shallow sheltered bays. Young fish up to lengths of 20-30 cm live inshore, in the vicinity of submerged vegetation (Hamblyn, 1962; Gee, 1966; Hopson, 1972). *Lates niloticus* (< 10 cm) have been caught in waters up to 60 cm deep. However, the highest densities are found in the shallow littoral zones. There is indication of diurnal vertical migrations of juvenile *L. niloticus* (< 10 cm). During the day they are concentrated near the bottom, but at night they migrate to the mid water level.

Nile perch *L. niloticus* species spawn almost all the year round with peaks during rainy season March- May and October- December in shallow littoral areas (depths 0-8 m) at temperatures ranging from 20 - 25° C (Hamblyn, 1962; Gee 1966; Hopson, 1972). Their eggs develop for 10 to 20 days in temperature 22 - 25° C and embryos hatch at sizes between 4 and 6 mm (Hopson, 1972). Smaller individuals hatch first (Hopson, 1972) and grow more slowly. Soon after hatching the perch larvae migrate from the littoral into the pelagic habitat. Before they return to the littoral area after metamorphosis, perch fry stay in the epilimnion for a month or even longer (Treasurer, 1988). The transparency of perch larvae is supposed to be an adaptation for life in the pelagic zone of lakes and inshore areas making them less visible to predators (Faber, 1967). This review indicates that few studies exist on fish larvae in Lake Victoria.

2.6 Growth Parameters

Proper assessment and management of a fishery requires an understanding of the population parameters of the species on which it is based, namely stock abundance, growth, recruitment and mortality (Sparre *et al.*, 1989; Hilborn & Walters, 1992), as these are the processes controlling the production. The number of fish is increased by reproduction of the adult stock, which results in juveniles being added into the stock or recruitment occurs. Likewise, the weight or biomass of the fish stock is increased by the growth of individual fish while the stock is being reduced in numbers and biomass by natural mortality and fishing mortality. The changes in population parameters are indicators of the adjustment in the life history strategy of the species in response to stress either from natural causes or fishing (Laevastu & Favorite, 1988; Wootton, 1990). Estimates of parameters such as growth rates, mortality and recruitment are necessary to determine fish production (Ricker, 1975; Pitcher & Hart, 1982). These parameters of a fish stock can be estimated either by using data on number of fish at different lengths, i.e. length-frequency data or CPUE - catch per unit effort data (Sparre *et al.*, 1989). These data can be collected directly from the landings of fishing vessels i.e. fishery-dependent data or from fisheries research vessel i.e. fisheries-independent data. To use CPUE data under surplus production models (Ricker, 1975) it must be accurately reflecting changes in abundance of fish in the stock and a long time-series of catch-and effort data must be available (Gayanilo & Pauly, 1997).

This objective aimed to establish the status of the Nile perch stock in the Kenyan waters and determine the levels at which might be sustainably exploited. Using the different assessment routines provided in FiSAT package, the objective attempts to

determine the population parameters of Nile perch and estimate the yield and the current exploitation levels.

2.7 Relationships between Environmental Parameters and Fish Distribution

2.7.1 Thermal and oxygen stratification

Results of previous studies indicate that the lake is thermally and oxygen stratified in the month of February/ March at the gulf mouth of Rusinga channel towards gull shoal in the Nyanza Gulf of lake Victoria, Kenya (Hecky *et al.*, 1996; Lungayia *et al.*, 2000; Mugidde, 2001; Gichuki *et al.*, 2001a,b, 2006). These researches indicates that thermal stratification has direct physical impact on the depth of the mixed layer, which in turn affects the vertical distribution of nutrients including oxygen and light availability in the water column. The strength and frequency of mixing governs the movement of nutrients from deeper waters into the euphotic zone as well as the development of anoxia (Hecky *et al.*. 1996, Mugidde, 2001; Mkumbo *et al.*. (2007), Gichuki *et al.*, 2006, 2001a+b; Lungayia *et al.* 2000) and the distribution of plankton and fishes which is enhanced during stratification. In addition microbial oxidation of organic materials in the hypolimnion of lakes and the resultant reduction of electron acceptors including an alternative to O₂, results in transformations of nitrate, sulfate, iron and carbon, which are significant in the lake sediments. The main products of oxidation in the lake sediments include nitrites, sulphides and methane, which are toxic to fish. When plankton and fish encounter these conditions, they may undertake several options namely; Relocation to the surface waters from the bottom where the oxygen values are higher (epilimnion) and away from the toxic substances (nitrites, sulphides) generated by various chemical reactions, which occur in the hypolimnion in the lake sediments in presence of high organic matter presence and in absence of oxygen. The low oxygen at the bottom prevented Nile perch from accessing the

feeding niches at the bottom. In summary, Kaufman (1992) indicated that Nile perch *L. niloticus* cannot tolerate dissolved oxygen less than 5 mg L⁻¹. In case of hypoxic conditions then the Nile perch *L. niloticus* would certainly be affected first by decreasing oxygen concentrations. Escaping to other areas in the lake which are well replenished with oxygen

2.7.2 Changes in Secchi depth and turbidity

Changes in the environment involving water quality especially turbidity may have brought about dramatic losses in biodiversity. Light penetration in the lake is controlled by phytoplankton abundance, which absorbs light for photosynthesis, and by suspended sediments (Hecky *et al.*, 1996; Mugidde, 2001; Mkumbo *et al.*, 2007; Gichuki *et al.*, 2006, 2008 a,b; Lungayia *et al.*, 2000). Therefore, the increased sediments loads and elevated algal biomass have direct effects on the fish habitat as well as fish production. Fish require good light conditions for visual recognition during mating and territorial defence. The changed light environment in Lake Victoria as indicated by the increased water turbidity and reduced transparency has reduced the effectiveness of colour signals between mates leading to the breakdown of the reproductive barriers and consequence erosion of the population explosion of Nile perch in Lake Victoria (Seehausen *et al.*, 1997)

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

The present study covered the Kenyan portion of Lake Victoria. The Kenyan portion of Lake Victoria is a narrow and shallow gulf known by many names: Victoria Nyanza (Graham, 1929), Kavirondo Gulf (Copley, 1953, Miller & Benda, 1981) Nyanza Gulf (Rinne & Wanjala, 1982; Ogari & Dadzie, 1988) and Winam Gulf (Okach & Dadzie, 1988). It comprises only 6 percent (4,100 km²) of the entire lake (68,000 km²) (Goldschmidt & Witte, 1992), comprising the semi-enclosed Nyanza Gulf and part of the main lake (Fig. 1a). The Nyanza Gulf is joined to the main lake via Rusinga channel. The Nyanza Gulf is shallow with an average depth of 6–8 m (Okemwa 1984) and lies between 34°13' and 34° 52' E and 0° 4' and 0°32' S. The Kenyan portion of Lake Victoria has several inflowing rivers including Sio, Nzoia, Yala, Nyando, Sondu-Miriu, Kuja and Mara (Fig. 1a). The main geographical, hydrological and physical characteristics of Lake Victoria are described by Crul (1995). The air temperature ranges between 17.1°C minimum and 34.8°C maximum. The hottest months are December to March. The water temperature and solar radiation are relatively constant throughout the year with mean of $22 \pm 3^{\circ}\text{C}$ and $1200 \pm 140 \text{ ME M}^{-1} \text{ S}^{-1}$, respectively (Crul, 1985). The annual precipitation ranges from 400 to 800 mm with long rains occurring from March to May and short rains from November to December. The lake is monomictic, experiencing complete annual mixing between the months of June to August. Besides, the annual mixing, wind induces strong shear stress at the bottom of the lake and vigorous vertical mixing within the gulf especially around Mid Gulf area (Okely *et al.*, 2010; Guya, 2013).

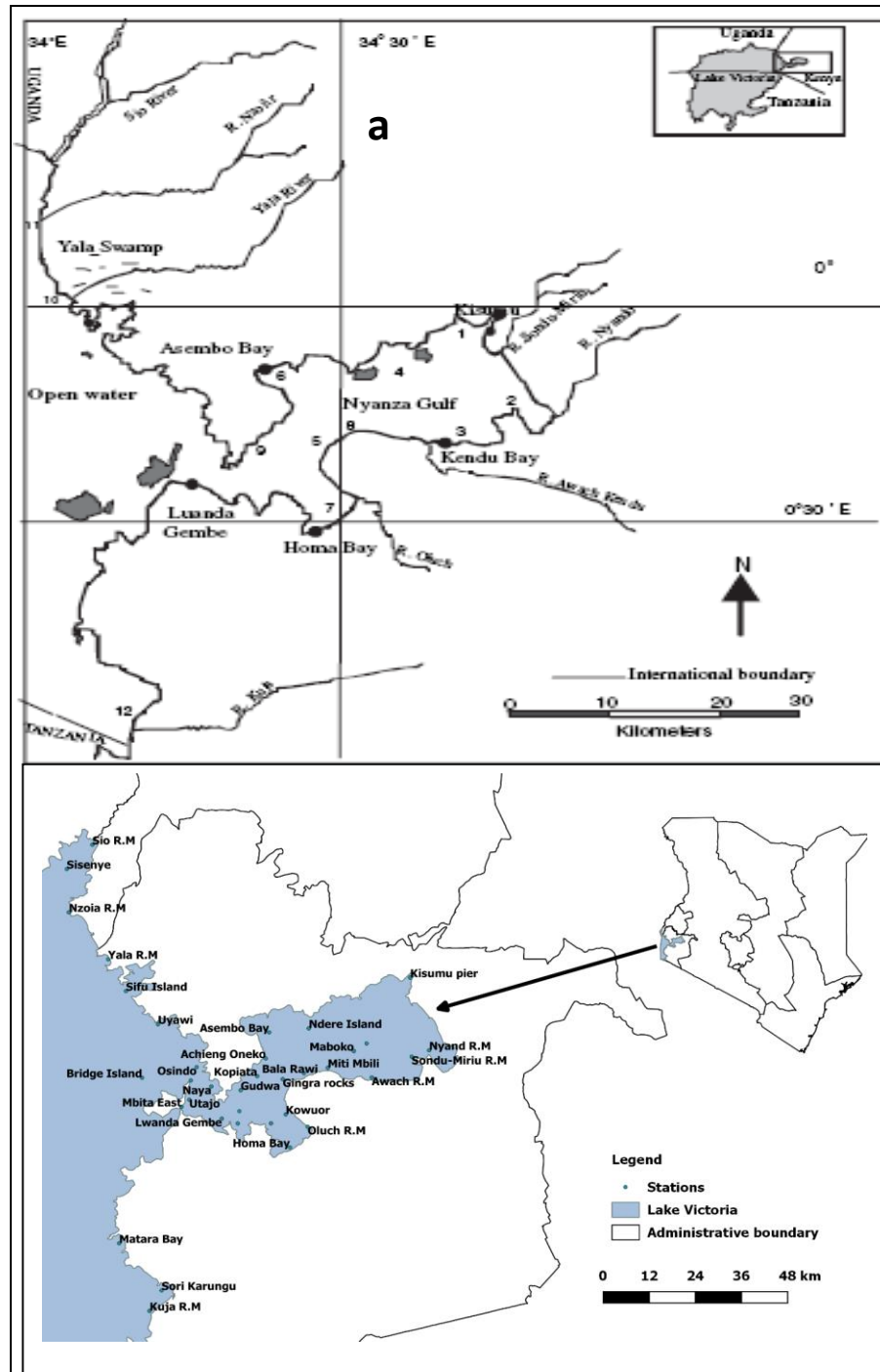


Figure 1: Map of Lake Victoria, Kenya showing the sampled stations. (a) Number on the map denotes (1 Kisumu Bay 2 Siondu miriu , 3 Awach River mouth, 4 Off Maboko, 5 Off Gingra rock, 6 Asembo Bay,7 Homa Bay, 8 Bala Rawi, 9 Madundu, 10 Yala River mouth, 11 Nzoia River mouth ,12 Kuja River mouth b) shows all stations by name. (Source: Author, 2018)

The lake plays an important role in modulating regional climate. Its thermodynamics and hydrodynamics are also influenced by climatic factors such as the Inter tropical Convergence Zone (ITCZ), El Nino/Southern Oscillation (ENSO), complex orographic forcing, and the Indian Ocean zonal temperature gradient anomalies (Anyah & Semazzi, 2009; Sun, 2014) on diel, seasonal and annual scales (MacIntyre *et al.*, 2014). The ITCZ that separates the northeast and southeast monsoons, crosses East Africa twice every year, once during March-April-May and again during October-November-December. This incursion and retreat of the ITCZ is responsible for the two main rainfall and dry seasons of the region.

The rainy season from March through to May is commonly known as the ‘long rains’; the second rainy season of October through to December is called the ‘short rains’ (Song *et al.*, 2004). The water budget is controlled mainly through precipitation over the lake surface, catchment inflow (Table 1), controlled out flow at a hydroelectric dam on River Nile and evaporation (Kendall, 1969; Swenson & Wahr, 2009; Tate *et al.*, 2010). The Lake does have a season of deep vertical mixing when the lake becomes isothermal. During June and July the established thermocline breaks down under the seasonal onset of the south-east trade winds and for a brief period at the end of July the main body of the lake becomes isothermal with respect to depth. The thermocline most often occurs at 30–40 m depth. Complete mixing occurs once a year (Talling, 1966). Lake Victoria is not physico-chemically homogenous. Much of the shoreline in the north and south is highly irregular. The northern shallow waters are intercepted by numerous islands. East and west of the lake, the basin rises over a thousand meters to highlands bordering the respective rift valleys, but to the north and south the watershed is less than 25 m above lake level (Kendall, 1969; Nyamweya *et al.*, 2016). Water quality varies spatially in Lake Victoria. Gulfs, near-shore areas

adjacent to big human settlements and river mouth areas are relatively turbid and eutrophic (Okely *et al.*, 2010). The diverse topography/terrain, prevailing weather/climatic conditions as well as river inflows and outflows influence water circulation patterns. This in turn determines the temporal-spatial water quality which can be linked to the distribution of biota in the lake (Okely *et al.*, 2010). For instance it is the purported area of initiation of the rapid increase in Nile perch *L. niloticus* (L) population in Lake Victoria. The Kenyan waters, in particular Winam Gulf was also the first portion of Lake Victoria to exhibit shallow-water hypoxia and associated fish kills (Ochumba, 1990; Kaufman, 1992; Hecky *et al.*, 1994), and it was the first area in Lake Victoria to experience overfishing of the Nile perch population (Kundu *et al.*, 2017).

Table 1: Morphometry, hydrological balance and geographical features of Lake Victoria

Characteristic	Measure
Position: Latitude	0 ⁰ 20' – 3 ⁰ 00'
Position: Longitude	31 ⁰ 39' – 34 ⁰ 53' E
Altitude (m above sea level)	1134
Catchment area (Km ²)	184,000
Lake basin area (km ²)	68,500
Lake area as % catchment	37
Shoreline (km)	3,440
Max. length (km)	400
Max. width (km)	240
Mean width (km)	172
Max. depth (m)	84
Mean depth (m)	40
Volume (km ³)	2,760
Inflow (Km ³ yr ⁻¹)	20
Outflow (Km ³ yr ⁻¹)	20
Precipitation (Km ³ yr ⁻¹)	114
Annual lake level fluctuations (m)	0.4 – 1.5
Max. rise in lake level (m)	2.4
Flushing time (years)	138
Residence time (years)	21

Sources: (Hecky & Bugenyi, 1992; Bootsma & Hecky, 1993; Crul, 1995)

3.2 Characteristics and Selection of the Sampled Stations

The characteristics of the stations and or sites selected are as shown in Table 2. A total of 12 sites were selected for sampling. The sites included some inshore areas on the river mouths of major rivers, and some were located in off-shores waters within the Nyanza Gulf. Some sites were also located away from human influences such as towns and fishing landing beaches. But the standard procedure for Lake Victoria choice of sampling stations are detailed in Table 3 formed the justification as to why sampling stations increased from 12 to 29. The allocation for Kenya in this method differs from the other two countries, because the number of stations in deep water would be too many (Table 3). Therefore, the number of deep water stations are artificially set at 2 and 1, respectively (LVFO, 2005). The final calculations must then be performed using the right hand side of the table, and expressed as percentages only after this has been done, because they depend entirely on the total number of stations planned for Kenyan waters. For instance, number in the 20-30 m depth zone in Kenyan waters is $(50-3)*402/3100 = 6$ (Table 3). Kenya is allocated 50 sampling stations but for this study 29 were possible for larvae sampling.

Table 2: Description of sampling stations in the Kenyan waters of Lake Victoria

Location (Station No)	Position	Depth (m)	Habitat influence
Kisumu Bay (1)	00 ⁰ 06'18"S 34 ⁰ 44'64"E	3.5	Town/inshore gulf
Sondu miriu (2)	00 ⁰ 17'20"S 34 ⁰ 45'28"E	3.0	River/inshore gulf
Awach River mouth (3)	00 ⁰ 17'20"S 34 ⁰ 45'28"E	4.0	River/inshore gulf
Off Maboko Island (4)	00 ⁰ 10'51"S 34 ⁰ 27'76"E	5.1	No town/river/offshore gulf
Off Gingra (5)	00 ⁰ 20'16"S 34 ⁰ 26'75"E	10.0	No town/river/offshore gulf
Asembo Bay (6)	00 ⁰ 12'36"S 34 ⁰ 24'60"E	3.0	No town/river/inshore gulf
Homa Bay (7)	00 ⁰ 31'05"S 34 ⁰ 36'38"E	8.0	Town/inshore
Bala Rawi (8)	00 ⁰ 20'06"S 34 ⁰ 29'44"E	10.0	No town/river/offshore gulf
Madundu (9)	00 ⁰ 24'12"S 34 ⁰ 20'40"E	20.0	No town//river/offshore gulf
Yala River mouth (10)	00 ⁰ 03'05"S 34 ⁰ 56'99"E	3.4	River/inshore open
Nzoia River mouth (11)	00 ⁰ 03'74"S 34 ⁰ 06'36"E	3.4	River/inshore open
Kuja River mouth (12)	00 ⁰ 54'50"S 34 ⁰ 07'37"E	8.4	River/inshore open

Table 3: Depth strata areas for the allocation stations In Lake Victoria.

Depth layer (m)	Equal allocation of stations to country				Depth Layer (m)	Equal allocation of stations to country			
	Uganda	Kenya	Tanzania	Total		Uganda	Kenya	Tanzania	Total
4-10	24.6%	53.7%	25.6%	34.6%	4-10	12	27	13	52
10-20	23.5%	15.3%	15.8%	18.2%	10-20	12	8	8	27
20-30	18.6%	12.2%	18.4%	16.%	20-30	9	6	9	25
30-40	13.3%	12.8%	20.2%	15.4%	30-40	7	6	10	23
40-50	15%	4.0%	15.0%	11.3%	40-50	8	2	8	17
50-80	5.0%	2.0%	4.0%	4.0%	50-80	3	1	3	6
TOT	100%	100%	100%	100%	TOT	50	50	50	150

3.3 Measurement of Physico-chemical Characteristics

Information on physico-chemical variables was measured using a multi parameter meter (Sea & Sun Technology GmbH. Arndtstr). The meter was used to measure temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), conductivity ($\mu\text{S cm}^{-1}$), turbidity (NTU), pH and depth (m) at each site before trawling or setting of nets were carried out. A back up water quality monitoring system (Yellow Springs Instruments- (YSI), 660-DM- YSI incorporated Yellow Springs Ohio - 45387 USA) was also used to provide extra information in shallow areas and river mouths where seining for larvae was done. Data obtained with the YSI was also used to calibrate the values obtained by the CTD in sampling water profile. A 20-cm diameter black-white secchi disc was used to estimate light penetration/transparency (m). Water samples were collected with a 3-litre van Dorn sampler at the surface and portion of water analysed for alkalinity and hardness using procedure outlined by GEMS (1992).

3.4 Collection of Fish Samples

3.4.1 Larval sampling

In 2011- 2013 monthly and diel (24 hrs) tows for fish larvae were carried out using a 3-metre long, 500 μm and 750 μm mesh size plankton net with a mouth area of 0.2 m^2 . At each of the inshore stations, three replicate oblique tows lasting 6 minutes were made, from close to the bottom (1-3 m) to just below the water surface at a speed of about $1 \text{ m}\cdot\text{s}^{-1}$. A calibrated flow meter was installed at the centre of the mouth of the net to measure water velocity that was used to calculate the volume of water sampled. Monthly sampling at all stations lasted for 10-14 days. After each tow, samples were preserved in 5% buffered formaldehyde solution prior to identification in the laboratory.

Additional fish larvae samples were collected using a 30 m long beach seine net (mesh size = 3 mm) at Usenge Beach. These samples were used to relate abundance and diel feeding regime of the larvae as detailed below. Seining was done once in January 2013. Collected samples were fixed using 5% formaldehyde (overnight fixation) then transferred to 96% isopropyle alcohol (long-term storage) until stomach content analysis in the laboratory. Larvae and juveniles were measured to the nearest 0.1 mm body length (BL) which represented notochord length in preflexion and flexion-stage larvae and total length in postflexion larvae/juveniles. Terminologies for developmental stages used in this thesis (Fig. 2) follow that of Kendall *et al.*, (1984). These include:

Preflexion larva: Developmental stage beginning at hatching through egg yolk absorption and ending at the start of upward flexion of the notochord.

Flexion larva: Developmental stage beginning with flexion of the notochord, development of the caudal fin and fin rays in majority of species, together with supporting bones and cartilages of the homocercal fin.

Postflexion larva: Developmental stage from formation of the caudal fin (distal margin of the hypural elements vertical) to attainment of full external meristic complements (fin rays).

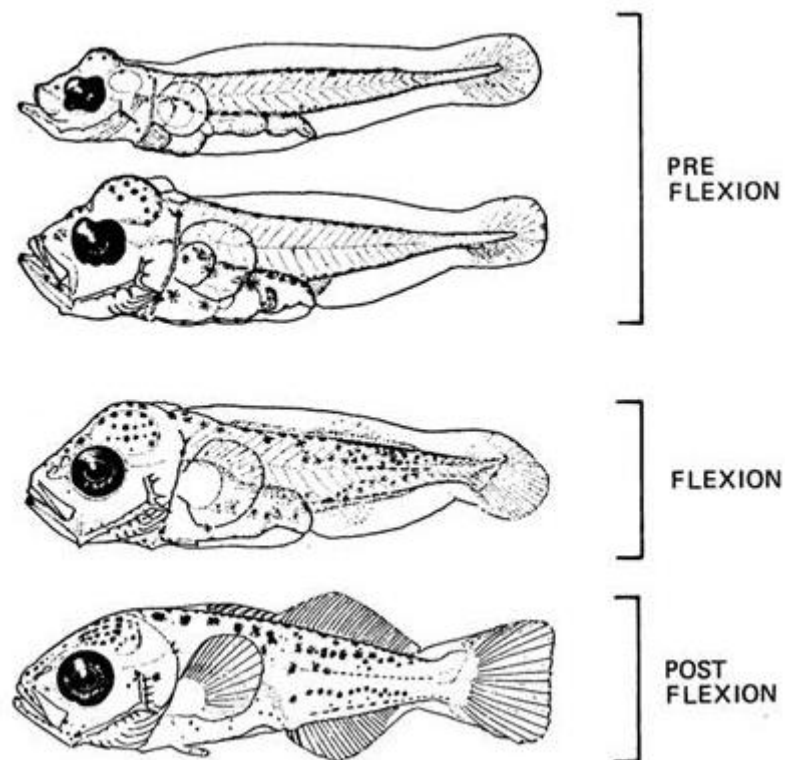


Figure 2 : Larval development in *Lates niloticus* showing the approximate length (TL mm) at which the principal morphological features first appear on the fish.

Structural and morphological features in developmental stages were observed under inverted microscope. Different fish were observed and lengths at which the feature occurred were recorded.

3.4.2 Diel sampling

Seining for the diel sampling of larvae was done at Usenge Bay (see Fig. 1) in 2013 over 24 hours period from 14:00, 18:00, 22:00, 02:00, 06:00, 10:00, 14:00 hours and haul finally at 18:00 on the second day. This provided set of data relevant during the 24 hours. The food in larvae was determined by dissecting the stomach under stereo microscope, emptying stomach contents, and observing under microscope. These data explained at what times larvae feeds.

3.4.3 Trawl sampling

The trawl net used was a conical net bag with a wide mouth fitted with sinkers and floats on the head-rope to open mouth of the net (Witte & Dansen, 1995; Sparre & Venema, 1998). When the fishing vessel was active, the net was kept open by two otterboards, wooden or iron structures which were towed by the warps attached forward of their centre so they tend to diverge. The two otterboards were connected to the net by bridles. These was up to 200 m long and sweep the lake bed over wide area. They frightened the fish towards advancing net and so increased its effectiveness. The shape of the net varies depending on the type of fish to be caught and on the types of bottom. The ground –rope was fitted with roller gear (bobbins) so that the trawl could be used on stony bottom without being damaged. The tail end of the gear from which the captured fish was removed is called the ‘cod end’. This is where most of the size selection took place (Sparre & Venema, 1998). In most cases relatively small mesh size 5 mm required in the ‘cod end’, in order to obtain a representative sample for the entire size range of the species under investigation

The trawl sampling survey was carried out quarterly for a period of twelve (12) days covering 29 stations from 2011 - 2015 in the Kenyan portion of Lake Victoria (Fig. 1; Table 1). Fish specimens were obtained using a bottom trawler (RV Uvumbuzi of 250 hp, length 18.5 m, 1500 tonnes and head rope 250 m) moving at an average speed of 3 nautical miles/ knots.

The process of sampling on the deck was as follows: a) The trawl net was retrieved. Data form was completed. b) Where the catch was of sufficiently manageable size (i.e. was handled in about 1½ hours, before the next trawl was started) the catch was sorted and the weight of each fish recorded. The lengths of all individuals were recorded in the length frequency distribution data sheet. c) Where the catch was too large for all the individual fish to be measured for length, sub-sampling was done. First, the larger individuals of the taxa were removed, and recorded their weight and lengths. Thoroughly mixed the remaining catch and a representative sub -sample of about 200 specimens was taken. Weighed this sub-sample (a). Weighed the remaining sample from which the subsample was obtained (b). The raising factor for the subsample was derived as $(a+b)/a$. The sub-sample was sorted into taxa, weighed and measured and entered the data. d) Biometric data on individual fish was collected as detailed in the section dealing with fish biology.

3.4.4 Gillnet sampling for juvenile and adult fishes

Multi-size gillnets targeting all sizes (2 fleets of size 1 to 10 inches) were set overnight from 7:00 p.m. to 6:30 a.m the following day. Fleets were set along the depth contour so as to maintain a constant depth. Each set of gill net had its catches recorded as fish caught in the first upper half of the net and ground rope caught fish in the lower half of the net. For each fish caught, the total length was measured to the

nearest millimetre and weight was measured to the nearest gramme and noted. Methods after Asila (2000) and Tweddle *et al.* (1999) were used in shallow and rocky areas which were accessed using a canoe mounted with an outboard engine. Geographical information system (GIS) coordinates were obtained for each of the sites using a hand held Global positioning system (GPS). This sampling was done biannually at 29 sites. The GIS software quantum GIS Desktop Version 2.8.11 was used to map the demarcated fish breeding site.

3.5 Stomach content Analysis

Stomach contents for the bigger specimens were analysed using modified method of Hyslop (1980). Each stomach was awarded an index of fullness from 0 to 20 regardless of fish size; empty stomach scored 0; quarter full 5; half full 10; three quarter full 15; and full 20 points. The stomachs were dissected and preserved in neutral 6 % formalin solution for analysis in the laboratory as indicated in section 3.6.3.

3.6 Laboratory Analysis

3.6.1 Water sample analysis

Alkalinity (mmol L^{-1}) was estimated by potentiometric titration of 200 ml of filtrate with 0.02 N HCl (3.65 gL^{-1}) to a pH of 4.5 using methyl orange (GEMS, 1992).

Alkalinity was calculated by:

$$\text{Alkalinity (mg L}^{-1}\text{)} = (A*N*50\ 000)/V$$

where, A is the mL of acid taken, V is the sample volume and N is the acid normality.

Hardness was estimated by titration with EDTA using Eriochrome T black mixture indicator. A buffer solution (1 mL) of 1 N ammonium hydroxide was added to the sample to give a pH of 10.1.

Hardness was calculated according to (GEMS, 1992) by the relationship:

$$\text{Hardness (mg L}^{-1}\text{)} = (A*B*50\ 000)/V.$$

where A = mL of titrant EDTA, B = mg carbonate equivalent 1 mL EDTA (EDTA normality) = Volume of sample.

Chlorophyll- a

For analysis of chlorophyll *a* an aliquot portion of the water sample was filtered through a membrane filter of pore size 0.45 μ m. A few drops of magnesium carbonate slurry was added to the sample to aid in filtration and to prevent the acidity development during extraction. The filter papers were folded on adsorbent pads and put in labeled aluminum foil and kept in a darkened desiccator. Chlorophyll *a* was extracted using acetone. Chlorophyll *a* absorbance were read at 750 nm, 665nm 640 nm and 630 nm on a spectrophotometer (Spectronic 21D).

Nutrient analysis

Nutrient analysis was carried out following the methods outlined in Wetzel & Likens (1991). For the determination of the soluble reactive species on the freshly collected samples, nutrient samples were filtered through membrane filters of 0.45 μ m pore size. Ammonium determination was carried out following the phenol hypochlorite method using nitroprusside as a catalyst. Nitrate and nitrite were measured following the cadmium reduction method. Total nitrogen in the samples was analyzed on unfiltered samples by digestion with concentrated sulphuric acid (by autoclave

procedure) to convert organic nitrogen to ammonium nitrogen and then analysis for total nitrogen carried out as outlined for ammonium nitrogen. Phosphate phosphorus was measured following the ascorbic acid method. For total phosphorus, the unfiltered water samples were oxidized by hot 5 % potassium persulfate ($K_2S_2O_8$) in distilled water. The tubes (samples, standards and blanks) were autoclaved for 30 minutes. They were further cooled at room temperatures with the caps slightly loosened. The total phosphate was then determined by the methods described above for inorganic phosphate.

3.6.2 Analysis of larval samples

In the laboratory, the *Lates niloticus* larvae from a known volume of filtered water were sorted and identified using stereo microscope. This was done by checking the distinct and discontinuous dorsal fin where the third spine is long and morphology of the mouth sets them apart (Hopson, 1972). The larvae are clear white with big head, slender body and pointed tail. Body deep (see Plate 1, 2) and somehow depressed. The total length of each larva was measured to the nearest 0.1 mm using a Vanier calliper. Density was expressed as numbers 100 m^{-3} for fish larvae and numbers m^{-3} for zooplankton.



Plate 3 : Picture of preflexion stage of *L. niloticus* larvae



Plate 4 : *Lates niloticus* larvae and eggs

3.6.3 Analysis of stomach contents

In the laboratory, the stomachs were opened up and the contents weighed (g) using an electronic balance (Oertling NA 264 weighing 0.0001-200g). The stomach contents were then emptied into a petri dish and with aid of binocular microscope (magnification x 40), food items were sorted into categories (i.e. fish remains, *Caridina*, molluscs, insects, organic matter and alga) identified and weighed. The importance of each food category was expressed as a percentage by dividing the total points awarded to all food types into number of points awarded on stomach analysis to food type in question according to Hyslop (1970).

3.7 Data Analysis

3.7.1 Water quality assessment

One - way ANOVA ($\alpha = 0.05$) (Zar, 2010) was used to test for significant differences in spatial variations in environmental variables among stations/sites. Post hoc Tukey test was used further to determine which sample means were significantly different

between stations. Variables tested were temperature, dissolved oxygen, chlorophyll-a concentration, and zooplankton abundance. These variates were further related to density and abundance of fish larvae using logistic linear regression and General linear model (GLM). Logistic regression GLM analysis was also used to determine the major factors that influence the abundance and distribution Nile Perch larvae in the study area. Non-metric multidimensional scaling (NMDS) ordination was used to explore variation in water quality parameters across sites. Dissimilarity matrices were derived for log-transformed water quality data to determine groupings among sites based on shared water quality characteristics.

3.7.2 Larval fish data analysis

Larval abundance data were $\log_{10}(x+1)$ transformed prior to analysis to fulfil normality requirements for parametric tests. Density of larval fishes and zooplankton was calculated by dividing total numbers counted in each sample by volume of lake water filtered (no. of revolutions of flow meter x volume in m^3 per revolution). For all statistical analyses a significance level of $\alpha < 0.05$ was used. To illustrate relationships between the water quality (predictor variables) and the Nile Perch larvae abundance (response variable), PCA was used.

3.7.3 Analysis of length frequency distributions

Comparison of distributions

To compare length distributions for *L. niloticus* juveniles from stations and from time to time, distributions within the ecological were pooled. These distributions were plotted on the same scale, and modal lengths compared, minimum and maximum lengths. Such an examination can reveal much about the way fish are growing over time (shown by shifts in modal lengths over time), or the progressive loss of larger

fish due to removals by mortality (shown by a reduction in the largest fish in the catch). In essence, if the length distributions do not show reasonably obvious and consistent modes, then an analysis of length frequency distributions are highly subjective and are unlikely to be successful (Sparre & Venema, 1998). It is thus necessary to compare mean lengths of different samples using Student's t test. Differences between length distributions were examined using the Kolmogorov-Smirnov Goodness-of-Fit Test, but for samples with large numbers of fish this tends to be overly sensitive (Zar, 2010) indicating differences between distributions that are not really indicative of genuine differences in biological processes (Sokal & Rolf, 1981).

Estimation of growth parameters from length data

A detailed description of the estimation of growth parameters of juveniles and adults (Length at maximum yield, total mortality Z, recruitment pattern and yield per recruit) is provided in Sparre and Venema (1998). The basis for estimation of the growth parameters was the von Bertalanffy Growth Formula (VBGF) which is expressed by the form (Sparre & Venema 1998):

$$L_t = L_\infty (1 - \exp(-K*(t - t_0)))$$

(where L_t is the predicted length at time t (years), L_∞ is the asymptotic length (cm), or the mean length the fish of a given stock would reach if they were to grow indefinitely, K is a growth coefficient (yr^{-1}), constant also called “stress factors” by Pauly (1980), t_0 is the age the fish would have been at zero length, t is the age (or the relative age, computed with $t_0 = 0$). L_∞ was initially estimated from $L_\infty = 0.95 L_{\text{max}}$ (Pauly & Murphy, 1982) where L_{max} is the size of the largest fish caught. The growth

parameters were estimated by length-frequency analysis (Pauly *et al.*, 1984; Sparre & Venema, 1998). Various methods of analysis are available, and have been incorporated into computer software packages. For example, the FAO-ICLARM Stock Assessment Tool (FISAT) (Gayanilo *et al.*, 1996) incorporates the Electronic Length Frequency Analysis (ELEFAN I and II) method.

Length at maximum yield

The length at maximum yield is the length class a fishery would obtain maximum possible catch weight per recruit:

$$L_{opt} = L_{\infty} (3 / (3 + M/K))$$

where L_{opt} is length corresponding to mean age in years at maximum at maximum yield per recruit (t_{opt}) in cm; M is the natural mortality having derived the growth coefficients (K) and asymptotic lengths (L_{∞}) natural mortality rates were estimated following Pauly's (1980) empirical equation;

$$\ln M = -0.0152 - 0.279 * \ln L_{\infty} + 0.6543 * \ln K + 0.463 * \ln T$$

where T (is the annual average lake surface temperature) for Lake Victoria is taken as 24 °C (Ochumba, 1984) and K is growth coefficient (yr^{-1}) were made on the restructured length frequency data using the surface response option in ELEFAN I sub-package in FiSAT with the highest index of fit (R_n range 0-1) selected. Length at maximum yield is of value as an indicator of growth overfishing as part of a comprehensive analysis of yield per recruit (Hilborn & Walters, 1992).

Maximum life span

The life span in years is the approximate maximum (t_{\max}) that fishes of a given population would reach. Using the parameters of von Bertalanffy growth function as estimated above, the life span was calculated as the age at 95 % of L_{∞} .

Total mortality Z

Total mortality coefficient (Z) was estimated using length converted catch curve (Pauly, 1980, 1984c). Length frequency data was converted to their corresponding ages by means of set growth parameters (L_{∞} & K of VBGF). The method consists of a plot of the natural logarithm of the number of fish in various age groups (N_i) against the corresponding age (t). Abundance at a given age decreases exponentially, making the slope an expression of mortality. Total mortality was estimated as the negative slope of:

$$\ln(N_i/\Delta_{ti}) = a + bt;$$

where:

$\ln N_i$ = natural logarithm of number of fish in length class i.

Δ_{ti} = time fish needs to grow through length class i.

$$\Delta_{ti} = (1/K) \ln[(L_{\infty}-L_1)/(L_{\infty}-L_2)]$$

t_i = time fish needs to grow through length class i $t_i = -1/K \ln[1-(L_i/L_{\infty})]$

t_i = is age corresponding to the midpoint of length class i.

a = y intercept, b = is the regression slope (estimation of Z)

Length converted catch curve (Pauly, 1983, 1984 a, b) converted length using the inverse VBGF.

$$t_L = t_0^{-1} + 1/K * \ln(1-L_i/L_{\infty})$$

where: t_L = is the predicted age (yrs) at length, t_0 = age at length = 0, K = the rate at which length tends towards the asymptote, L_i = length (cm) at age t_L , L_∞ = the mean length of fish would reach if they were to grow indefinitely. Selection of points to be used in the regression followed these rules:

- i) The first point in the regression should be the point immediately to the right of the highest point on the catch curve plot. Points were chosen by software ELEFAN II in the FISAT Software
- ii) Any point within 5 % of L_∞ was discarded, as these generated unrealistically high age.
- iii) One single outlier was rejected within the regression where straight line was fitted.

These analyses were done using the FISAT II Software. The natural mortality coefficient (M) was estimated using empirical formula (Pauly, 1980), linking the natural mortality with von Bertalanffy parameters, K (yr^{-1}), L_∞ (cm) and mean annual temperature ($T^\circ \text{C}$) of water in which fish stock live (in this case 24°C). Fishing mortality coefficient (F) was computed from the relationship $F = Z - M$, while exploitation rate will be calculated from the relationship $E = F/Z = F/(F+M)$.

Recruitment pattern (length converted catch curve)

The recruitment pattern was estimated from length frequency data by a method which involved: 1) backward projection onto the time axis of a set of length-frequency data; 2) summation of each month of the frequencies was projected onto each month; 3) subtraction, from each monthly sum, of the lowest monthly sum to obtain a zero value where apparent recruitment was lowest; and 4) expressing monthly recruitment in percent of annual recruitment (Pauly *et al.*, 1984).

Yield per recruit analysis

The relative yield-per-recruit model presented in the following is based on the Beverton and Holt model of 1966, modified by Pauly & Soriano (1986). The Beverton-Holt yield-per-recruit model (Beverton & Holt, 1957) was used to predict effects of changes in fishing effort on future yields. Relative yield-per-recruit (Y'/R) was computed from the formula (Beverton & Holt, 1957) and (Y'/R) analysis was run in FISAT II:

$$Y'/R = SP_i((Y'/R)_i \cdot G_i^{-1}) - ((Y'/R)_{i+1} \cdot G_i)$$

where, (Y'/R)_i refers to the relative yield-per-recruit computed from the lower limit of class i using and:

$$\frac{Y'}{R} = EU^{M/K} \left\{ 1 - \frac{3U}{1+m} + \frac{3U^2}{1+2m} - \frac{U^3}{1+3m} \right\}$$

where U and m are defined as:

$$U = 1 - \left(\frac{L_c}{L_\infty} \right)$$

$$m = (1-E) / \left(\frac{M}{K} \right) = \left(\frac{K}{Z} \right)$$

P_i is the probability of capture between L_i and L_{i+1}, while G_i is defined by

$$G_i = \prod r_j$$

where:

$$r_j = (1-c_i)^{S_i} / (1-c_i^{-1})^{S_i}, \text{ and}$$

$$S_i = (M/K)(E/(1-E))P_i.$$

here, B'/R is estimated from

$$(B'/R)_i = (1-E) \cdot A/B$$

where

$$A = \left\{ 1 - \frac{3U}{1+m} + \frac{3U^2}{1+2m} - \frac{U^3}{1+3m} \right\}$$

$$B = \left\{ 1 - \frac{3U}{1+m'} + \frac{3U^2}{1+2m'} - \frac{U^3}{1+3m'} \right\}$$

where,

$$m' = 1/(M/K) = m/(1-E).$$

E_{\max} , $E_{0.1}$ and $E_{0.5}$ are estimated by using the first derivative of the function. The outputs included plots of Y'/R vs E (=F/Z) and of B'/R vs E, from which the E_{\max} , $E_{0.1}$ and $E_{0.5}$ (as defined above) are also estimated using FiSAT II.

3.7.5 Food and feeding habits

Stomach content and fullness

The variation of different food items with regard to size classes and time were analysed. Stomach fullness of *L. niloticus* larvae caught in the 24-hour regime, was expressed as percentage of fish weight viz: The frequency of occurrence of a particular food item was calculated by expressing the stomachs containing this item as percentage of all stomachs containing food.

$$SF = (SC/\text{Fish weight (g)}) \cdot 100$$

where,

$$SC = \text{stomach contents weight (g)}.$$

Food/ diet composition was described from stomach samples based on the weight of the prey items identified to the lowest taxon(Schoener, 1970; Hyslop, 1980; Wallace, 1981; Lucena *et al.*, 2000. Categories of prey were *Caridina nilotica*, insects grouped as Odonata along with other Ephemeroptera, Trichoptera, molluscs inclusive of gastropods and bivalves, cladocerans, fish remains and plant material.)

CHAPTER FOUR

RESULTS

Objective 1: The effects of limnological factors on spatial variation in abundance of larvae and juveniles of *L. niloticus* in Lake Victoria, Kenya

4.1 Physico-chemical Water Quality Parameters

Mean values of some of the physical-chemical parameters measured are given in (Table 4). The study area was divided into three sections for determination of water quality: C1 = the inner, nearshore Gulf, C2 = the mid Gulf, and C3 = the outer, offshore Gulf (open lake). Secchi depth values increased from the inner gulf to the open lake, and values ranged between 0.25 m in C1 in 2012 and 3.5 m in C3 in 2013. The lowest value (0.2 m) was recorded at Kisumu Pier in C1 in 2015 while the highest value(3.5 m) occurred at Gingra Rock in C3 also in 2015. Values for turbidity decreased from the inner Gulf sites to the offshore open lake sites. Turbidity values ranged from 8.3 NTUs in C3 in 2015 to 111.1 in the open lake. Turbidity with a maximum of 498 NTUs in C1 was also recorded in 2015. Turbidity ranged from 14.3 NTU in C3 in 2013 to 111.1 NTU in C1 in 2015 when the highest value of 498 NTUs was recorded at Kowuor. There was an inverse relationship between Turbidity and Secchi depth.

Mean chlorophyll *a* concentrations ranged between 11.8 $\mu\text{g L}^{-1}$ recorded in C3 in 2013 and 66.7 $\mu\text{g L}^{-1}$ in C1 in 2012. The highest value of chlorophyll *a*, 104 $\mu\text{g L}^{-1}$ occurred at Ndere in C1 in 2012. Mean dissolved oxygen (DO) concentrations during the surveys ranged between 5.1 mg L^{-1} in cluster 2 (C2) in 2013 and 7.6 mg L^{-1} in C3 in 2012. The highest DO value 11.2 mg L^{-1} was recorded in C1 and C3 in 2012 and

2013, respectively. However, low DO values of 3.1 mg L^{-1} 3.5 mg L^{-1} were recorded in bottom waters of Achieng' Oneko (C2) and C1, respectively, in 2013.

Table 4: Mean values (and maximum values in brackets) of some of the physico-chemical parameters in the different clusters of the study area. ND denotes no data. (C1 = Inner Gulf stations, C2 = Mid Gulf stations, C3 = Offshore open Lake stations)

Cluster	2012			2013			2015		
	C1	C2	C3	C1	C2	C3	C1	C2	C3
Secchi (m)	0.25 (0.2-3.5)	0.31 (0.2-3.5)	2.4 (0.2-3.5)	0.4 (0.2-3.5)	0.5 (0.2-3.5)	1.6 (0.2-3.5)	0.3 (0.2-3.5)	0.4 (0.2-3.5)	1.31 (0.2-3.5)
Turbidity (NTU)	ND	ND	ND	80.8 (8.3-498)	80.3 (8.3-498)	14.3 (8.3-498)	111.1 (8.3-498)	52.7 (8.3-498)	8.3 (8.3-498)
Chla ($\mu\text{g L}^{-1}$)	66.7 (11.8-104)	41.9 (11.8-104)	29.3 (11.8-104)	20.9 (11.8-104)	13.9 (11.8-104)	31(11.8-104)	ND	ND	ND
DO (mg L^{-1})	7.2 (3.1-11.2)	6.5 (3.1-11.2)	7.6 (3.1-11.2)	7.2 (3.1-11.2)	5.1 (3.1-11.2)	5.3 (3.1-11.2)	6.34 (3.1-11.2)	7.3 (3.1-11.2)	7 (3.1-11.2)
Cond. ($\mu\text{S cm}^{-1}$)	150 (98-210)	153 (98-210)	112.4 (98-210)	153.3 (98-210)	142 (98-210)	98 (98-210)	168.3 (98-210)	174.6 (98-210)	135.8 (98-210)
NO ₃ N ($\mu\text{g L}^{-1}$)	103.6 (0.5-198)	95 (0.5-198)	73.9 (0.5-198)	123.9 (0.5-198)	55.2 (0.5-198)	26 (0.5-198)	113 (0.5-198)	58.6 (0.5-198)	8.53 (0.5-198)
NH ₄ H ($\mu\text{g L}^{-1}$)	128 (17.7-472)	106.9 (17.7-472)	17.7 (17.7-472)	147.7 (17.7-472)	63.7 (17.7-472)	43.8 (17.7-472)	91.1 (17.7-472)	180.3 (17.7-472)	56.4 (17.7-472)
PO ₄ P ($\mu\text{g L}^{-1}$)	92.3 (25.1-145)	95.1 (25.1-145)	25.3 (25.1-145)	74.4 (25.1-145)	74.2 (25.1-145)	29.8 (25.1-145)	45.1 (25.1-145)	45.5 (25.1-145)	26.1 (25.1-145)

There was an increase in temperature from the inner gulf stations to the C3 open lake stations. The values decreased in the open lake stations to the south (Appendix IV).

There was a general decrease in conductivity from the inner gulf to the open lake. Stations with a river influence were characterized by lower conductivity (Table 4). The mean conductivity values ranged between $98 \mu\text{S cm}^{-1}$ in C3 in 2013 and $174.6 \mu\text{S cm}^{-1}$ in C2 in 2015. The highest value of $210 \mu\text{S cm}^{-1}$ occurred at Kisumu pier in 2015 in C2. There was a decrease in the levels of both Total Dissolved Solids (TDS) and Total Suspended Solids (TSS) from the Inner Gulf sites to the open lake sites (Appendix VI). Within Kisumu bay the total dissolved solids were higher than the suspended solids (Appendix VI). The sites within the open lake waters, had higher primary production (measured as chlorophyll *a*) than the Gulf stations (Table 4).

For most sites, the most dominant form of nitrogen was ammonium. Mean values of nitrates ($\text{NO}_3\text{-N}$) ranged between $15 \mu\text{g L}^{-1}$ in C3 in 2015 and $123.9 \mu\text{g L}^{-1}$ in C1 in 2013. The highest $\text{NO}_3\text{-N}$ concentration of $198 \mu\text{g L}^{-1}$ occurred at Kisumu pier in C1 in 2013.

The mean nitrite ($\text{NO}_2\text{-N}$) concentrations varied between 0.7 and $17.1 \mu\text{g L}^{-1}$ with a mean of $4.1 \mu\text{g L}^{-1}$. In 2012, observed nitrite concentrations ranged between 0.5 and $23.0 \mu\text{g L}^{-1}$ with a mean of $11.1 \mu\text{g L}^{-1}$. In 2013, nitrite concentrations ranged from 2.5 and $21.3 \mu\text{g L}^{-1}$ with a mean of $11.9 \mu\text{g L}^{-1}$. Mean values of ammonium ($\text{NH}_4\text{-N}$) ranged from $17.7 \mu\text{g L}^{-1}$ in C3 in 2012 to $180.3 \mu\text{g L}^{-1}$ in C2 in 2015 when the highest value of $472 \mu\text{g L}^{-1}$ was also recorded at Gingra Rock in C2.

Total nitrogen values were higher in the inner Gulf stations and low in the open lake stations (Table 4). High concentrations of soluble reactive Phosphorus (SRP) was

observed in the open waters and outer gulf sites. The Total Phosphorus (TP) values were high in the inner Gulf stations, mid Gulf stations and southern stations respectively. Total nitrogen (TN) concentrations for the year 2015 varied between 856.9 and 2,538.7 $\mu\text{g L}^{-1}$ and a mean of 1,330.3 $\mu\text{g L}^{-1}$. In 2013, the observations varied between 204.2 and 2,349.6 $\mu\text{g L}^{-1}$ with a mean concentration of 511.6 $\mu\text{g L}^{-1}$. TN concentrations in 2012 ranged between 482.8 and 2496.6 $\mu\text{g L}^{-1}$. Mean values of Phosphates ($\text{PO}_4\text{-P}$) ranged between 26.1 $\mu\text{g L}^{-1}$ in C3 in 2015 and 91.5 $\mu\text{g L}^{-1}$ in in C2 in 2012. The highest concentration of $\text{PO}_4\text{-P}$ was 145 at Maboko in C2 in 2012.

Total phosphorus (TP) concentration during the study period varied between 29.1 $\mu\text{g L}^{-1}$ at Mbita West 1 in C3 and 244.9 $\mu\text{g L}^{-1}$ at Gingra Rock in C2 with a mean of 95.5 $\mu\text{g L}^{-1}$. In 2013, TP concentrations ranged between 26.3 and 192.0 $\mu\text{g L}^{-1}$ and a mean of 92.7 $\mu\text{g L}^{-1}$. In 2012, the observed concentrations ranged from 52.3 to 322.3 $\mu\text{g L}^{-1}$ and a mean of 172.7 $\mu\text{g L}^{-1}$. Silicate (Si-O_2) in 2015 ranged between 0.2 and 15.3 mg L^{-1} with a mean of 7.7 mg L^{-1} . In 2013, silica ranged between 1.4 and 23.4 mg L^{-1} with a mean concentration of 13.0 mg L^{-1} , while in 2012 the concentrations varied from 1.8 to 33.9 mg L^{-1} and a mean of 16.9 mg L^{-1} .

Dimension 1 of the NMDS matrix displayed positive loadings with turbidity and was associated with sites such as Samunyi, Kowuor, Oluch and Homabay (Fig. 3 and 4). Secchi and maximum depth were loaded negatively along Dimension 1 and were associated with stations such as Mbita East and Mbita West. Turbidity was negatively associated with Secchi depth, as expected (Fig. 3).

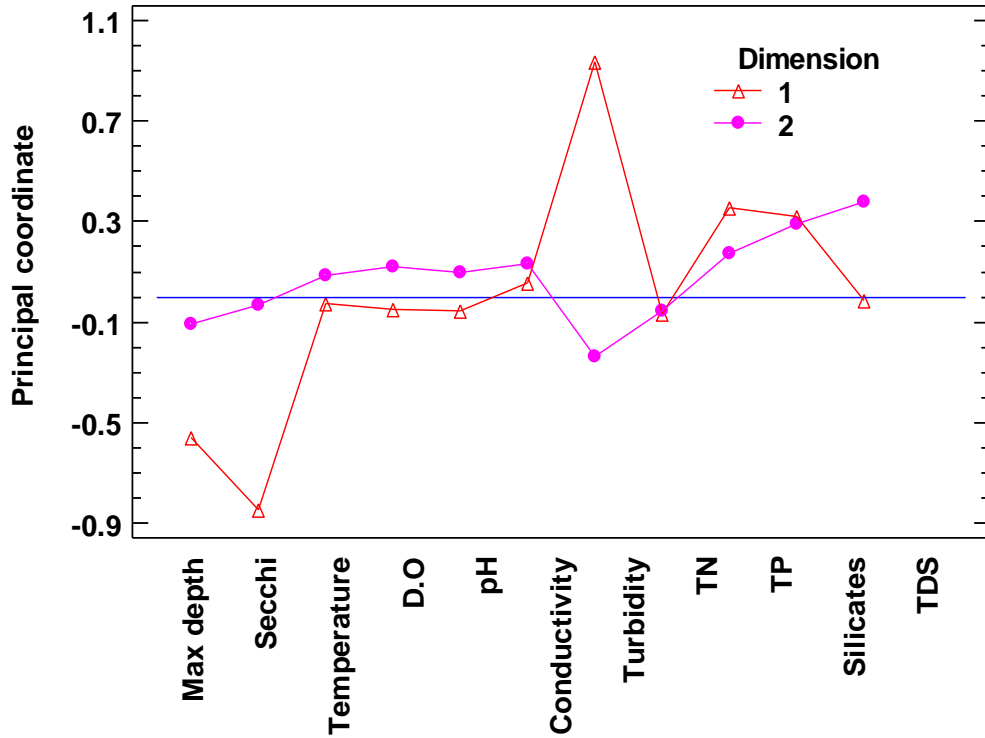


Figure 3: Principal coordinates projections (vector projections) of water quality parameters in Lake Victoria, Kenya

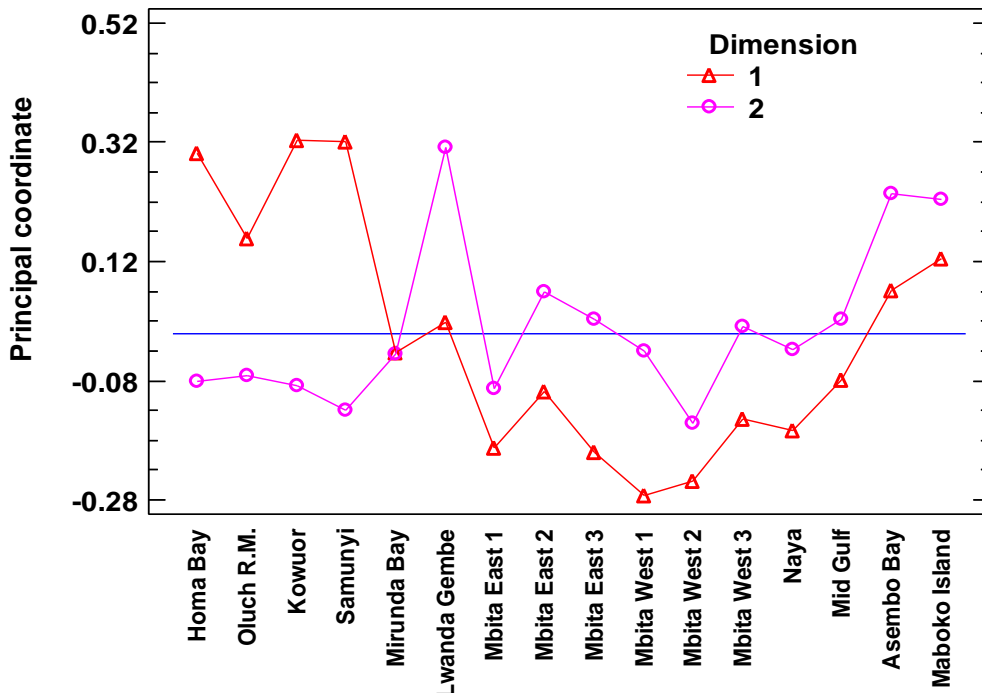


Figure 4: Principal Coordinates showing dimension 1 and 2 vector projections by stations in Lake Victoria, Kenya

Mosaic plots were used as a starting view of multidimensional part-to-whole data sets into a single graph (Fig. 5). It's important to view all of the parts at once. The widths of the rectangles represent the proportion of physical- chemical parameters with each and their stations across the plot. The area of each rectangle is proportional to the frequency of each combined group. It is obvious that total nitrogen (TN) values were higher in Mbita west compared to all other stations. Turbidity from the size of the rectangle were visualized as high in Samunyi, Homa Bay and Kowuor stations. Total dissolved solids (TDS) was high in Lwanda Gembe station. Whereas conductivity showed no variation among stations judging from the size of the boxes. The set of bar graphs are presented to reveal the same relationships in a way that can be more easily and accurately perceived and understood (Fig. 5).

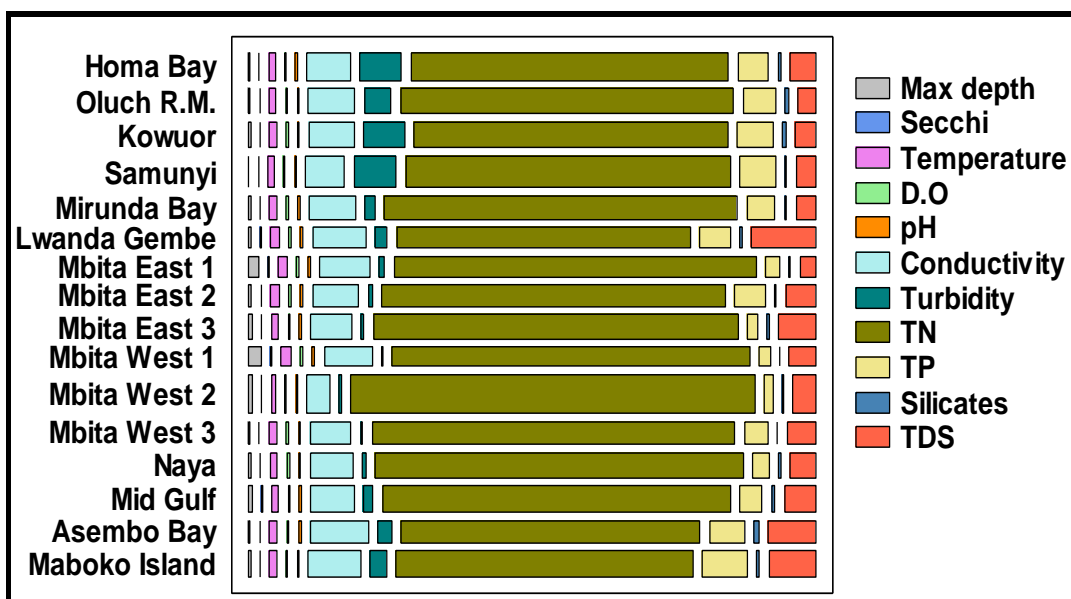


Figure 5. The mosaic display to show the values (cell frequencies) in a contingency table cross-classified by one or more “factors”.

Objective 2: The distribution and abundance of larvae and juveniles of *L. niloticus* in Lake Victoria, Kenya

4.2 Distribution of Eggs, Larvae and Prey in Relation to water quality

Canonical correspondence analysis (CCA) ordination of water quality and abundance of of *L. niloticus* I larvae in the Kenyan sector of Lake Victoria (Fig. 6), identified pH, turbidity, temperature, conductivity and alkalinity as the key parameters influencing distribution of larvae. Factor 1 in CCA ordinations accounted for most of the variation (97.8 %) distinguishing most lake sites with high abundance in the gulf and those in the main Lake (Fig. 6). Variables most related to Factor 1 were the main drivers of distribution and abundance of larvae. Factor 2 accounted for 1 % of variability.

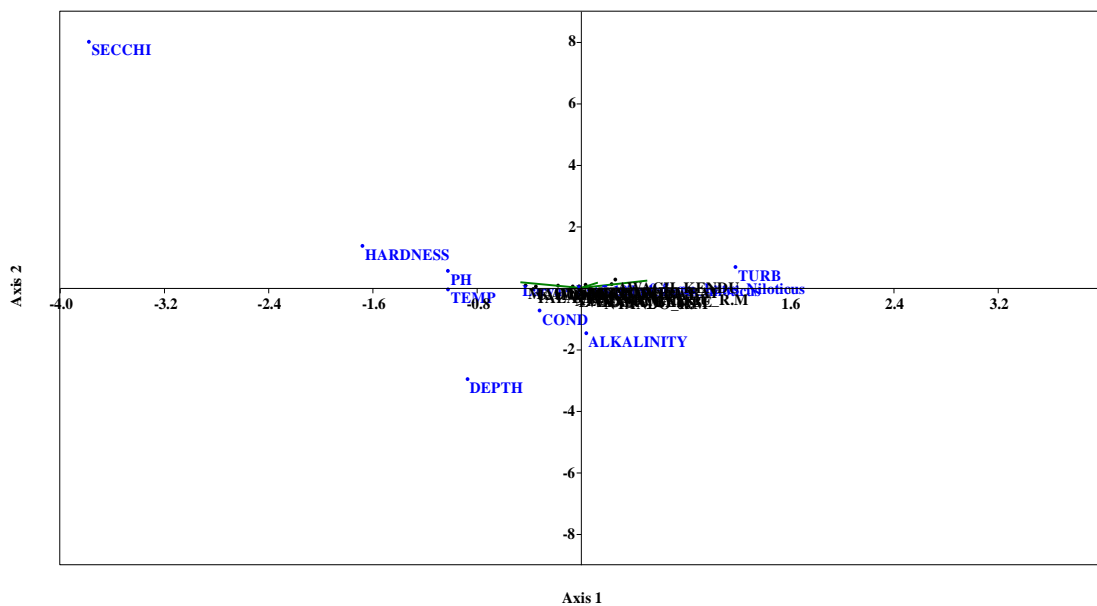


Figure 6: CCA of *Lates niloticus* ordination with physical chemical parameters in the Kenyan sector of Lake Victoria in 2012

Logistic regression outputs show the estimated coefficients (parameter estimates), standard error of the coefficients, z-values, and p-values associated with water quality effects on larvae abundance (Table 5). The odds ratio and a 95% confidence interval for the odds ratio. The coefficient associated with a predictor was the estimated

change in the logit with a one unit change in the predictor, assuming that all other factors and covariates were the same.

The first set of estimated logits, labeled Logit (1), were the parameter estimates of the change in logits of TDS relative to the reference event, *L. niloticus*. The p-values of 0.00 and 0.417 for Measurements and *L. niloticus* larvae, respectively, indicate that there is sufficient evidence to conclude that a change in measurements from TDS or Turbidity affected *L. niloticus* larvae abundance (Table 5). The second set of estimated logits, labeled Logit (2), are the parameter estimates of the change in logits of Secchi depth relative to the reference event, *L. niloticus*. The p-values of 0.000 and 0.939 for measurements and *L. niloticus*, respectively, indicate that there is sufficient evidence that the parameter Secchi depth and turbidity influenced larvae abundance and distribution. The positive coefficient for Secchi depth/Turbidity indicates *L. niloticus* tend to prefer TDS/Turbidity and water depth/ Turbidity. The estimated odds ratio of 0.10 implies that the odds of finding *L. niloticus* larvae in areas influenced by secchi depth/turbidity is about 10 % higher for larvae.

The negative coefficient associated with TDS and deeper areas indicates that larval fish tend not to prefer turbid waters (Table 5). The G statistic of the regression indicate that $G = 203.737$, $p < 0.05$ indicating that at $\alpha = 0.05$, there is sufficient evidence that at least one coefficient was significantly different from 0. In this case, the p-value for the Pearson test was 1.0 and the p-value for the deviance test was 1.0, indicating that there is evidence to suggest the model fits the data. If the p-value was less than selected level, the test would indicate that the model does not fit the data.

Table 5: Nominal Logistic Regression: Parameters versus Measurements, *L.niloticus* larvae (a) response information (b) Logistic Regression Table (c) Goodness of Fit Tests. Note: TDS = Total dissolved solids

(a) Response Information									
Variable	Value	Count							
Par	Turbidity.	35 (Reference Event)							
	TDS	35							
	Secchi depth	35							
	Maximum depth	35							
	Total	140							
(b) Logistic Regression Table									
Predictor	Coef	SE Coef	Z	P	Odds Ratio	95% CI			
						Lower	Upper		
Logit 1: (TDS/Turb.)									
Constant	-2.389	0.642	-3.72	0.000					
Measurement	0.0443	0.010	4.29	0.000	1.05	1.02	1.07		
Lates niloticus	-0.0015	0.002	-0.81	0.417	1.00	1.00	1.00		
Logit 2: (Secch.Depth/Turb.)									
Constant	5.401	1.103	4.90	0.000					
Measurement	-2.350	0.589	-4.00	0.000	0.10	0.03	0.30		
Lates niloticus	0.0002	0.002	0.08	0.939	1.00	1.00	1.00		
Logit 3: (Max Depth/Turb.)									
Constant	0.800	0.405	1.98	0.048					
Measurements	-0.0511	0.0189	-2.71	0.007	0.95	0.92	0.99		
Lates niloticus	-0.0002	0.0013	-0.18	0.854	1.00	1.00	1.00		
Log-Likelihood = -92.213									
Test that all slopes are zero: G = 203.737, DF = 6, P-Value = 0.000									
(c) Goodness-of-Fit Tests									
Method	Chi-Square	DF	P						
Pearson	300.683	402	1.000						
Deviance	184.425	402	1.000						

4.3 Larvae Abundance and Size structure

The distribution of fish larvae by station sampled from September 2011 to June 2013 in the Kenyan waters of Lake Victoria are presented in Table 6. A total of 12,073 individual larvae of *L. niloticus* were sampled. In general, abundance of *L. niloticus* larvae were usually highest in stations associated with river mouths and sheltered bays and declined considerably in open waters. In August/ September 2012 highest abundance of *L. niloticus* larvae of totalling 3897 No. m³ was recorded. This was followed by the month of February 2012 where 2835 No. m³ were collected. This was

also followed by November/ December 2012 when 2013 No. m³ were caught. The lowest number of 374 No. m³ individual counts were recorded in September 2011. In December 2013 the individuals encountered were 489 No. m³. In April 2012 Nile perch larvae were observed at six stations (Awach river mouth, Asembo Bay, Bala Rawi, Oluch river mouth, Sukru Island and Mirunda Bay) only (Table 6). The highest consistent larval densities for *L. niloticus* was observed at Kisumu Pier (Kisat river mouth), Asembo Bay, Awach River mouth, Mirunda Bay, Bala Rawi, Mitimbili, Maboko, Oluch River mouth, Lwanda Gembe and off Gingra rock (Table 6).

L. niloticus larvae totaling 4017 were sorted out during the study into the larval developmental stages. Out of this, 3358, representing 83.6 %, were preflexion stage, 462 (11.5 %) were flexion and 197 (4.9 %) were in postflexion stage. The mean length frequency distributions of Nile perch larvae ordered by early life history stages Preflexion, Flexion, Post-flexion and Juveniles in Lake Victoria, Kenya are presented (Fig. 7). The overlaps in length measurements of the different stages of larvae was observed as they transitioned to other stages of their development. There was no clear cut length which could be assigned to a particular stage because of these overlaps in their lengths. They can be described by their length range which overlapped the other stages (Fig. 7).

Table 6: Distribution of fish larvae by station sampled from September 2011 to June 2013 in Lake Victoria, Kenya (No. /m³).

STATION	September 2011	February 2012	Apr-2012	28 Jun- 11 Jul 2012	Aug/Sep 2012	Nov-Dec 2012	Jan-2013	Jun-2013	Dec2013
Ksm Pier		21		46	608			222	190
Nyando RM		13		38					66
Sondu Miriu		18		4					
Awach RM	15	54	3	4	333	167			21
Bala Rawi	30	113	302	69	132	44		1	
Gingra Rock	2	1		1	54	20			
Kowuor	0	3		3	130	77		1	
Mirunda Bay	86	555	103		6	166			79
Yala RM	0	552			198	26	100		0
Nzoia RM		16		29	8	30			14
Usenge Bay		0					413		
Kadimo Bay		595					56		0
Mid Gulf					210	97		1	
Naya	1	0			97	109			
Maboko	31	0		3		81		14	
Mitimbili	1	278		134	152	78		22	
Homa Bay	66	127		12	276	40		211	42
Madundu	78	122			220				
OluchRM	21	208	147	13	204	14		55	9
Lwanda Gembe	43	32		2	694	62			
Asembo Bay		127	1	128	18	614			63
Sukru Island			1	4					
Ndere Island				100	52	125		1	
Soklo Point				58		14			
Kuja RM				3	170	8			0
Samunyi RM					69			46	5
Kopiata				6	21	43		1	
Utajo				1	233	194			
Achieng Oneko				6	12	104			
TOTAL	374	2835	557	664	3897	2113	569	575	489

The length distributions of Nile Perch caught in standard larval fish surveys conducted using nets with 500 μm mesh and nets with 750 μm mesh (Appendix VIII) showed that smaller sized fish were caught in high numbers in 500 μm net than those caught in 750 μm .

The percentage relative abundance of *L. niloticus* larvae per month for each sampling station during 2011-2013 in Lake Victoria, Kenya are presented in Figure 8. In September 2011 higher abundances were recorded at Kuja river mouth, mid gulf, Gingra rock, Kisumu pier, Awach river mouth stations. whereas in the month of February 2012 high relative abundances were observed in Sondu-miriu river mouth Kadimo bay, Mirunda bay and Yala river stations (Fig. 8). While in July 2012 higher relative abundances were recorded at Sukru Island, Ndere Island and Soklo point stations. Whereas in December 2012 higher abundances of larvae were recorded at Maboko Island, Asembeo bay, Achieng Oneko and kopiata. In January 2013 high relative abundances were recorded at the mouth of Sondu Miriu River (Fig. 8)

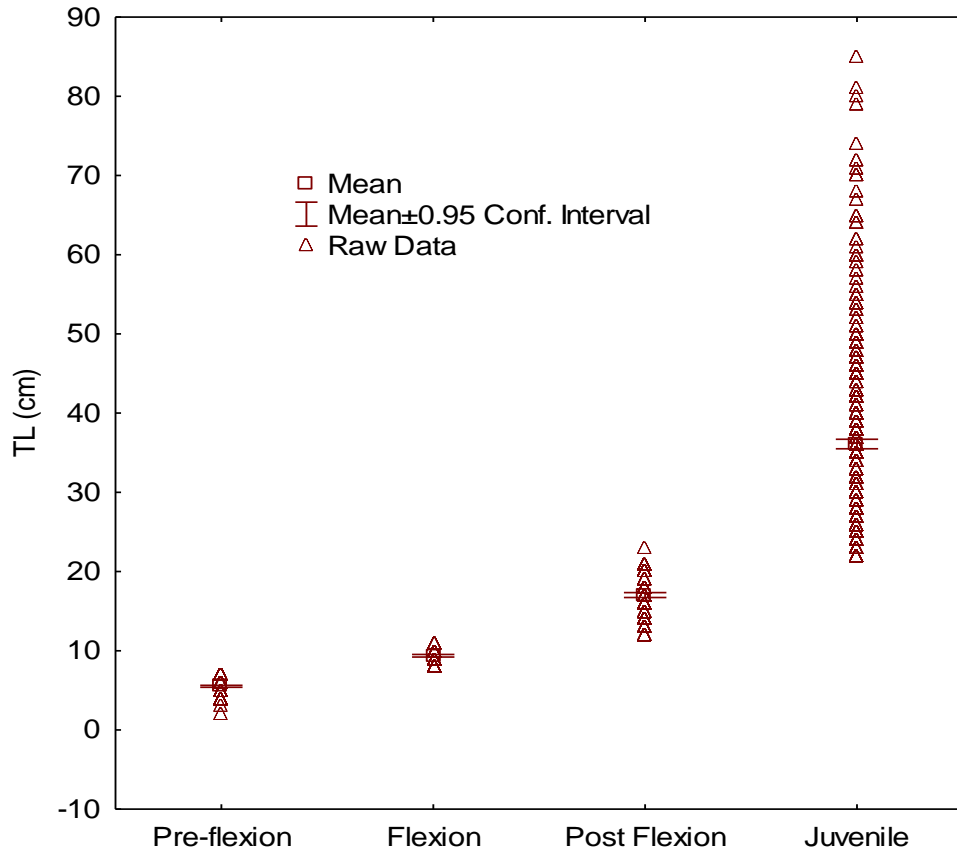


Figure 7: Mean length distribution of Nile perch larvae ordered by early life history stages (Pre-flexion, Flexion, Postflexion and Juveniles in Lake Victoria, Kenya. Showing overlaps in lengths as they transition

Results of Tri- monthly relative abundance of *Lates niloticus* larvae for each sampling station during 2011-2013 sampling period in Lake Victoria, Kenya are presented in Figure 8. In January-December sampling months Kisumu Pier and Usenge Bay had the highest relative abundance of 400 while Homabay had 250, as the rest of the stations had a relative abundance of below 100. In the months of July-December Kisumu Pier, Awach RM, Lwanda Gembe and Asembo Bay recorded relative abundance of 500 and above while Utajo had a relative abundance of 400, whereas the rest of the stations had a relative abundance of 300 and below. In the months of September- April sampling period Mirunda Bay had the highest abundance, followed by Kadimo bay and Balarawi that had a relative abundance of 400. During this period the remaining 20 Stations recorded a relative abundance of 0-100 (Fig.8).

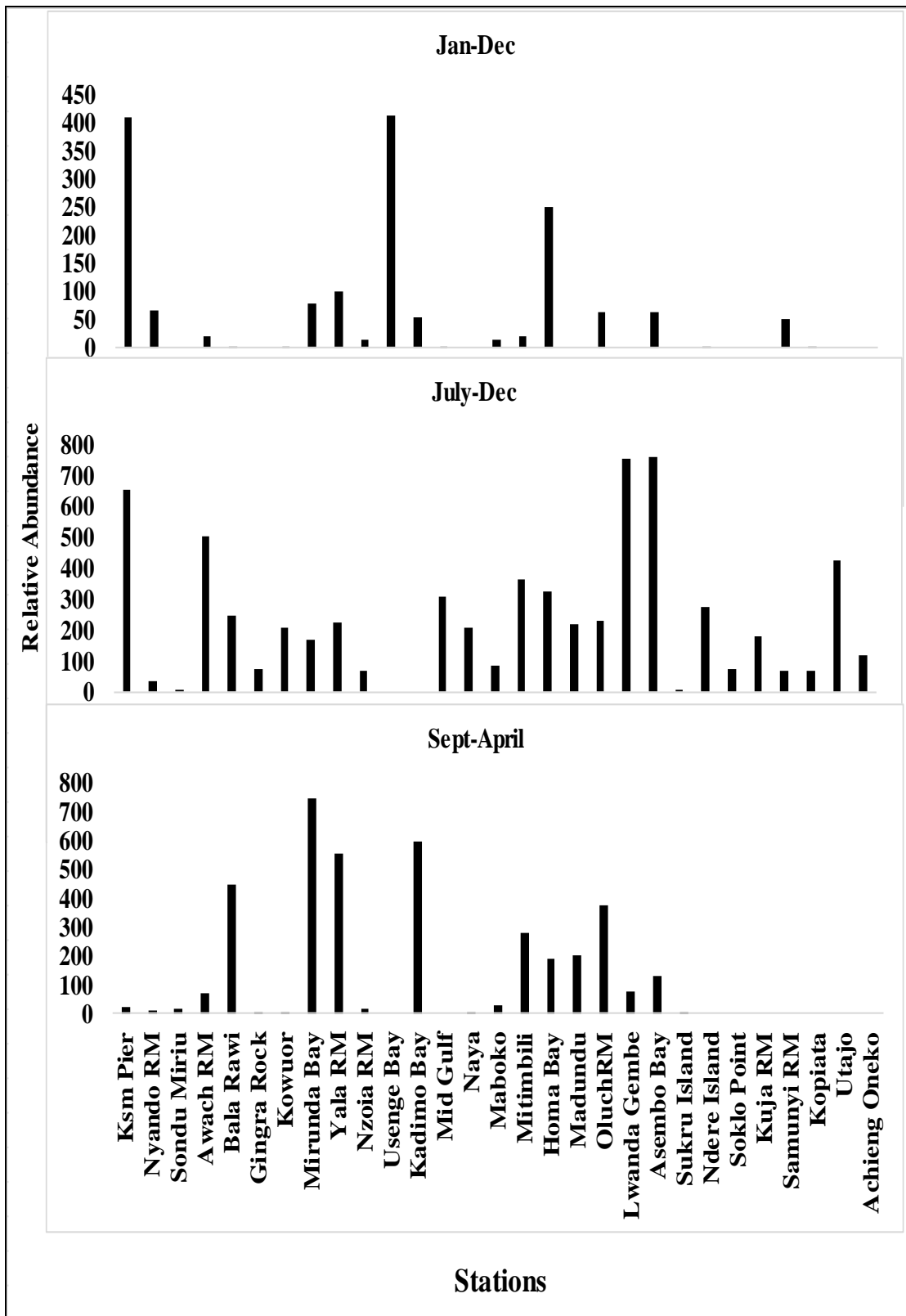


Figure 8: Pooled tri - monthly relative abundance of *Lates niloticus* larvae for each sampling station during 2011-2013 sampling period in Lake Victoria, Kenya

There was an increase in sizes from the youngest (pre-flexion) to the oldest (post-flexion) larval stages (Fig. 9). Juveniles mean sizes recorded were higher than any of the larval stages in the study area. The non-overlapping whiskers of boxplots indicates that mean sizes across larval stages were statistically significant (Fig. 9).

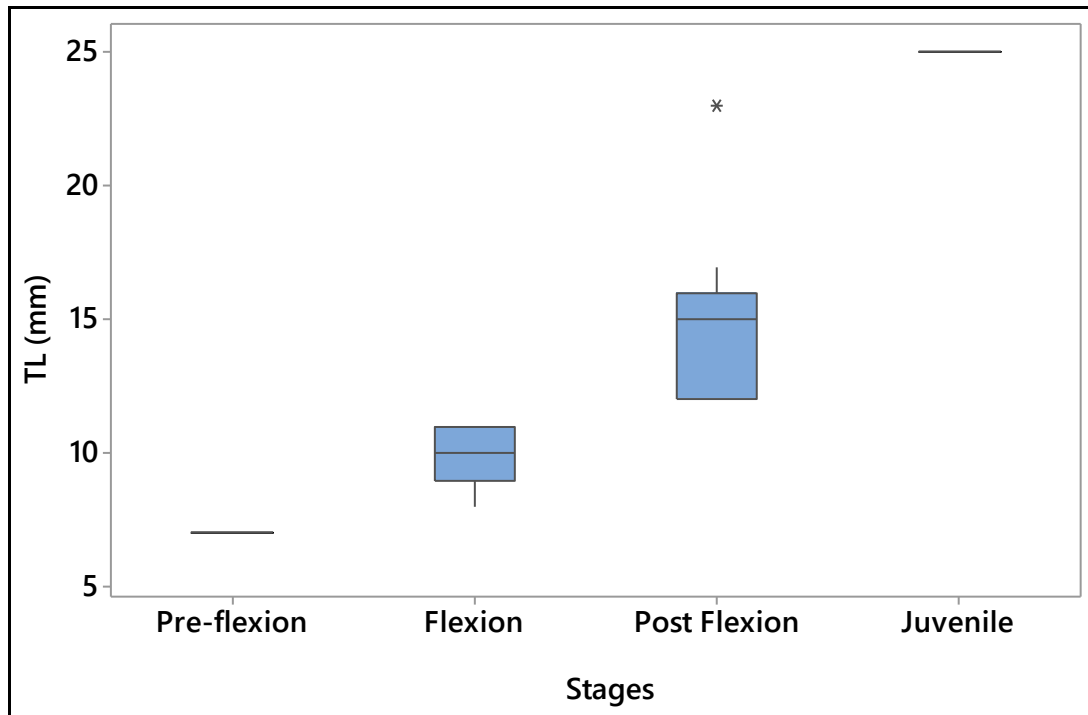


Figure 9: Boxplot distribution characteristics of different stages of Nile perch larvae sampled in 2013 grouped data in Lake Victoria Kenya

The mean size (total length in mm) distributions of *L. niloticus* larvae were significantly different between stations (Fig. 10; $F_{0.05}(32, 1820)$, $p < 0.05$). Mean sizes in most of the stations were below 40 mm TL. The results show that river mouths stations such as Kisat, Nyamasaria and Samunyi recorded higher larvae mean size distributions, followed by sheltered bays such as Mirunda and Asembo.

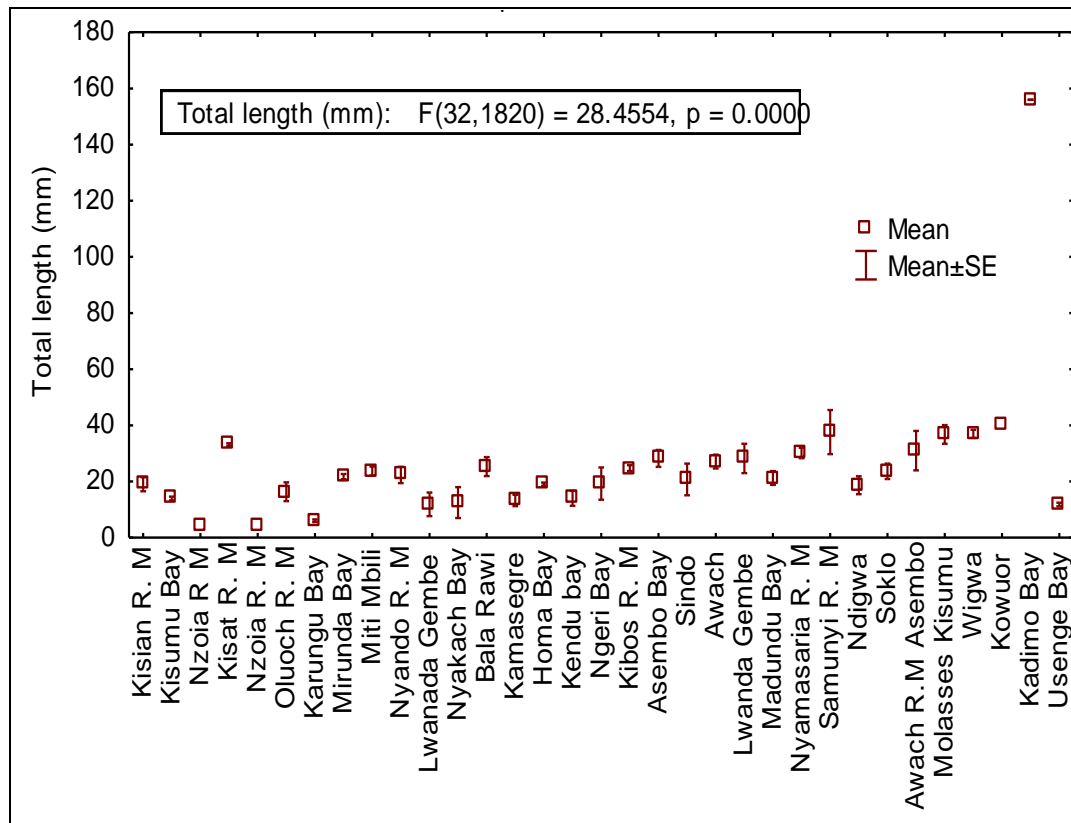


Figure 10: Mean size distribution of Nile perch larvae sampled in 2013 grouped by station in Lake Victoria Kenya

The mean variation of total length of *L. niloticus* larvae sampled over 24 hours are shown Figure 11. The mean sizes observed varied with smaller mean sizes encountered at 4pm on the first day of sampling, at 4 am and 8 am respectively. Whereas the larger mean sizes were in the samples caught at 8 pm, 12 am, 12 pm and 4 pm the following day The mean size were significantly different with the hours (Total length mm $F_{0.05}(4, 85) = 14.6859, p < 0.05$).

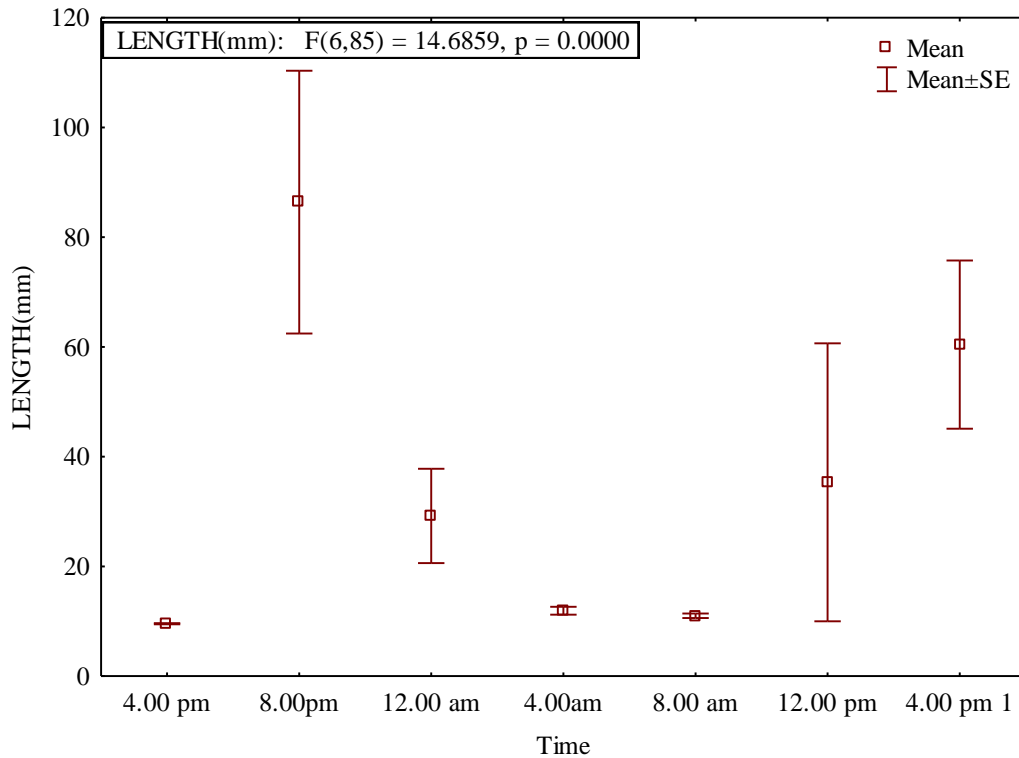


Figure 11: Mean size of *Lates niloticus* larvae sampled over 24 hours in January 2013

4.4 Variation in mean length of Nile Perch juveniles with depth

There was an increase in length of Nile Perch juvenies with water depth in Lake Victoria (Fig. 12). The relationship between length of fish and water depth showed a positive correlation ($r = 0.458$, $p < 0.05$). Length of *L. niloticus* increased with depth up to 40 m where observations were made (Fig. 12; Appendix IV). An increase in length of fish with depth, coupled with a reduction in numbers with depth are shown in Figure 12, there were indications that shallow waters have high numbers of fish which are mainly small hence lower weight. This is an indication of large quantities of juvenile fish concentrations in depths below 20 m.

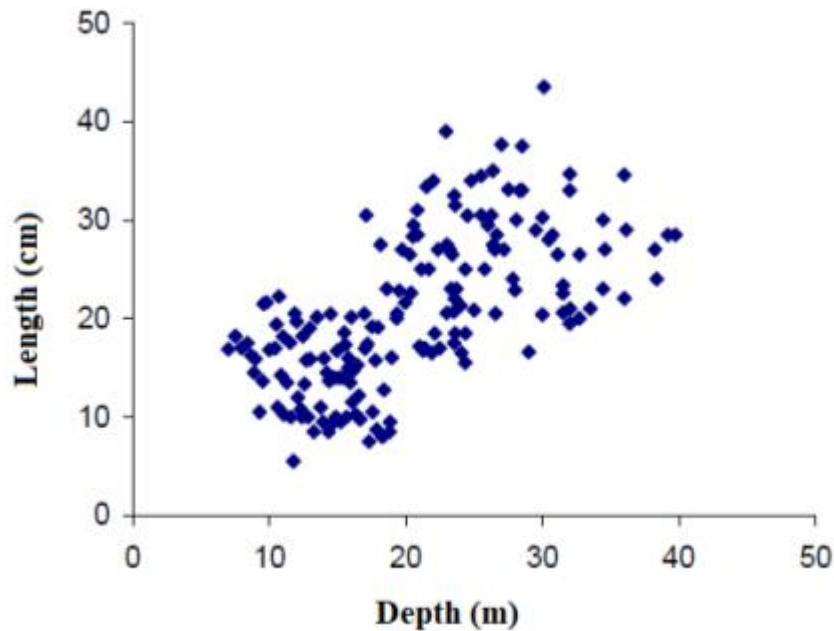


Figure 12: Length of Nile perch juveniles harvested at various depths using a bottom trawl net in Lake Victoria, Kenya

Results of the length frequency distribution showing how juvenile Nile perch fish were distributed vertically in the water column in the experimental gillnets set at depths 0-1 m, 1-2 m and 2-3 m (Fig. 13) showed size class of 10.5 – 20.5 cm TL were more abundant generally. Highest numbers were caught at the top followed by bottom, whereas the rest of size class had a frequency of 10 and below (Fig.13)

The length frequency distributions of Nile perch juveniles caught in the experimental gillnets set at 100 m, 200 m and 500 m from the shore line are presented in Figure 14. This provided indications of how Nile perch juveniles were distributed horizontally from the shoreline to offshore in the lake. The results showed size class of 10.5-20.5cm TL were caught frequently in high numbers in nets set 200 m away from shoreline which was followed by fishes caught at distance of 100 m from shoreline. Sizes of 0-35 cm TL were not caught at 500 m from shoreline. This was indicative that fishes below 35 cm TL were occupying areas close to the shoreline.

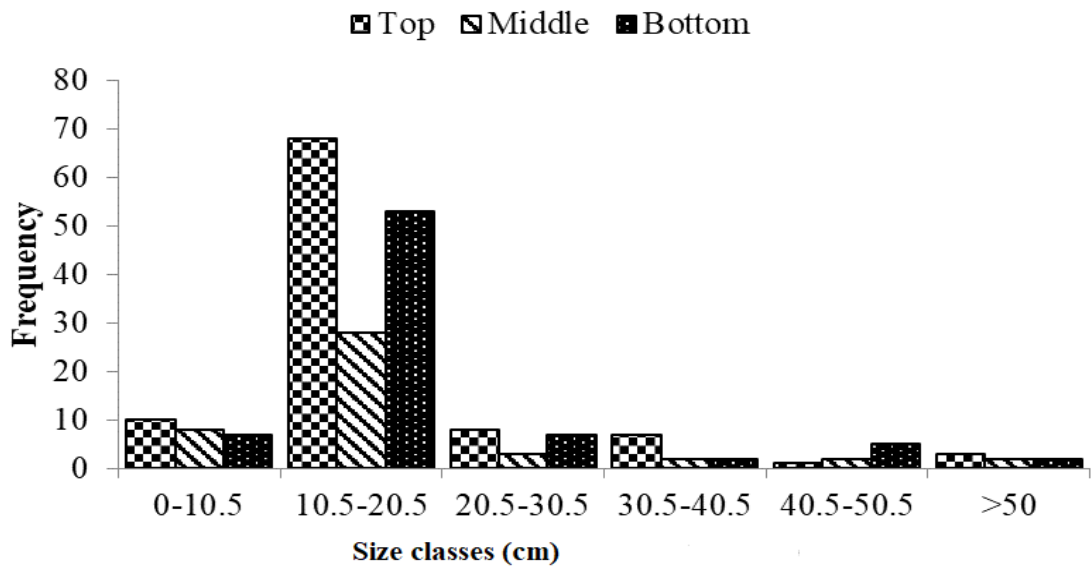


Figure 13: Length-frequency distributions of Nile perch in the experimental gillnet catches set at different depth (Top 0-1m, middle 1-2m, bottom 2-3 m) in Lake Victoria, Kenya.

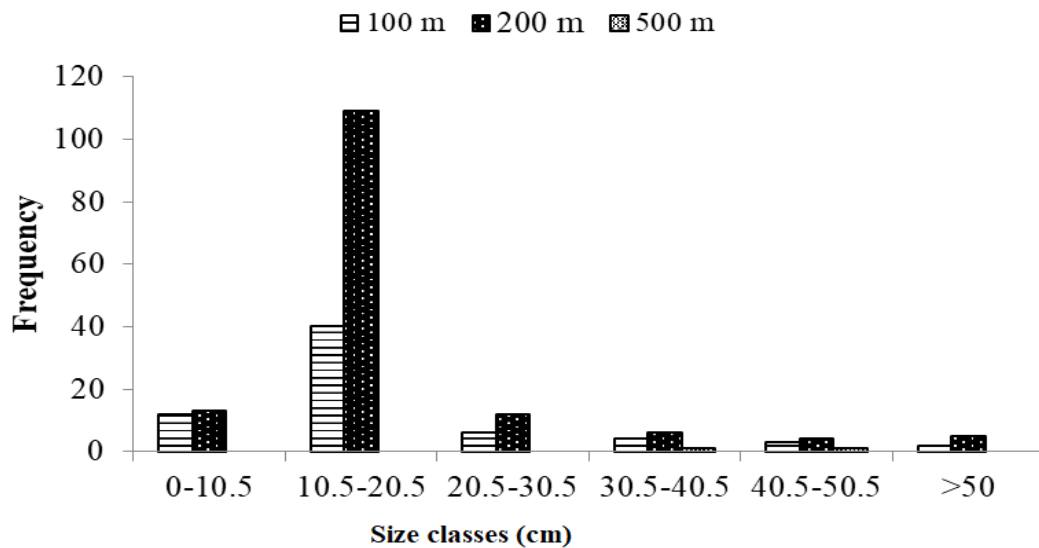


Figure 14: Length-frequency distributions of Nile perch in the experimental gillnet catches set at 100 m, 200 m and 500 m from shoreline in Lake Victoria, Kenya

The frequency distribution of the Nile perch juveniles caught in experimental gillnets set parallel and perpendicular to the shoreline in Lake Victoria , Kenyan waters is shown in Fig. 15 the results from this experiments showed that sizes 0-20.5 cm TL as the most abundant were caught at the top parallel and middle perpendicular net settings which caught highest numbers of fish. The highest frequency was realized in size class 10.5 - 20.5 in top parallel and middle perpendicular regions of the net setting.

Results of different moon phases are shown (Fig. 16) that is full moon and last quarter phases with results of highest catches from sizes class of 10.5 - 20.5 cm TL came from the new moon phase which was followed by last quarter for size classes 20.5 - 30.5 cm TL category were caught during full moon phase only.

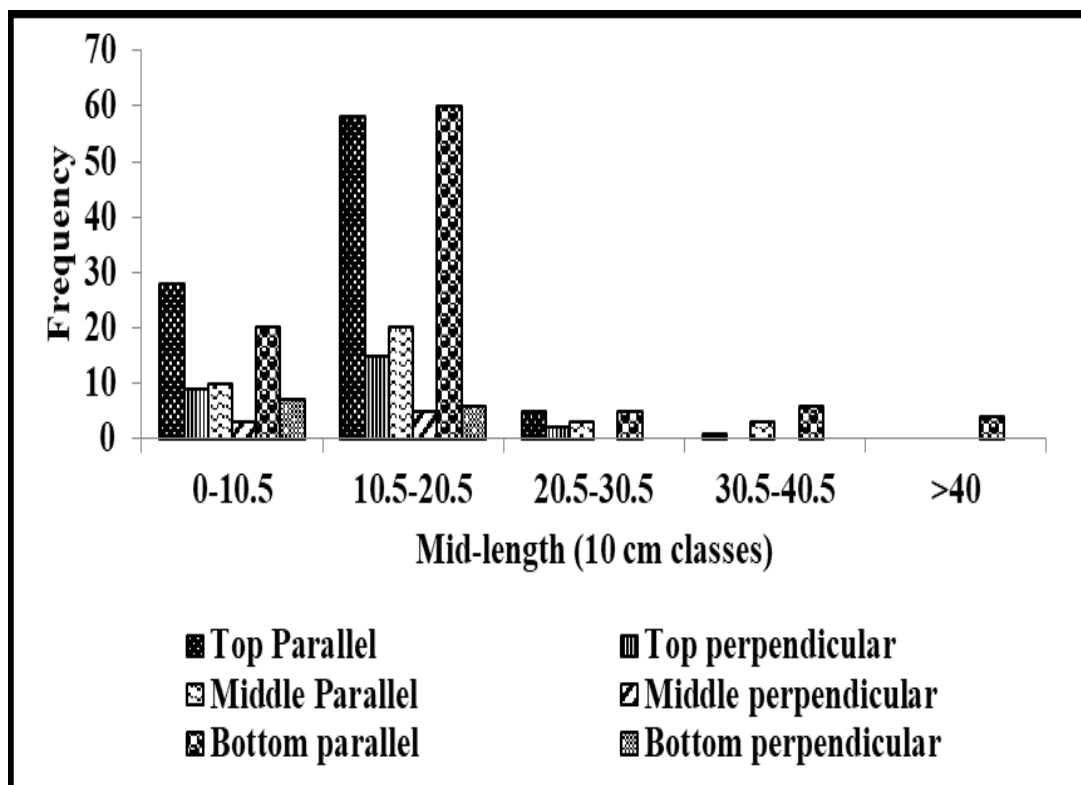


Figure 15 : Frequency distribution of Nile perch juveniles caught in gillnets set parallel and perpendicular to the shoreline in Lake Victoria, Kenya

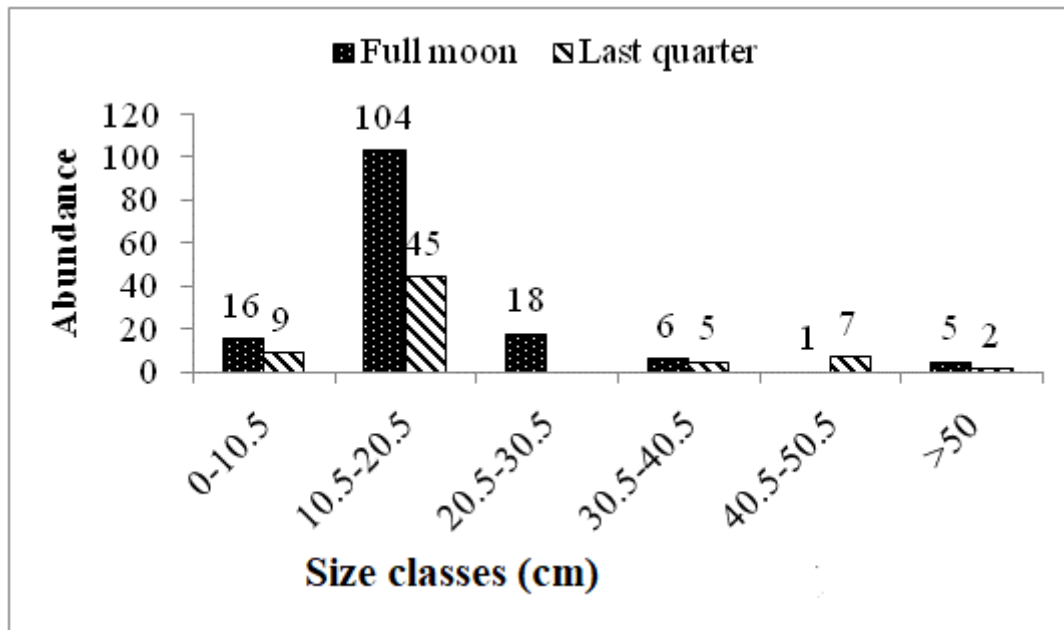


Figure 16 : Abundance of Nile perch during full and last quarter lunar phases in Lake Victoria, Kenya

Objective 3: The spatial / bathymetric distribution, abundance and population characteristics of *L. niloticus* juveniles and adults stages and their prey the Zooplankton in Lake Victoria, Kenya

4.5 Spatio-temporal distribution of zooplankton

Zooplankton is the main food for Nile Perch larvae in Lake Victoria. The highest and lowest number (density) of zooplankton recorded was 250 and 13 individuals L^{-1} at Kisumu pier and Remba Island, respectively (Fig. 17). Zooplankton abundance was generally higher in the gulf than in the open waters. It was also noted that all the peak abundances in the lake were at river mouths and sheltered bays.

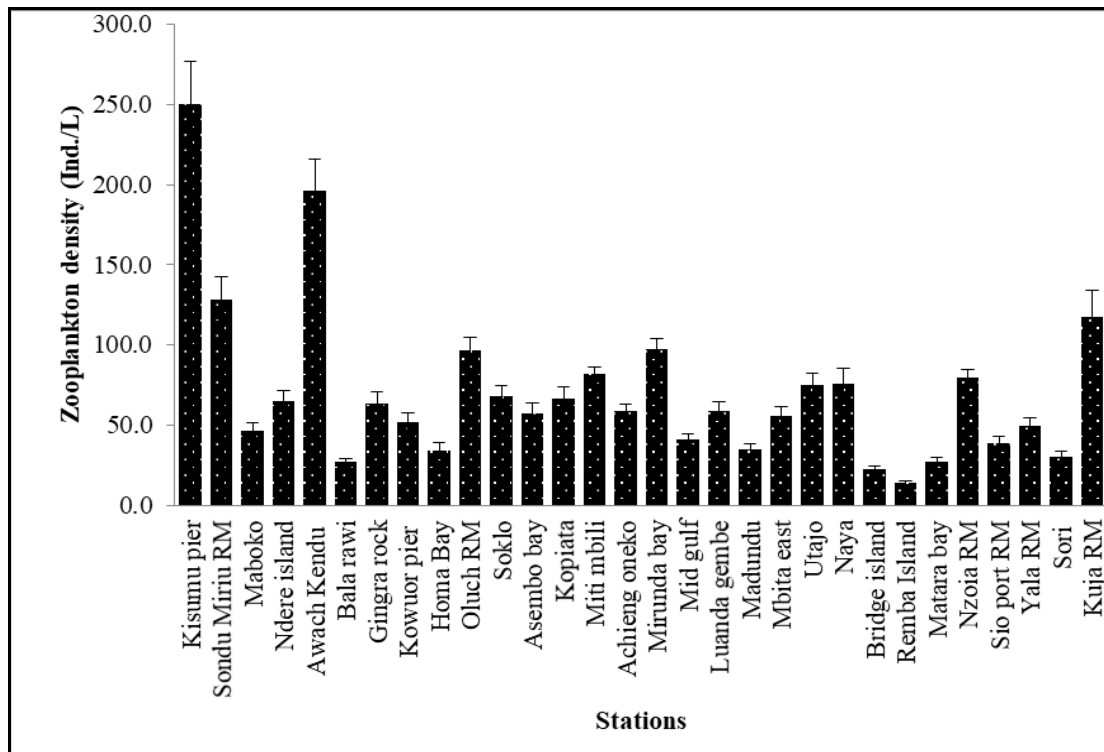


Figure 17 : Zooplankton densities in different sampling stations in Kenyan waters

Canonical correlations of zooplankton with water quality parameters are presented in Table 7. Turbidity in the column samaunyi had the highest value of 192 NTU. This was significantly different from the other stations $p < 0.05$. In Homa Bay turbidity of 164 NTU was recorded (Appendices I, II, III). At Kowuor station turbidity of 150 NTU was recorded while the rest of the stations turbidity levels below 100 NTU were observed. Depth observed ranged from 2 m in Samunyi to 34 in Mbita West Sechi depth was from 0-2 m while surface water temperature ranged from 26-29. D.O observed was 6-8, p.H was 7-8. Most of the columns were not significantly different from each other.

Table 7: Canonical Correlations of zooplankton species with the water quality parameters

	<i>Max depth</i>	<i>Secchi</i>	<i>Temperature</i>	<i>D.O</i>	<i>pH</i>	<i>Conductivity</i>	<i>Turbidity</i>	<i>TN</i>	<i>TP</i>	<i>Silicates</i>	<i>TDS</i>	<i>TOTAL</i>
Homa Bay	4	0	26	6	7	174	164	1261	122	9	104	1877
Oluch R.M.	5	0	26	7	7	168	95	1201	118	12	64	1703
Kowuor	7	0	26	7	7	166	150	1142	132	11	76	1724
Samunyi	2	0	29	6	8	177	192	1482	163	7	92	2158
Mirunda Bay	6	0	26	7	7	155	36	1197	96	7	68	1605
Lwanda Gembe	7	1	26	7	8	156	34	857	89	7	188	1380
Mbita East 1	30	1	26	6	8	148	16	1070	41	5	48	1399
Mbita East 2	8	1	26	7	8	140	11	1039	92	4	92	1428
Mbita East 3	12	1	26	7	7	145	10	1293	36	7	132	1676
Mbita West 1	34	2	26	6	8	128	2	959	29	0	72	1266
Mbita West 2	18	2	26	6	8	129	14	2257	51	1	132	2644
Mbita West 3	3	1	27	8	8	135	8	1202	79	0	96	1567
Naya	7	1	27	9	7	153	12	1315	59	7	92	1689
Mid Gulf	14	1	26	7	8	164	35	1315	82	13	120	1785
Asembo Bay	5	0	26	7	8	186	43	953	113	15	152	1508
Maboko Island	7	0	26	7	7	196	60	1106	168	11	176	1764
TOTAL	169	11	421	110	121	2520	882	19649	1470	116	1704	27173

4.6 Spatial Distribution of Larvae

The presence of larvae in an area likely indicated a nursery ground for this species. Samples obtained indicated two cohorts of fish in the distribution (Fig. 18). The < 5cm TL group (small) was distributed with an outward trend from the shore, whereas the inner gulf stations had the highest abundance of larvae, with a decline offshore. The stations in the southern part of the lake also showed elevated abundance of this size group. The slight catch variation observed in the large size range (< 10 cm TL) implied that the very young of Nile perch were more concentrated inshore and probably move out to the offshore areas as they grow in size. The youngest fish < 3 cm TL were absent from the sites outside the Gulf and in sites to the north but were prominent (including the < 1 cm TL size class near Sori- Karungu and Muhuru bays. The above statement on the apparent spatial size distribution on inshore-offshore juxtaposition can be supported by the observed size ranges in Figure 18. There was a general grow out from the inshore sites into the offshore sites suggesting that Nile perch breeds inshore and the larvae disperse outwards to the open lake.

The spatial distribution of NP larvae densities and abundance from surface tows are presented in the krigged GIS map (Fig. 19). The trend is more or less similar showing areas closely associated with rivers and sheltered bay with high densities than the open lake. Both sheltered bays and river mouths had relatively high proportions of juveniles indicating that they are nursery grounds. Based on the findings fish breeding nursery ground were mapped as shown in Figure 20.

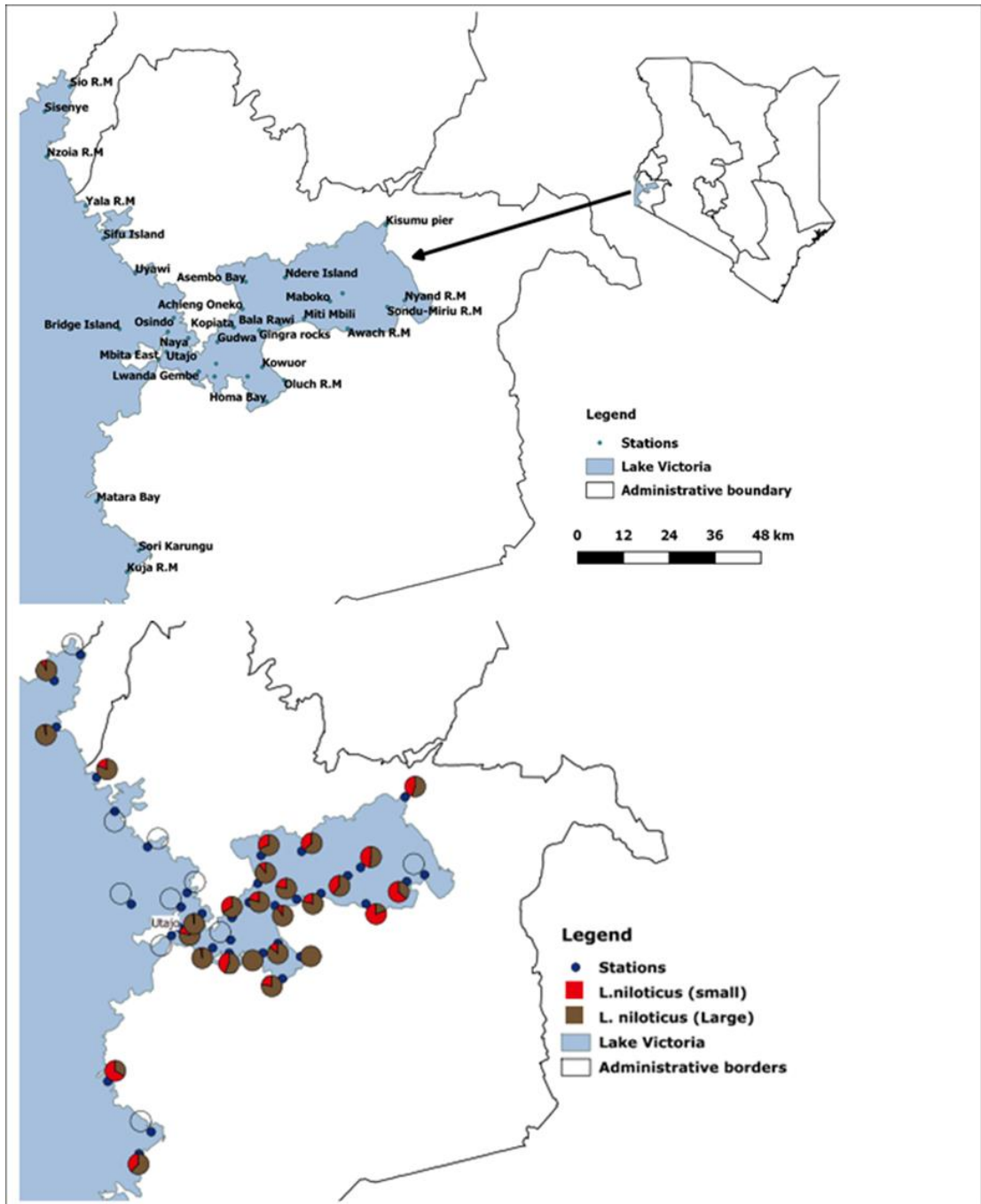


Figure 18 : Spatial distribution of Nile perch post larvae abundance by sizes of 0-5 cm and 5-10 cm in Lake Victoria, Kenya

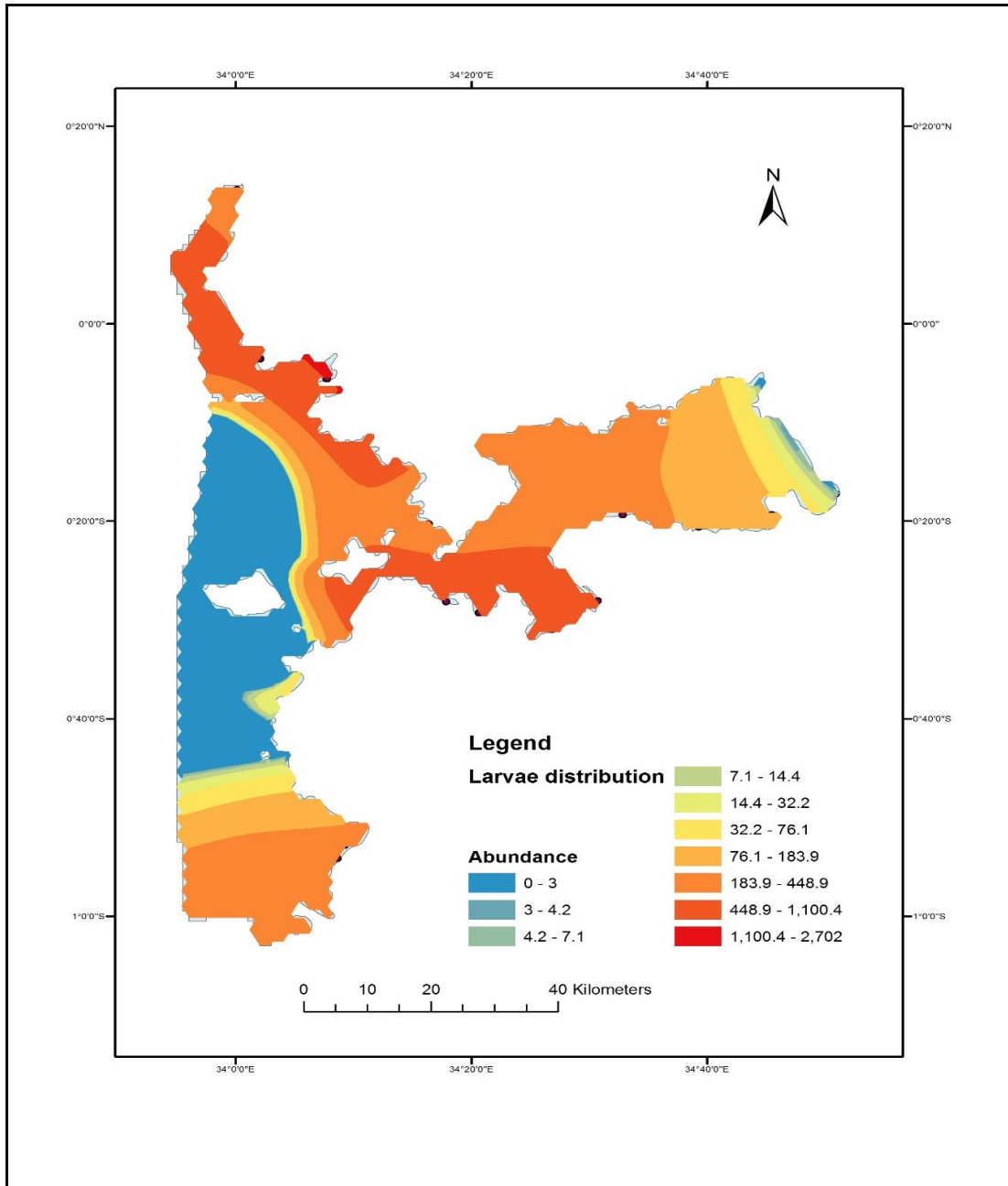


Figure 19: Spatial densities of Nile perch larvae densities and abundance from Surface tows in Lake Victoria, Kenya (Source: Author, 2014)

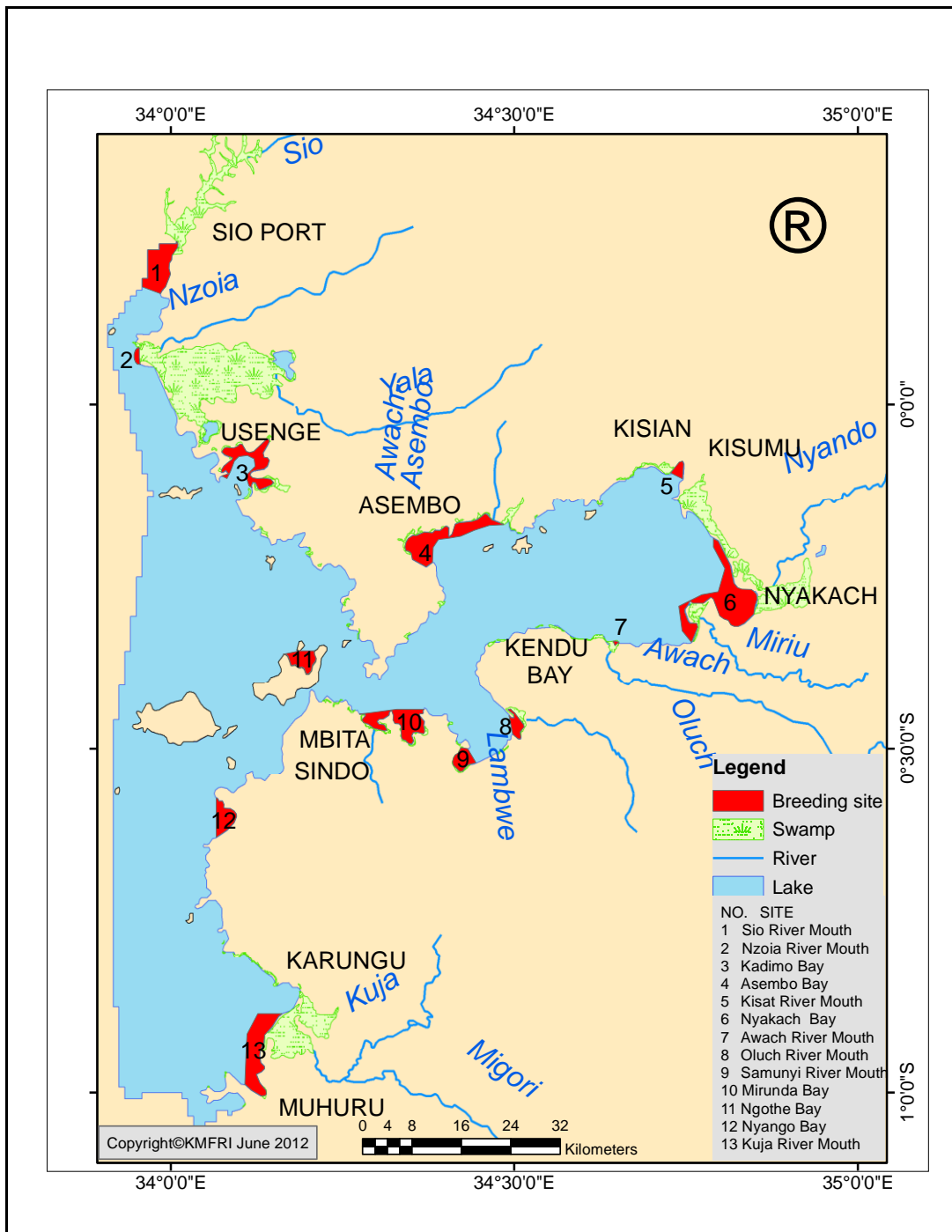


Figure 20: Identified and demarcated *Lates niloticus* fish breeding and nursery grounds in Lake Victoria, Kenya (Details in figure 21 above) Source: Author, 2014

4.7 Population Growth Characteristics

4.7.1 Growth parameters

The samples for each month from 2014 to 2015, were combined to form a composite sample for this study and, are presented in Appendix IX. The K-scan routine indicated an asymptotic length (L_{∞}) of 169 cm TL and a growth curvature (K) value of 0.22 year⁻¹. These results gave a growth performance index (ϕ) of 3.53 for *L. niloticus* in Lake Victoria. The Von Bertalanffy growth curve resulting from a combination of 169 cm TL asymptotic length and growth curvature of 0.22 year⁻¹ are shown in Figure 21.

4.7.2 Mortality estimates and probability of capture

The total mortality coefficient (Z) of *L. niloticus* from length-converted catch curve indicates an annual estimate of 0.96 year⁻¹ with a confidence interval from 0.89 to 1.03 year⁻¹. Natural mortality (M), fishing mortality (F) and exploitation rate (E) were found to be 0.42 yr, 0.54 year⁻¹ and 0.57, respectively (Fig. 22). The probability of capture showed that at least 25 % of fish of 44.01 cm TL, 50 % of the fish of 46.09 cm TL and 75 % of all fish of 47.29 cm TL are retained on encounter with the gear (Fig. 22). All fish above 50 cm TL were retained with the gear.

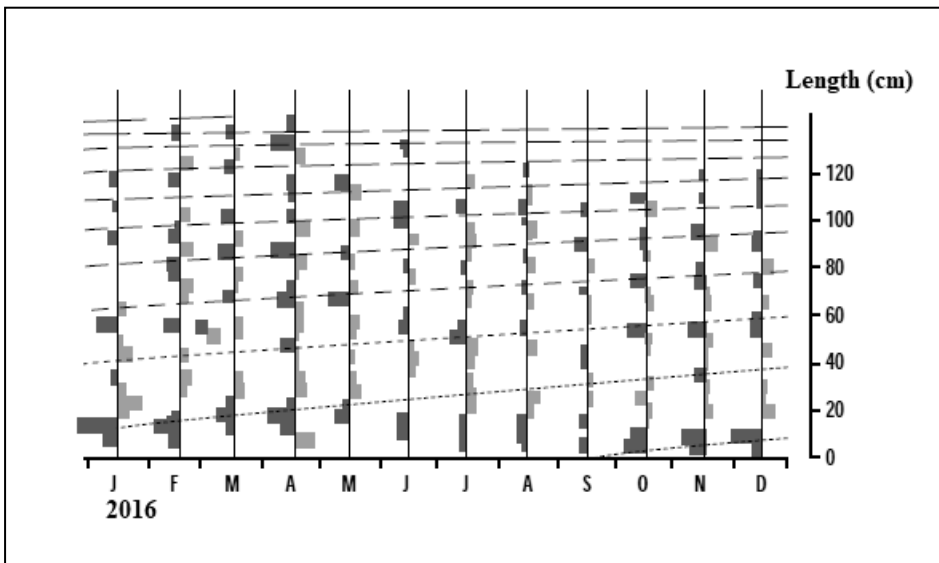


Figure 21 : The growth curves (continous lines) of cohorts of *Lates niloticus*, in Lake Victoria, Kenya superimposed over restructured length frequency data. Peaks (black) are positive points and troughs (grey) are negative points. $R_n = 0.34$, $L_\infty = 169$ cm

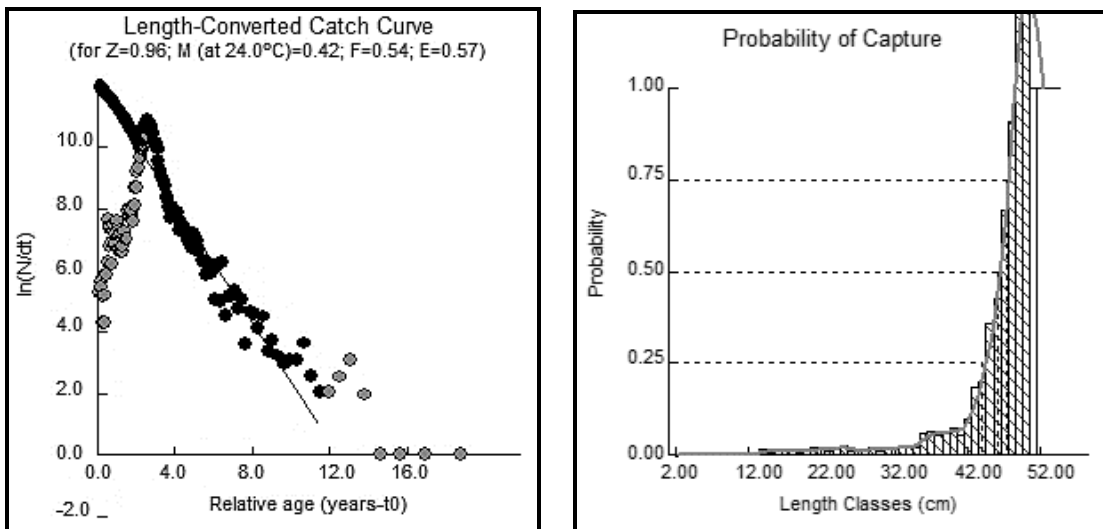


Figure 22 : Left: Values of total mortality (Z), natural mortality (M), fishing Mortality (F) coefficients and exploitation rates (E) from length-converted catch curve. Right: Logistic curve showing 25 %, 50 % and 75 % capture length (cm TL) of *L. nilotic*

4.7.3 Recruitment pattern and Relative Yield Per Recruit/Biomass Per Recruit

Recruitment pattern showed that there were two peak recruitment periods, a minor one in March, accounting for 12.04 %, and a major peak in July, accounting for 22.04 % of the total annual recruitment (Fig. 23). The Beverton and Holt relative yield per recruit model (Fig. 24) showed that the indices for sustainable yields are 0.32 for optimum sustainable yield ($E_{0.5}$), 0.60 for the maximum sustainable yield (E_{max}) and 0.51 for economic yield ($E_{0.1}$).

The comparison in growth and population parameters of *L. niloticus* in Lake Victoria between 1991 and 2015 are presented in Table 8. Overall L_{∞} cm TL has been declining over the years, while K (yr^{-1}) has been increasing. The other parameters (Z [yr^{-1}], F [yr^{-1}] and E [F/Z]) do not show a clear trend (Table 8).

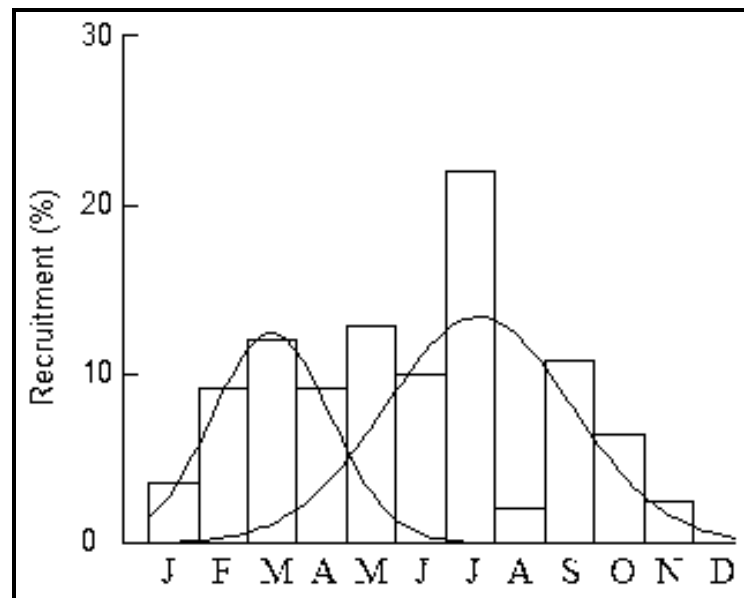


Figure 23 : Annual percentage recruitment

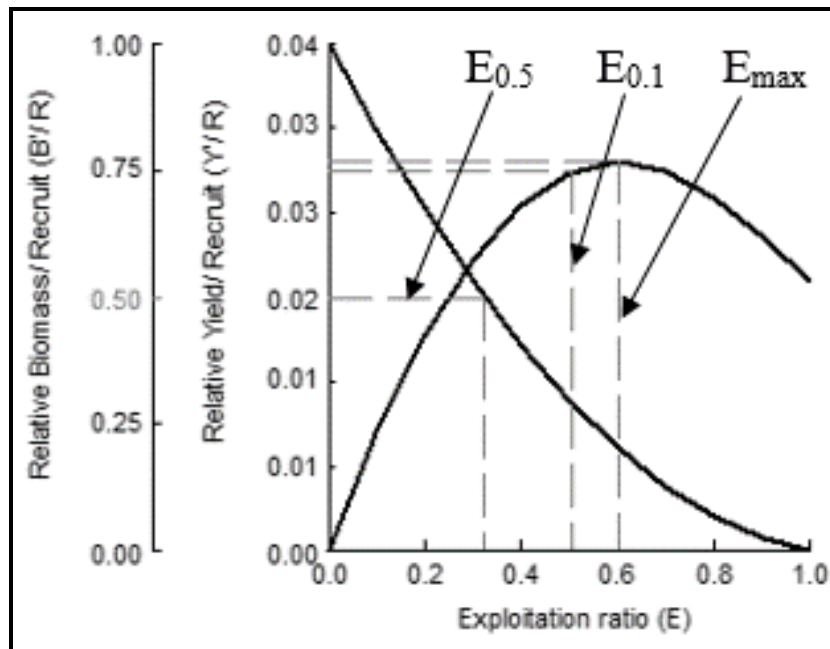


Figure 24 : Beverton & Holt's relative yield-per-recruit and average biomass per Recruit models, showing levels of yield indices: E_{0.5} – optimum sustainable yield, E_{0.1} - maximum economic yield & E_{max} – maximum sustainable yield.

Table 8: Changes in growth and population parameters of *L. niloticus* in Lake Victoria, 1991-2015

Lake & period	L_{∞} cm TL)	K (yr ⁻¹)	Z (yr ⁻¹)	F (yr ⁻¹)	E (F/Z)	L_{m50}		Source
						Male	Female	
Victoria (Kenya)-1988	205	0.19	1.60	1.26	0.78	74	102	Njiru <i>et al.</i> 2008
Victoria (Tanzania)-1990	185	0.17				60	110	Njiru <i>et al.</i> 2008
Nyanza Gulf (Kenya)-1991	169	0.18	0.72	0.35				Rabuor <i>et al.</i> 2003
Victoria (Uganda)-2002	256	0.29	1.91	1.44	0.75	64	73	Njiru <i>et al.</i> 2008
Victoria (Tanzania)-2002	216	0.19	1.93	1.64	0.85	54	77	Njiru <i>et al.</i> 2008
Victoria (Kenya)-2002	204	0.21	1.78	1.42	0.80	55	78	Njiru <i>et al.</i> 2008
Victoria (Uganda)-2003	221	0.17	2.18	1.88	0.86	57	76	Njiru <i>et al.</i> 2008
Victoria (Tanzania)-2006	178	0.20	2.17	1.81	0.83	60	85	Njiru <i>et al.</i> 2008
Victoria (Uganda)-2006	153	0.24	2.12	1.88	0.89	58	70	Njiru <i>et al.</i> 2008
Victoria (Kenya)-2006	145	0.24	1.91	1.71	0.89	55	62	Njiru <i>et al.</i> 2008
Victoria (Kenya)-2015	169	0.22	0.96	0.54	0.57			This study

Objective 4: Food composition of *L. niloticus* larvae, juveniles and sub- adults in Lake Victoria, Kenya

4.8 Food and Feeding Habits

A total of 1382 (68 %) out of the 2020 juvenile/adult fish analysed during 2012/16 had stomachs with food items while 638 (32 %) were empty. The diet of Nile perch consisted primarily of *Caridina nilotica*, haplochromines, *Rastrineobola argentea*, unidentified fish and other prey items in varied proportions. *C. nilotica* was the most preferred food item (59 %) and *R. argentea* was the least (5 %) (Fig. 25 a). By comparing with results of 2014/15, *C. nilotica* (44 %) and tilapia (8 %) contributed the highest and lowest proportions, respectively (Fig. 25 b).

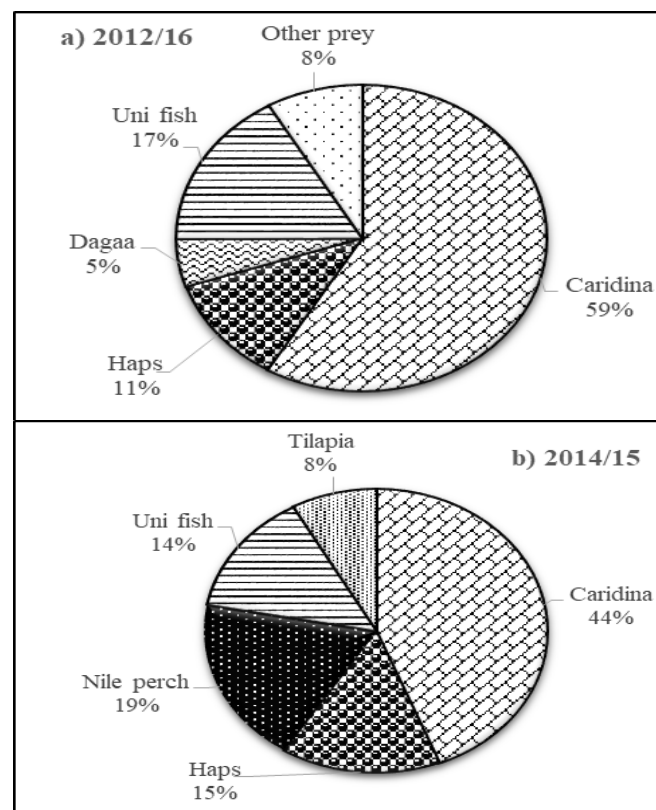


Figure 25 : Percent contribution by weight of major food item in overall diet of *Lates niloticus* in 2012 -2016 from Lake Victoria. Source: this study (2012/16), 2014/2015 (Outa et al., 2017) Note: (Haps = haplochromines, Uni fish = unidentified fish).

4.8.1 Diel feeding

The 24-hr feeding intensity of larval *L. niloticus* shows stomach content fullness increasing from 1 am to 4 pm (Fig. 26). Kruskal-Wallis one-way analysis of variance by ranks showed significant differences in stomach fullness. The calculated H value and the table value were: calculated H = 28.57 and tabled H = 23.21 (.01 confidence level).

Inspection of larval guts showed diet composition was dominated by cladocerans (63 %) while copepods comprised 36 %, and calanoids 1 % (Figure 27). On average, larvae had the three prey items in their guts, with a maximum of 3 and a minimum of 1.

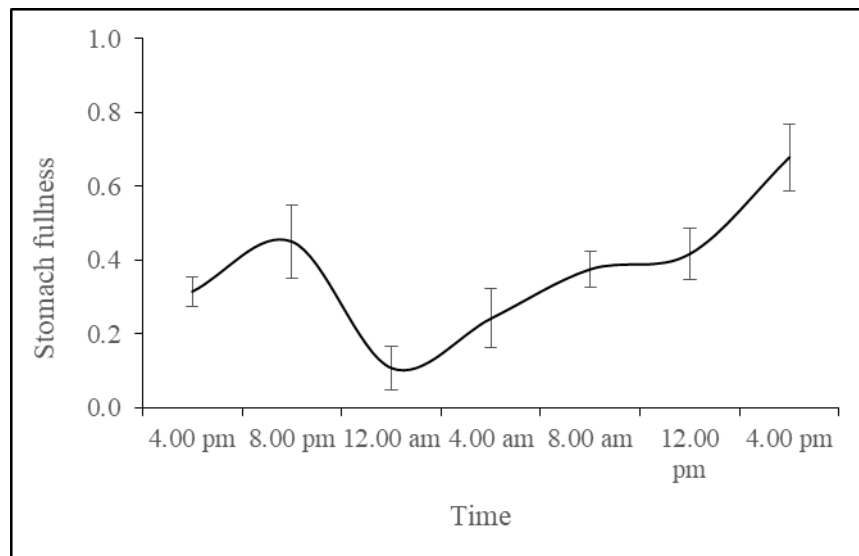


Figure 26 : Diurnal feeding regime of *L. niloticus* larvae from Lake Victoria, Kenya. Vertical lines indicate the mean \pm SD.

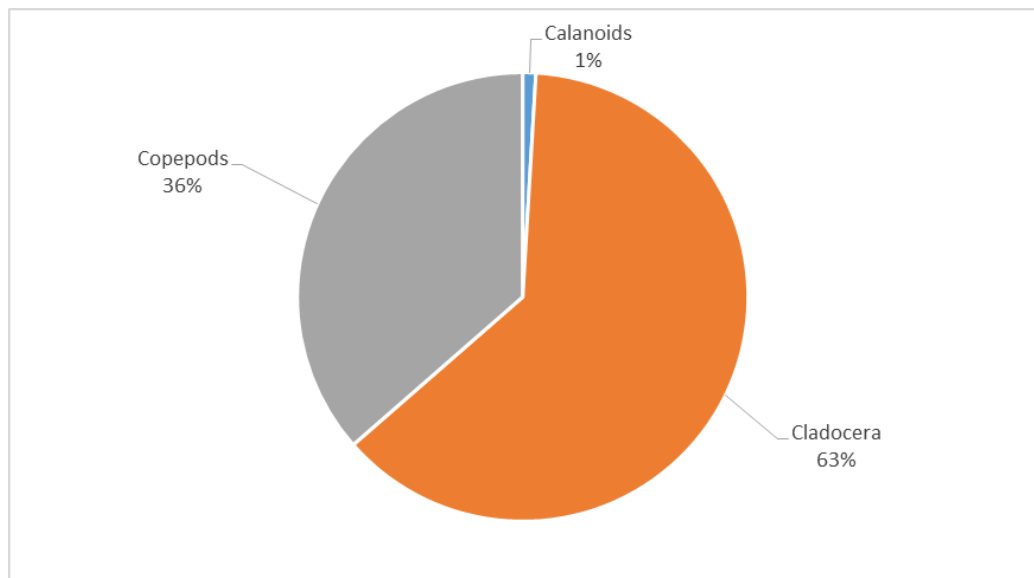


Figure 27 : Food composition in guts of larvae collected during diel sampling.

Objective 5: Ontogenetic shifts in structural development and food composition of *L. niloticus* in Lake Victoria, Kenya

4.8.2 Ontogenetic shifts in diet/ food composition

Ontogenetic shifts in diet/ food composition is presented in Figure 28. Zooplankton was only observed in the diet of fish in the length class 1 - 5 cm TL (20 %), while *C. nilotica* was the dominant food item in the diets of almost all size classes, but decreased as fish sizes increased. Fish prey was important food item as Nile perch increased in size and cannibalism was only evidenced from size classes above 35 cm TL. In the stomachs of *L. niloticus*, *C. nilotica* was most frequent in all sizes as importance decreased with increase in size. *C. nilotica* changed roles with fish remains as the sizes of fish increase in Nile perch. Insects seemed to decrease in importance with increase in size compared to molluscs which increased in frequency as the fish size increased (Fig. 28). On average $21.2 \pm 5.6\%$ of all studied stomachs were empty. The average percentage of empty stomachs per cm class was positively correlated with fish length (Pearson correlation coefficient: $r = 0.459$, $p = 0.011$, $n = 30$) and ranged from 8.5 % in the 3 cm class to 32.4 % in the 23 cm class. Zooplanktivorous Nile perch (< 5 cm TL) collected in 2012/16 consumed copepods, cladocerans and rotifers while in 1988 they fed on calanoids and cyclopoids only (Table 9). In the study of 2012/16, the diets of fishes of 1 cm consisted of copepods, cladocerans and rotifers. At 2 cm the diet changed to copepods and cladocerans only (Fig. 29). In 1988/89 proportion of the relatively large calanoids increased with Nile perch size, and made up between 35 and 80% of the diet in fishes of 3 – 4 cm (Fig. 29).

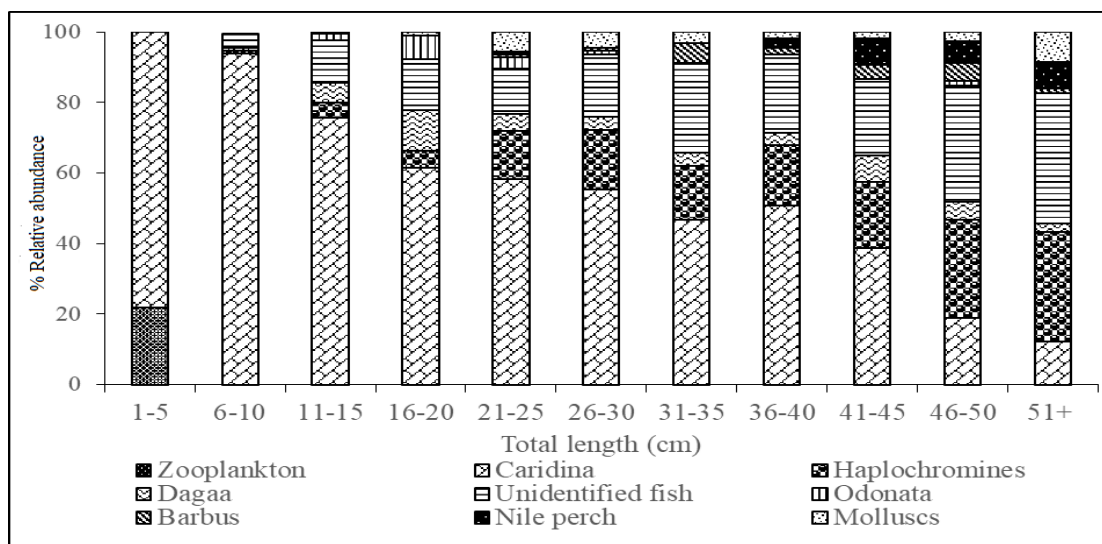


Figure 28 : Food of *Lates niloticus* of different lengths from Lake Victoria, Kenya 2012/16

Table 9: Percentage composition of zooplankton in the diet of small Nile perch in 2012/16 and 1988/89

Prey items	Copepods	Cladocerans	Rotifers	Calanoids	Cyclopoids
Nile perch (1 cm)	33.9	58.9 (0)	7.4	0(8.1)	0(91.9)
Nile perch (2 cm)	43.8	56.2(0)	0	0(8.1)	0(91.8)
Nile perch (3 cm)	0	0(0)	0	0(35.9)	0(64.0)
Nile perch (4 cm)	0	0(0)	0	0(80.2)	0(19.8)

Values in brackets are derived from Katunzi *et al.* (2006).

Comparisons of frequency of occurrence of prey items in Nile perch diet for the data collected during 1988/1989, 2006/2008 and 2012-2016 are presented in Figure 29. In this study (2012/16), Nile perch of 6 to 25 cm TL fed more frequently on *C. nilotica* compared to 1988/1989 and 2006/08 (Fig. 29). The occurrence of *C. nilotica* in the diet of Nile perch during 2006/08 declined as the fish increased in size unlike the other periods. In 2006/08 haplochromines were fed on more than in 2012/16 by Nile perch of 6 cm to 30 cm TL as size increased (Fig. 29). The frequencies of occurrence

of dagaa in Nile perch stomach were highest in 1988/89 and lowest in 2006/08 for size of upto 30 cm TL (Fig. 29). Moreover, for Nile perch ranging from 6 to 30 cm TL, in 1988/89 the frequency of occurrence of dagaa increased with Nile perch size, but this was not the case in 2006/08 and 2012/16. The proportion of Odonata in the diet of Nile perch of size class 16-20 cm TL and 21-30cm TL were highest in 2012/16 and 1988/89, respectively (Fig. 29).

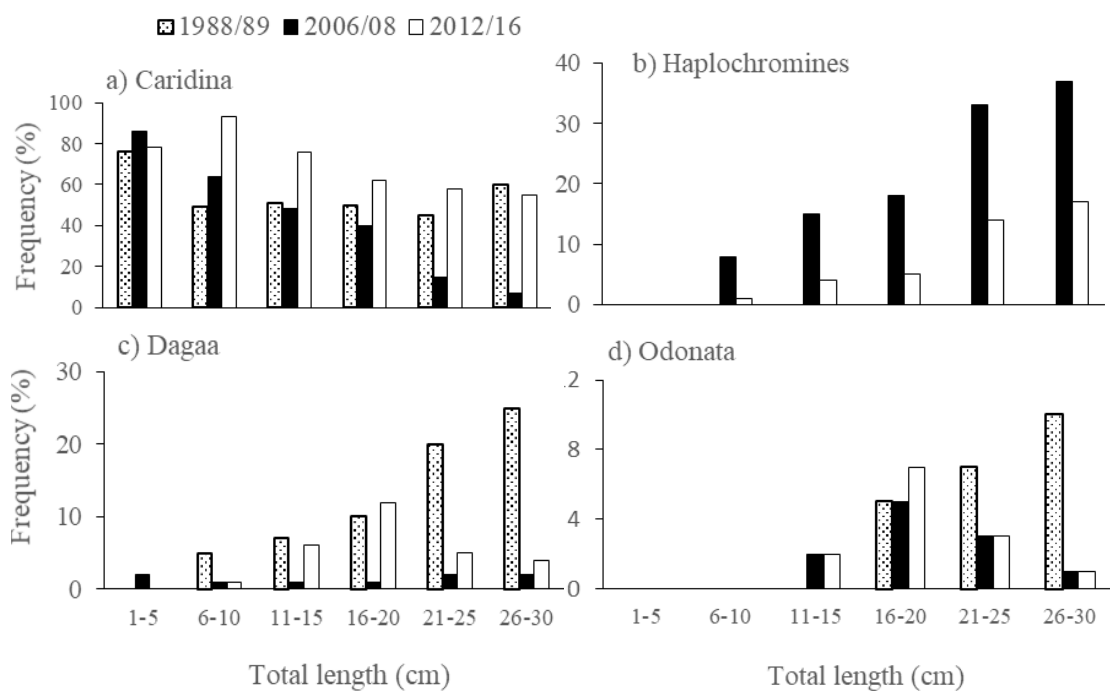


Figure 29 : Frequency of occurrence of the main prey types of Nile perch up to 30 cm TL in 1988/89 (Katunzi et al., 2006), 2006/08 (Kishe-Machumu et al., 2012) and 2012/16 (this study).

4.9 Ontogenetic Changes in food items in adult Nile Perch

There were clear differences in the frequency of occurrence of the prey types in the Nile perch stomachs in relation to predator size (Fig. 30). Over the whole study area, zooplankton formed an important food source for Nile perch larvae of up to 17 mm.

Fishes of 50 mm to 8.6 mm switched to *Caridina* as the dominant food item and small fishes (including *R. argentea*) in small quantities. At 130 mm fishes switched to feeding and selecting on haplochromis predominantly.

4.9.1 Ontogenetic changes in morphological features

The Larval development in *L. niloticus* showing the approximate length (TL mm) at which the principal morphological features first appeared in Lake Victoria, Kenya (Table 10). The developmental sequence in which the various structural features are formed is presented (Table 10). In general the ontogeny of *L. niloticus* particularly the sequence of structural, morphological differentiation and development; at 2.8 - 3.0 mm TL four developments occurred which included eye pigment, distal expansion of pectoral fins, functional mouth and gills. At 4.5 – 4.6 mm TL swim bladder and the hypural primordia was observed. At the length of 5.4 - 5.6 the interneurals of branched dorsal and anal fins , preopercular spines , teeth and the heterocercal tail developed. While at 6.2 - 6.4 mm TL caudal, branched dorsal and anal fin rays and pelvic fin buds were clearly visible. At the length of 7.2 - 7.5 mm TL pelvic fin buds and homocercal tail, interneural of spinous dorsal fin rays were visible on the young *L. niloticus* larvae. At lengths of 8.8 - 9.1 mm TL rays of pelvic and spinous dorsal fins were present and finally at 15.5 - 17.0 mm TL scales were developed on the fish larvae and the larvae at this point resembles the adults although mottled in colour.

Table 10 : Larval development in *Lates niloticus* showing the approximate length (TL mm) at which the principal morphological features first appear on the fish.

Structural feature	Length (mm)
Pectoral fin buds	2.8-3.0
Eye pigment	3.0-3.3
Distal expansion of pectoral fins	3.0-3.3
Functional mouth and gills	3.0-3-3
Feeding activity	3.0-3-3
Swim bladder	4-5-4.8
Hypural primordia	4-5-4.8
Interneurons of branched dorsal and anal fin rays	5-4-5.6
Preopercular spines	5.4-5.6
Teeth	5.4-5.6
Heterocercal tail	5-4-5-6
Caudal, branched dorsal and anal fin rays	6.2-6.4
Pelvic fin buds	6.2-6-4
Homocercal tail	7.2-7.5
Interneurons of spinous dorsal fin rays	7.2-7.5
Rays of pelvic and spinous dorsal fins	8.8-9.1
Scales	15.5-17.0

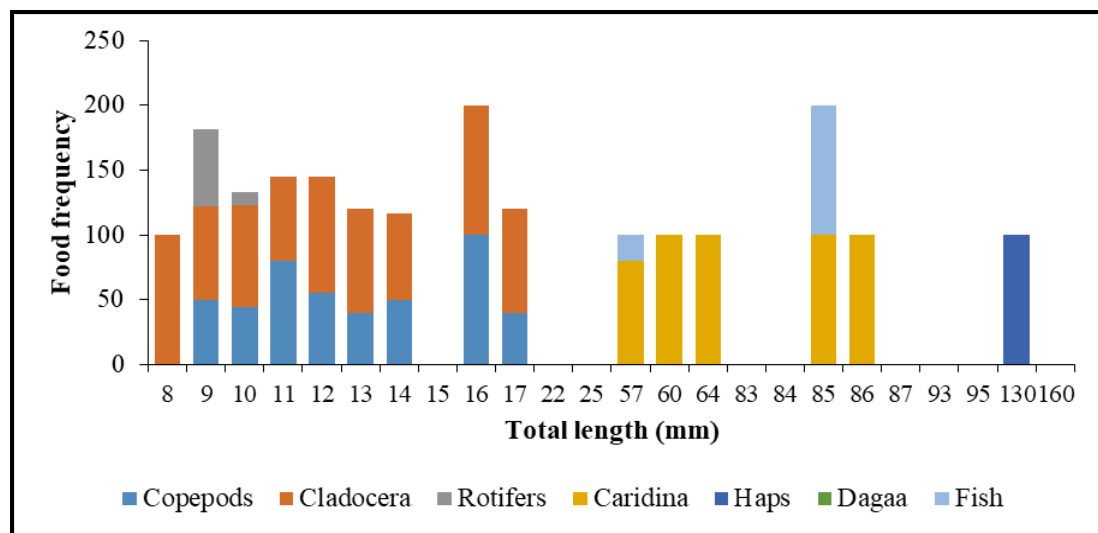


Figure 30: Ontogenetic shift in prey items observed in the stomach of wide length range of Nile perch larvae caught in the Kenyan waters (n = 2316). (Haps = Haplochromine, Dagaa = *R. argentea* and fish = unidentified fish)

CHAPTER FIVE

DISCUSSION

5.1 Physico-chemical Water Quality Parameters

As indicated by the data, the pattern of change in Lake Victoria's physical and chemical parameters is extremely variable and unpredictable across sampling sites. This may be attributable to the shallow mean depth and landscape context of the Kenyan part of the lake, which is strongly influenced by variability in seasonal/diurnal wind patterns (Okely *et al.*, 2010). Run-off from agricultural land, inputs of industrial effluent, the relatively urban setting, and the nature of its inflows also combine with natural processes to generate these patterns. Bottom sediments are frequently resuspended by the winds, with nutrients associated with these particles being remineralized during this process, thereby comprising the majority of the significantly correlated variables. Inputs from soils and sediments, mainly from catchment run-off, as well as shoreline erosion, resuspension of bottom sediments by waves and currents, and a range of human activities (Mwamburi 2016) may have resulted in the high turbidity, low transparency and excessive concentrations of TN and TP in the open lake. This pattern is also exhibited by the high chlorophyll-a concentrations at sites in C1 and C2, compared to C3. The dissolved oxygen (DO) concentrations were relatively high, which can be explained by the high primary productivity resulting from eutrophication and vigorous local mixing of the water body, mainly in the Winam Gulf. The average DO values observed in the present study ranged from 5.1 to 7.6 mg L⁻¹ in C3, with a maximum of 11.2 mg L⁻¹, being similar to previously recorded measurements in the same areas, which ranged from 6 to 11 mg L⁻¹ (Lung'ayia *et al.*, 2001). Slightly lower DO levels (3 mg L⁻¹) were observed in the

bottom waters at some localities within C1 and C2, probably attributable to microbial decomposition of dead organic matter derived from plankton and macrophytes. The DO levels were generally within the permissible WHO levels ($\geq 2.0 \text{ mg L}^{-1}$) for fisheries (Table 4). Electrical conductivity, TN and TP levels were higher in the shallow waters and moderate in the mid-gulf, possibly attributable to inputs of minerals resulting from weathering processes, erosion from increasingly cultivated land, remineralization from resuspended bottom sediments and anthropogenic activity (Mwamburi, 2016). These factors greatly stimulate phytoplankton productivity, resulting in higher chlorophyll-a levels within the Gulf than in C3 (open lake; Ochumba 1990). The electrical conductivity levels were within the permissible WHO levels for fisheries. Increased turbidity levels and macrophytes in the inland waters of the lake were likely related to the high concentration of parameters like total suspended solids and chlorophyll-a (Lung'ayia *et al.*, 2001). Increased turbidity and algal levels in Winam Gulf validated the declining ecological integrity of the zone, as indicated by its physical–chemical characteristics.

According to the nominal logistic and the GLM- logistic it was inferred that turbidity significantly affected *L. niloticus* abundance. This was confirmed by NMDS results turbidity was clustered with same few stations where the abundances of larvae was low.

5.2 Distribution and Abundance of Larval Fish

From the obtained results fish larvae and juveniles it is clear that most Nile perch breeding areas were associated with the river mouths and shallow sheltered bays. The fact that most of the breeding grounds are within the Winam Gulf demonstrates that it is a very important area for fish recruitment. The river mouths provide travel corridors

for migratory species during rainy season. The breeding of most of the fishes are notable by the relatively high abundance of their juveniles and / or ripe individuals at river mouths and within the rivers.. The findings of this young of the year fish assemblage in river mouths are consistent with earlier observations (Ochumba & Manyala, 1992; Mugo and Tweddle, 1999; Gichuki *et al.*, 2001; Ojuok, 2005; Ojwang, 2006; Ojwang *et al.*, 2007).

The zooplankton of river mouths was predominant food for almost all fish juveniles (Owili & Omondi, 2003). These together with Nile perch (*L. niloticus*), historically a riverine fish species commonly found in the rivers of Lake Victoria, are known to spawn within particular pelagic realms of the lake.

The swampy areas, particularly the remaining wetlands are recognized as refugia to some of the native fish populations, mostly those that are tolerant of extreme environmental conditions (Chapman *et al.*, 1996). The structural complexities of the swampy habitats coupled with periodic low oxygen levels protect a number of fish species from both excessive human exploitation and predation from larger sized Nile perch (Chapman *et al.*, 1996; Schofield & Chapman, 1999; Balirwa, 1998). Wetlands of Lake Victoria, Kenya differ considerably in terms of fish diversity.

The Bays supported breeding of *L. niloticus* because they have sandy, shallow and sheltered substrata with submerged plants like *Potamogeton* and *Ceratophyllum* which acts as good substrates for larval attachment. The knowledge generated from this and indigenous studies supported the mapping of fish breeding grounds and nursery areas, which indicated the need to harmonise both empirical data and these local understanding of fish dynamics by the local population. Use of the indigenous knowledge has pointed out that there are several breeding areas within various

beaches, but given the fact that there is a general decline in the fisheries people often fish in those areas for their livelihoods (Manyala & Bolo, 1998). The communities agree that several species that were not there during the Nile perch boom are currently present in high numbers, particularly in the breeding areas, and now form the part of fish that they harvest.

The fishing areas also double as breeding grounds as witnessed in areas around Kuja river mouth, Nzoia and Yala river mouths among others. This poses a big challenge on how the areas can be conserved without creating conflicts between the fishers and the managers.

The present study provides first-hand information that will be used by both fishing communities and the scientific communities to set both conservation and management matters as a priority area if fishing has to be done sustainably. It is for this reason that GIS maps have been generated in order to complement what we already have in our data bases concerning the exploitation of commercial fishery in Lake Victoria.

5.2.1 Temporal distribution

The total abundance, size composition and densities *L. niloticus* larvae in the Kenyan waters varied throughout the course of the year. The spawning activity of local adult populations is probably the major determinant of this broad-scale temporal variation in abundance. The timing of spawning activity appeared to be related to zooplankton production cycles, as it has been in many other studies (Townsend, 1984; Jenkins, 1986; Haldorson *et al.*, 1993; Horstman & Fives, 1994). The reproductive strategy of *L. niloticus* appeared to involve synchronizing peaks in larval abundance with peaks in prey abundance (Cushing, 1975). This is likely to improve the survival rates of larval fish by maximizing food availability. However, the larval stages were pre-

emptive or ubiquitous, with larvae occurring prior to peaks in zooplankton production or during periods of low prey abundance.

If this annual variability in peak abundance is indicative of fluctuations in year-class strength then the resulting recruitment variability will impact on the structure of adult populations (Sale *et al.*, 1985; Doherty & Williams 1988; Doherty, 1991; Sale 1991). Any annual variability in larval supply is likely to have long-lasting effects on the dynamics of local adult populations (Underwood & Denley, 1984). Despite many fine-scale differences in occurrence and peaks of abundance, there were close similarities between the inshore and the offshore stations in the temporal distribution of the larval stages. The geographic separation and very different current and exposure regimes of the two locations did not result in marked differences in temporal distribution, with most having a broad overlap in temporal distribution between Gulf and open water stations. Although high mortality rates could explain decreases in abundance at a station, horizontal movement is most likely responsible for this temporal variation because abrupt increases also occurred. However, this horizontal movement must occur on a temporal scale finer than the two weeks for intermediate states not to be detected by monthly sampling.

Descriptions of offshore distribution on a finer temporal scale are required to elucidate patterns of horizontal movement. The abundance of larvae in surface waters (i.e., the uppermost 2 m) at inshore sites was relatively consistent between consecutive days. This suggests that the processes producing temporal variation in abundance operate on a broader time scale. However, at inshore sites there were large variations in the abundance of larval fish in surface waters within a 24 hr period, probably because of diel vertical migration. The extent and nature of diel vertical

migration require further investigation on a broader spatial scale, but also on a finer temporal scale, so that more precise patterns of nocturnal movement of larval fish, their prey and predators can be detected.

5.3 Spatial distribution of Larval fish

The abundance of the larval stages was not uniform over the narrow distance from the river mouth. The larger larval sizes were consistently more abundant further from shore. The smaller larval sizes were always found in highest abundance attached to submerged macrophytes few metres from land. However, the presence, at up to several kilometres from the shoreline, of larvae of adult fish that spawn in sheltered nearshore suggests a mechanism of offshore transport must exist. A bay recirculation cell (cf. Smith *et al.*, 1999) may be one mechanism of offshore dispersal. This cell could act by transporting larvae in subsurface waters offshore and those in surface waters towards shore.

Although the abundance of larval stages varied with distance from shore, there is little evidence from my study to support the generalisation that larvae that are more abundant nearshore hatch from demersal eggs, whereas those that are more widely distributed are derived from pelagic eggs (Leis & Miller, 1976; Marliave, 1986; Kingsford & Choat, 1989; Suthers & Frank, 1991; Brogan, 1994 a; Gray, 1998) this was considered to be the result of differing dispersal requirements.

However, the larval stages of species that are dispersed offshore and returned to the nearshore environment by advection may utilize alongshore currents to transport them to suitable settlement habitats. Acting within the broader-scale distribution patterns of larval fish were fine-scale processes. These processes are usually undetected by broad scale surveys, but may contribute to the often considerable variation observed in large

scale studies (Fasham 1978, Haury *et al.*, 1978; Fortier & Leggett, 1984; Williams & English, 1992; Lennert-Cody & Franks, 1999). Both the horizontal and vertical distribution of larval fish in this study were likely influenced by processes operating on a fine scale.

This aggregation, together with the shoreward movement of slicks, suggests that they may transport larval fish towards the shore. The decreased abundance of larval fish in an area after the passage of a surface slicks shows they are capable of modifying broad-scale distribution patterns. Although the aggregation and movement of internal waves may influence spatial variability on a much broader scale. The results obtained using different sampling methods indicate that, clearly there is no single method is appropriate for all ichthyoplankton sampling. This study relied predominately on horizontal plankton tows at the surface, seining at fixed depths and trawling with a codend cover for sampling the larval stages of fish.

5.4 Population Characteristics

It is evident from the findings of the present study that the asymptotic length (L_{∞}) of 124 cm TL of *L. niloticus* caught from Lake Victoria has been greatly reduced over the past years. Similarly, there was a sharp decrease in the numbers of fish above the slot size of 50–85 cm TL, based on the length frequency distribution. Njiru *et al.*, (2009) reported that fish below and above the slot size has continued being caught and processed, thereby confirming the slot size is hardly adhered to by both the fishers and the processors. Reductions in the sizes of *L. niloticus* are likely attributed to the illegal gears and methods used in the fishery (Yongo *et al.*, 2017).

The natural mortality coefficient (M) of 0.42 reported in the present study is comparable with the value of 0.37 reported by Rabuor *et al.* (2003) in their study on

Nile perch in the Nyanza Gulf of Lake Victoria. Natural fish mortality is attributable to factors not associated with fishing, including predation, competition, cannibalism, diseases, spawning stress, starvation and pollution stress (Yongo & Outa, 2016). The present study reported a 50% probability of capture of the fish of 46.09 cm TL, which is lower than its length at first maturity (L_{m50}) in Lake Victoria (Njiru, Kazungu, Ngugi, Gichuki, & Muhoozi, 2008; Table 11). This implies the fishing gears are catching high proportions of immature fish. The recruitment peaks showed by Nile perch in the months of March and July actually coincide with the rainy seasons along the Lake Victoria basin. Thus, recruitment of Nile perch could be influenced by food availability and favourable environmental conditions. Rabuor *et al.*, (2003) observed the highest peak for recruitment of Nile perch in November, December and January in the Nyanza Gulf of Lake Victoria, with a minor one in June, indicating recruitment of two cohorts per year. According to Kische-Machumu *et al.*. (2012), the apparent preference for haplochromines as prey has considerably reduced the degree of cannibalism, which may have a positive impact on Nile perch recruitment. The impact of population parameters on the biomass and yield is best reflected in the Beverton and Holt's yield-per-recruit model (Beverton & Holt, 1966). At the current mortality rates, the observed exploitation rate (E) of 0.57 is less than optimum sustainable yield ($E_{0.5}$) of 0.32, but not much different from maximum sustainable yield (E_{max}) 0.60 and economic yield ($E_{0.1}$) of 0.51. These results agree with Rabuor *et al.*, (2003), who reported the Nile perch population in the Nyanza Gulf may now be exhibiting some kind of demographic equilibrium. The period of the main recruitment pulse lasts from September to January of the following year. A minor pulse takes place in June. This is supportive of Gee (1964, 1965) who suggested that Nile perch in Lake Victoria probably spawn twice a year. Gee (1964) suggests that the spawning periods

are mainly in the rainy seasons. This is true for the main pulse, which occurs before and during the short rainy season (October to December).

5.5 Food and Feeding Habits

The food of Nile perch collected during 2012/16 was dominated by *C. nilotica* (59 %) with little contributions from haplochromines, *Rastrineobola*, and other fish prey. The results agree with those of Outa *et al.*, (2017) who also reported dominance of *C. nilotica* (44 %) in the diet of Nile perch collected from the Nyanza Gulf of Lake Victoria during 2014/15. These observations suggests that *C. nilotica* is the preferred prey item of Nile perch in the absence of haplochromine cichlids, therefore, the shift from haplochromines to *C. nilotica* as the main prey was due to the decline of the haplochromines. Analysis of stomachs in relation to fish size showed shifts in diet at three levels from zooplankton to *C. nilotica*, then to fish prey including haplochromines, fish prey and juvenile Nile perch as fish size increased. Zooplankton was only present in the stomach of young fish in the length class 1-5 cm TL. Changes in diet requires morphological and physiological features that are not yet well developed in young fish, thus, they can easily digest zooplankton that also satisfy their demand for protein (Yongo *et al.*, 2016). The contribution of *C. nilotica* in the diet declined progressively from Nile perch of 1-5 cm TL up to 51+ cm TL, and this is because the adult fish were increasingly feeding on other prey items including haplochromines, *R. argentea*, juvenile Nile perch, molluscs, insects and *Barbus* . Results of this study (2012/16) for Nile perch of up to 30 cm TL were comparable with the findings of Katunzi *et al.* 2006 in 1988/89 and as those of Kische-Machumu *et al.* (2012) in 2006/08. Nile perch of 6 to 25 cm TL fed more frequently on *C. nilotica* in 2012/16 compared to 1988/1989 and 2006/08, and this could be an indication that *C. nilotica* is the most available prey item for Nile perch in the Kenyan

side of the lake following decline of haplochromine cichlids. The frequency of occurrence of *C. nilotica* in the diet of Nile perch up to 30 cm TL did not show a trend across size classes in 1988/1989, but a negative trend observed in 2006/08 and 2012/16 could be result of resurgence of haplochromines in the lake as evidenced by the positive trend in occurrence of haplochromines during the same periods. The contribution of *R. argentea* and *odonata* in the diet of Nile perch has remarkably reduced due to continued preference for *C. nilotica* and haplochromines.

5.6 The ontogenetic shift in structural development and diet

There was a general ontogeny of *L. niloticus* larvae particularly in the sequence of structural morphological differentiation and development. Larval development in *Lates niloticus* showed the approximate length (TL mm) at which the principal morphological features first appear in Lake Victoria, Kenya at 2.8.-3.0 mm four developments occurred thus eye pigment, distal expansion of pectoral fins. This is the period a functional mouth and gills developed in lates larvae thus signalling the beginning of feeding and foraging activity in these fish species. This was evidenced by the fact that yolk-sac was absorbed at 4.5 mm TL meaning that without early feeding practice the larvae would starve to death in a matter of days to come. The mophomorphosis continued until the larvae was 15.5 -17.0 mm TL when the larvae resmsbled an adult fish

There was shift according to size of the fish, which fed on different items as fish sizes increased. There was clear ontogenetic shift in Nile perch in which fish below 4 cm fed on zooplankton, 10 - 20 cm fed exclusively on *Caridina* and lengths above 20 fed on fish, similar trend was reported by Ogutu-Ohwayo (2004), according to Owili and Omondi (2003). Nile perch of 4 cm and below feeds purely on zooplankton. The

observed shift during ontogeny from zooplankton to increasingly larger prey is a common feature in fish (Wanink & Joordens, 2003). Foraging strategy deployed by *L. niloticus* of different sizes of fish was in the sizes targeted by different fish as evidenced by the ontogenetic shift in this fish as it grew from small sized fish to bigger fish.

The results of this study further indicated distinct and clear ontogenetic shifts in the diets and changes in foraging patterns of Nile perch, the same have been described and reported by other authors (Ogari & Dadzie, 1988; Ogutu-Ohwayo, 2004; Katunzi *et al.*, 2006). This was observed at three different levels as fish transitioned from larvae to juvenile and to adults. In some instances Nile perch ate zooplankton until a size of 3 cm TL. In the pelagic larvae of 4-14 mm cladocerans dominated, whereas in the inshore post-larvae > 1 cm, cyclopoid copepods. Calanoid copepods were rare in the diets. In fish of more than 7 cm TL the shrimp and fish became increasingly important and in *L. niloticus* of more than 60 cm, fish were the dominant prey from observations although not part of this study. In inshore areas the shift from shrimps to fish was more abrupt and because fish dominated already above 36 cm TL.

Zooplanktivory was confined to Nile perch < 5 cm. The proportion of cyclopoid copepods decreased and that of calanoids increased with size of the fish; zooplankton was followed by midge larvae. Shrimps, dragonfly nymphs, daga and small Nile perch were eaten by all size classes above 5 cm (Katunzi *et al.*, 2006). In 1988-1989, when haplochromine cichlids were absent in the Gulf, the switch to fish (juvenile Nile perch and *R. argentea*) in shallow inshore areas (< 4 m) occurred around 10 cm SL, whereas in deeper, offshore areas (> 12 m) Nile perch shifted to the shrimp *C. nilotica*, which remained the dominant prey up to at least 50 cm (larger fish were not

included in the study by Katunzi *et al.*, 2006). In the Kenyan part of the lake, in years when haplochromines were absent, shrimps were the dominant prey up to 50 cm TL and were common up to 80 cm TL (Hughes, 1986, 1992 b; Ogari & Dadzie, 1988). Nile perch larger than 100 cm were mainly piscivorous. This study found similar trend.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

1. Winam Gulf had higher TP, TN, turbidity, conductivity and zooplankton densities than the open lake. Turbidity & Secchi influenced distribution & abundance of *L. niloticus* larvae & juveniles in the lake.
2. Larvae of *L. niloticus* preferred shallow warm water at river mouths and in bays for survival of larvae. The rivermouths and bays also likely offered protection from waves and predators, and the higher primary production due to elevated nutrient inputs from the catchment likely increased zooplankton populations that are the main food for the larvae and juveniles.
3. Horizontal patterns of distributions of the early stages of *L. niloticus* with preference of within 200 m. Combining distribution and abundance data is useful for identifying breeding areas for conservation
4. There were clear morphological changes and ontogenetic shifts in diet composition with size for both larvae and juveniles of Nile Perch.

6.2 Recommendations

Following the results of this study, the following recommendations are made;

1. The area within 200 m from the shore along the lake should be protected through legal prohibition of fishing and any other activity in the lake. This is an important breeding ground for Nile Perch in Lake Victoria.
2. Studies of near-shore hydrodynamics are required to provide more insights on factors influencing the abundance and distribution of larvae and juveniles of Nile Perch in Lake Victoria.
3. The extent and nature of diel vertical migration require further investigation to determine whether it is related to predator avoidance, feeding or energetics as has been observed for zooplankton.
4. Management measures should be based on the findings of this and other studies for sustainability of the Nile Perch and other fisheries in Lake Victoria. The findings of this study are particularly important for the conservation and successive recruitment of the Nile Perch fishery in the lake.

REFERENCES

- Abila, R.O. and Jansen, E.G. (1997). From local to global markets: The fish exporting and fishing meal industries of Lake Victoria. Structure, strategies and socio-economic impacts in Kenya, IUCN Eastern Africa programme. Socio-economics of Lake Victoria fisheries: Report No.2, The World Conservation Union, Nairobi.
- Abila, R. O. (2000). The development of the Lake Victoria fishery: A boom or bane for food security? IUCN Report No. 8. Nairobi, Kenya.
- Acere, T.O. (1985). Observations on the biology of Nile Perch (*L. niloticus*), and the growth of its fishery in the northern waters of Lake Victoria. *FAO Fisheries Report* 335, 42-61.
- Anderson, A. M., (1961). Further observations concerning the proposed introduction of Nile perch into Lake Victoria. *East African Agricultural and Forestry Journal* 26,195–201.
- Anyah R O, Semazzi F., (2009). Idealized simulation of hydrodynamic characteristics of Lake Victoria that potentially modulate regional climate. *International Journal of Climatology*. 29, 971–981. doi: 10.1002/joc.1795.

- Asila, A. A. and Ogari, J., (1987). Growth parameters and mortality rates of Nile perch (*Lates niloticus*) estimated from length-frequency data in the Nyanza Gulf (Lake Victoria). In Contributions to Tropical Fisheries Biology, edited by S. Venema, J. Moller-Christensen and D. Pauly. Papers by the participants of FAO/DANIDA Follow-up Training Courses. *FAO Fisheries Report*, (389):,272–87.
- Asila, A. A. and Okemwa, E., (1999). Growth parameters for *Lates niloticus* (L.), *Bagrus docmak* (Forsk.) (Forsk.), *Oreochromis niloticus* (L.), *Clarias gariepinus* (Burchell) and *Synodontis* species derived from tag returns. pp. 204-207.
- Asila, A.A., (2000). Report on the frame survey conducted in March 2000 in the Kenya Waters of Lake Victoria. Draft 1. Kenya Marine and Fisheries Research Institute.
- Asila. A. A. and Ogari. J., (1988). Growth parameters and mortality of Nile perch (*Lates niloticus*) estimated from length-frequency data in the Nyanza Gulf (Lake Victoria). *FAO Fisheries Report* 389, 272-287.
- Balirwa, J. S., Chapman, C. A., Chapman, L. J., Cowx, I. G., Geheb, K., Kaufman, L., Witte, F. (2003). Biodiversity and fishery sustainability in the Lake Victoria basin: An unexpected marriage? *BioScience*, 53(8), 703–715.
[https://doi.org/10.1641/00063568\(2003\)053\[0703:BAFSIT\]2.0.CO](https://doi.org/10.1641/00063568(2003)053[0703:BAFSIT]2.0.CO)
- Balirwa, J.S. (1995). The Lake Victoria environment: its fisheries and wetlands - review. *Wetlands Ecology and Management* 3, 209-224.

- Barel, C. D. N., Dorit, R., Greenwood, P. H., Fryer, G., Hughes, N., Jackson, P. B. N., Kanawabe, H., Lowe-McConnell, R. H., Witte, F. & Yamaoka, K. (1985). Destruction of fisheries in Africa's lakes. *Nature* 315, 19–20
- Beverton, R. J. H., (1959). Report on the state of the Lake Victoria Fisheries. *Mimeo.* Fisheries Laboratory. Lowestoft. 1- 69 pp
- Beverton, R. J. H., & Holt, S. J. (1966). Manual of methods for fish stock assessment. Part II. Tables of yield function. *FAO Fish. Biol. Techn. Pap.* 38, 10 (Ver. 1), 1–67.
- Bootsma, H.A. and Hecky, R.E. (1993). Conservation of the African Great Lakes: A Limnological Perspective. *Conservation Biology* 7(3), 644-655.
- Brogan, M. W. (1994a). Distribution and retention of larval fishes near reefs in the Gulf of California. *Marine Ecology Progress Series* 115, 1-13.
- Buchanan-Wollaston, H. J. 1923. The spawning of plaice in the southern part of the North Sea. Ministry of Agriculture, Fisheries and Food (UK), Fisheries Investigations (Series 2), 5(2), 36pp.
- Bwathondi, P.O.J. (1988). The state of Lake Victoria fisheries, Tanzania sector. *FAO Fish. Rep.*, no. 388, pp. 29–35.
- Chapman, L.J., Chapman, C. A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L. and Keiter. A.E. (1996). Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conservation Biology* 10, 554-561.
- Cowx, I., and Knaap, M. Van Der. (2003). Improving fishery catch statistics for Lake Victoria. *Aquatic Ecosystem Health and Management* 6 (3), 299–310

- Copley, H., (1953). The Tipia fishes of the Kavirondo Gulf. *J. East Afri. Nat. Hist. Soc.* 2257-67.
- Crul R C M. (1995). Limnology and Hydrology of Lake Victoria. Paris: UNESCO Publishing.
- Cushing, D. H. (1975). *"Marine ecology and fisheries"*. Cambridge University Press, Cambridge.
- DFO, (2004). Atlantic Mackerel of the Northwest Atlantic in 2003. DFO Can. Sci. Advis. Sec. Stock Status Rep. 2004/018.
- Doherty, P. J. and D. M. Williams (1988). The replenishment of coral reef fish populations. *Oceanography and Marine Biology: An Annual Review* 26, 487-551.
- Fasham, M. J. R. (1978). The statistical and mathematical analysis of plankton patchiness. *Oceanography and Marine Biology: An Annual Review* 16, 43-79.
- Froese, and Pauly, D. (2012). FishBase. World Wide Web electronic publication
- Fortier, L. and W. C. Leggett (1984). Small-scale covariability in the abundance of fish larvae and their prey. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 502-512.
- Fossum, P. 1992. The recovery of the Barents Sea capelin (*Mallotus villosus*) from a larval point of view. *ICES J. Mar. Sci.*, 49, 237-243.

- Fuiman, L. A. 2002. Special considerations of fish eggs and larvae. 1-32 In: L. E. Fuiman & R. G. Werner (eds.) *Fishery science: The unique contributions of early life stages*. Blackwell Publishing. Iowa, USA. 326 pp.
- Gayanilo, F. C., Sparre, P., & Pauly, D. (1996). *FAO-ICLARM stock assessment tools (FISAT)*, Rome (126 pp., +3 diskettes).
- Gee, J.M. (1964). Nile perch investigations. *EAFFRO Annual Report 1962/63*:14–24
- Gee, J.M. (1969). A comparison of certain aspects of the biology of *Lates niloticus* (L.) in some East African lakes. *Rev. Zool. Bot. Afr.* 80, 244–262.
- GEMS, (1992). *Global Environmental monitoring system (GEMS) WATER Operation Guide*, 3rd Edition
- Gichuki, J.; Guebas, FD., Mugo J, Rabuor C.O., Triest, L, Dehairs. F., (2001a). Species inventory and the local uses of the plants and fishes of the Lower Sondu Miriu wetland of Lake Victoria, Kenya. *Hydrobiologia* 458, 99–106.
- Gichuki, J.W, Triest, L., Dehairs. F., (2001b). The use of stable carbon isotopes as tracers of ecosystem functioning in contrasting wetland ecosystems of Lake Victoria, Kenya. *Hydrobiologia* 458, 91–97.
- Goldschmidt, T. and Witte, F. (1992). Explosive speciation and adaptive radiation of haplochromine cichlids from Lake Victoria: an illustration of the scientific, value of a lost species flock. *Mitt. Internat. Verein. Limnol.* 23: 101-107.
- Goudswaard, K., Witte, F., & Katunzi, E. F. B., (2008). The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): Chronology and causes. *Environmental Biology of Fishes*, 81(2), 127–139.

- Goudswaard, K.P.C., Witte, F., Katunzi, E.F.B., (2006). The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. *Environ. Biol. Fish* 81, 127–139.
- Goudswaard, P. and Witte, F., (1985). Observations on Nile perch *Lates niloticus* (L.) 1758, in the Tanzanian waters of Lake Victoria. FAO Fisheries Report, (335), 62–5.
- Graham, M., (1929). The Victoria Nyanza and its fisheries. A report on the fishing Surveys of Lake Victoria of 1927 to 1928. Crown agents colonies, London. 225 pp.
- Gray, C. A. (1998). Diel changes in vertical distributions of larval fishes in unstratified coastal waters off southeastern Australia. *Journal of Plankton Research* 20, 1539-1552.
- Greenwood, P. H., (1966). The fishes of Uganda. Kampala, The Uganda Society, 131 p. 2nd rev. ed.
- Guya, F.J., (2013). Bioavailability of particle-associated nutrients as affected by internal regeneration processes in the Nyanza Gulf region of Lake Victoria. *Lakes and Reservoirs: Research and Management*. 18, 15.
- Haldorson, L., M. Pritchett, D. Sterritt and Watts, J., (1993). Abundance patterns of marine fish larvae during spring in a southeastern Alaskan bay. *Fishery Bulletin* 91, 36-44.
- Hamblyn, E. L., (1961). Nile perch investigation. Annual Report EAFFRO 1961 23–8.

- Hashem, M. T., and Hussein. K. A. (1973). Some biological studies of the Nile perch (*Lates niloticus* C. & V.) in the Nozhahydrodome. *Bull. Inst. Oceanogr. Fish.* (Cairo), 3, 364-393.
- Haury, L. R., McGowan J. A, and. Wiebe, P. H., (1978). Patterns and processes in the time-space scales of plankton distributions. In "Spatial pattern in plankton communities". (J. Steele, ed.), pp. 277-327. Plenum Press, New York.
- Hecky, R.E., Bugenyi, F.W.B., Ochumba, P., Talling, J.F., Mugidde, R., Gophen, M. and Kaufman, L., (1994). Deoxygenation of the deep waters of Lake Victoria. *Limnol. Oceanogr.* 39, 1476–1480.
- Hempel, G. (1973). Fish egg and larval surveys. FAO Fisheries Technical Paper No. 122, 82 pp.
- Hilborn, R., and. Walters, C. J. (1992). Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall. New York, NY. 570 pp.
- Holden, M.J., (1963). Report on the fisheries of Lake Albert. Report to Uganda Government (mimeo).
- Hopson, A.J., (1972). A study of Nile perch (*Lates niloticus*) (L.), Pisces Centropomidea) In Lake Chad. Overseas Research Publication 19, Overseas Development Administration, London, UK 93pp
- Hopson, A.J., (1982). The biology of *Lates niloticus* (L.) in Lake Turkana. In: *A Report on the Findings of the Lake Turkana Project 1972–75*, pp. 1285–1299, (Hopson, A.J., ed.) Overseas Development Administration, London.

- Horstman, K. R. and Fives J. M., (1994). Ichthyoplankton distribution and abundance in the Celtic Sea. *International Council for the Exploration of the Sea. Journal of Marine Science* 51, 447-460.
- Hughes, N.F., (1992). Growth and reproduction of the Nile perch, *Lates niloticus*, an introduced predator, in the Nyanza Gulf, Lake Victoria. *Environmental Biology of Fishes* 33, 299–305.
- Hughes, N.F., (1983). A study of the Nile perch, an introduced predator, in the Kavirondo Gulf of Lake Victoria. Oxford University, Nile Perch Project, Oxford. 75pp.
- 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 in the Nyanzan Gulf. *J. Fish Biol.* 29, 541–548.
- Hughes, N.F. (1992). Growth and reproduction of the Nile perch, *Lates niloticus*, an introduced predator, Nyanza Gulf, Lake Victoria, East Africa. *Environ. Biol. Fish* 33, 299–305.
- Hyslop, E.J. (1980). Stomach content analysis- a review of methods and their application. *Journal of Fish Biology* 17, 411-429.
- ICES. (2003). Report of the working group on mackerel and horse mackerel egg surveys. ICES CM 2003/G: 07. 57 pp.

- Ikwaput-Nyeko, J., Kirema_Mukasa, C., Odende, T., and Mahatane, A., (2009). Management of Fishing Capacity in the Nile Perch Fishery of Lake Paper presented to the Lake Victoria. *African Journal of Tropical Hydrobiology and Fisheries* 12, 67–73.
- Jansen, E.G. (1997). The fishing population in the Kenyan part of Lake Victoria report to the East African Freshwater Fisheries Research Organization Department of social anthropology, University of Bergen.
- Jenkins, G. P., (1986). Composition, seasonality and distribution of ichthyoplankton in Port Phillip Bay, Victoria. *Australian Journal of Marine and Freshwater Research* 37, 507-520.
- Katunzi E.F.B., Van Densen W.L.T., Wanink J.H. and Witte F., (2006). Spatial and seasonal patterns in the feeding habits of juvenile *Lates niloticus* (L.), in the Mwanza Gulf of Lake Victoria. *Hydrobiologia*, 568, 121–133.
- Kaufman L. S., (1992). Catastrophic change in species-rich freshwater ecosystems, the lessons of Lake Victoria. *BioScience* 42, 846-852
- Kayanda, R., A. M. Taabu, R. Tumwebaze, L. Muhoozi, T. Jembe, E. Mlaponi, and Nzungi P., (2009). Status of the major commercial fish stocks and proposed species-specific management plans for Lake Victoria. *African Journal of Tropical Hydrobiology and Fisheries* 21,15–21.
- Kenchington, F.E., (1939). Observations on the Nile perch (*Lates niloticus*) in the Southern Sudan. *Proceedings of the zoological society of London, Ser. A* 109, 157-168.

- Kendall R L., (1969). An ecological history of the Lake Victoria Basin. *Ecological Monographs*. 39 (2),121– 176. doi:10.2307/1950740
- Kendall R. L., (1969). An ecological history of the Lake Victoria Basin. *Ecological Monographs*. 1969; 39(2),121–176. doi: 10.2307/1950740
- Kingsford, M. J. and Choat, J. H., (1989). Horizontal distribution patterns of presettlement reef fish:are they influenced by the proximity of reefs? *Marine Biology* 101, 285-297.
- Kishe-Machumu, M. A., Witte, F., Wanink, J. H., & Katunzi, E. F., (2012). The diet of Nile perch, *Lates niloticus* (L.) after resurgence of haplochromine cichlids in the Mwanza Gulf of Lake Victoria. *Hydrobiologia*, 682 (1), 111–119. <https://doi.org/10.1007/s10750-011-0822-1>
- Kitchell, J., and Schindler, D., (1997). The Nile perch in Lake Victoria: interactions between predation and fisheries. *Ecological Applications* 7(2), 653–645.
- Kolding, J., P. van Zwieten, O. Mkumbo, G. Silsbe, and R. Hecky., (2008). Are the Lake Victoria fisheries threatened by exploitation or eutrophication? Towards an ecosystem-based approach to management. Pages 309–354 in G. Bianchi and H. R. Skjoldal, editors. *The ecosystem approach to fisheries*. <http://dx.doi.org/10.1079/9781845934149.0309>
- Kundu, R.; Aura, C. M.; Nyamweya, C., Agembe, S.; Sitoki, L., Lung'ayia, H. B. O.; Ongore, C.; Ogari, Z., and Werimo, K., (2017). Changes in pollution indicators in Lake Victoria,Kenya and their implications for lake and catchment management. *Lakes and Reservoirs: Research and Management* 2017 22, 199–214

Lake Victoria Fisheries Research Project Phase II (LVFRP/TECH/01/16). Technical Document No. 16.

LeCren, C.D., (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in perch, *Perca fluviatilis*. *Journal of Animal Ecology* 20, 201-209.

Leis, J. M. (1991a). The pelagic stage of reef fishes: The larval biology of coral reef fishes. In "The ecology of fishes on coral reefs". (P. F. Sale, ed.), pp. 183-229. Academic Press Inc., San Diego.

Leis, J. M. and Miller J. M., (1976). Offshore distributional patterns of Hawaiian fish larvae. *Marine Biology* 36, 359-367.

Lennert-Cody, C. E. and Franks P. J. S., (1999). Plankton patchiness in high-frequency internal waves. *Marine Ecology Progress Series* 186, 59-66.

Levins, R., (1968). Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton pp120.

Ligtvoet W. & Mkumbo O.C., (1990) Synopsis of ecological and fishery research on Nile perch (*Lates niloticus*) in Lake Victoria, conducted by the HEST/TAFIRI. FAO Fisheries Report 430, 35–74.

Ligtvoet, W. and Mkumbo, O.C., (1990). Stock assessment of the Nile perch in Lake Victoria. p. 35–74. In: CIFA, Report of the 5th session of the Sub-committee for the Development of the Fisheries in Lake Victoria, Mwanza, Tanzania, 1989 September 12–14. FAO Fish Rep. 430, FAO, Rome.

- Ligtvoet, W. and Witte. F. (1991). Perturbation through predator introduction: effects on the food web and fish yields in Lake Victoria (East Africa), p. 263-268. In O. Ravera (ed.) Terrestrial and aquatic ecosystems. Perturbation and recovery. Ellis Horwood, Chichester
- Ligtvoet, W., Mous, P.J., Mkumbo, O.C., Budeba, Y.L. Goudswaard, P.C., Katunzi, E.F.B., Temu, M.M, Wanink, J.H. and Witte, F., (1995). The Lake Victoria fish stocks and fisheries. In: F. Witte and W.L.T. van Densen (eds). Fish Stocks and Fisheries of Lake Victoria. A Handbook for Field Observations. Samara Publishing, Cardigan, UK, pp. 11-53 pp.
- Lowe-McConnell, R. H., (1987). *Ecological studies in tropical fish communities*. (P. S. Ashton, S. P. Hubbell, D. H. Janzen, P. H. Raven, and P. B. Tomlinson, Eds.) *Science* 11: 382. Cambridge University Press.
- Lucena, F. M.; Vaske, T.; Ellis, J. R.; O'Brien, C. M., (2000). Seasonal variation in the diets of bluefish, *Pomatomus saltatrix* (Pomatomidae) and striped weakfish, *Cynoscion guatucupa* (Scianidae) in southern Brazil: implications of food partitioning. *Env. Biol. Fish* 57, 423-424.
- LVFO. (2007). Regional Plan of Action for the Management of Fishing Capacity in Lake Victoria (RPOA-Capacity); LVFO, Jinja.
- LVFO. (2016). Regional Frame Survey for the Management of Fishing Capacity in Lake Victoria (RPOA-Capacity); LVFO, Jinja.
- Lung'ayia H., Sitoki L. & Kenyanya M., (2001). The nutrient enrichment of Lake Victoria (Kenyan waters) *Hydrobiologia* 458, 75-82.

- Lung'ayia H.B.O., M'Harzi A., Tackx M., Gichuki J. & Symoens J.J., (2000) Phytoplankton community structure and environment in the Kenyan waters of Lake Victoria. *Freshwater Biology* 43, 529–543.
- MacIntyre S, Romero J R, Silsbe G M, Emery B M., (2014). Stratification and horizontal exchange in Lake Victoria, East Africa. *Limnology and Oceanography*. 59 (6):1805–1838. doi:10.4319/lo.2014.59.6. 1805.
- Manyala, J. O., Ojuok, J.E., (2007). Survival of the Lake Victoria *Rastrineobola argentea* in a rapidly changing environment: Biotic and abiotic interactions. *Aquatic Ecosystem Health and Management* 10 (4), 407–415.
- Marliave, J. B., (1986). Lack of planktonic dispersal of rocky intertidal fish larvae. *Transactions. American Fisheries Society* 115, 149-154. Masterman, A. T. (1892). Report on the pelagic eggs
- Marshall, B. E., & Mkumbo, O. C., (2011). The fisheries of Lake Victoria: Past present and future. *Nature & Fauna*, 26, 8–13. FAO, Rome.
- Masese, F. O. and McClain, M. E. (2012). Trophic resources and emergent food web attributes in rivers of the Lake Victoria Basin: a review with reference to anthropogenic influences. *Ecohydrol.* 5, 685–707 (2012)
- Matsuishi, T. L. Muhoozi, O. Mkumbo, Y. Budeba, M. Njiru, A. Asilla, A. Othina, Cowx I.G., (2006). Are the exploitation pressures on the Nile perch fisheries resources on Lake Victoria a cause for concern? *Fisheries Management and Ecology*. 13, 53- 71

- Mkumbo, O. C., & Marshall, B. E., (2015). The Nile perch fishery of Lake Victoria: Current status and management challenges. *Fisheries Management and Ecology*, 22, 56–63. <https://doi.org/10.1111/fme.12084>
- Mkumbo, O.C., (2002). Assessment and management of Nile perch (*Lates niloticus* L.) stocks in the Tanzanian waters of Lake Victoria. PhD, thesis, Hull University, UK. 289 pp
- Mkumbo, O.C. and Ligetvoet, W., (1992). Changes in the diet of Nile perch, *Lates niloticus* (L), in the Mwanza Gulf, Lake Victoria. *Hydrobiologia*, 232, 79–83.
- Mugidde R. (2001) Nutrient status and planktonic nitrogen fixation in Lake Victoria, Africa. PhD Thesis. University of Waterloo, Ontario, Canada. 191pp.
- Mugo, J., Tweddle, D., (1999). Preliminary surveys of the fish and the fisheries of the Nzoia, Nyando and Sondu Miriu Rivers. Part 1. Report of the third FIDAWOG workshop held at Triangle Hotel Jinja, 29th March- 1st April 1999. Technical Document No. 6 LVFRP/TECH/99/06. Lake Victoria Fisheries Research Project Phase 2 pp 1060116.
- Muhoozi, L. I., (2002). *Exploitation and management of the artisanal fisheries in the Ugandan waters of Lake Victoria*. PhD Thesis. University of Hull, Hull, UK. 260 pp
- Muyodi F. J., Bugenyi, F. W. B. and Hecky R.E (2010). Experiences and lessons learned from interventions in the Lake Victoria Basin: The Lake Victoria Environmental Management Project *Lakes & Reservoirs: Research and Management* 2010 15, 77–88

- Mwamburi J., (2016). Spatial variations in sedimentary organic matter in surficial lake sediments of Nyanza Gulf (Lake Victoria Kenya) after invasion of water hyacinth. *Lakes and Reservoirs: Research and Management* 21, 94-113.
- Njiru M, Kazungu, J., Ngugi, C.C., Gichuki, J. and Muhoozi, L., (2008). An overview of the current status of Lake Victoria fishery: opportunities, challenges and management strategies. *Lakes and Reservoirs: Research and Management* 13: 1–12.
- Njiru, M., Getabu, A., Taabu, A. M., Mlaponi, E., Muhoozi, L., & Mkumbo, O. C., (2009). Managing Nile perch using slot size: Is it possible? *African Journal of Tropical Hydrobiology and Fisheries*, 12 (1), 9–14.
- Njiru, M., J. Ojuok, a. Getabu, T. Jembe, M. Owili, and Ngugi C., (2008). Increasing dominance of Nile tilapia, *Oreochromis niloticus* (L) in Lake Victoria, Kenya: consequences for the Nile perch *Lates niloticus* (L) fishery. *Aquatic Ecosystem Health & Management* 11, 42–49.
<http://dx.doi.org/10.1080/14634980701878090>
- Njiru, M., P. Nzungi, A. Getabu, E. Wakwabi, A. Othina, T. Jembe, and Wekesa S., (2007). Are fisheries management, measures in Lake Victoria successful? The case of Nile perch and Nile tilapia fishery. *African Journal of Ecology* 45, 315–323. <http://dx.doi.org/10.1111/j.1365-2028.2006.00712.x>
- Njiru, M., Sitoki, L., Nyamweya, C.S., Jembe, T., Aura, M.C., Waithaka, E. and Masese, F., (2012). *Habitat degradation and changes in Lake Victoria fisheries*. Nova Publishers, Environmental Degradation: Causes, Issues and Management. 1- 34 pp

- Nonaka, I., Toyama, R., & Konno, N. (2000). SECI, Ba and Leadership: a Unified Model of Dynamic Knowledge Creation. *Long Range Planning*, Elsevier Science Ltd, 33(1), 5- 34
- Ntiba N. M, M., K.W. and T., M.C., (2001). *Management issues in the Lake Victoria watershed*. *Lakes & Reservoirs Research and Management* 6, 211-216.
- Nyamweya C, Desjardins C, Sigurdsson S, Tomasson T, Taabu-Munyaho A, Sitoki L., (2016). Simulation of Lake Victoria Circulation Patterns Using the Regional Ocean Modeling System (ROMS). *PLoS ONE* 11(3): e0151272. doi:10.1371/journal.pone.0151272
- Ochumba P.B.O., (1990). Massive fish kills within the Nyanza Gulf of Lake Victoria, Kenya. *Hydrobiologia* 208, 93-99.
- Ochumba P.B.O., (1996). Measurement of water currents, temperature, dissolved oxygen and winds on the Kenyan Lake Victoria. In: Johnson TC, Odada EO, editors. *The limnology, climatology and paleoclimatology of the East African Lakes*. Amsterdam: Gordon and Breach; 1996. pp. 55–167.
- Ochumba, P. B.O., Manyala, J. O., (1992). Distribution of fishes along the Sondu-Miriu River of Lake Victoria, Kenya with special reference to upstream migration, biology and yield. *J. Aquacul. Fish. Manag.* 23, 701–719.
- Ochumba, P.B.O., (1987). Periodic massive fish kills in the Kenyan part of Lake Victoria. *Water Quality Bulletin* 12,119-122, 130.

- Ochumba, P.B.O., (1995). Limnological changes in Lake Victoria since the Nile perch introduction. p. 33-43. In: T.J. Pitcher and P.J.B. Hart (eds.) The impact of species changes in African Lakes. Chapman & Hall Fish & Fisheries Series 18.
- Ofulla V.A; & Adoka, Ong'wen, N; Anyona, D. O.; Abuom, P.; Karanja, D. V., John Okurut, T.; Matano, Ally-Said; Dida, G.; Jembe, T. and Gichuki, J., (2013). Spatial distribution and habitat characterization of schistosomiasis host snails in lake and land habitats of western Kenya. Lakes & Reservoirs Research and Management. 18, 197-215.
- Ogari, J., (1985). The biology of *Lates niloticus* (Linn.) in the Nyanza Gulf of Lake Victoria (Kenya) with special reference to the food and feeding habits. M.Sc Thesis, University of Nairobi, Kenya.
- Ogari, J. & Dadzie, S., (1988). The food of the Nile perch, *Lates niloticus* (L.), after disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). J. Fish. Biol. 32, 571–577.
- Ogari, J. & Dadzie, S., (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 of Fish Biology* 32, 571–577.
- Ogari, J. and Asila, A.A., (1992). Status of fisheries of Lake Victoria Kenya sector. p. 15-23. In CIFA. Report of the sixth session of the sub-committee for the development and management of the fisheries in Lake Victoria, 10-13 February 1992, Jinja, Uganda. FAO Fish. Rep. 475. FAO, Rome.

- Ogutu-Ohwayo, R. (1984). The reproductive potential of Nile perch, *Lates niloticus* L., and the establishment of the species in lakes Kyoga and Victoria (East Africa). *Hydrobiologia* 162, 193-200.
- Ogutu-Ohwayo, R. (1990). 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. <https://doi.org/10.1111/j.1095-8649.1990.tb05926.x>
- Ogutu-Ohwayo, R. (1996). Adjustments in Fish Stocks and in Life History Characteristics of the Nile perch, *Lates niloticus* L. in Lakes Victoria, Kyoga and Nabugabo. PhD Thesis, University of Manitoba, Winnipeg, Canada. 213 pp.
- Ogutu-Ohwayo, R. (2004). Management of the Nile perch, *Lates niloticus* fishery in Lake Victoria in light of the changes in its life history characteristics. *African Journal of Ecology*, 42, 306–314. <https://doi.org/10.1111/j.1365-2028.2004.00527.x>
- Ogutu-Ohwayo, R., (1985). The effects of predation by Nile perch, *Lates niloticus* (Linne´) introduced into Lake Kyoga (Uganda) in relation to the fisheries of Lake Kyoga and Lake Victoria. FAO Fisheries Report 335: 18–41.
- Ogutu-Ohwayo, R., (2004). Management of the Nile perch, *Lates niloticus* fishery in Lake Victoria in light of the changes in its life history characteristics. *African Journal of Ecology* 42: 306–314.

- Ojwang, W. O., Nyamweya, C., Ojuok, J., Agembe, S., and Werimo, K., (2011). *Biological Baseline Survey of Nile Perch (Lates niloticus Linnaeus 1758) In the Kenyan Waters of Lake Victoria* (p. 30). Kisumu, Kenya: LVEMP II.
- Ojwang, W.O., Kaufman, L., Soule, E., Asila, A. A., (2007). Evidence of stenotopy and anthropogenic influence on carbon source for the major riverine fishes of Lake Victoria. *Journal of Fish Biology* 70, 1430–1446.
- Ojwang, W.O., Ojuok, J. E, Mbabazi, D. and Kaufman L., (2010). Ubiquitous omnivory, functional redundancy and the resiliency of Lake Victoria fish community. *Aquatic Ecosystem health & management* 13(3), 1-8.
- Okach, J. I. O. and S. Dadzie (1988). The food and feeding habits and distribution of a siluroid catfish, *Bagrus docmac* (Forsskäll) in Kenyan waters of Lake Victoria. *J. Fish Biol.* 32, 21-26.
- Okedi, J., (1971). Further observation on the biology of the Nile perch (*Lates niloticus* L.) in Lake Victoria and Kyoga, EAFFRO Annual Report, pp. 42–55.
- Okely, P., Imberger, J. and J. P. Antenucci. 2010, *Processes affecting horizontal mixing and dispersion in Winam Gulf, Lake Victoria*. *Limnology and Oceanography* 55, 1865–1880.
- Okemwa, E.N., (1984) Potential fishery of the Nile perch *Lates niloticus* Linne. (Pisces: n Centropomidae) in Nyanza Gulf of Lake Victoria East Africa. *Hydrobiologia* 108, 121- 126.
- Okemwa, E.N., (1984). The state of fishery in Nyanza Gulf of Lake Victoria, East Africa. *Kenya Aquatica* 2, 39-45.

- Outa, N. O., Yongo, E., & Jameslast, A. K. (2017). Ontogenic changes in prey ingested by Nile perch (*Lates niloticus*) caught in Nyanza Gulf of Lake Victoria, Kenya. *Lakes & Reservoirs: Research & Management*, 2017 (20), 1–5.
- Overholtz, W. J., L. D. Jacobson, G. D. Melvin, M. Cieri, M. Power, D. Libby, and K. Clark. 2004. Stock assessment of the Gulf of Maine - Georges Bank Atlantic herring complex, 2003. Northeast Fish. Sci. Cent. Ref. Doc. 04-06. 290 pp.
- Owili, M. A., Omondi, R., 2003. Predator-prey relationship between zooplankton and *Rastrineobola argentea* and juvenile *Lates niloticus* in the lake-river interface habitats in the Nyanza Gulf of Lake Victoria. *Aquatic Ecosystem health and Management*.
- Pauly, D., (1980). On the interrelationship between natural mortality, growth parameters, mean environmental temperature in 175 fish stock. *Journal du Conseil. Conseil Permanent International Pour L'exploration de la mer*, 39, 175–192. <https://doi.org/10.1093/icesjms/39.2.175>
- Pauly, D., (1987). A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. In D. Pauly & G. R. Morgan (Eds.), *Proceedings, length-based methods in fisheries research ICLARM Conference* 13 (486, pp. 7–34).
- Pauly, D., & Munro, J. L., (1984). Once more on growth comparison in fish and invertebrates. *Fish Bytes*, 2, 21.

- Pauly, D., & Soriano, M. L., (1986). Some practical extensions to Beverton and Holt's relative yield-per-recruit model. In J. L. Maclean, L. B. Dizon, & L. V. Hosillo (Eds.), *The first Asian fisheries forum* (pp. 491– 496). Manila, Philippines: Asian Fisheries Society.
- Pauly, D., Ingles, J., & Neal, R., (1984). Application to shrimp stocks of objective methods for the estimation of growth, mortality and recruitment- related parameters from length-frequency data (ELEFAN I and II). In J. A. Gulland & B. I. Rothschild (Eds.), *Penaeid shrimps – Their biology and management* (pp. 220–234, 312). Farnham, UK: Fishing News Books.
- Rabuor, C. O., Gichuki, J., & Moreau, J., (2003). Growth, mortality and recruitment of Nile perch *Lates niloticus* (L. Centropomidae) in the Nyanza Gulf of Lake Victoria: An evaluation update. *Naga, WorldFish Center Quarterly*, 26 (4), 8–12.
- Ricker, W.E., (1973). Linear regressions in fishery research. *J. Fish. Res. B. Can.* 30, 409–34.
- Rinne, J.N. and B. Wanjala, (1982). Observations on movement patterns of Tilapia spp. in Nyanza Gulf, Lake Victoria. East Africa. *J. Fish. Biol.* 20, 317-332.
- Rutherford, E. S., (2002). Fishery management, pp. 206-221 In: L. E. Fuiman & R. G. Werner (eds.) *Fishery science: The unique contributions of early life stages*. Blackwell Publishing. Iowa, USA. 326 pp.
- Sabate's, A., Olivar, M.P., (1996). Variation of larval fish distributions associated with variability in the location of a shelf-slope front. *Marine Ecology Progress Series* 135, 11–20.

- Sale, P. F. (1991). Reef fish communities: open non-equilibrial systems. In "The ecology of fishes on coral reefs". (P. F. Sale, ed.), pp. 564-598. Academic Press, New York.
- Sale, P. F., G. P. Jones, J. H. Choat, J. M. Leis, R. E. Thresher and Williams D. M., (1985). Current priorities in ecology of coral reef fishes. *Search* 16, 270-274.
- Sampey, A.; Mckinnon, A.; Meekan, M.; and McCormick, M., (2007). Glimpse into guts: A first overview of the feeding of tropical shorefish larvae. *Marine Ecology Progress Series*. 339, 243-257.
- Schoener, T. W., 1970: Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51, 408 – 418.
- Schofield P.J. & Chapman L.J., (2000). Hypoxia tolerance of introduced Nile perch: implications for survival of indigenous fishes in the Lake Victoria basin. *African Zoology* 35, 35–42.
- Schofield, P.J. and Chapman, L.J., (1999). Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. *Environmental Biology of Fishes* 55, 343-358.
- Seehausen O., Van Alphen J.J.M. & Witte F., (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277, 1808–1811.
- Sitoki L., Kurmayer R. & Rott E., (2012). Spatial variation of phytoplankton composition, biovolume, and resulting microcystin concentrations in the Nyanza Gulf (Lake Victoria, Kenya). *Hydrobiologia* 691, 109–122.

- Smith, K. A., M. T. Gibbs, J. H. Middleton and Suthers, I. M., (1999). Short term variability in larval fish assemblages of the Sydney shelf: tracers of hydrographic variability. *Marine Ecology Progress Series* 178, 1-15.
- Smith, T. D., (1994). *Scaling fisheries: The science of measuring the effects of fishing, 1855-1955*. Cambridge University Press. New York, NY. 392 pp.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry: The principles and practice of statistics in biological research*. 3rd Edition, W. H. Freeman and Co, New York. 477 pp
- Sparre, P. and Venema, S.C., (1998). *Introduction to tropical stock assessment*. FAO Fisheries Technical Paper No. 306/1. Rome, FAO. 376 pp.
- Sun X, Xie L, Semazzi F H M, Liu B., (2014). A numerical investigation of the precipitation over Lake Victoria Basin using a coupled Atmosphere-Lake Limited-Area Model. 2014.
- Suthers, I. M. and Frank, K. T., (1991). Comparative persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova Scotia, Canada. *Marine Biology* 108, 175-184.
- Swenson S, Wahr J., (2009). Monitoring the water balance of Lake Victoria, East Africa, from space. *Journal of Hydrology*. 370 (1–4),163- 176. Available from: <http://dx.doi.org/10.1016/j.jhydrol.2009.03.008>. doi:10.1016/j.jhydrol.2009.03.008
- Talling J., F., (1966). The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Internationale Revue Gesamte Hydrobiologia*. 51, 545–621. doi:10.1002/iroh.19660510402

- Talling J.F., (1966). The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Int. Revue ges. Hydroiol.* 54 (4), 545-621.
- Talling J.F., (1987). The phytoplankton of Lake Victoria (East Africa). *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 25, 229-256.
- Tate E, Sutcliffe J, Conway D, Farquharson F., (2010). Water balance of Lake Victoria: update to 2000 and climate change modelling to 2100. *Hydrological Sciences Journal.* 49,563–574. Available from: <http://www.tandfonline.com/doi/abs/10.1623/hysj.49.4.563.54422>.
- Townsend, D. W., (1984). Comparison of inshore zooplankton and ichthyoplankton populations of the Gulf of Maine. *Marine Ecology Progress Series* 15, 79-90.
- Tweddle, D., Ridgway S. and Asila, A., (1999). The design of multimesh, multidepth gillnet fleets
- Underwood, A. J. and Denley, E. J., (1984). Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In "Ecological communities, conceptual issues and the evidence". (D. R. Strong, D. Simberloff, L. G. Abele and A. B. Thistle, eds.), pp. 613. Princeton University Press.
- Verschuren, D., T. C. Johnson, H. J. Kling, D. N. Edgington, P. R. Leavitt, E. T. Brown, M. R. Talbot, and R. E. Hecky., (2002). History and timing of human impact on Lake Victoria, East Africa. *Proceedings of the Royal Society of London Biological Sciences* 269, 289–294. <http://dx.doi.org/10.1098/rspb.2001.1850>

- Von Bertalanffy, L., (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10,181–213.
- Wallace, R. K., (1981). An Assessment of diet-overlap indexes. *Trans. Amer. Fish. Soc.* 110, 72 – 76.
- Wanink J.H., Kashindye J.J., Goudswaard P.C. & Witte F., (2001). Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*. *Freshwater Biology* 46, 75–85.
- Welcomme, R., (1967). Observations on the biology of the introduced species of *Tilapia* in Lake Victoria. *Revue de Zoologie et de Botanique Africaines* 76, 249–279.
- Welcomme, R. L., (2003). River fisheries of Africa: Their past, present, and future. Pages 145-175. In: Crisman TL, Chapman LJ, Chapman CA, Kaufman L, eds. *Conservation Ecology and Management of African freshwaters*. Gainesville: University Press of Florida
- Welcomme, R.L., (1988). International introductions of inland fish species. *FAO Fisheries Technical Paper*, 294, 1-318.
- Welcomme, R.L., (1967). The relationship between fecundity and fertility in the mouth brooding cichlid fish *Tilapia leucosticta*. *J. Zool., Lond.*, 151, 453-68
- Elliott, E. M., and D. Jimenez. 1981. Laboratory manual for the identification of ichthyoplankton from the Beverly - Salem Harbor area. Dept. of Fisheries, Wildlife and Recreational Vehicles, Massachusetts. 230 pp.

- Werimo, K., (1998). *Nile perch oil characteristics, composition and use*. FAO Expert Consultation on Fish Technology in Africa. 6, Kisumu (Kenya), 27-30 Aug 1996. Rome: Food and Agricultural Organization of the United Nations.
- Wetherall, J.A., J. J. Polovina and S. Ralston. 1987. Estimating growth and mortality in steady state fish stocks from length-frequency data. ICLARM Conf. Proceed. 13; 53-74.
- Williams, D. M. and English S., (1992). Distribution of fish larvae around a coral reef: direct detection of a meso-scale, multi-specific patch? *Continental Shelf Research* 12, 923-937.
- Witte F., Goldschmidt, T., Goudswaard, P.C., Ligetvoet, W., van Oijen, M.J. and Wanink, J.H., (1992). Species extinction and concomitant ecological changes in Lake Victoria. *Metter lands journal of zoology* 42, 214-232.
- Witte F., Wanink J.H. & Kische-Machimu M., (2007a). Species distinction and the biodiversity crisis in Lake Victoria. *Transactions of the American Fisheries Society* 136, 1146–1159.
- Witte F., Wanink J.H., Kische-Machumu M., Mkumbo O.C., Goudswaard P.C. & Seehausen O. (2007b) Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria. *Aquatic Ecosystem Health and Management* 10, 416–433.
- Witte, F., Goldschmidt, T., and Wanink, J., (1992). The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* 34,1–28.

- Witte, F., Goldschmidt, T., Wanink, J., van Oijen, M., Goudswaard, K., Witte-Maas, E., & Bouton, N., (1992). The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes*, 34, 1–28. <https://doi.org/10.1007/BF00004782>.
- Witte, F., Msuku, B. S., Wanink, J. H., Seehausen, O., Katunzi, E. F. B., Goudswaard, P. C. and. Goldschmidt, T., (2000). Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. *Reviews in Fish Biol. Fisheries* 10, 233-24.
- Wootton, R. J. (1998). Ecology of teleost fishes. Dordrecht:Kluwer Academic Publisher: 386 pp.
- Worthington, E. B., (1929). A Report on the Fishing Survey of Lakes Albert and Kyoga, March to July, 1928.London: Crown Agents for the Colonies.
- Zar, J. H. (2010). *Biostatistics Analysis*. 4th EditionPrentice Hall, New Jersey 620 pp
- .

Appendix I: Canonical Correlations of zooplankton species and the nutrients

<i>Number</i>	<i>Eigenvalue</i>	<i>Canonical Correlation</i>	<i>Wilks Lambda</i>	<i>Chi-Square</i>	<i>D.F.</i>	<i>P-Value</i>
1	0.990294	0.995135	0.0000015924	193.579	133	0.0005
2	0.930623	0.964688	0.00016406	126.372	108	0.1092
3	0.870405	0.932955	0.00236475	87.6827	85	0.3995
4	0.739479	0.85993	0.0182472	58.0543	64	0.6856
5	0.682461	0.826112	0.0700412	38.5507	45	0.7402
6	0.612276	0.782481	0.220575	21.917	28	0.7851
7	0.431103	0.656584	0.568897	8.17882	13	0.8318

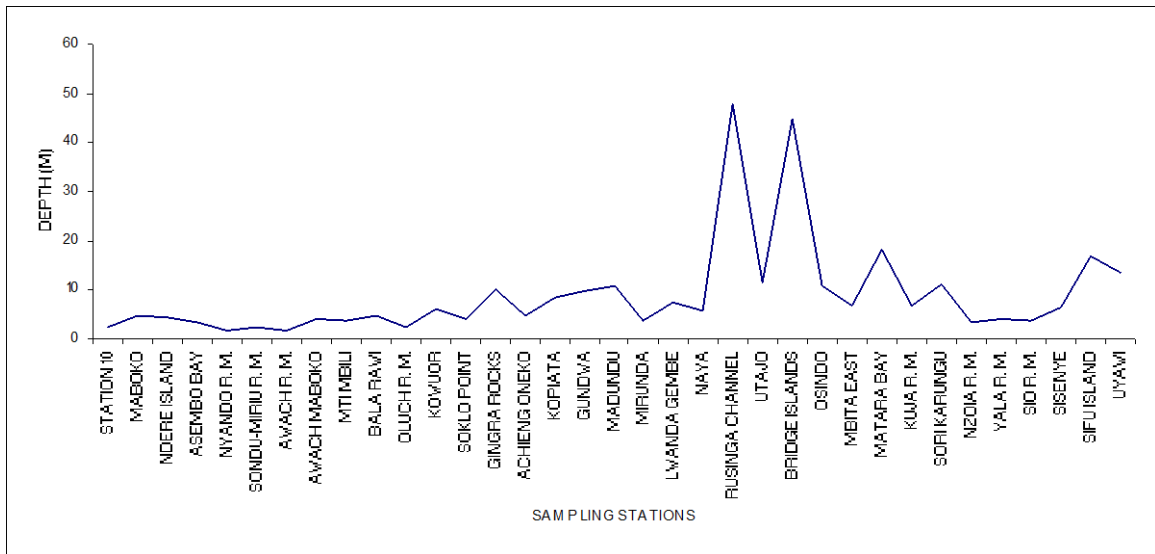
Appendix II: Coefficients for Canonical Variables of water quality and zooplankton

<i>Diaphanasoma excisum</i>	0.012178	-0.506825	0.657895	0.0604152	-0.524764	0.0561829	-0.518632
<i>Moina micrura</i>	-2.60354	-5.00674	-1.5535	-3.25799	-5.63331	-4.87003	0.788202
<i>Ceriodaphnia cornuta</i>	0.859601	0.25114	-0.905658	0.698238	0.433562	-0.202432	1.0215
<i>Bosmina longirostris</i>	0.839468	0.922303	-1.3336	-0.623537	-0.374618	0.289595	-0.197415
<i>Daphnia barbata</i>	1.35336	0.922434	-1.17191	-0.0893561	1.30485	0.533033	0.0272789
<i>Daphnia longispina</i>	-0.0958714	-0.0550818	0.388324	-0.0752731	-0.359714	-0.151227	0.0831043
<i>Daphnia lumhortzi</i>	4.40628	6.04374	2.35901	4.36747	7.35013	6.79035	-0.822637
<i>Brachionus calyciforus</i>	0.107101	0.198482	0.374323	-0.105369	-0.25482	-0.0523992	0.165722
<i>Brachionus falcatus</i>	-0.551769	-0.654375	1.5431	0.606322	0.229969	-0.26988	0.404011
<i>Brachionus angularis</i>	-1.19077	-1.37892	0.544413	-1.15308	-1.79077	-1.78118	0.25077
<i>Brachionus plicatilis</i>	-3.79719	-3.22114	4.25274	0.711728	-2.67968	-2.82118	-2.12665
<i>Brachionus caudatus</i>	1.60114	1.83153	-0.32071	1.36423	1.94974	2.03803	-0.303371
<i>Brachionus patulus</i>	5.77346	5.34733	-6.85832	0.222585	4.30926	4.76659	2.95676
<i>Keratella tropica</i>	-0.825953	-1.45349	-0.884696	-1.15752	-3.02568	-1.36225	0.205371
<i>Keratella cochlearia</i>	-0.306912	-0.485545	-0.739648	-0.620694	-0.552164	-1.98123	0.407561
<i>Euchlanis sp.</i>	-0.255637	-0.431664	0.280844	0.177648	-0.392888	0.0374806	0.214036
<i>Polyrthra sp.</i>	-4.30105	-3.09279	7.21548	0.378574	-1.10219	-1.57057	-2.61909
<i>Filinia sp.</i>	-0.429775	0.323211	-0.312979	-0.111638	0.0210331	0.465462	-0.993874
<i>Asplanchna sp.</i>	-0.0500383	0.248797	0.0212	0.262929	0.773102	0.527973	-0.649489

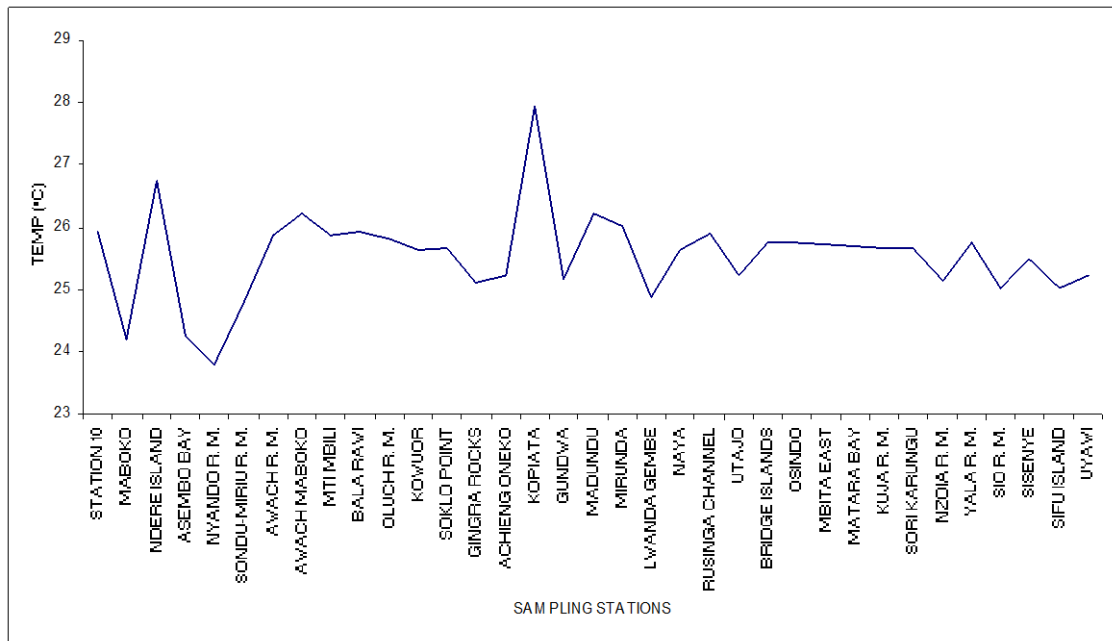
Appendix III : Coefficients for Canonical Variables of the Second Set

TN	-0.63298	0.169239	-0.246806	0.33401	0.645859	-0.0245664	-0.922539
Nitrates	-0.174409	-0.101763	-1.62164	-0.831647	-0.160294	0.520192	-1.29513
Nitrites	0.648952	0.79816	-0.424341	-0.439585	0.753943	-1.75192	1.89055
TP	0.221955	-0.0607476	-0.730187	0.723384	-1.70631	-0.106935	0.485442
SRP	-1.49258	-0.40012	0.35831	-0.379614	0.752009	0.817369	0.137799
Silicates	0.577352	-1.29165	1.71727	1.03165	-0.352516	0.0604845	-0.983278
Chloro.A	0.462079	0.186534	0.206703	0.16995	1.05714	0.719161	0.268192

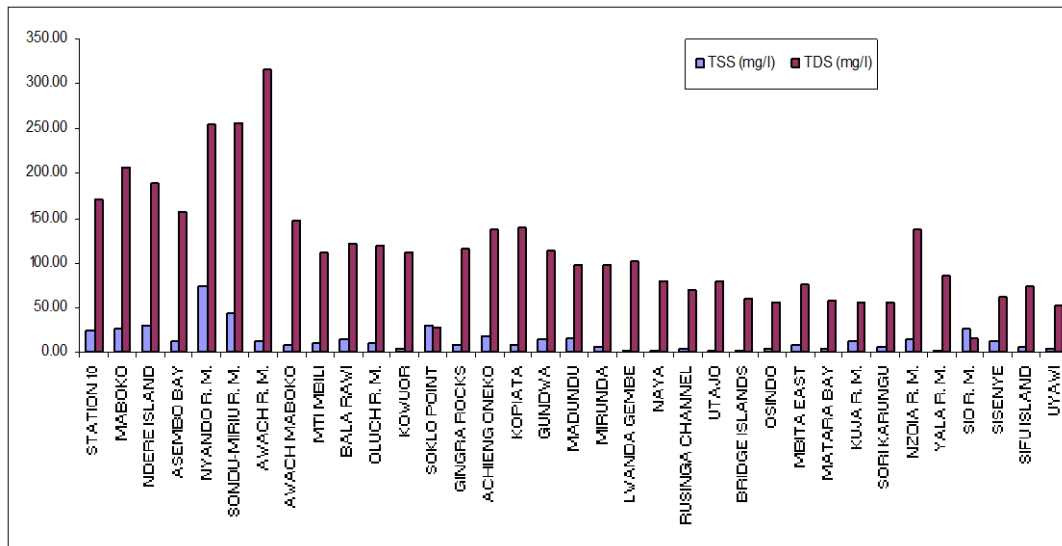
Appendix IV: Variation in depth for the investigated stations



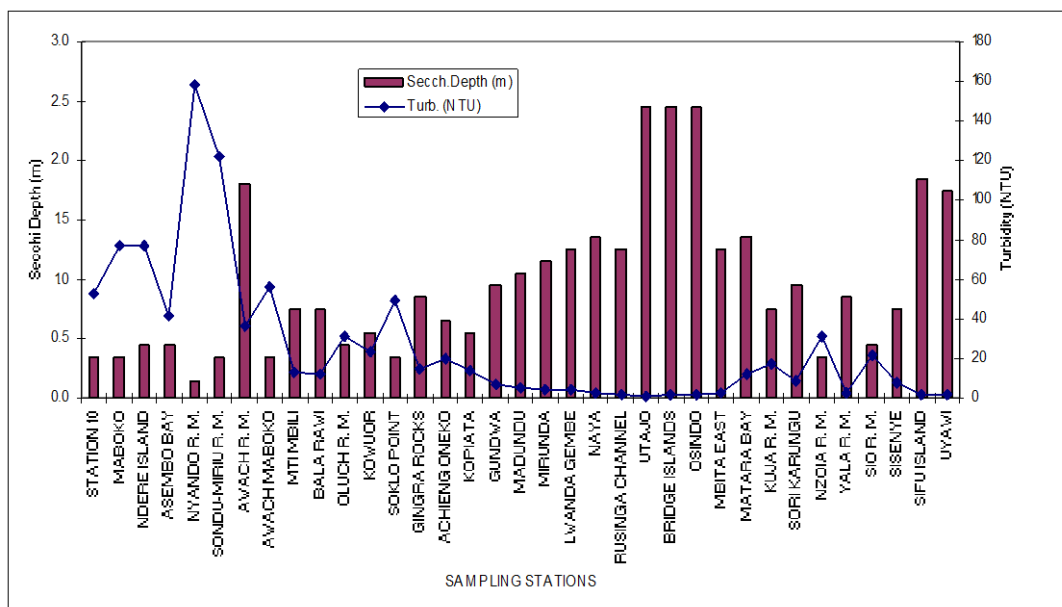
Appendix V: Variation in Temperature for the investigated stations



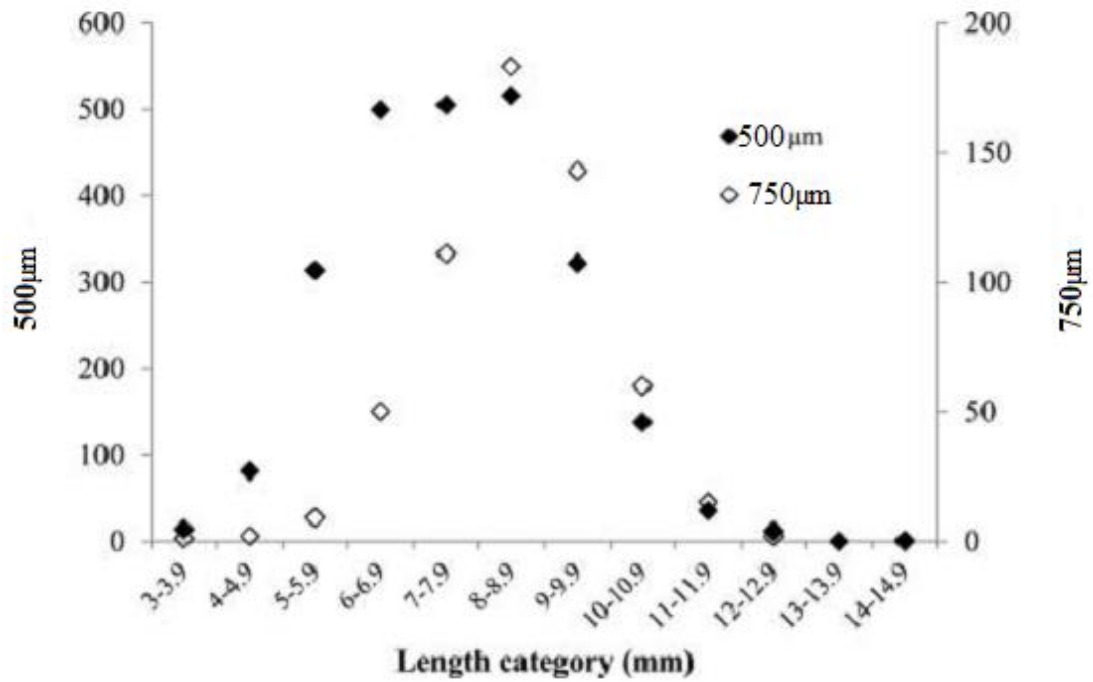
Appendix VI: Variation in TSS and TDS for the investigated stations



Appendix VII: Variation in Turbidity and Secchi depth for the investigated stations



Appendix VIII: Length frequencies of Nile Perch caught in standard larval fish collected using tow nets with 500 μm mesh and nets with 750 μm mesh



**Appendix IX: Monthly composite length frequency data of *L. niloticus*
representing samples collected from 2014 to 2015 pooled together**

Length-class TL (cm)	Jan	Feb	Mar	April	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
<30	5	5	1	5	2	1	49	11	5	1	60	2
30-40	9	6	9	11	9	9	39	14	11	6	20	0
40-50	30	58	45	52	39	154	132	122	184	102	147	28
50-60	213	346	293	264	254	262	526	324	403	342	333	122
60-70	37	79	75	76	56	54	119	86	105	86	51	28
70-80	14	26	17	14	8	19	42	29	25	15	32	10
80-90	8	10	7	8	3	9	19	8	11	15	11	5
90-100	5	4	3	3	1	6	9	3	2	4	8	0
100-110	3	0	1	0	0	3	1	3	2	1	2	1
110-120	0	1	1	2	1	1	1	1	0	1	2	0
120-130	0	0	0	2	0	0	1	0	0	0	0	0
Total	324	535	452	437	373	518	938	601	748	573	666	196