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An ecosystem-based approach to balancing cage aquaculture, capture fisheries, and biodiversity conservation in Lake Victoria, Kenya

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Dissertation

AN ECOSYSTEM-BASED APPROACH TO BALANCING CAGE AQUACULTURE, CAPTURE FISHERIES, AND BIODIVERSITY CONSERVATION IN LAKE VICTORIA, KENYA

by

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DEDICATION

To my father and mother who set me off on the road to this Ph.D a long-ago; my wife Kerubo, and my children Ositu, Nyabuti, and Mwambi for all their support, love, and enduring my absence throughout this endeavor.

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AN ECOSYSTEM-BASED APPROACH TO BALANCING CAGE AQUACULTURE, CAPTURE FISHERIES, AND BIODIVERSITY CONSERVATION IN LAKE VICTORIA, KENYA

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ABSTRACT

Lake Victoria is known for its cichlid fish species flock of 500 or more, which have been drastically decreased due to mass extinction. The lake's fisheries transformed from artisanal to industrial, with exotic species displacing the indigenous flock, changes linked to local and global anthropogenic consequences. Cage aquaculture has been established in the lake as a result of dwindling catch fisheries, a growing human population, and increased demand for fish. This dissertation investigates: 1) the distributional ecology of fishes along a limnological gradient in Lake Victoria, Kenya; and 2) the effects of cage aquaculture in the lake on limnology and fish communities, as well as the scientific and social correlates of proper implementation and growth. In April/May and July/August 2017, fish distribution patterns in the lake were surveyed using gillnets at eleven littoral sites and trawls at thirty lake-wide locations. From November 2018 to July 2019, four sites arrayed on an inshore-offshore gradient were sampled using paired cages and control stations. Using established protocols, water quality variables were sampled and analyzed. The status of variables and their associations were investigated using descriptive and exploratory statistics in the R statistical programming language. There was a limnological gradient, with nutrient concentrations, chlorophyll-a, and turbidity decreasing dramatically from the inner gulf to the outer waters. In the gulf's eutrophic waters, indigenous catfishes and cyprinids were abundant, while Nile perch and haplochromines were abundant in the open less eutrophic waters. Along the inner gulf-open lake gradient, Nile perch population structure, size at 50% maturity, and feeding patterns differed. There were no significant variations in environmental metrics between the paired cage farms and the controls, implying that inputs like sewage and agricultural runoff contribute more to eutrophication and the state of the gulf. Near cages, the average monthly total fish biomass was higher than in control areas. In the inner gulf, non-haplochromine fishes were many and diversified, with some species being particularly prevalent near cages. Based on biophysical constraints and overlap between cage aquaculture, fisheries, and biodiversity conservation in the lake, it was projected that cages could yield 250,000 metric tons of Nile tilapia per year. The findings indicate that, when correctly managed, cage aquaculture in Lake Victoria has a positive impact on both biodiversity and economic prosperity in the region.

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LIST OF ABBREVIATIONS

AGLs	African Great Lakes
ANOVA	Analysis of Variance
APHA	American Public Health Association
BOD	Biological Oxygen Demand
BU	Boston University
°C	Degree Celsius
CHANS	Coupled Human and Natural Systems
Chlo	Chlorophytes
Chlo.a	Chlorophyll-a
cm	Centimeters
Col.	Collinearity
Cond	Conductivity
cont	Content
Cyno	Cyanophytes
Diat	Diatoms
Dino	Dinoflagellates
DO	Dissolved Oxygen
EAC	East African Community
EBFM	Ecosystem-Based Fisheries Management
EBM	Ecosystem-Based Management
EDTA	Ethylene Diamine Tetraacetic Acid
EPA	Environmental Protection Agency
Eug	Euglenoids
FAO	Food and Agriculture Organization
FCRs	Feed Conversion Ratios
FiGR	Fish Genetic Resources
FTU	Formazin Turbidity Units
g	Grams

GAqP	Good Aquaculture Practices
GF/C	Glass Microfiber filters
GIS	Geographic Information System
GPS	Global Positioning System
H	Shannon Diversity Index
H_2SO_4	Sulphuric Acid
Haps	Haplochromines
HCL	Hydrochloric Acid
HDPE	High-Density Polyethylene
IDPs	Internally Displaced People
IG	Inner gulf
IG_RM	Inner gulf near river mouth
IS	Inshore
IS_RM	Inshore near river mouth
IUUs	Illegal Unreported and Unregulated
J	“Evenness” Of the Community
KMFRI	Kenya Marine and Fisheries Research Institute
KNBS	Kenya National Bureau of Statistics
LBDA	Lake Basin Development Authority
LVBC	Lake Victoria Basin Commission
LVFO	Lake Victoria Fishery Organization
m	Meters
MCL	Maximum Contaminant Level
MG	Mid Gulf
mg l^{-1}	Milligrams Per Liter
MG_RM	Mid Gulf River Mouth
MT	Metric Tonnes
mV	Millivolts
NH_4^+	Ammonium

NO_2^-	Nitrites
NO_3^-	Nitrates
NSF	National Science Foundation
ORP	Oxidation-Reduction Potential
OS	Offshore
PCA	Principal Components Analysis
PCs	Principal components
pH	-log10 [H+] (Negative Log10 of Hydrogen Ions Concentration
PO_4+	Phosphates
R.V	Research Vessel
S	Total Number of Species
SDGs	Sustainable Development Goals
SiO_2	Silicon
SOPs	Standard Operating Procedures
SRP	Soluble Reactive Phosphorous
SRSi	Soluble Reactive Silicon
SSA	Sub-Saharan African
ST	Standard Length
Stom	Stomach
TDS	Total Dissolved Solids
Temp	Temperature
TL	Total Length
TN	Total Nitrogen
TP	Total Phosphorous
Tukey’s HSD	Honestly Significant Differences
Turb	Turbidity
UN	United Nations
UNEP	United Nations Development Program
W	Weight

WFC	WorldFish Center
YSI	Yellow Springs Instruments
Zyg	Zygnematecea
$\mu g\ l^{-1}$	Micrograms per Liter
$\mu S\ cm^{-1}$	MicroSiemens per Centimeter

CHAPTER ONE: THE ENVIRONMENTAL CONTEXT FOR CAGE AQUACULTURE IN THE KENYAN WATERS OF LAKE VICTORIA: RECENT CHANGES IN LIMNOLOGY, FISHERIES, AND FISH BIODIVERSITY.

1.1 Introduction

Lake Victoria is the largest of the African Great Lakes and the second-largest freshwater lake in the world (after Lake Superior) in terms of surface area (~69,000 km^2). It also harbors one of the two most productive fisheries in the world (the other being Cambodia's Tonle Sap), providing the lakeside nations of Kenya, Uganda and Tanzania (with Rwanda and Burundi being part of the catchment) with food security and foreign revenue. Lake Victoria supports a riparian community of about 45 million people who depend on it directly and indirectly for food in the form of fish, economic livelihoods, climate regulation, and other ecosystem services (Sun *et al.*, 2014). Since the late 1970s, the Lake Victoria ecosystem has been subject to serial traumas including climate change, cultural eutrophication, exotic species, and overfishing. These have profoundly altered the outlook for its hundreds of endemic fish species and its fisheries and dependent human population.

With wild capture fisheries now in decline, a new industry has emerged based on the rearing of Nile tilapia (*Oreochromis niloticus*), an introduced species, in floating cages in the lake. This dissertation explores 1) the distributional ecology of fishes along a limnological gradient in Lake Victoria, Kenya; 2) Cage aquaculture in the lake - its effects on limnology and fish communities; the production capacity for the industry if practiced rationally and sustainably; and some of the scientific and social correlates of doing so properly. Cage aquaculture can address a host of biological and social ills in the lake, or it could itself become another among them. This introductory chapter provides background on the lake basin system and its recent ecological and management history. The most interesting question here is just how the advent of cage aquaculture can build upon this history, helping to ensure that changes to come are for the betterment of human well-being in the region, avoiding those pitfalls capable of redirecting the system to the detriment of its peoples and natural assets. One of the most significant changes to the lake was the introduction of Nile perch (*Lates niloticus*) from other parts of Africa. Nile perch is a huge, predatory fish in the family Latidae (formerly included within the Centropomidae). It is essentially a freshwater barramundi, whose establishment and subsequent spectacular success in Lake Victoria has been accused of much of the troublesome changes that the lake has seen since the late 1970s. However, it was just one of several important drivers of the degradation of the Lake Victoria ecosystem that peaked during the latter third of the 20th Century. Thus, cage aquaculture has come to the lake during a time of ongoing, turbulent change.

1.2 Environmental context

Until the mid to late 1970s, the lake was mesotrophic. Since then, it has been highly eutrophic due to a combination of human influences, including deforestation and soil erosion in the catchment, the introduction of exotic species and pollutants, over-extraction via fisheries, habitat destruction, modification and fragmentation, resource use conflicts, and anthropogenic climate change (Barel *et al.*, 1985; Kaufman, 1992; Witte *et* *al*., 1992; Goldschmidt *et al*., 1993; Kitchell *et al*., 1997; Balirwa *et al*., 2003; Seehausen, 1997, 2003; Hooper *et al*., 2005; Cornelissen *et al*., 2015; Downing *et al*., 2015; van Zwieten *et al*., 2016; Nyamweya *et al*., 2020). The lake's limnology and fisheries changed profoundly in the early to mid-1980s, with associated impacts on the diversity of its flora and fauna. There has been a massive shift in Lake Victoria's fish community and water quality over the past five decades. These limnological and ecological changes have adversely affected the provisioning of ecosystem services, putting livelihoods in the riparian communities at risk.

1.3 Lake Victoria Pre-Nile perch introduction

1.3.1 Lake Victoria's indigenous fish species before Nile perch

Before introducing the Nile perch, Lake Victoria was a biodiversity hot spot, home to an astounding diversity of cichlids with over 500+ endemic haplochromine species (Kaufman, 1992; Witte *et al*., 2007). There were also two endemic tilapiines, *Oreochromis esculentus* and *Oreochromis variabilis*, and 38 non-cichlid species, of which ten were endemic (Kudhongania and Chitamwebwa, 1995; van Oijen, 1996). The latter included two cyprinids that became commercially important species: *Labeo victorianu*s ('ningu') and *Rastrineobola argentea* ('omena'). The riparian communities exploited the lake's fishes, but this had little effect on the stocks in pre-colonial times, as human population densities were low and the traditional harvesting methods were inefficient (Taabu-Munyaho *et al*., 2016; Nyamweya *et al*., 2020). Soon after the arrival of European explorers and settlers on the lakeshores, there was an influx of people to work on emerging plantations. The unfolding development brought extreme anthropogenic pressure to the ecosystem on several fronts, including greatly intensified fishing pressure (Graham, 1929). The Ugandan Railway's arrival in Kisumu in 1901 set the stage for other significant events that beset the lake. There was a population irruption around the lake as migrants moved in, and with the consequent introduction of flax gill nets by the British in 1905 to replace the local villagers’ papyrus nets and fish traps. With this innovation, overfishing soon became a severe problem. The catches dropped and fishers turned to nets with ever-smaller mesh sizes, thus destroying both the breeding adults and young of many native species (Graham, 1929). This was exacerbated by the introduction of non-selective beach seine nets (the 1920s) that further intensified fishing in littoral zones and damaged the breeding and nursery grounds of the indigenous cichlids (Graham, 1929).

The initial comprehensive research survey in Lake Victoria carried out in the late 1920s (Graham, 1929) gave a baseline from which ecosystem change could be estimated; and showed the lake had clear waters and provided excellent conditions for the feeding and spawning of cichlids that were abundant. The tilapiines *Oreochromis esculentus* (‘ngege’) and *O. variabilis* (‘mbiru’) were the pillars of the small-scale fishery. The early 1920s witnessed the introduction of gillnets, with the initial fishery targeting *Oreochromis esculentus* and *Oreochromis variabilis*. At the same time, *Labeo victorianus* (‘ningu’) were trapped during their spawning movements up the rivers, to devastating effect. Graham (1929) warned of the dangers of overfishing. Intensive gillnetting of gravid *L. victorianus* as they migrated up the affluent rivers to breed led to the demise of the fishery, and the species was commercially extinct by the mid-1960s (Cadwalladr, 1965; Ogutu-Ohwayo, 1990). The indigenous tilapia stocks were depleted in areas of intensive fishing (Fryer, 1974). In a move intended to boost fisheries, the non-native tilapiines *Coptodon zillii, C. rendalli, Oreochromis leucostictus and O. niloticus* were introduced in the 1950s. Introductions of Nile perch (*Lates niloticus*) to Lake Victoria began in 1954 and expanded in the early 1960s (Welcomme, 1968; Balirwa, 1992; Lowe-McConnell, 1993; Pringle, 2005a, b). In the early 1970s, the species was still not fully established. Data from the Nyanza Gulf (now Winam Gulf) in the 1970s show a catch dominated by indigenous fish species (Table 1-1). Nile perch were in small numbers in 1970 but were well established by 1977. The Nile perch population increased by 3.5 times between 1975 and 1977, while the catches of catfish (*Bagrus*) and lungfish (*Protopterus*) collapsed in 1977, falling by 84% and 98%, respectively. In the same period, haplochromines declined by 12%, but by 1982–1983 they had collapsed totally, while Nile perch had increased 10-fold (Table 1-1). While intensive fishing (especially the longline fishery) may have contributed to the collapse of native fish stocks in some areas, there also seems to have been selective predation by the Nile perch. This was indicated by a rapid decline in smaller individuals of both endemic tilapiine species, with larger individuals persisting for longer (Goudswaard and Witte, 1997). Initially, the decline and loss of haplochromines and other indigenous species were attributed to predation by the introduced Nile perch (Barel *et al.*, 1985; Payne, 1987; Achieng, 1990; Ligtvoet *et al.*, 1991; Kaufman, 1992; Kudhongania *et al.*, 1992, Marshall, 2018). Other researchers have observed that overfishing, eutrophication, and climate change likely contributed (Hecky *et al.*, 1994; Bundy and Pitcher, 1995; Witte *et al.*, 2007; van Zwieten *et al.*, 2016). For several decades now, other indigenous species (*Mormyrus kannume, Labeobarbus altianalis, Schilbe mystus, Clarias gariepinus, Bagrus docmak,* and *Protopterus aethiopicus*) have declined drastically in the lake and the ever-shrinking fringing wetlands (Yongo *et al.*, 2018; Nyamweya *et al.*, 2020; Outa *et al.*, 2020).

	Biomass (kg ha^{-1})					
Fish species	1969-1970 (n = 19)	1975 (n = 69)	1977 (n = 167)	1982-1983 (n=54)	1989-1990 (n = 43)	2017 (n = 30)
Haplochromines	35.8	32.7	28.7		0.1	0.1
Nile perch	+	0.8	2.8	29.0	32.7	15.5
Tilapias[1]	0.1	0.3	1.0	1.4	0.8	0.03
Bagrus docmak	15.0	15.1	2.5	1.8	0.1	0.04
Protopterus aethiopicus	3.7	10.7	0.3		+	0.1
Other species	2.2	0.5	0.6	0.1	0.8	0.5
Total	56.8	60.1	35.9	32.3	34.5	16.3

[1] *Oreochromis variabilis* and *O. niloticus*

Table 1-1. Biomass (kg ha^{-1}) of major fish species in the Nyanza Gulf (Winam Gulf), Kenya, of Lake Victoria in 1969-1990. Data from bottom trawl surveys; n = number of hauls; + = densities <0.1 kg ha^{-1}, blank cells = no catch. Adapted from Ochumba, 1995; Taabu-Munyaho *et al*., 2016, KMFRI unpublished data**.**

1.3.1.1 Overfishing

At one point, it was thought that overfishing might be the leading cause of haplochromine decline in the lake (Acere, 1988; Harrison *et al*., 1989; Kudhongania and Chitamweba, 1995). The view has been used to back the argument that haplochromine decline was a necessary forerunner to the Nile perch eruption (Silsbe and Hecky, 2008; van de Wolfshaar *et al*; 2014). However, this suggestion could not explain the decline of haplochromines in lightly fished areas, and those where no fishing took place (Witte *et al*., 2007; van Zwieten *et al*., 2016).

The human population in the Lake basin has been progressively increasing (Table 1-2). In 1960, only about 8.7 million people were inhabiting the riparian catchment. Currently, the population has more than quadrupled, with over 45 million people settled in the watershed. On average, the population increases at a rate of 3.8% per annum (Nyamweya *et al*., 2020). The burgeoning population has seen the number of fishers, fishing crafts, and gear increase steadily in the lake over time, leading to increased fishing effort. Overall, illegal, unreported and unregulated (IUUs) gear like small seines that usually target small pelagics in the lake has increased. The observed increase is consistent with an increase in fishers and fishing crafts (Nyamweya *et al*., 2020).

Year	Population density (Persons/km^2)	Population (millions)	Source
1960	45	8.7	UNEP
1970	61	11.8	
1980	84	16.2	
1990	115	22.2	
2000	159	30.7	
2010	218	42.1	Bremner *et al*., (2013)
2020	220	42.4	
2030	315	60.8	
2040	396	76.5	
2050	589	113.2	

Table 1-2. Human population trends in Lake Victoria basin. The population density in the Lake Victoria watershed is one of the highest in the world, increasing at a rate of 3.8% per annum (Adapted from Nyamweya *et al*., 2020).

1.3.1.2 Early signs of eutrophication

The sudden eutrophication of the lake was attributable to Nile perch. Still, evidence of eutrophication from the 1950s onwards led some researchers to conclude that it resulted from climatic changes (Taabu-Munyaho *et al*., 2016). Fossil assemblages of chironomids also prove that deep-water anoxia became more prevalent around that time (Lehman, 1998; Verschuren *et al*., 2002; Stager *et al*., 2009; Hecky *et al*., 2010). The results of cores from Lake Victoria and cross-checked with Talling's notebooks, found an inflection point in eutrophication during the late 1970s (Hecky *et al*., 1994). There were occasions when upwelling brought toxic water to the surface, causing unpleasant smells and fish kills (Kitaka, 1971; Ochumba and Kibaara, 1989). These events may have been an early indication that eutrophication had already begun because there is evidence from sediment cores that this process had started before the Nile perch explosion (Stager *et al*., 2009; Hecky *et al*., 2010). The importance of climate change, notably during a period of low wind stress from about 1977 to 1983, has been emphasized as a factor in the eutrophication of Lake Victoria. Its influence on mixing depths, increased stratification stability and deoxygenation of deeper waters; could have triggered an abrupt transition in the lake by mobilizing phosphorus-rich detritus buried in the sediments (Silsbe and Hecky, 2008; Hecky *et al*., 2010). It has also been proposed that Nile perch populations were initially suppressed because of intense predation by the then still abundant haplochromines (van Zwieten *et al*., 2016; Marshall, 2018).

The history and causes of eutrophication in Lake Victoria can also be inferred from diatom records from the lake. These show that a transition from *Aulacoseira-*

dominated planktonic assemblages to dominance by long *Nitzchia spp*., occurred along the Kenyan coast from the 1940s to the early 1950s and late 1970s offshore, suggesting a time-transgressive process (Stager *et al*., 2009). These changes are not readily attributable to Nile perch population growth during the early 1980s, but more likely reflect responses to long-term nutrient enrichment and climatic instability in the region (Stager *et al*., 2009). The diversity of planktonic communities has since declined dramatically, and a namesake variety of *Aulacoseria nyassensis* may now be nearly extirpated. Although local planktonic communities varied considerably in the past, the current domination of diatom assemblages by *Nitzschia* is unprecedented in the 15,000-year history of Lake Victoria (Stager *et al*., 2009).

1.4 Lake Victoria post-Nile perch introduction

1.4.1 Collapse of indigenous fish species

The collapse of the haplochromines in the early 1980s, fish that initially made up the bulk of the fish biomass, was one of Lake Victoria's most spectacular change indicators (Figure 1-1). It involved a massive loss of both horizontal (i.e., number of species) and vertical (i.e., trophic levels) diversity, and it appeared that many haplochromine species had become extinct (Ogutu-Ohwayo and Hecky, 1991; Goldschmidt and Witte, 1993; Mbabazi *et al*., 2004; Witte *et al*., 1992, 2007). The populations of most other native species also collapsed around this time, as the biomass of all other species decreased other than the Nile perch, Nile tilapia, and *omena* (Table 1-1). This was possible because of fishing efforts and Nile perch predation (Taabu-

Munyaho *et al.*, 2016). Decreased oxygen concentrations in the deeper water (>40 m) were thought to have contributed to the haplochromine decline (Kaufman and Ochumba, 1993; Hecky *et al.*, 1994; Bundy and Pitcher, 1995; Ochumba, 1995). The decreases in catfish may have resulted from the increased use of longlines (i.e., an increase in fishing effort), as suggested by Marten (1979). Reduced diversity can trigger extinctions and reduce ecosystem functions (Duffy *et al.*, 2007; Srivastava and Bell, 2009; Jabiol *et al.*, 2013). This would have been the scenario in Lake Victoria, where the rapid disruption of complex interactions within its diverse fish community involved many species at every trophic level (Ligtvoet and Witte, 1991; Witte *et al.*, 1992).

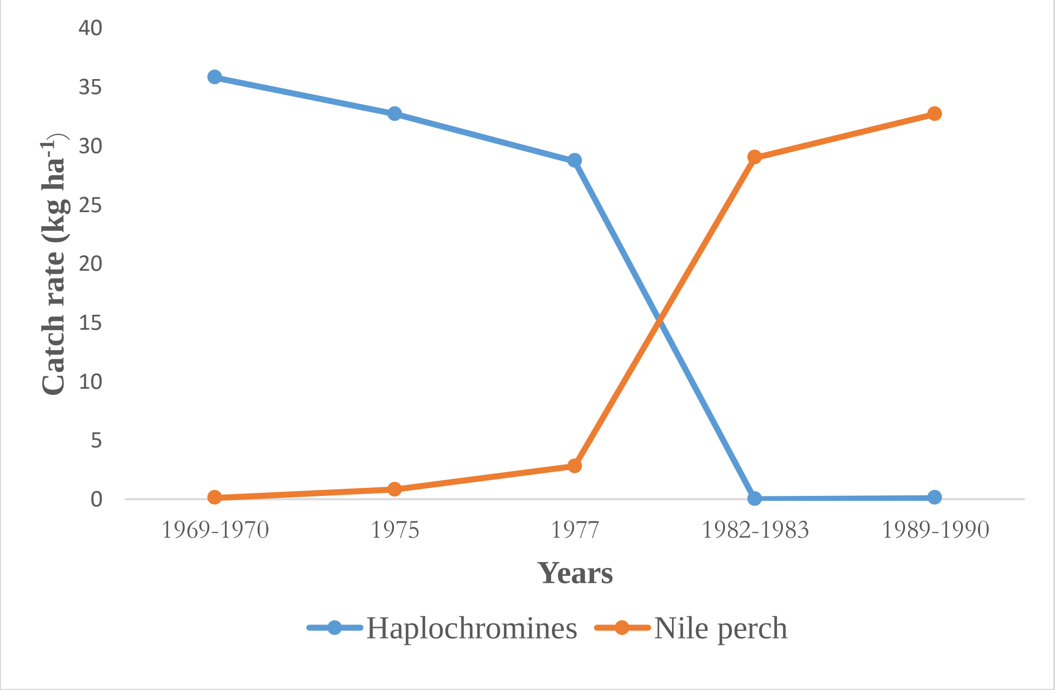


Figure 1-1. Biomass (kg ha^{-1}) of haplochromines and Nile perch in bottom trawls in Nyanza Gulf, Kenya, of Lake Victoria 1969–1990. Nile perch were in small numbers in 1970 but well established in 1977. By 1982–1983, the haplochromines had collapsed while Nile perch had increased 10-fold. Modified from Ochumba, 1995**.**

Fish store a high proportion of ecosystem nutrients in their tissues, transport nutrients farther and faster than many other aquatic animals, and excrete dietary nutrients in dissolved forms that are readily available to primary producers (Vanni, 2002). The destruction of native fishes in Lake Victoria would have released a significant quantity of nutrients into the lake, which became available for algal growth and contributed further to eutrophication. At least in part, the algal blooms of the 1980s in Winam Gulf could have been caused by the loss of the phytoplanktivorous and detritivorous haplochromines, which like the already-vanished ngege, grazed phytoplankton. In their absence algal blooms, especially of cyanobacteria, became common (Ochumba and Kibaara, 1989; Sitoki *et al*., 2010).

1.4.2 Eutrophication post Nile perch introduction in Lake Victoria

Before 1980, the lake was an oligotrophic-mesotrophic waterbody with relatively low primary productivity (Talling and Talling, 1965; Talling, 1966), but after 1980 it was highly eutrophic, with dense blooms of cyanobacteria and severe deoxygenation of its deep waters (Hecky, 1993; Hecky *et al*., 1994). These ecological changes can be ascribed to anthropogenic activities because of three nearly simultaneous occurrences: 1) a population irruption of the introduced Nile perch (*Lates niloticus*), 2) collapse of the indigenous species and 3) significant physicochemical and other ecological changes (Balirwa *et al*., 1995, 2003; Witte *et al*., 2012; Taabu-Munyaho *et al*., 2016; Kudhongania *et al*., 2019). These changes were unprecedented in scope and rapidity (Barel *et al*., 1985; Ogutu-Ohwayo, 1990; Kaufman, 1992; Witte *et al*., 1992) and have been a significant focus of attention by the scientific community. The water quality changed dramatically, with phosphorous concentrations around 2.5–3.0 times greater in the 1990s than in the 1960s, while silica decreased by almost 90% and 60% in inshore and offshore waters, respectively, over the same period (Table 1-3).

Limnological parameter	1960–1961		1990s	
	Inshore	Offshore	Inshore	Offshore
TP (µmol l^{-1})	1.2	1.1	2.8	3.0
Si (µmol l^{-1})	74	66	10	25
Chl-a (µg l^{-1})	13	3	71	13.5
PP (mg O_2 m^{-2} h^{-1})	11	7.4	22	14

Table 1-3. Nutrient and primary productivity data for Lake Victoria in 1960–1961 and the 1990s. TP = total phosphorous, Chl-a = chlorophyll a, Si = silica, PP = primary productivity. Adapted from Hecky *et al*., 2010; Taabu-Munyaho *et al*., 2016.

Most dramatically, chlorophyll-*a* concentrations increased 5-fold while primary productivity at least doubled, reflecting the increased density of phytoplankton, primarily cyanobacteria. Deoxygenation of deeper water became more pronounced, occurring at shallower depths than before (Hecky *et al*., 1994) and contributing to fish kills (Ochumba and Kibaara, 1989; Ochumba, 1990). Decreased oxygen concentrations in deeper water (>40 m) were thought to have contributed to the haplochromine decline (Kaufman and Ochumba, 1993; Heckey *et al*., 1994; Bundy and Pitcher, 1995). On the other hand, hypoxic deep waters could have provided a refuge for haplochromines to evade the Nile perch because they tolerate lower dissolved oxygen levels than do Nile perch. While this could be true, haplochromine biomass in shallow areas was always higher than in the deepest waters (Kudhongania and Cordone, 1974). Furthermore, the deep-water refugium hypothesis can be challenged because Nile perch have been observed as sonar targets and also were caught in water with oxygen concentrations well below 2 mg l^{-1} (Kaufman, pers.

com; Wanink *et al*., 2001), showing that they can move into hypoxic waters from time to time. Even so, such low oxygen concentrations could have first affected both Nile perch and *Rastrineobola*, as they are less tolerant of low oxygen concentrations than were many of the haplochromines (Wanink *et al*., 2001; Witte *et al*., 2005). Nevertheless, both of these species thrived after the lake became eutrophic.

Algal blooms also reduce water transparency, a potentially serious consideration for haplochromine fishes that rely heavily on vision for mate selection. Water with a narrow spectral width may have constrained the functional diversity of color signals, limiting the number of species that could be sexually isolated and thus increasing the frequency of intermediate phenotypes between sympatric forms (Seehauseen *et al*., 1997). However, losses among rock-dwelling haplochromines, which were better able to evade Nile perch, were less severe than among the open-water species (Witte *et al*., 2007), suggesting that reduced visibility is not the only factor involved; both groups should have been affected by algal blooms and turbidity. In any event, the introduction of the Nile perch into Lake Victoria was involved in various ways in the ecological damage that ensued, including a reduction in the diversity of the resource base at several trophic levels.

1.4.3 The catchment as a cultural eutrophication driver

The cause of cultural eutrophication in the lake was linked to the rapid growth of the lake basin's human population, which led to increased nutrient loading to the lake through deforestation, land clearance, erosion of nutrient-rich soils into the lake, forest burning, and the growth of cities and towns (Verschuren *et al*., 2002). Anthropogenic activities including settlement on the shoreline, urbanization, intensive cultivation, animal husbandry and wetlands clearance have accelerated the rate of nutrient inputs, leading to changes in the chemical, physical and biological properties of Lake Victoria water (Bootsma and Hecky, 1993; Hecky, 1993; Muggide, 1993; Sitoki *et al*., 2010: Mwamburi *et al*., 2020). Winam Gulf, Kenya, is historically the most densely populated and heavily polluted lake region (UNEP, 2006). Both non-point and point nutrient sources are involved.

1.4.3.1 Non-point sources

The major source of catchment nutrients in Lake Victoria is agricultural runoff. Excess nitrogen and phosphorous are washed from agricultural farms into the rivers and eventually into the lake during rainstorms (Sitoki *et al*., 2010). Agricultural practices and farms in the catchment include tea plantations, maize farms, horticultural farms, and rice paddies at irrigation schemes; effluents compound these from paper factories, and sugar cane plantations that dot the catchment. Deforestation in the catchment has also contributed to increased runoff and silt deposition into the rivers and eventually into the lake (Mwamburi *et al*., 2020). Wetlands clearance along the river banks and the shoreline has exacerbated the situation and now little is left of buffer zones or natural filters (Nyamweya *et al*., 2020). Drastic seasonal changes in rivers and effluents have frequently interrupted the breeding of potamodromous species (Outa *et al*., 2020).

1.4.3.2 Point sources

These include discharges from industrial wastes, domestic effluents, and construction debris. Examples include discharges from factories, industries, and faulty sewerage treatment plants via pipes, channels, conduits, drains and direct discharge into the lake. The pollutants include industrial chemicals, suspended solids, heavy metals, pesticides and other hazardous materials, leading to water quality deterioration (Lung'ayia *et al*., 2001) and a change in phytoplankton species composition from one dominated by diatoms (Talling, 1966) to that presently dominated by cyanobacteria, especially in Winam Gulf (Sitoki *et al*., 2012).

1.4.4 Water hyacinth (*Eichhornia crassipes*)

The invasive water hyacinth *(Eichhornia crassipes)* was first reported in Lake Victoria in 1989. It was accidentally introduced into the lake from South America in the 1980s, growing massively in 1992–1993 and reaching a maximum in 1997–1998 (Kateregga and Sterner, 2006). Its spread was attributed to the lake's eutrophic condition (Williams and Hecky, 2005) and by 1998, it covered about 180 km^2 of the lake. Though diminished because of biological control and manual and mechanical removal, it is still a nuisance (Albright *et al*., 2004; Wilson *et al*., 2007), especially in Winam Gulf. Water hyacinths are one of many invasive species that affect ecological processes and present a significant threat to native biodiversity in the Lake Victoria Basin (Ogutu-Ohwayo *et al*., 1997). Water hyacinth reproduces rapidly and covers large swathes of the lake, forming dense mats of plants that block sunlight needed for the survival of life below the surface

(Ongore *et al*., 2018). These changes have led to severe eutrophication, and anoxia in some parts of the lake, especially Winam Gulf (Gichuki *et al*., 2012; Nyamweya *et al*., 2020). The water hyacinth has also had dramatic effects on other activities in the lake, such as fisheries, recreational use, transport, drinking water, and other ecosystem services. Its interwoven network of mats and dead plants traps silt, providing substrate for the growth and proliferation of other macrophytes such as hippo-grass (*Vossia cuspidata*). These macrophytes aggregate together to form massive moving islands on the lake's surface, posing a great threat to fishing and transportation on the lake, and by extension are a threat to livelihoods in the lake's riparian communities. Floating islands made of these mats (water hyacinth, water lettuce, hippo grass, and papyrus) can be huge, spreading to about 200 – 800 meters across. The main reason why the water hyacinth and hippo grass are flourishing at the levels they are now is because the lake water is highly fertile and immensely silted. This profusion of floating macrophytes, however troublesome, can also function as a blessing in disguise as they reduce the nutrients and toxins humans churn into the lake. The root problems are anthropogenic, including deforestation, unsuitable agriculture, and pollution.

1.4.5 Other potential drivers

Other potential sources of nutrient loading into the lake include atmospheric deposition, fishing activities, forest burning, washing of cars and clothes along the shoreline, and increasingly of late, cage aquaculture.

1.4.5.1 Climate change and global processes

Nitrogen can be freely fixed into aquatic systems (atmospheric nitrogen) contributing to eutrophication. Some species of cyanobacteria can fix nitrogen from the atmosphere just as legumes do on land. Other processes like lightning yield nitrates and other atmospheric residues that are deposited into the lake through precipitation. Climatic changes and global processes contribute to this and can impact the thermal stability of the lake (Ogutu-Ohwayo *et al*., 1997; MacIntyre, 2013; MacIntye *et al*., 2014).

1.4.5.2 Fishing activities

Motorized boats and vessels operating on the lake contribute to pollution by direct discharge into the lake (oils and toilet wastes). This adds more nutrients to the lake. Overexploitation of certain fish species may cause an imbalance in food chains or food webs, interfering with nutrient recycling in the lake.

1.4.5.3 Use of phosphorus-based detergents

Many riparian household communities perform washing chores on the lakeshore (i.e., clothes and utensils). Another common scenario is washing lorries, vans, cars, motor bikes, and bicycles on the lakeshore or the banks of rivers and streams affluent to the lake. Most of the detergents used are phosphorus-based, thus adding phosphorus and other chemicals and oils into the lake.

1.4.5.4 Forest burning

Widespread deforestation and biomass burning in most of the Eastern and Central African nations add nutrients to Lake Victoria via ash blown by winds (Delmas et al., 1991; Hao and Liu, 1994). In the lake, where water input by rainfall exceeds river inflow by a greater ratio (6:1), direct atmospheric deposition of phosphorus on the lake may be significant (Tamatamah *et al*., 2005). Land use in Lake Victoria basin has seen intensification of existing agricultural land, especially in the highlands; reduction of vegetation in protected areas; reduction in forestland, and increase in settled areas through sprawling informal urban centers, especially along beaches (UNEP, 2006). These changes have occurred amid varied social, environmental, and economic drivers (Odada *et al*., 2006).

1.4.6 Biomass trends of the major fish stocks in Lake Victoria

Figure 1-2 shows the biomass trends of the major fish stocks and the atyiid prawn *C. nilotica* in Lake Victoria from 1999 to 2017. Generally, the biomass for Nile perch, *omena*, and haplochromines has been increasing from 2008 up to around 2014, after which Nile perch biomass slightly decreased in 2015 and 2016. *Omena* exhibits a decline after 2015, possibly due to overfishing.

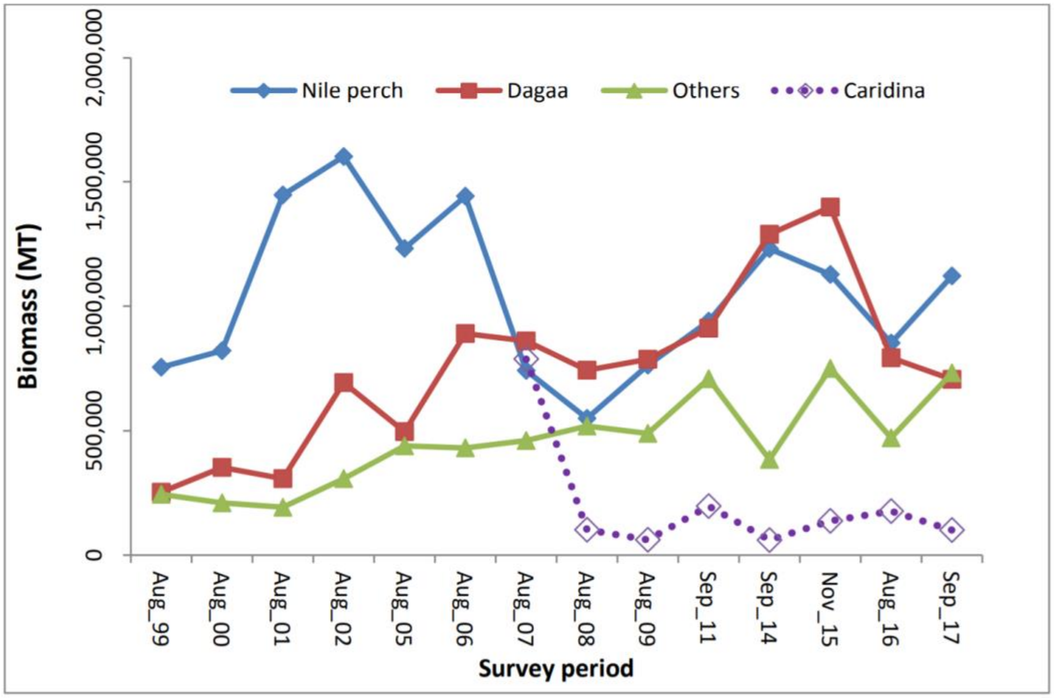


Figure 1-2. Trends in biomass of the major fish stock taxa in Lake Victoria estimated through acoustic surveys (August 1999–September 2017). Biomass data are not available for years 2003–2004, 2009, and 2012–2013 (Adapted from LVFO, 2017 report).

In catch data, the apparent abundance of any one species can appear to increase initially as an artifact of fishing effort. However, beyond a certain level, the catches decline as the species is beginning to show signs of overfishing (Nyamweya *et al*., 2020). Observations have shown recovery and resurgence of some species, especially groups of haplochromines, possibly a result of predatory release occasioned by the declining Nile perch stocks thought concurrent with this has also been a return to more regular mixing and oxygenation of the lake’s deeper waters. Tilapias and other fish species exhibit a declining trend in catches, indicating that these groups are overfished. Considering all species together, catches are still increasing with increasing harvesting capacity. Nevertheless, catch composition is shifting towards one dominated by small pelagics- an emerging trend in the African Great Lakes (AGLs) and, indeed, throughout the world's freshwater and marine waters. The high-value species and sizes are declining. The significance of this is reduced income for fishing communities unless more value is harnessed from the abundant small pelagics. Total annual fish catches in Lake Victoria amount to around one million tonnes, with about 230,000 tonnes of landed Nile perch fueling an export fishery that generates substantial foreign revenue (LVFO, 2016).

1.4.7 Haplochromine recovery and biodiversity in Lake Victoria post Nile perch introduction

The "new' Lake Victoria that emerged after the Nile perch explosion had a depauperate fish fauna (lacking in diversity of species, biomass, and genes), effectively reduced to just three species in the commercial fishery, Nile perch, Nile tilapia and *omena* (Ligtvoet *et al*., 1991). One other native species shows a notable increase in this era: the tiny prawn *Caridina nilotica*. The primary productivity of the lake increased and the food chains were simplified leading to an increase in total catch from 100,000 tonnes per annum in 1980 (Wilson, 1993; Kitchell, *et al*., 1997) to around 600,000 tonnes in 1990 and to around 1,000,000 tonnes per annum by 2010; and the Nile perch dominated the catch during its irruption phase of 1980–1990 (Taabu-Munyaho *et al*., 2016). However, the Nile perch boom did not last long, and since 2010 its catches and those of Nile tilapia have plummeted, with *omena* now dominating the catch (Taabu-Munyaho *et al*., 2016). With declining Nile perch biomass under intensive fishing, some haplochromines species have shown recovery (Witte *et al*., 2007). This would be attributable to demographic changes brought about by fishing, which eliminated larger Nile perch that preyed upon haplochromines to a greater extent than the smaller ones (Kishe-Machumu *et al*., 2012; Mkumbo and Marshall, 2015). The increase in the number of fishers, increase in effort and the use of illegal, unreported and unregulated (IUUs) gear led to overfishing and degradation of fishing habitats (LVFO, 2009; Medard, 2019; Outa *et al*., 2020). Other possible contributors to partial haplochromine recovery include adaptations to eutrophic conditions and changes in the phytoplankton community (van Rijssel and Witte, 2013). Silsbe and Hecky (2008) postulated that the recovery may have resulted from a shift towards species better adapted to eutrophic conditions, a hypothesis supported by the current abundance of detritivorous haplochromine species (Van der Meer *et al*., 2012; van Rijssel *et al*., 2015, 2016; Natugonza *et al*., 2021). Gill surface area in the pelagic zooplanktivorous haplochromine *Yssichromis pyrrhocephalus* was 70% larger in specimens collected in 1993–2001 (eutrophic lake) than those collected in 1977–1981 lending some support to this view (Witte *et al*., 2008). However, it is not known in how many recovering haplochromine species the gill area increased. Maybe the increase in gill area was a pre-adaptation to low oxygen concentrations for fish living under papyrus mats escaping Nile perch predation, or an adaptation to increased use of the hypoxic zone during diel vertical migrations. The change in the phytoplankton community from diatom to cyanobacterial dominance could reduce the digestibility and nutrient density of detritus. Sediment pollution in Mwanza and Nyanza Gulfs (Kishe and Machiwa, 2003; Campbell *et al*., 2003) can have greatly impacted detritivores. The recovery of some haplochromine species is a salient development in post-Nile perch Lake

Victoria. Although it was feared that these fishes might have disappeared completely, they reappeared in Kenyan commercial catches as early as 1988 (Ogutu-Ohwayo, 1995), and now comprise part of the fisheries across the lake.

1.4.8 Importance of the state of Lake Victoria to the advent of cage aquaculture in the lake

Despite their proximity to the lake, the Lake Victoria riparian communities have had challenges accessing fish as food. This is a paradox, but it is the reality that communities live with. The Nile perch boom in the 1990s changed fisheries from a barter trade fishery to an export market-oriented fishery (Medard, 2019). Given the declining catches from capture fisheries of Nile perch and Nile tilapia (both introduced species), the last decade has seen the introduction of cage aquaculture on the lake to augment fish production (Figure 1-A1). There are over 4,000 cages on the Kenya part of Lake Victoria (Hamilton *et al.*, 2020) farming Nile tilapia, whose landings have drastically plummeted from wild catches. However, cage aquaculture can be disruptive if done wrongly, causing eutrophication and other problems. The uneaten feeds and fish sewage from the cages can be a potential source of pollution. On the other hand, cages could serve as rich foraging grounds and act as refugia, especially in overfished areas, with the potential to swell the fishery and enhance biodiversity.

The lake continues to be subject to cultural eutrophication resulting from anthropogenic nutrient enrichment. Until the mid to late 1970s, the lake was mesotrophic. Since then, the lake has been highly eutrophic on the whole, due to a combination of human influences including catchment degradation, the introduction of exotic species and pollutants, over-extraction via fisheries, and anthropogenic climate change. Eutrophication is extreme in the inner Winam Gulf near the city of Kisumu (Kenya's third most populous), thus creating a limnological gradient from the Gulf to the open waters of the lake. Installing cages in the lake-especially in the Gulf-might exacerbate already eutrophic conditions. On the other hand, additional environmental damage attributable to cage aquaculture might be greatest under the relatively oligotrophic conditions of the open lake. For the lake to maintain a sustainable fishery, while allowing recovery in biodiversity conservation and ensuring food security there is a need to understand the spatial and temporal interactions between cage farms, wild fisheries, and biodiversity under the range of limnological conditions in the lake.

This dissertation explores 1) the distributional ecology of fishes along a limnological gradient in Lake Victoria, Kenya; 2) cage aquaculture in the lake - its effects on limnology and fish communities, and the scientific and social correlates of doing it properly. It determines 1) How environmental spatial variability influences fish diversity and community structure in the lake, 2) How aquaculture farms interact with the larger aquatic system (limnology, fisheries biology, biodiversity and spatial ecology), and 3) Biophysical limits and trade-offs among the overlapping ecosystem uses in the lake (i.e., cage aquaculture, wild fisheries, and other ecosystems goods and services), and how all of these may relate to sustainable development goals (SDGs). The dissertation focus is on the Kenyan waters of Lake Victoria, but the results have implications for the entirety of this lake as well as other global freshwater ecosystems.

CHAPTER TWO: DISTRIBUTIONAL ECOLOGY OF FISHES ALONG A LIMNOLOGICAL GRADIENT IN THE KENYAN WATERS OF LAKE VICTORIA.

2.1 Introduction

Lake Victoria is well known for its rich endemic fish fauna, dominated by haplochromine cichlids (Cichlidae:Pseudocrenilabrinae), and also for the disappearance of a large portion of this fauna in the mid-1980s, with many species likely extinct. The modern lake is highly limnologically heterogeneous, with areas that range from slightly to extremely eutrophic, due largely to anthropogenic influence (Taabu-Munyaho *et al*., 2016; Nyamweya *et al*., 2020). One of the strongest limnological gradients is present in the Kenyan waters of the lake, with eutrophication decreasing from inshore to offshore (Okechi *et al*., *in press*). The gradient and its ecological and biodiversity correlates are attributable to anthropogenic activities, including cultural eutrophication, species introductions, and climate change. The fishery and biodiversity of Lake Victoria have changed profoundly over the past several decades. In the 1960s, the indigenous tilapia species *Oreochromis esculentus* (known in the local Luo language as *ngege*) accounted for about 92 percent of the total fishery yield in Winam Gulf. This dropped to only 3 percent by 1973 (Garrold, 1961; Wanjala and Marten, 1974). In the mid-1970s, haplochromine cichlids were numerically the dominant fishes in Winam Gulf, and indeed over much of the lake. Their abundance was attributed to a short generation time, versatile feeding habits, and rapid adaptation to a variety of lacustrine environments and food sources (Brooks, 1950; Greenwood, 1951; Wanjala and Marten, 1974). In the early

1950s and 1960s, nonnative species were introduced into the lake to boost the fishery of the two endemic tilapiines (*Oreochromis esculentus* and *Oreochromis variabilis*), cyprinids, catfish, and other native food fishes, which had all declined. The introduced species included exotic tilapiines including the Nile tilapia (*Oreochromis niloticus*), *O. leucostictus, Coptodon zillii* and possibly *C. rendalli* plus the Nile perch (*Lates niloticus*) (Fryer, 1959, 1961; Cadwallar, 1965; Welcome, 1967; Lowe McConnell, 2009). Around the early to mid-1980s, the native haplochromine species flock plummeted in diversity and abundance (Barel *et al*., 1985; Ogutu-Ohwayo, 1990; Kaufman, 1992; Goldschmidt and Witte, 1993; Kaufman and Ochumba, 1993; Mbabazi *et al*., 2004; Witte *et al*., 2007). Nile perch and Nile tilapia established and became dominant in the commercial fishery, along with a single native species, the omena (*Rastrineobola argent*ea) (Ogutu-Ohwayo 1990; Kaufman, 1992). Catchment activities like wetland clearance, dams, effluents pouring into the rivers, and drastic seasonal changes in rivers have interfered with the life cycles of fluviatile and potamodromous fishes. Yields of other endemic species that have also shown decline include the large catfishes *Bagrus docmak* and *Clarias gariepinus*, and the lungfish (*Protopterus aethiopicus*).

The decline in native fish stocks is attributable to a combination of causes, including overfishing, and catchment degradation (Downing *et al*., 2014; Nyamweya *et al*., 2020). Meanwhile, demand for fish protein has continued to increase because of rapid human population growth and growing awareness of the nutritional and health benefits associated with fish consumption (Akintola *et al*., 2013). Fishermen are switching to progressively smaller meshes in gillnets, whereas juvenile Nile perch are increasingly exploited by illegal beach seine fisheries in many areas. Some haplochromine populations are recovering in those areas where major fisheries have been most intense, and for species of haplochromines that take advantage of structural refugia, such as rocky habitats. Although haplochromines play a big role ecologically in the food web in the Lake Victoria fishery, data on the species composition and biology of the surviving haplochromines are scarce. While up to half of the original fauna has disappeared with many species possibly extinct, a resurgence of haplochromine cichlids has been observed, especially in the open waters of the lake. Some species groups have recovered spectacularly, including some detritivores, zooplanktivores, and insectivores, though species diversity within each group is often low (Kishe-Machumu *et al*., 2012, 2015; van Rijssel and Witte, 2013; Witte *et al*., 2013). It is important to investigate whether the resurgence and recovery are related to the decline in *L. niloticus* abundance as inferred from the catches, or if it is more closely related to environmental and climatic changes. In 2017, the entire lake was surveyed within a few months, the first synoptic lake-wide study of Lake Victoria fish fauna. The work was a massive simultaneous cooperative effort of the three-lakeside nations (Kenya, Uganda, and Tanzania). In total 41 stations were sampled in the Kenyan waters of the lake; 11 in the littoral zone using gillnets and 30 in the open lake using a bottom trawl. This chapter examines the nature of the environmental heterogeneity in the lake, and how it influences fish abundance, diversity, population size structure (size at 50% maturity), and feeding habits. It is hypothesized that 1) an inshore – offshore environmental gradient exists in the Lake. 2) the environmental gradient will separate fish in their abundance, size structure and feeding habits; and separate overall species diversity.

2.2 Methods

2.2.1 Study design

A survey of the Kenyan waters of Lake Victoria was conducted in April/May and July/August 2017. The study design incorporated the following: 1) A survey of fish communities in the entire lake (all three countries' waters) using gill nets for the nearshore, and trawls for offshore areas. 2) An accompanying limnological survey, covering environmental variables and habitat characterization. This chapter focuses on the Kenyan waters, where a total of 41 stations were sampled; 11 in the littoral zone using gillnets and 30 in the open lake using a bottom trawl (Figure 2-1). The gillnets were designed according to Lake Victoria Fishery Organization's Standard Operating Procedures (SOPs) (LVFO, 2005a), including guidelines for collecting and monitoring biological as well as ecological information on the fishes (LVFO, 2005b). The physicochemical parameters and habitat characterization were determined *in situ* and water samples were collected for nutrient laboratory analysis. Sampling sites were geo-referenced using a Garmin Global Positioning System (GPS) and can therefore be used for future sampling comparisons. Diverse habitats were selected depending on habitat type and area covered. Gillnet and bottom trawl survey sites were clustered into the inner gulf, mid-gulf and open lake based on their limnological heterogeneity (Figure 2-1).

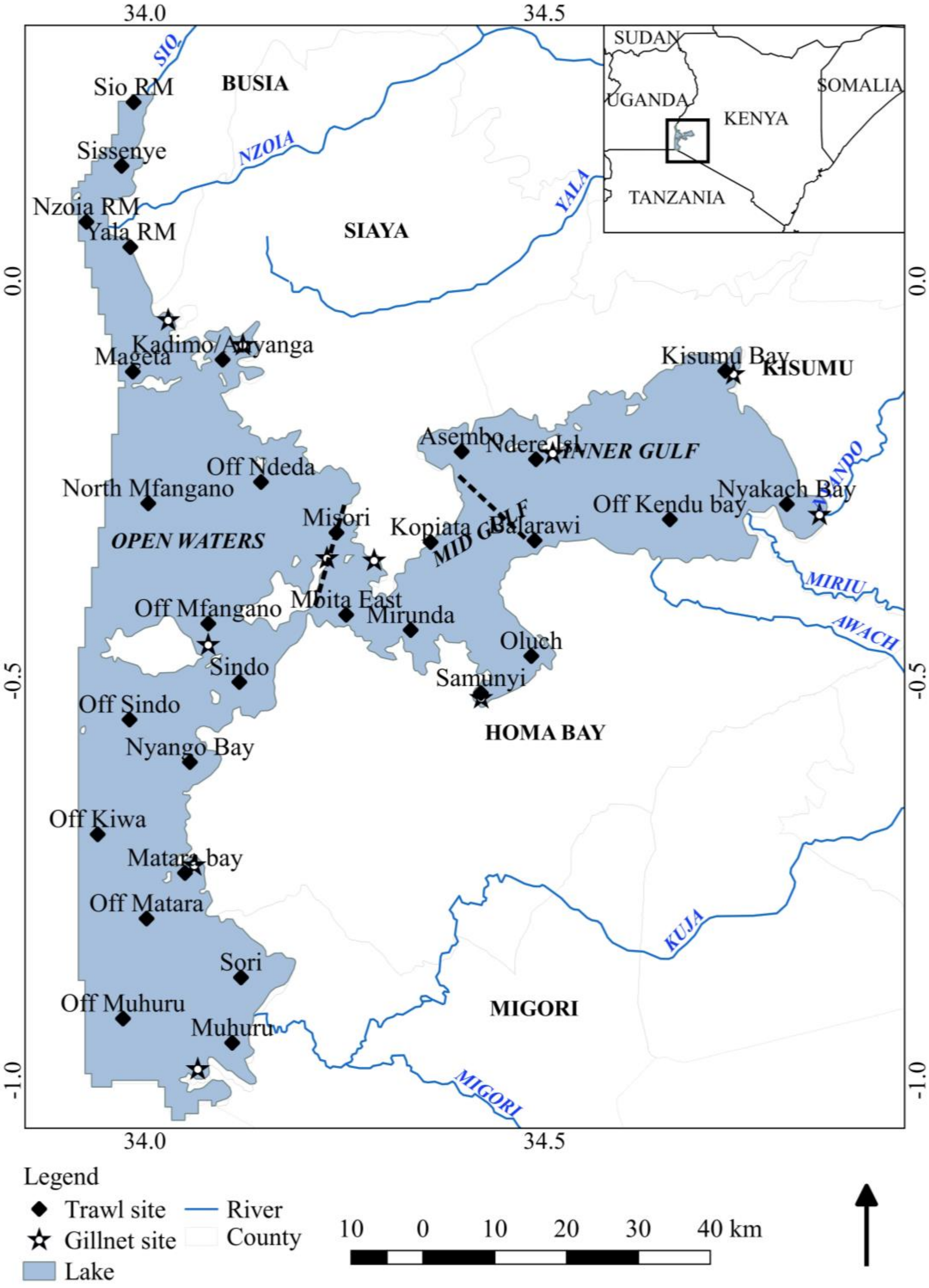


Figure 2-1. Gillnets and bottom trawl survey sampled stations in Lake Victoria, Kenya (April/May and July/August 2017). The stations were clustered into inner gulf, mid-gulf and open lake using dotted lines.

2.2.2 Sampling environmental variables and water quality parameters

Physicochemical water quality parameters were sampled using standard methods for water quality monitoring (APHA, 1985; Wetzel, 1991). Replicate measurements for each physicochemical parameter were taken in situ at 1m depth using a YSI 650–MDS multi-parameter-YSI 6600 system. The parameters measured included: depth, pH, dissolved oxygen (DO), temperature, turbidity, conductivity, total dissolved solids (TDS), chlorophyll-a, alkalinity, salinity, and oxidation-reduction potential (ORP). Water transparency was measured using a standard Secchi disk, by obtaining the mean disappearance and reappearance depth down the water column. Water samples were collected using a one-liter capacity Van Dorn water sampler for the determination of nutrients, total hardness, total alkalinity as well as phytoplankton analysis. Determination of alkalinity and hardness followed published titrimetric methods (APHA, 1985). An aliquot of surface water sample (50 ml) was titrated with a standardized hydrochloric acid (HCl) to a pH of 4.5, using a mixed indicator of 0.2 g Methyl red and 1g of Bromocresol green in 95% ethanol, for total alkalinity, and Di-Sodium EDTA 0.02 M, with the addition of a small amount of indicator (Eichrome Black T dye) for total hardness. Water samples for nutrient analysis were placed in high-density polyethylene (HDPE) bottles, fixed using sulfuric acid (H_2SO_4) and kept at 4°C until laboratory analysis and final quantification. Total nitrogen (TN) and total phosphorous (TP) were analyzed using potassium persulphate digestion to oxidize both the organic and inorganic contents to analyzable form. Glass microfiber (GF/C) filter papers were used to filter the samples. The filtrates were used for the analysis of dissolved nutrients (NH_4 + -N, NO_3 - -N, NO_2 -

-N, and SRSi) using spectrophotometric methods as outlined in APHA (1985). Ammonium, NH_4 + -N was analyzed using manual phenate method, NO_2+, NO_3 - -N by cadmium reduction technique and SRSi using colorimetric method. The unfiltered sample was used to analyze phosphates (PO_4+ -P) as TP using the ascorbic-acid method.

2.2.3 Fish sampling

2.2.3.1 Gillnet survey

Eleven stations covering the entire littoral Kenyan lake were surveyed during April/May 2017 and were pre-determined based on substrate type that included sandy, muddy and vegetated bottom types. During the survey, multifilament and monofilament gillnets were deployed. The multifilament set comprised four fleets left to soak overnight and retrieved in the morning. The second set comprised monofilament nets which were set in the morning. For the multifilament nets, each fleet had 7 panels of mesh sizes (1.5”–7”), measuring 45 m long for each net. The monofilament nets were organized into three fleets. Each fleet had five panels (mesh sizes: 0.5”, 1”, 1.25”, 1.5” and 2”). Two fleets were set parallel to the shoreline, while the third fleet was set perpendicular to the shoreline (Tweddle *et al.*, 1999). Each fleet was left to soak for an hour and staggered to allow for processing of one fleet at a time while the rest soaked. After hauling, all the fish samples (except haplochromines) were sorted and identified to species level (Greenwood, 1966; Trewavas, 1983; Witte and Densen, 1995). The haplochromine was initially recorded as a group (Haplochromis spp.) due to the difficulty of immediate identification to species level in the field. Later in the laboratory, the haplochromines from each of the stations were identified as best as possible, then quantified morphometrically to determine the broad pattern of trophic and body form variation at each station. Total catch, species identity, and wet weights of the fish were recorded from each site.

2.2.3.2 Bottom trawl sampling

The trawl survey was conducted for eleven days in July/August 2017 on Winam Gulf and the open waters of Lake Victoria within the Kenyan border to investigate the distribution and association patterns of fish species in the lake. A total of 30 sites in the Kenyan portion of the lake were trawled and fish specimens were obtained using a bottom trawler (R. V. Uvumbuzi of 210 hp) moving at an average speed of 3 nautical miles knots. Trawling depth was controlled by varying the lengths of the towing warps as different depths were encountered. Bottom type (substratum) was recorded as vegetative, mud, sand, gravel, or rock as found on the cod-end and otter boards. Towing was done for 30 minutes and after each haul, fish caught were identified, counted, measured, weighed and their stomach contents examined.

2.2.3.3 Gillnet and trawl surveys sample processing

All fish landed were identified and sorted to species level (except haplochromines). For each fish caught, total length (TL, cm), standard length (SL, cm) and total weight (W, g) were measured and recorded. The fish were dissected, sexed, and maturity status determined. The gonads were removed, weighed, and categorized according to developmental stages. The eviscerated mass of the fish was recorded. Stomach contents for the bigger specimens were determined immediately, while those from the smaller specimens were examined thereafter under a stereo microscope (x 40 magnification).

2.2.3.4 Population structure and reproductive biology

Length frequency distributions for *L. niloticus* were compared for Winam Gulf and open waters before combining the data for the entire areas sampled. Size at 50% maturity for the commercial species Nile perch was estimated for both sexes via a least-squares fit of the frequency of mature individuals by length to a logistic curve (Kolding and Skaalevik, 2010).

2.2.3.5 Food and feeding habits

Gut contents of individual fish in three length groups (2–14, 15–40, and ≥ 41cm) were analyzed using a modified point method following Hyslop (1980). The number of stomachs in which each prey item occurred was expressed as a percentage of the total within their length group. The stomach was awarded an index of fullness ranging from 0 (empty), 5 (1/4 full), 10 (1/2 full), 15 (3/4 full), 20 (full stomach). The contribution of various prey items was estimated as a percentage of the total volume of the contents.

2.2.4 Data analysis

Microsoft Excel was used for descriptive statistics and visualization using graphs and tables. Differences among observations from various sampling sites were tested using ANOVA at $p < 0.05$. Tukey's HSD test was used to determine post-hoc differences for significant results. Relationships among selected water quality variables were explored using simple correlations. Principal Component Analysis (PCA) was used in classifying sampling sites for both gillnet and bottom trawl to the inner gulf, mid gulf, open lake, and associated fish species. All statistical analyses were performed in RStudio version 1.3.1093 (RStudio Team, 2020). A summary of the survey and analyses is shown in a conceptual framework (Figure 2-2, Figure 2-A1).

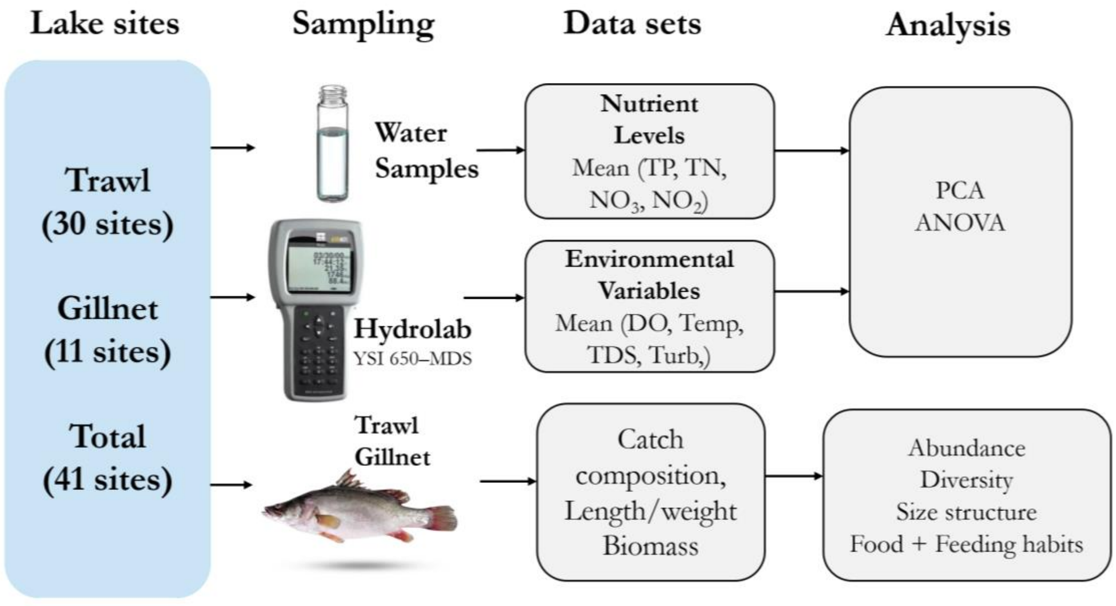


Figure 2-2. A summary conceptual framework of Lake Victoria fish sampling survey and analyses.

2.3 Results

2.3.1 Environmental variables and water quality parameters across Lake Victoria, Kenya

Environmental sampling confirmed the presence of an inshore-offshore environmental gradient across the Kenyan waters of Lake Victoria (Figure 2-3). Samples from the inner portion of Winam Gulf formed a distinct cluster to the left side of the graph, and the open lake a distinct cluster to the right. PC1 explains much of this variability in the inner gulf, and was characterized at one extreme (the innermost gulf) by high values of turbidity, salinity, total dissolved solids (TDS), conductivity, and chlorophyll-a, and nutrients (total phosphorous, nitrates, nitrites and silica).

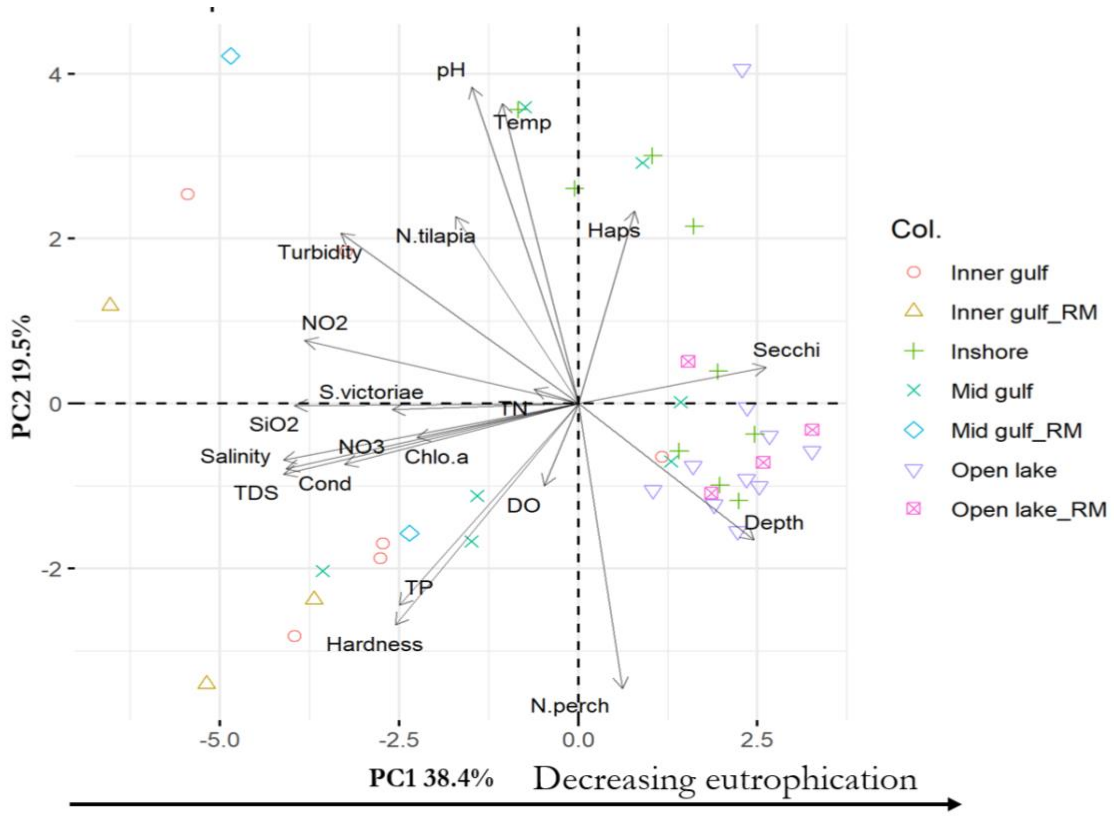


Figure 2-3. PCA biplot of all measured variables. PC1 explains 38.4% of the total variation and PC2 explains 19.5% of the total variation during the survey.

PC1 is attributable to nutrient loading, and water clarity with low PC1 scores having high loading and low clarity, and characterized by high values of turbidity, salinity, TDS, conductivity, chlorophyll-a and nutrients in the inner gulf. PC2 accounts for temperature, pH, and hardness, reflecting a stable open water environment. Nile perch and haplochromines were negatively correlated with turbidity and nutrients, whereas Nile tilapia and *Synodontis victoriae* were positively correlated with TDS, and turbidity.

The open lake, on the other hand, was characterized by high water transparency, temperature, pH, and dissolved oxygen (Figure 2-3). Visualization of the contributions of the raw variables to PC1 and PC2 are as depicted in Figures 2-4a, b.

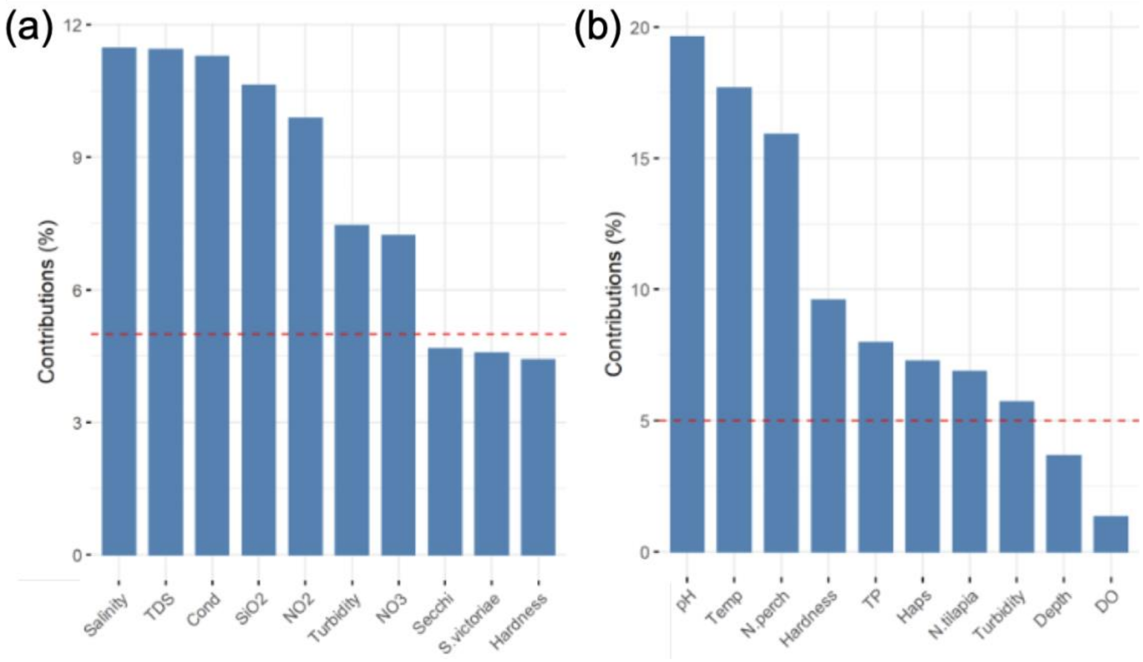


Figure 2-4a, b. Visualizing contributions of variables to PC1 (a) and PC2 (b). PC1 is chatacterized by high values of salinity, TDS, conductivity, turbidity and nutrients; whereas PC2 is characterized by high values of pH, temperature, and hardness.

2.3.2 River mouth influence on the inner gulf and open lake

To determine if the river mouth had affected lake water attributes, sampling stations were divided into seven zones: inner gulf (IG), inner gulf near river mouth (IG_RM), mid gulf (MG), mid gulf near river mouth (MG_RM), inshore (IS), inshore near river mouth (IS_RM), and offshore (OS) or open lake. It was predicted that the inner gulf river mouth would show higher levels of nutrients and low water transparency, with a shift toward more oligotrophic, clear water in the open lake. A PCA analysis shows that open lake stations clustered differently from inner gulf stations. Inshore and offshore stations differentiated along PC2, whose main contributing variables were pH, temperature and dissolved oxygen (Figure 2-5).

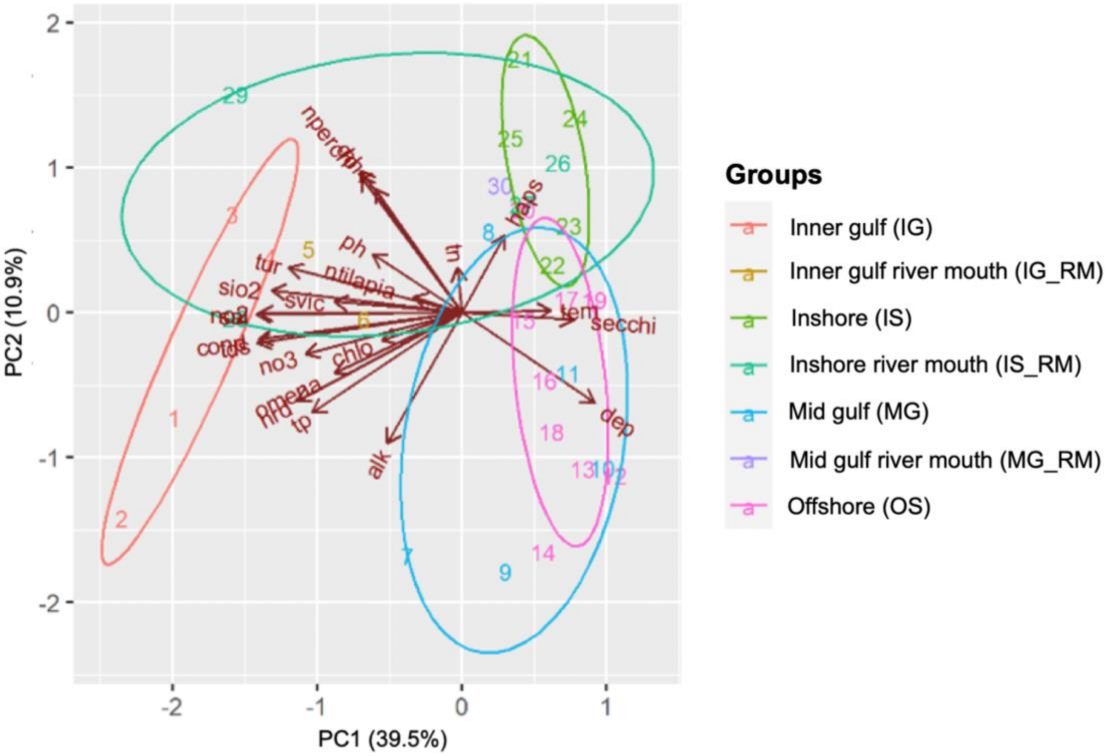
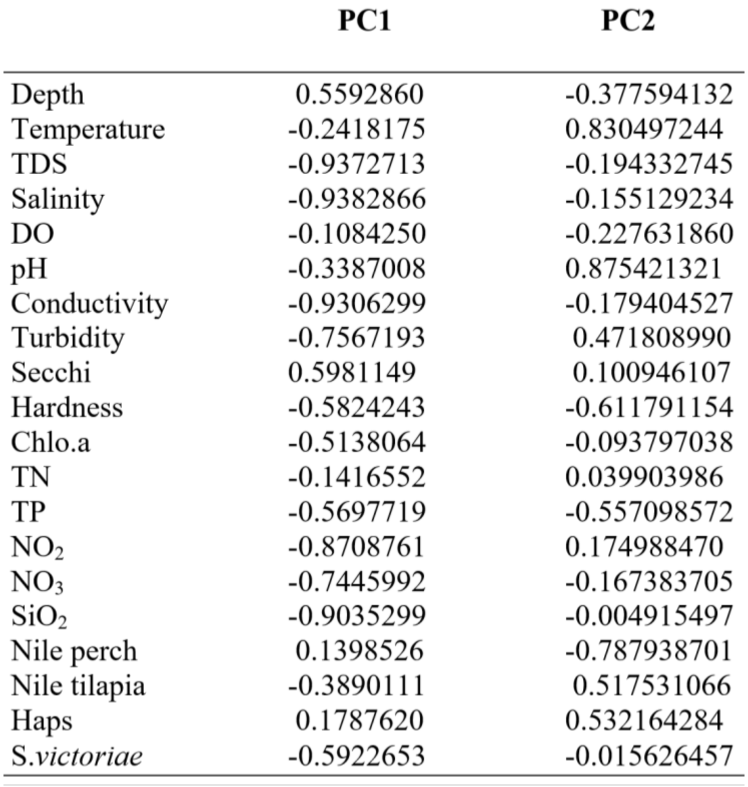


Figure 2-5. A PCA analysis showing separation of ecological zones in the lake based on environmental variability near river mouths in the inner gulf, mid gulf, inshore, and offshore in Lake Victoria, Kenya.

However, as shown by factor loading for PC1 and PC2 the separation between the inner gulf and open lake was along PC1, which was closely correlated to turbidity, conductivity, salinity, total dissolved solids, and nutrients (nitrites, nitrates, total phosphorous and silica) (Table 2-1, Figure 2-A2).



	PC1	**PC2**
Depth	0.5592860	-0.377594132
Temperature	-0.2418175	0.830497244
TDS	-0.9372713	-0.194332745
Salinity	-0.9382866	-0.155129234
DO	-0.1084250	-0.227631860
pH	-0.3387008	0.875421321
Conductivity	-0.9306299	-0.179404527
Turbidity	-0.7567193	0.471808990
Secchi	0.5981149	0.100946107
Hardness	-0.5824243	-0.611791154
Chlo.a	-0.5138064	-0.093797038
TN	-0.1416552	0.039903986
TP	-0.5697719	-0.557098572
NO_2	-0.8708761	0.174988470
NO_3	-0.7445992	-0.167383705
SiO_2	-0.9035299	-0.004915497
Nile perch	0.1398526	-0.787938701
Nile tilapia	-0.3890111	0.517531066
Haps	0.1787620	0.532164284
S.*victoriae*	-0.5922653	-0.015626457

Table 2-1. Correlations between variables and the first two dimensions (PC1 and PC2). PC1 is chatacterized by high values of salinity, TDS, conductivity, turbidity, and nutrients. PC2 is characterized by high values of pH, temperature, and hardness.

Mean values of some of the measured physical and chemical variables are shown in Table 2-2. A one-way ANOVA performed on the two first PCs to determine if the near river station categories differed in PC1 or PC2, showed that the station categories differed significantly only on PC1. There were highly significant differences in PC1 between station pairings: open lake and inner gulf, open lake_RM and inner gulf, mid gulf and inner gulf_RM, open lake and inner gulf_RM, open lake_RM and inner gulf_RM, and open lake and mid gulf (one-way ANOVA, $p < 0.001$; Tukey HSD, $p < 0.001$ for all comparisons).

	Inner gulf	Inner gulf - RM	Midgulf	Midgulf -RM	Inshore	Inshore -RM	Open lake
Alkalinity (mg/L)	69.50 (10.75)	73.00(15.56)	65.60(12.76)	62.00	68.00(12.00)	61.50(14.27)	64.73(11.84)
Conductivity(µS/cm)	142.25(23.8)	180.00(24.4)	123.20(20.5)	143.00	93.67 (2.52)	82.50(27.01)	93.36 (9.10)
Depth (m)	5.44 (3.01)	4.3 (1.27)	9.93 (1.37)	4.55	11.53 (7.29)	10.59 (5.05)	29.30(10.14)
DO (mg/L)	7.87 (0.53)	8.05 (1.65)	5.58 (1.27)	7.32	5.06 (1.78)	7.04 (0.60)	5.83 (1.42)
Hardness (mg/L)	38.50 (12.79)	56.00(16.97)	36.80 (9.86)	42.00	32.00 (2.00)	32.50 (1.91)	33.82 (6.23)
ORP (mV)	93.25 (10.97)	92.00(11.31)	88.40 (7.70)	71.00	81.00(13.23)	87.50(14.66)	92.82 (7.63)
pH	6.36 (0.20)	6.31 (0.08)	6.29 (0.21)	6.30	6.21 (0.20)	6.14 (0.32)	6.07 (0.20)
Salinity (mg/L)	0.07 (0.01)	0.09 (0.01)	0.06 (0.01)	0.07	0.04 (0.01)	0.04 (0.01)	0.04 (0.01)
Secchi (m)	0.61(0.03)	0.45 (0.21)	0.93 (0.32)	0.60	1.53 (0.75)	1.23 (0.43)	2.21 (0.87)
Temp. (°C)	23.80 (0.45)	24.08 (0.73)	23.85 (0.46)	24.38	24.17 (0.25)	24.18 (0.50)	24.19 (0.21)
TDS (mg/L)	0.10 (0.02)	0.12 (0.01)	0.08 (0.02)	0.09	0.06 (0.00)	0.05 (0.02)	0.06 (0.01)
Turbidity (FTU)	12.81 (6.19)	18.46 (0.35)	8.35 (4.40)	8.52	6.06 (3.05)	6.54 (6.50)	3.18(2.13)
Ammonium (µg/L)	26.82 (19.92)	22.44 (2.21)	17.63 (6.90)	19.00	11.50 (7.68)	13.22 (8.01)	16.62(12.25)
Chlo_a (µg/L)	10.61 (5.29)	12.23 (9.92)	9.42 (5.19)	7.50	6.16 (1.09)	9.44 (6.71)	5.38 (2.14)
Nitrates (µg/L)	13.05 (4.22)	15.09 (1.50)	13.24 (8.55)	14.33	2.21 (1.09)	2.82 (1.50)	6.54 (6.75)
Nitrites (µg/L)	8.65 (5.80)	10.40 (0.86)	5.36 (3.65)	7.67	0.90 (0.17)	1.91 (1.24)	1.72(0.50)
Silica (mg/L)	9.97 (6.08)	16.01 (3.20)	8.80 (6.72)	14.30	2.71 (2.10)	3.33 (2.16)	3.01 (0.85)
SRP (µg/L)	48.79 (20.48)	68.86 (1.01)	45.43(20.86)	53.43	21.52(12.15)	12.36 (3.58)	30.18(11.34)
TN (µg/L)	349.18(66.9)	256.00(55.8)	414.00(89.7)	433.27	371.46(25.6)	391.91(159.)	319.21(71.7)
TP (µg/L)	128.78(60.7)	202.73(3.03)	106.00(41.9)	174.86	99.62(36.26)	65.93(41.23)	90.28(42.45)

Table 2-2. Mean values (and standard deviation in brackets) for physicochemical and nutrient parameters for the different ecological zones in the lake (inner gulf, inner gulf_RM, mid gulf, mid gulf_RM, inshore, inshore_RM and open lake), Lake Victoria, Kenya (RM = River mouth).

Figure 2-6 shows water physicochemical parameter values in the gulf and open waters of Lake Victoria. Water conductivity was significantly different between all location pairings in the open lake and inner gulf river mouth (one-way ANOVA, $p < 0.001$; Tukey HSD, $p < 0.001$ for all comparisons), with a high mean value of 180.0 ± 24.4 µS cm^{-1} (inner gulf river mouth) and a low value of 82.5 ± 27.0 µS cm^{-1} (inshore river mouth). The location also had a highly significant effect on total dissolved solids (TDS), with higher significant differences in TDS between the open lake and inner gulf river mouth (one-way ANOVA, $p < 0.001$; Tukey HSD, $p < 0.001$ for all comparisons), having a high mean value of 0.12 ± 0.01 mg l^{-1} (inner gulf river mouth) and a low value of 0.06 ± 0.01 mg l^{-1} (open lake). There were significant differences in turbidity between the open lake and inner gulf river mouth (one-way ANOVA, $p < 0.05$); Tukey HSD, $p < 0.001$) decreasing from a high mean of 18.46 ± 0.35 FTU in the inner gulf river mouth to a low mean of 3.18 ± 2.13 FTU in the open lake. Salinity had highly significant differences between the open lake river mouth and inner gulf river mouth pairings (one-way ANOVA, $p < 0.001$; Tukey HSD, $p < 0.001$) and there were significant differences in hardness between the open lake river mouth and inner gulf river mouth (one-way ANOVA, $p < 0.05$; Tukey HSD, $p < 0.05$ for all comparisons). Though there was variation in dissolved oxygen (DO), the differences were not significant between the open lake and inner gulf stations (one-way ANOVA, $p > 0.05$); and water temperature did not significantly vary among all the stations in the lake.

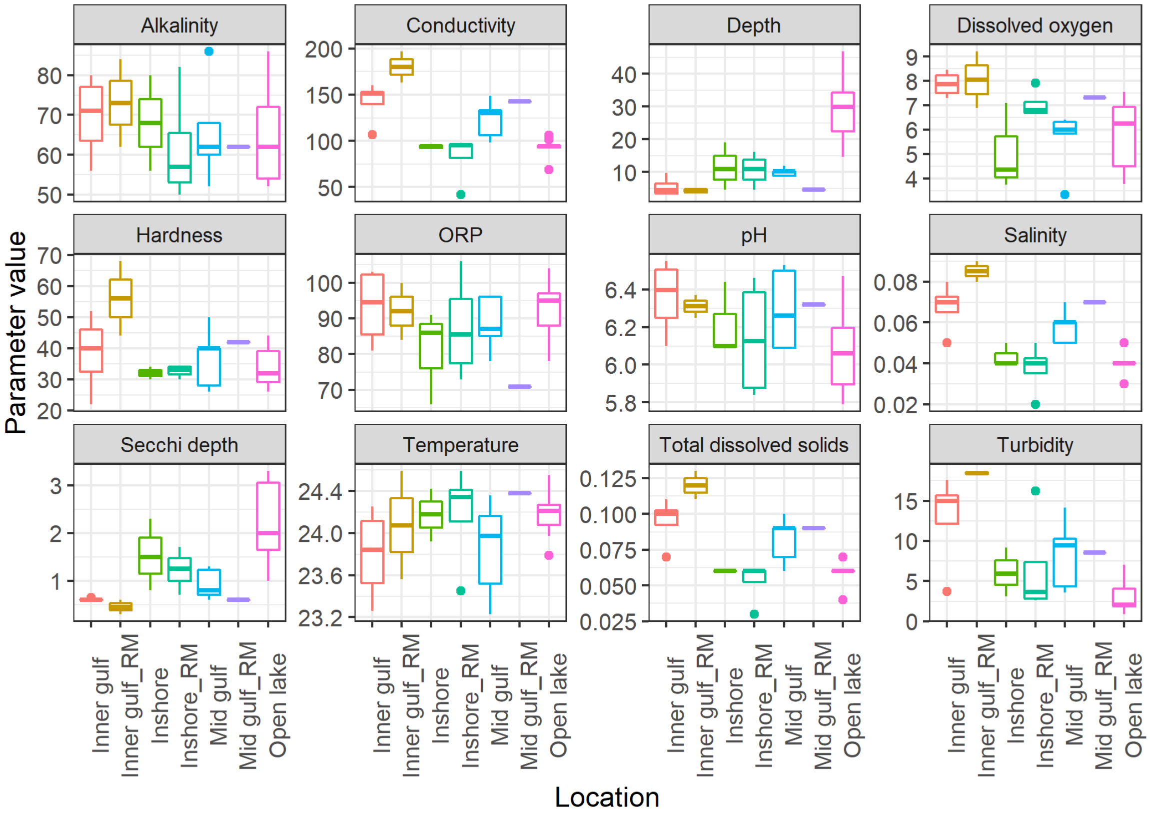


Figure 2-6. Physicochemical parameters in Lake Victoria, Kenya (April/May; July/August 2017). Temperature (°C), pH, turbidity (FTU), total dissolved solids (mg l^{-1}), conductivity (µS cm^{-1}), dissolved oxygen (mg l^{-1}), salinity (mg l^{-1}), alkalinity (mg l^{-1}), hardness (mg l^{-1}), oxidation-reduction potential (ORP) (mV), Secchi disk (m), and depth (m).

2.3.3 Nutrients and primary production

Figures 2-7 show the nutrients and cholorophyll-a levels in the lake's sampled zones. The inner gulf and open lake have very different nutrient concentrations, with the inner gulf having higher levels, resulting in an inshore-offshore gradient. Between the pairings of the open lake and inner gulf, and open lake river mouth and inner gulf river mouth, there were extremely significant differences in nitrates (NO_3), nitrites (NO_2), total phosphorous (TP), and silicates (SiO_2) (one-way ANOVA, $p < 0.001$; Tukey HSD, $p < 0.001$ for all comparisons). The inner gulf river mouth had the greatest mean nitrite levels of 10.40 ± 0.86 µg l^{-1}, while the inshore had the lowest (0.90 ± 0.17 µg l^{-1}). The inner gulf river mouth had the highest mean nitrates (15.09 ± 1.50 µg l^{-1}) while the inshore had the lowest (2.21 ± 1.09 µg l^{-1}). The inner gulf river mouth had the highest mean TP (202.73 ± 3.03 µg l^{-1}) while the inshore had the lowest (65.93 ± 41.23 µg l^{-1}). The inner gulf river mouth had the highest mean silicates (16.01 ± 3.20 mg l^{-1}) while the inshore had the lowest (2.71 ± 2.10 mg l^{-1}). The inner gulf and open lake stations had significantly different chlorophyll-a concentrations (one-way ANOVA, $p < 0.05$), and the inner gulf river outlet had a lot of variability (Figures 2-7). The inner gulf river mouth had the highest mean chlorophyll-a concentrations (12.23 ± 9.92 µg l^{-1}) while the open lake had the lowest (5.83 ± 2.14 µg l^{-1}) (Table 2-2).

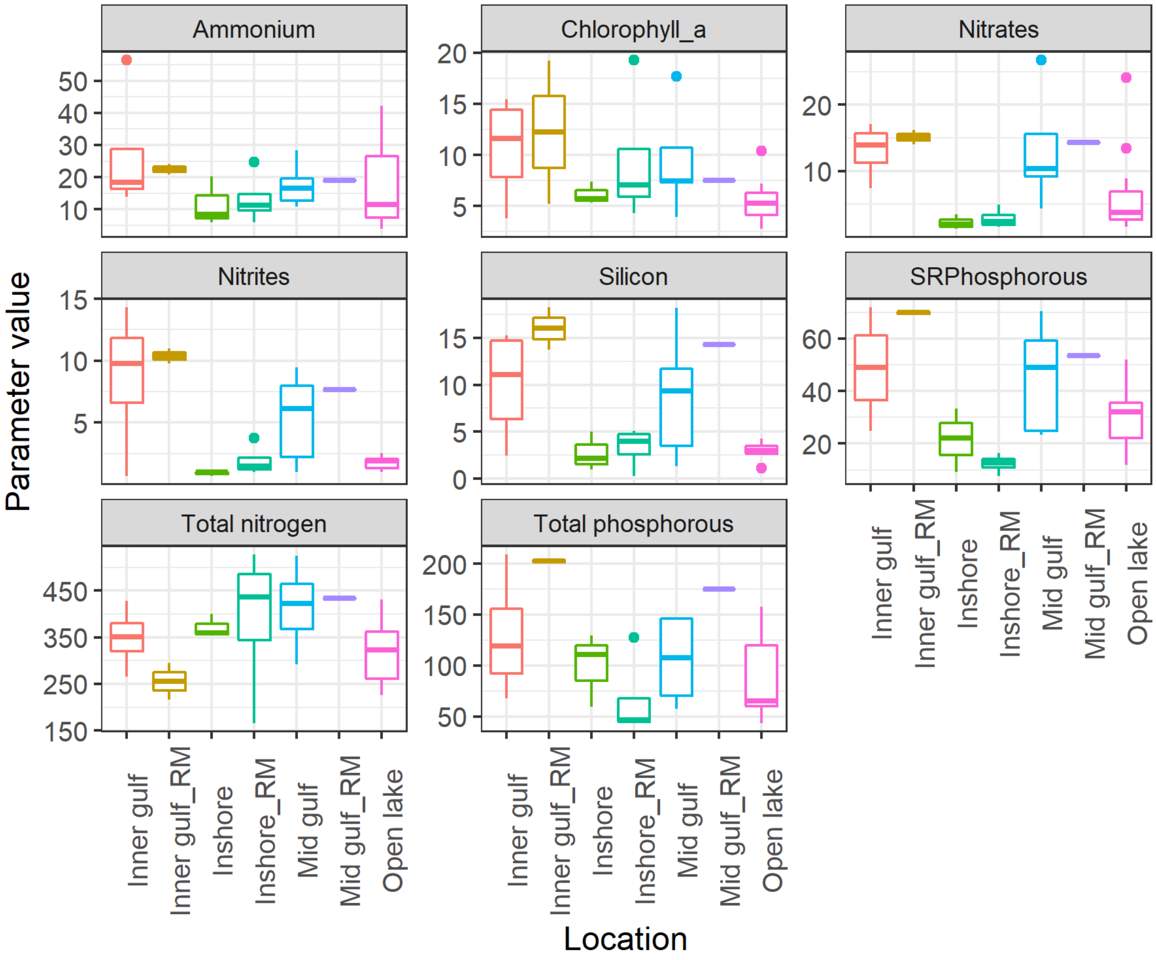


Figure 2-7. Nutrient enrichment in Lake Victoria, Kenya (April/May and July/August 2017). Units for nitrates, nitrites, soluble reactive phosphorus (SRP), ammonium, total nitrogen, total phosphorus, and chlorophyll_a are in µg l^{-1}, while silicates (SiO_2) are in mg l^{-1}.

2.3.4 Fish species abundance and diversity across the spatial-environmental gradient

In total, an assemblage of diverse haplochromines and eighteen (18) other species were caught during bottom trawl and gillnet surveys. The haplochromines will be identified to the species level; but included representatives of the genera (after Greenwood, 1951, 1966) *Ptyochromis* and *Platytaeniodus* (oral molluscivores), the insectivores and sometime pharyngeal crushers of *Paralabidochromis, Psammochromis, Gaurochromis* and *Astatotilapia*, pharyngeal molluscivores *Astatoreochromis* and possibly *Labrochromis*, herbivores *Xystichromis* and *Neochromis,* the zooplanktivores *Yssichromis*, several species of the detritivores *Enterochromis*, and a very few piscivorous members of the Greenwood genera *Harpagochromis* (Figure 3-A3). The use of the Greenwood (1959) genera is maintained for the ease of communication, recognizing that recent genomic studies by McGee *et al* (2016, 2020) will eventually result in a new taxonomic revision and recognition of certain evolutionary complexities within the surviving fauna. Non-haplochromines caught include: *Lates niloticus, Enteromius profundus, Rastrineobola argentea, Oreochromis niloticus, Oreochromis variabilis, Coptodon zillii, Xenoclarias sp., Synodontis victoriae, Synodontis afrofischeri, Clarias gariepinus, Schilbe mystus, Brycinus sadleri, Brycinus jacksonii, Bagrus docmak, Mormyrus kannume, Protopterus aethiopicus*, and *Labeo victorianus,* plus the atyiid prawn *Caridina niloticus* and a variety of bivalve and gastropod mollusks (Figure 2-A3). Overall, fish species abundance (Figures 2-8a, b) and diversity (Figure 2-9) varied spatially across the environmentally heterogeneous lake. Haplochromine cichlids and *L. niloticus* were most abundant in the open lake, while the indigenous non-cichlid species were most abundant in the inner gulf (Figure 2-8a, b).

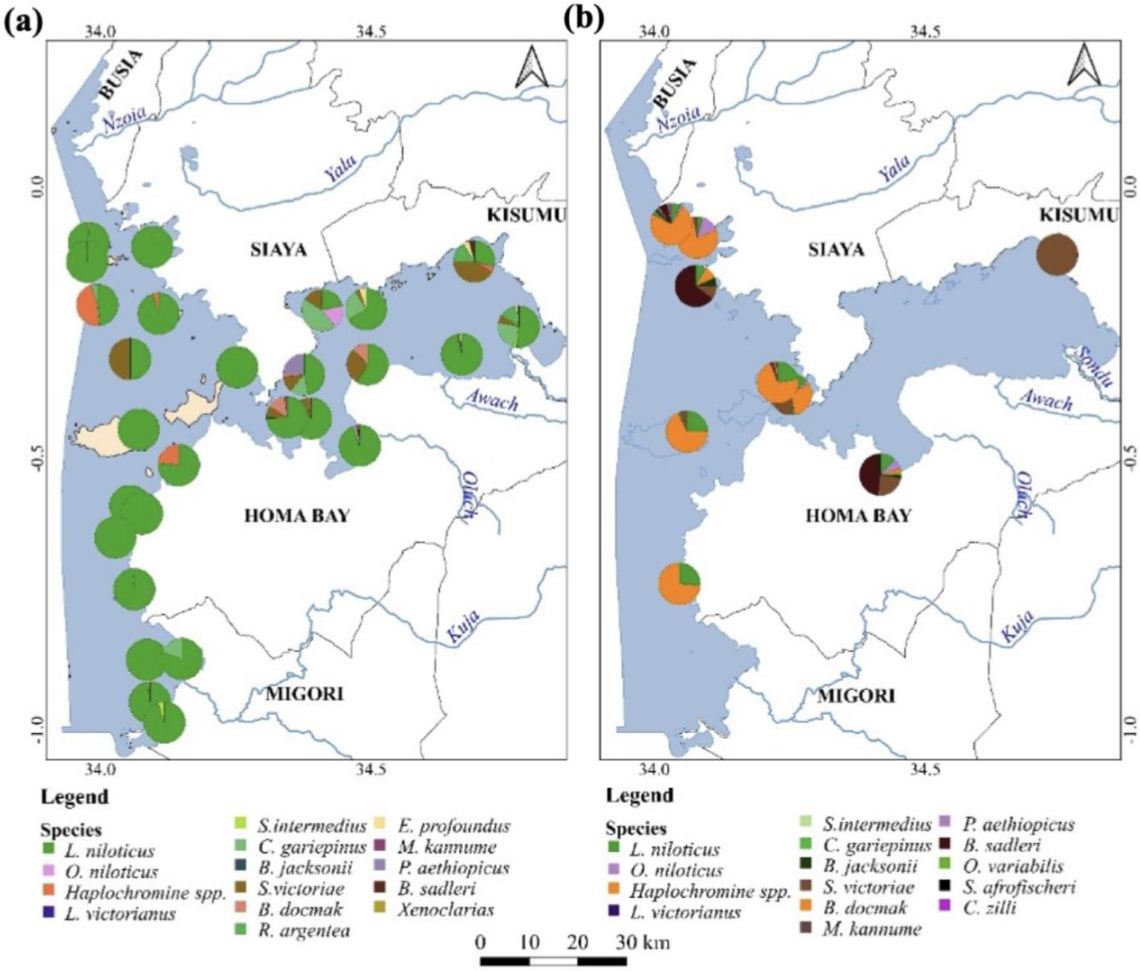


Figure 2-8a, b. Spatial fish species relative abundance for bottom trawl net (a) and gillnets (b) during July/August 2017 survey in Lake Victoria, Kenya.

In terms of diversity, the non-haplochromine species (mostly native species) were more diverse in the inner gulf, and the haplochromines were much more diverse in open waters (Figure 2-9). In the field, haplochromines were tagged for later identification.

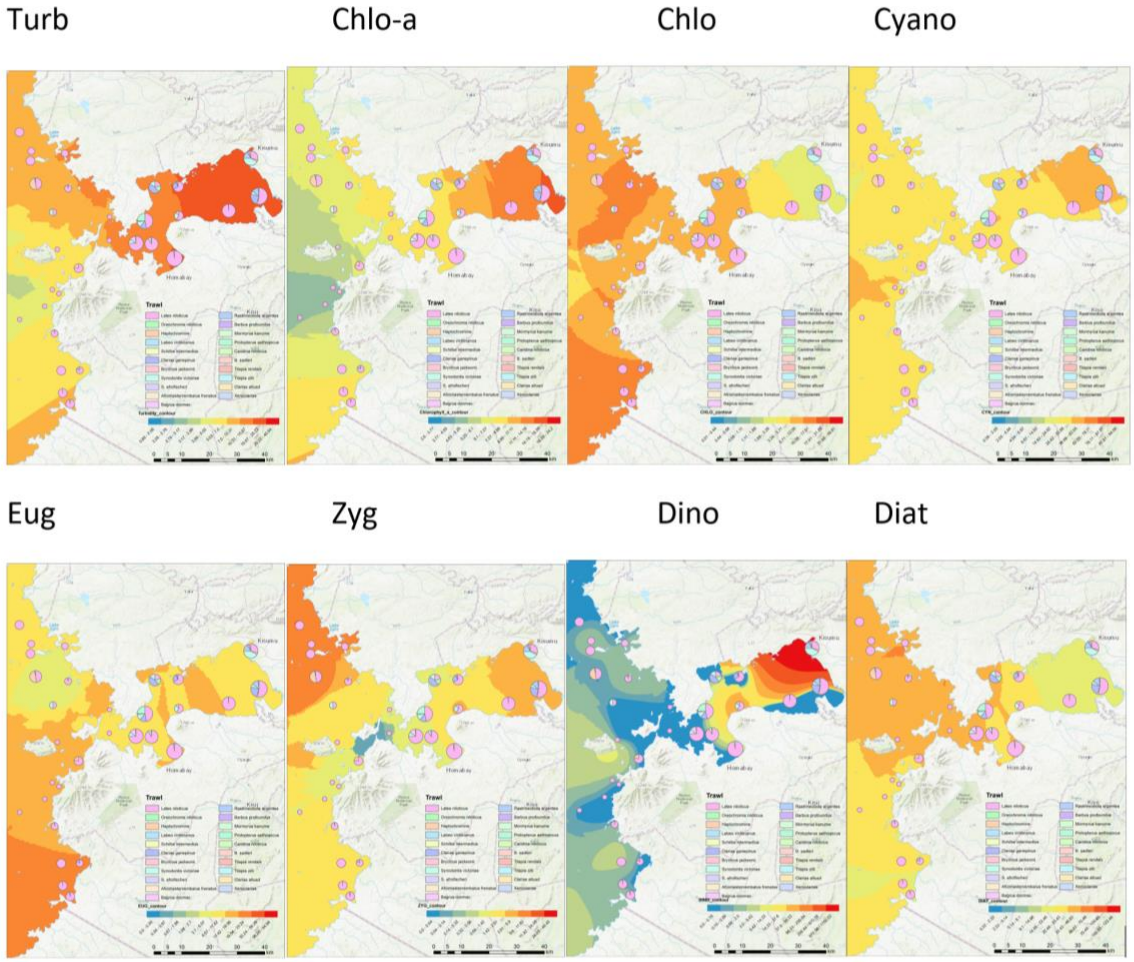
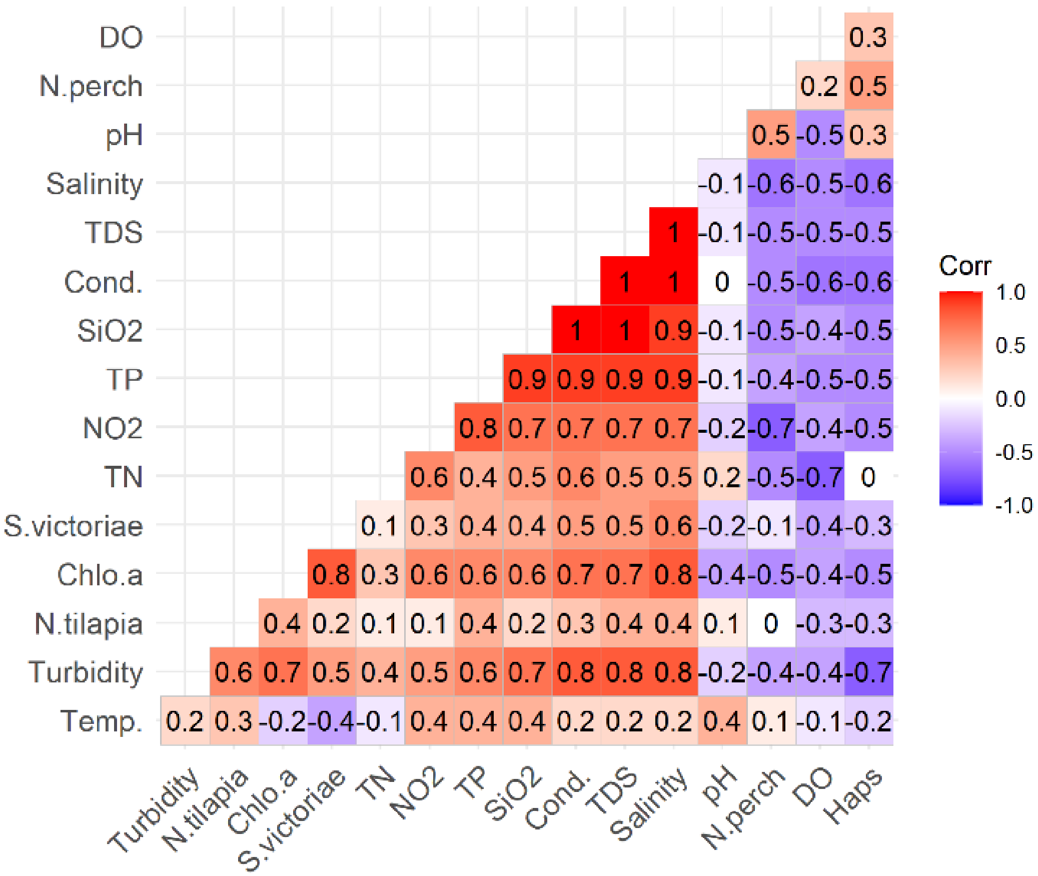


Figure 2-9. Spatial fish species diversity, turbidity, chlorophyll-a, and phytoplankton groups (chlorophytes, cyanophytes, euglenoids, zygnematecea, dinoflagellates and diatoms) during July/August 2017 survey, in Lake Victoria, Kenya. The dense red/brown colors indicate high concentrations and the dense blue colors indicate low concentrations.

Figure 2-10 shows a correlation matrix of environmental variables and fish species' relative abundance. Nile perch and haplochromines were negatively correlated with turbidity, conductivity, and nutrients, whereas Nile tilapia and *Synodontis victoriae* were positively correlated with TDS, turbidity, and nutrients.



	Turbidity	N.tilapia	Chlo.a	S.victoriae	TN	NO2	TP	SiO2	Cond.	TDS	Salinity	pH	N.perch	DO	Haps
DO															0.3
N.perch														0.2	0.5
pH													0.5	-0.5	0.3
Salinity												-0.1	-0.6	-0.5	-0.6
TDS											1	-0.1	-0.5	-0.5	-0.5
Cond.										1	1	0	-0.5	-0.6	-0.6
SiO2									1	1	0.9	-0.1	-0.5	-0.4	-0.5
TP								0.9	0.9	0.9	0.9	-0.1	-0.4	-0.5	-0.5
NO2							0.8	0.7	0.7	0.7	0.7	-0.2	-0.7	-0.4	-0.5
TN						0.6	0.4	0.5	0.6	0.5	0.5	0.2	-0.5	-0.7	0
S.victoriae					0.1	0.3	0.4	0.4	0.5	0.5	0.6	-0.2	-0.1	-0.4	-0.3
Chlo.a				0.8	0.3	0.6	0.6	0.6	0.7	0.7	0.8	-0.4	-0.5	-0.4	-0.5
N.tilapia			0.4	0.2	0.1	0.1	0.4	0.2	0.3	0.4	0.4	0.1	0	-0.3	-0.3
Turbidity		0.6	0.7	0.5	0.4	0.5	0.6	0.7	0.8	0.8	0.8	-0.2	-0.4	-0.4	-0.7
Temp.	0.2	0.3	-0.2	-0.4	-0.1	0.4	0.4	0.4	0.2	0.2	0.2	0.4	0.1	-0.1	-0.2

Figure 2-10. Correlation matrix showing the relationship between physicochemical and nutrient variables, and fish relative abundance (for Nile perch, Nile tilapia, haplochromines and *S. victoriae*) in Lake Victoria, Kenya. Nile perch and haplochromines were negatively correlated with nutrients and turbidity. Nile tilapia and *Synodontis victoriae* were positively correlated with nutrients and turbidity.

The fish biomass from the gillnets and bottom trawl was categorized into indigenous and introduced species. The introduced species comprised Nile perch and tilapiines (*O. niloticus*, *O. leucostictus*, *C. zillii*). This was to determine the proportion of the indigenous species in the catch, considering predation pressure on the group, particularly on haplochromine cichlids and some of the smaller catfishes. From the gillnet catches in the littoral zone, the combined indigenous species (though not commercially exploited) comprised higher biomass than the commercially exploited species (Figure 2-

11a). Catches for the indigenous species were low in biomass in the trawl gear, which was mainly deployed in deep waters (Figure 2-11b). However, the trawl catches sometimes had large numbers of small-sized haplochromines, mostly *Enterochromis,* and *Gaurochromis,* with some *Yssichromis*. Non-cichlid indigenous species were found more in the inner gulf, and *L. niloticus* (introduced) was more abundant in the open waters.

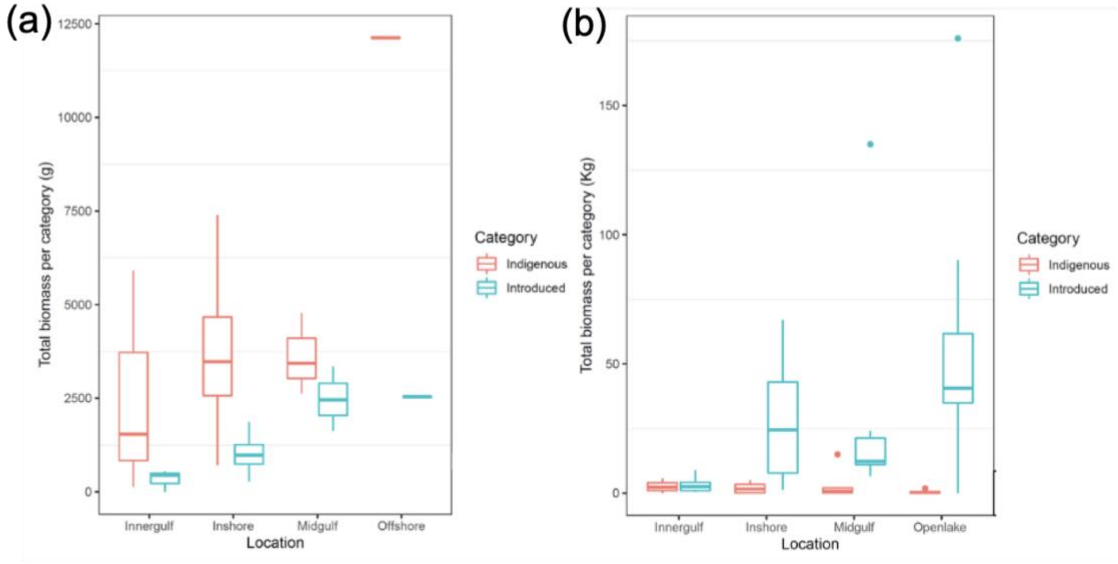


Figure 2-11a, b. Fish distribution by biomass of indigenous and introduced species from gillnet (a) and bottom trawl (b) catch surveys of 2017 in Lake Victoria, Kenya.

2.3.5 Fish species size structure across the spatial-environmental gradient

The size structure of *L. niloticus* showed considerable spatial variability. In the inner gulf, catch distribution was unimodal and dominated by fish less than 15 cm in total length. In the mid gulf and open waters, the length distributions were bimodal but with bigger individuals overall (Figure 2-12). For the other species, the numbers caught in the trawl were too few for a size distribution analysis to be very meaningful (Figure 2-A3).

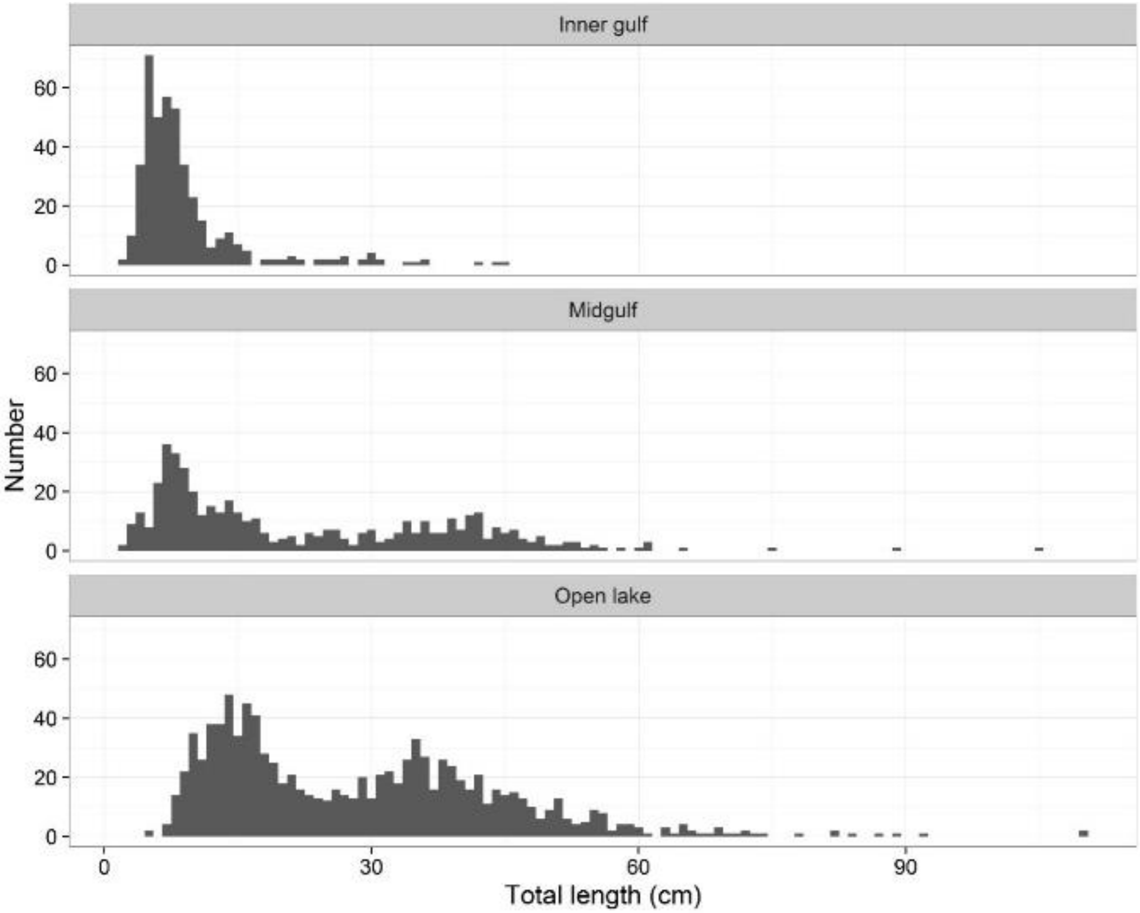


Figure 2-12. Size structure of Nile perch in different zones (inner gulf, mid gulf and open lake) during the 2017 survey of Lake Victoria, Kenya. Catch distribution was unimodal in the inner gulf with individuals less than 15 cm, but bimodal in the mid gulf and open lake with bigger individuals.

2.3.6 Fish Size at 50% maturity across the spatial-environmental gradient

Maturity determination was possible only for *L. niloticus* due to its abundance. A total of 1,944 specimens of Nile perch were analyzed. Maturing individuals numbered 203 mostly males. 17 fish were in a mature state, and 5 of these were ripe. All the rest were immature. Assuming determination of maturity stage 4 and above, the sampled specimens had only 1.5% *L. niloticus* that were mature. Length at 50% maturity for females and males was estimated at 85.5 cm and 61.0 cm TL, respectively (Figure 2-13).

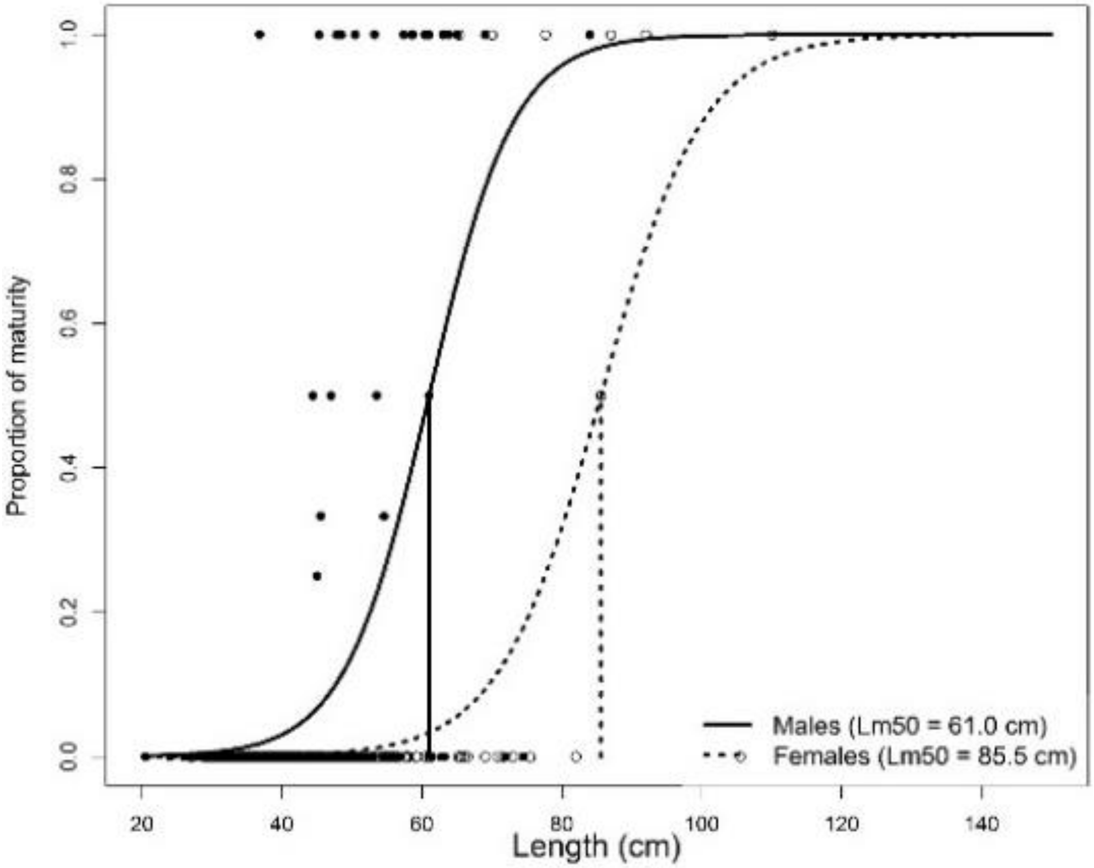


Figure 2-13. Size at 50% maturity for *L. niloticus* was estimated at 85.5 cm TL for females and 61.0 cm TL for males during 2017 bottom trawl sampling in Lake Victoria, Kenya.

2.3.7 Feeding habits of *Lates niloticus* in Lake Victoria across the spatial-environmental gradient

The diet of Nile perch in relation to the eutrophication gradient in Winam Gulf was investigated. To determine the diet of *L. niloticus*, 427 specimens were dissected and their stomach contents examined; 35 were from the inner gulf, 135 from the mid gulf, and 257 from open waters. In the inner gulf, 94.3% had stomach contents, none everted, and

5.7% of the stomachs were empty. In the mid gulf, 63% had stomach contents; none everted, and 37% were empty. In the open waters, 30.4 % had stomach contents; 45.1% everted, and 24.5% empty (Figure 2-14).

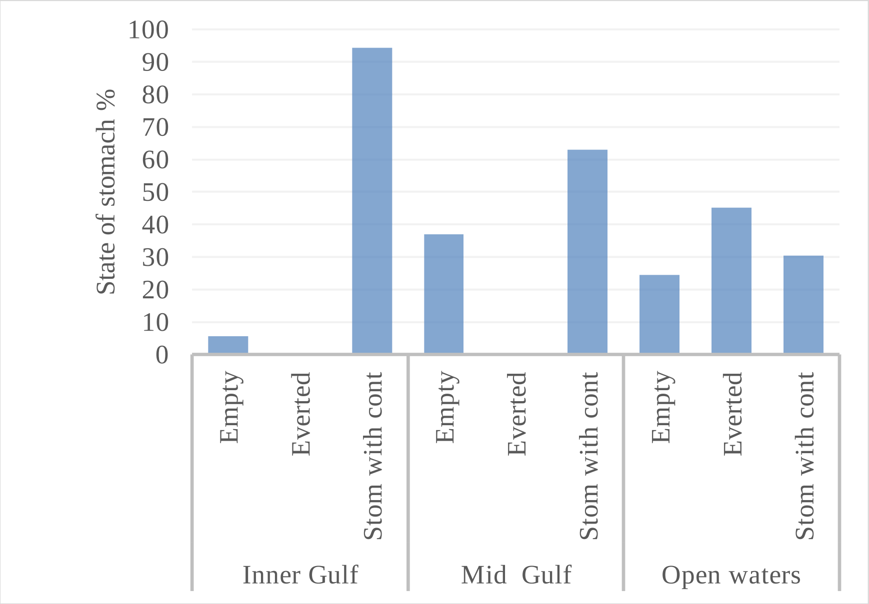


Figure 2-14. State of the stomach in dissected *L. niloticus* from 2017 bottom trawl survey Lake Victoria, Kenya.

The stomach data were categorized into different sizes of fish, and zone (inner, mid and open waters) and analyzed separately (Figure 2-15). In the inner gulf, the class interval 0–14 cm TL fed almost exclusively on *Caridina nilotica* (90.9%) with a few feeding on haplochromines (9.1%). The next larger size class of Nile perch, 15–40 cm also fed largely on *C. nilotica* (42.9%) but with a heavy mixture of unidentified fish remains (25%) while *Xenoclarias* in particular comprised 21.4% of the fish's diet. The class ≥ 40 cm TL had one representative that had fed heavily on *Rastrineobola argentia*. In the mid gulf, 0–14 cm TL class had one representative that had fed on crabs. The class 15–40 cm TL main diet was *C. nilotica* (62.7%) and assorted fishes (19.6%). Class ≥ 40 cm TL fed almost evenly on *C. nilotica* 28.6%; various fishes 33.3% and *R. argentea* in particular 28.6%. In open water, the class 0–14 cm TL was missing. The other two classes 15–40 cm TL and ≥ 40 cm TL consumed 86.3% and 82.9% of assorted fishes respectively. In the open waters, the haplochromines contributed significantly to the diet, accounting for 5.5% and 12.2% respectively (Figure 2-15).

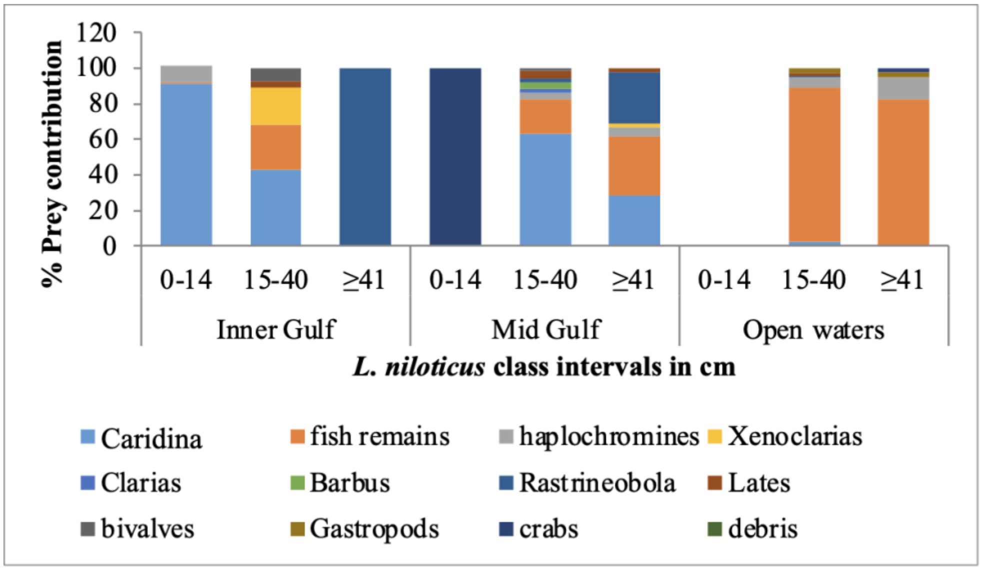


Figure 2-15. Diet of *L. niloticus* in different zones for different sizes of fish from 2017 bottom trawl survey in Lake Victoria, Kenya.

2.4 Discussion

The Lake Victoria ecosystem has been in flux since shifting from mostly mesotrophic to highly eutrophic during the early to mid 1980s (Hecky, 1993; Hecky *et al*., 1994; Kaufman and Ochumba, 1993; Stager *et al*., 2009; Sitoki *et al*., 2010, 2012; Nyamweya *et al*., 2020). Accompanying this change, the lake's fisheries have expanded from artisanal to industrial and from native to exotic species, particularly the introduced Nile perch and Nile tilapia, and the small native cyprinid, *Rastrineobola argentea*

(Medard *et al.*, 2019). Meanwhile, the fish assemblage has changed profoundly, from an indigenous species assemblage dominated by several hundred species of endemic haplochromine cichlids, two endemic tilapiines, and a variety of catfishes, mormyrids and cyprinids, to a mixed assemblage of natives and exotics overwhelmingly dominated by the exotics. More recently, several caveats have been added to the now-classic story of human lack of foresight, rampant exploitation, and mass extinction. Haplochromine biomass has resurged somewhat, though up to several hundred endemic species may have been lost. Nile perch are exhibiting signs of growth overfishing, and Nile tilapia, possibly even recruitment overfishing. However, surveys show that Lake Victoria is not uniform in either its physicochemical attributes or its biology. A limnological gradient from deep in embayments like Winam Gulf out into the open lake, is not at all surprising. What is, is how this gradient has become so extreme, and along with it, an exaggeration of the accompanying gradient in fish species diversity that would normally be expected. The modern lake is highly limnologically heterogeneous, with areas that range from slightly to extremely eutrophic, due largely to anthropogenic influences at varying scales, from local pollution to global climate change.

The inshore-offshore nutrient gradient is present and marked with high concentrations in the inner gulf river mouths and decreasing levels towards the open waters of the lake (Table 2-2). The fish biology tracks this gradient in overall community structure and the size at 50% maturity and feeding habits of Nile perch. Water quality parameters were distinctly different in the inner gulf, mid gulf, and open lake depicting a spatial inshore-offshore gradient. In the gulf, lake water conductivity varied spatially, with much higher mean levels of 180 ± 24.04 µS cm^{-1} occurring near river mouths where watershed influences are most significant. However, the conductivity of the lake's water has not changed appreciably over the last 50 years, remaining at around 100 µS cm^{-1} throughout the period in most of the lake and around 150 µS cm^{-1} in the Nyanza Gulf (Sitoki *et al.*, 2010). The mean pH in the inner gulf was 6.36 ± 0.20 and 6.07 ± 0.20 in the open lake. The pH values were quite a bit lower than those in Talling's (1966) data pre-1980, where pH values of 7.0 to 8.0 were recorded for the upper half of the water column. The low pH favored the ammonium ion with mean concentrations of 26.82 ± 19.92 µg l^{-1} in the inner gulf and mean concentrations of 11.50 ± 7.68 µg l^{-1} in the inshore (Table 2-2). The mean for total dissolved solids (TDS) was a high value of 0.12 ± 0.01 mg l^{-1} in the inner gulf and a low value of 0.06 ± 0.01 mg l^{-1} in the open lake. Abundant plant and other organic debris recovered in huge amounts in the bottom trawl gear may also have contributed to the high levels of TDS and can lead to low dissolved oxygen levels in the water column via organic matter decomposition, especially in littoral zones. Mean water turbidity was high in the inner gulf river mouth (0–5 m water depth) and decreased from 18.46 ± 0.35 NTU to 3.18 ± 2.13 NTU in the open lake (more than 30 m). The high turbidity in the inner gulf is due to suspended solids deposited by rivers draining from the catchment in addition to phytoplankton. The rivers transport materials from both lakeside anthropogenic activities and effluents from onshore human settlements. Low turbidity in the open waters can be ascribed to the inshore deposition of particulate matter and the dilution effect of the deep offshore waters (Mwamburi *et al.*, 2020). The effect of high turbidity is a reduced light penetration into the water column, explaining the inverse correlation between electrical conductivity and Secchi depth (Figure 2-3). Dissolved oxygen concentrations in the lake did not show any consistent trends with location, as relatively high daytime levels were observed even in the inner shallow gulf. This can be attributable to turbulence and mixing due to wind action in the shallow areas. Dissolved oxygen availability in the water column greatly influences fish distribution in the lake, especially for species intolerant to low dissolved oxygen concentrations (van Rijssel *et al*., 2016). From earlier acoustic studies, it was revealed that *L. niloticus* catches increased with an increase in oxygen concentration, and few fish were caught when dissolved oxygen was below 2.5 mg l^{-1} (Njiru *et al*., 2012). Levels of hypoxia are mainly determined by primary productivity, depth, and temperature of the water body (Wetzel, 2001).

The nutrient values for total phosphorus (TP), total nitrogen (TN), ammonium (NH_4), nitrites (NO_2), nitrates (NO_3) and silicates (SiO_2) were significantly higher in the inner gulf river mouth than in the open lake ($p < 0.001$; Table 2-2). Near shore grass, other organic debris and effluents brought in by rivers are possible contributing factors to the elevated nutrient levels. TDS, turbidity, conductivity, hardness, salinity and alkalinity showed positive correlations with nutrients (TP, SRP, nitrates, nitrites and silicates), especially in the inner gulf (Figure 2-3; Figure 2-5). Mean chlorophyll-a concentrations were higher in the inner gulf river mouth 12.23 ± 9.92 µg l^{-1} and significantly different between the inner gulf river mouth and the open lake 5.38 ± 2.14 µg l^{-1} ($p < 0.05$). The high levels of algal biomass (chlorophyll-a) observed in the lake and with extensive coverage of the water surface especially in the inner gulf by macrophytes (water hyacinth

– *Eichhornia crassipes* and Hippo grass – *Vossia cuspidata*) can increase direct uptake of the nutrients, with much lower levels measured in the lake water. Water mixing in the lake is a factor in nutrient levels and species distributions. The factors influencing horizontal mixing, exchange and dispersion processes in inshore and offshore areas of Lake Victoria were studied by Okley (2010) and MacIntyre (2014). In the simulation of water currents in the main lake, current velocities are highest at the center of the lake and also in the western inshore waters indicating enhanced water circulation in those areas, whereas water circulation patterns in the gulfs are more localized, and characterized by relatively slow water current velocities, probably because they are sheltered and shallow (Nyamweya *et al*., 2016). In this study, the recorded total phosphorus (TP) in the inner gulf river mouths was above 100 µg l^{-1} (i.e., 202.73 ± 3.03 µg l^{-1}) an indication of the eutrophic nature of the inner gulf. An increase in nutrient levels leads to the proliferation of algal blooms, especially in the inner gulf. This is corroborated with the Secchi depth and surface turbidity measurements that increase and decrease away from the inner gulf respectively.

A spatial analysis of the phytoplankton community shows that, chlorophyll-a, cyanophytes and dinoflagellates were dominant in the inner gulf, whereas diatoms and chlorophytes dominated the open lake (Figure 2-9). This is consistent with previous studies (Ochumba, 1990; Gophen *et al*., 1993; Lung'aiya *et al*., 2001; Sitoki *et al*., 2012). *Microcystis* accounted for the largest part (>50–90%) of cyanobacteria biovolume and was seasonally persistent in Kisumu Bay (Sitoki *et al*., 2012). Gikuma-Njuru and Hecky (2005) found that in both littoral and pelagic areas, cyanobacteria were the dominant planktonic primary producers, contributing between 54% and 65% of the total phytoplankton abundance, with diatoms contributing 20% to 40% of the total abundance and the main lake having relatively higher diatom abundance than the gulf. The diversity of planktonic diatom communities has declined markedly, particularly with regard to *Aulacoseira nyassensis,* which are nearly extirpated (Stager *et al*., 2009). This is notable because *Aulacoseira* was a major food of the endemic *ngege* (*Oreochromis esculentus*), a species of tilapia that was the most important food fish regionally until its near-extirpation from the main lake. Although local phytoplankton communities did vary considerably in the past, *Nitzchia* has long dominated the diatom assemblages (Stager *et al*., 2009; Sitoki *et al*., 2012).

The establishment of cyanobacteria in the inner gulf would be one reason for the decline of the indigenous tilapiine *O. esculentus*, which as mentioned above, fed largely on chain diatoms. Unlike *O. niloticus,* both it and its co-endemic congener *O. variabilis* lack a well-developed epibranchial organ specialized to filter and concentrate minute cells such as cyanobacteria (Goodrich *et al*., 2000). The presence of floating macrophytes, also spatially affects the optical properties of lake water and other natural transport and redistribution processes of the particulate materials within the gulf. The suspended solids play a fundamental role as different materials and pollutants can aggregate in these solids and brought in suspension, altering the state of the aquatic ecosystem and the use of the freshwater resources. Excessive suspended materials might condition primary productivity by hindering light penetration in the water column depending on the inherent optical properties of particles and TDS concentrations

(Giardino *et al*., 2017). Increased particulate and dissolved organic matter has a great influence on underwater light behavior, besides direct effects on light-dependent aquatic organisms. High algal blooms reduce visibility. This limits the ability of some groups of fish like haplochromine cichlids to use color choices to choose proper mates, leading to hybridization and loss of biodiversity (Seehausen *et al*., 1998; Maan *et al*., 2010; Witte *et al*., 2013). It might also interfere with feeding and prey/predator detection.

An assemblage of diverse haplochromine cichlids (still undergoing taxonomic evaluation) plus nineteen other non-haplochromine species were caught during the gillnet and bottom trawl surveys (Table 2-A1; Table 2-A2). Spatial variability was manifest in both fish species abundance and diversity. In the inner gulf, catches were low and consisted of mainly diverse indigenous non-cichlid species. The high species diversity may be attributable to the riverine and wetland species and a low abundance of the big size classes of the predatory *L. niloticus* in the inner gulf. The non-haplochromine species diversity decreased along the inshore-offshore gradient, with few species observed in the open waters. Overall fish abundance was highest in the open lake followed by the mid-gulf. In all the four zones of the Kenyan waters (inner gulf, mid gulf, inshore and open lake) *L. niloticus* was the dominant species followed by haplochromines, with the abundance of the two exhibiting a similar spatial pattern. This is not surprising in that both benefit from good water quality environments. It could also be related to the strong predator-prey relationship between the two, the latter being the preferred prey of the former (Nyamweya *et al*., 2016).

The inner gulf had greater non-haplochromine fish species richness with a high abundance of catfishes *Clarias gariepinus* and *Synodontis victoriae,* and lungfish *Protopterus aethiopicus*. Water in this area is highly turbid and eutrophic relative to the mid gulf and open lake. This portion of the lake is also shallow and the high level of turbidity is attributable to silt, debris and nutrients washed in by rivers with high effluent concentrations from agricultural activities and agrochemical industries in the catchment. It also receives wastes from onshore human settlements (villages, towns, and cities), including wastes from leaking Kisumu City's waste treatment plant.

The size structure of *L. niloticus* showed spatial variability (Figure 2-12). In the inner gulf, catch distribution was unimodal and dominated by a small size class (< 15 cm TL and probably one-year-olds). This size structure could be an indication of growth overfishing in the inner gulf, and or the use of nearshore areas as a nursery for this species. The inner gulf could also be a breeding ground for *L. niloticus* (Balirwa *et al*., 2003). In the mid gulf, the length distribution was bimodal, and with generally larger individuals than those seen in the inner gulf. This trend continued into the open lake, with more and bigger individuals than in the mid gulf. These observed differences in the population structure of *L. niloticus* in different zones underscore the importance of spatial considerations when formulating management measures for the fishery and the lake at large (Nyamweya *et al*., 2017). The suggestion is in agreement with Taabu-Munyaho *et al.* (2014) who observed that the lake is highly heterogeneous such that it can be considered as being composed of "many small lakes". Overall, the size structure reveals a population dominated by one year-old fish (5–25 cm TL), a typical scenario for *L. niloticus* in Lake Victoria (Taabu-Munyaho *et al*., 2005). Such a situation implies adequate recruitment despite intense fishing pressure, suggesting the presence of growth overfishing but not recruitment overfishing. Management measures should therefore continue to protect the vast amount of small fish in the population; but also allow enough of them to grow to a desirable size for harvest (LVFO, 2016).

To protect the Nile perch stock and ensure continued recruitment, it is necessary to establish and monitor size at 50% maturity. Length at 50% maturity for females and males was estimated at 85.5 cm and 61.0 cm TL, respectively (Figure 2-13). The observed size at 50% maturity for both sexes was an increase from what past recent surveys reported (Hughes, 1992a; Njiru *et al*., 2008). However, sampling needs to be done over months to get a better handle on seasonal and inter-annual trends. Aloo *et al.* (2017) summarizes previous studies on the reproductive biology of *Lates niloticus*. The size at 50% maturity has been decreasing (Table 2-A3), a situation that is generally attributable to increased fishing pressures, changes in food availability, and the lake environment. In the past, it was noted that the size at first maturity among females is close to the size at which *L. niloticus* shifts to larger prey (Hopson, 1972; Ogutu-Ohwayo, 1994). Consumption of larger prey could be related to a need to increase the energy input required for reproduction. As a management strategy to regulate exploitation, slot size has previously been set for males and females at 54–64 cm TL and 62–85 cm TL respectively (Njiru *et al*., 2008). Increasing fishing pressure can cause a shift in Nile perch reproductive physiology, meaning they reach sexual maturity at a younger age. Fishing pressure selects against large, late-maturing individuals. Fishing pressure can also impact Nile perch fecundity, as smaller individuals generally have lower fecundity due to smaller eggs or larvae, plus of course fewer gametes. Besides fishing, water quality could play an important role in Nile perch distribution and even decrease the size at maturity (Ogutu-Ohwayo, 1999). Given the eutrophic nature of the gulf, measures need to be in place to improve water quality for improved growth and reproduction of the Nile perch and other endemic species that are important as native food.

The juvenile Nile perch in the inner gulf fed almost exclusively on *Caridina nilotica*. In the mid gulf, the size class 15–40 cm TL fed on *C. nilotica* and mixed fishes, class ≥ 40 cm TL fed evenly on *C. nilotica*, *R. argentea* and other assorted fishes. The bigger Nile perch in the open waters fed on assorted fish with haplochromines contributing significantly to the diet of the Nile perch (Figure 2-15), but not quite so much as should be expected from earlier data. Data from a 1969–1971 trawling program in Lake Victoria revealed that haplochromines contributed 83 percent of the Nile perch diet (Kudhongania and Cordone, 1974). After the collapse of the haplochromines, there was a notable increase *in Caridina* (Goudswaard *et al*., 2006), and it was suggested that they replaced the detritivorous haplochromines (Lehman *et al*., 1996; Goudswaard *et al*., 2006). *Caridina* became an important food item for the Nile perch, and has even become a significant component of the fishery in some areas (Ogari and Dadzie, 1988; Ogutu-Ohwayo 1990,1999; Hughes, 1992b; Mkumbo and Ligtvoet, 1992; Moreau *et al*., 1993; Katunzi *et al*., 2006; Kishe-Machumu *et al*., 2012). In this study, the interaction between haplochromines and Nile perch is confirmed by their positive correlation. Besides fish, the Nile perch in this study were found to feed on bivalves, gastropods, crabs and debris.

Though other fish species caught during the survey were few in number, they were dissected and examined to learn what comprised their diet. *Synodontis victoriae* was dominant in habitats characterized by detritus from sinking hippo grass and water hyacinth. During bottom trawling in the inner gulf, macrophytes (mainly water hyacinth) clogged the net, with more than 85 per-cent of the catch volume constituted by decomposing macrophytes netted and landed on board. *S. victoriae* fed on an array of materials that included detritus, macrophytes, mollusks, gastropods, insect larvae, corixidae bugs, and *C. nilotica*. The catfish *C. gariepinus* was also caught in the inner gulf and it fed on *L.niloticus* juveniles, *C. nilotica. R. argentea*, and Odonata insects. Another large native catfish, *Bagrus docmak*, was caught in the mid gulf and open waters, where it fed on *C. nilotica, L. niloticus* juveniles, and *R. argentea*. Evidently, the two catfish species are feeding similarly to *L. niloticus* of comparable gape size, but it remains to be seen if competition is a significant factor affecting their demographics. The smaller, midwater catfish *Schilbe mystus* was found to be feeding on insects and *C. nilotica*.

In the 1980s, *L. niloticus* in Lake Victoria was reportedly feeding on haplochromines as its main diet (Okedi, 1970; Okemwa, 1983; Ogari and Dazie, 1988). The disappearance of more than 200 haplochromine species was roughly coincident with, but likely not entirely caused by the introduction and eventual rise to prominence of *L. niloticus*. The fish later shifted its diet to *C. nilotica* when haplochromine stocks got depleted (Hughes, 1992b). The introduction of the predatory food fish *L. niloticus*, coupled with major environmental perturbations, culminated in the extinction of hundreds of species of cichlids; an event termed as the greatest vertebrate extinction yet witnessed by the scientific community, a claim unfortunately likely to be surpassed (Ogutu-Ohwayo, 1990; Kaufman, 1992). The two introduced species (*L. niloticus* and *O. niloticus*) could have outcompeted the indigenous species, another possible cause for the disappearance of so many species (Acere, 1988), though the actual dynamics were likely complex, and may have been compounded by the limnological impact of climate change (McIntyre *et al*., 2014).

In the recent past, Ngwala (2014) observed that *L. niloticus* has shifted to again feeding on haplochromines in the Tanzanian waters of Lake Victoria. A resurgence of haplochromine cichlids has been reported in many localities lake-wide, though this recovery is selective and represents only a segment of the original fauna (Kishe-Machuma *et al*., 2012, 2015; Chapman *et al*., 2003). In this study, juvenile *L. niloticus* mainly fed on *C. nilotica*. For the bigger *L. niloticus*, mixed fish was the main dietary item. The feeding habits of *L. niloticus* need to be related to existing environmental conditions in the gulf to predict the future of the Nile perch fishery. Winam Gulf is faced with the problems of overfishing and eutrophication leading to frequent algal blooms and invasion by large mats of water hyacinth and hippo grass (Gichuki *et al*., 2010; Sitoki e*t al*., 2012, Mwamburi et al., 2020). The deteriorating water quality in the gulf is not a healthy environment for the fish community. The ontogenetic shift of *L. niloticus* from feeding on invertebrates to piscivory occurred at about 30 cm TL in Lake Nabugabo (Schofield and Chapman, 1999). In Lake Chamo, Ethiopia, the shift from invertebrates to piscivory was between 48.5 cm to 73.2 cm TL (Dadebo *et al*., 2005). In the Gulf, the shift appears to occur in the range of 30–40 cm TL class interval. Haplochromines are still, or once again, a major prey for the Nile perch. The apparent preference for haplochromines as prey has reduced the degree of cannibalism considerably, which may have a positive impact on Nile perch recruitment (Kishe-Machumu *et al*., 2012). However, the presence or absence of a food type is not the only factor that determines species distribution; instead, abiotic environmental factors may influence feeding performance. Depth and depth-related factors like light conditions and dissolved oxygen concentrations are equally important variables in determining species distribution (Witte *et al*., 2007).

One of the insights that crystalize from this dissertation is the dire need for a paradigm shift in resource management in Lake Victoria; the change from single-species to an ecosystem-based fisheries management approach (EBFM). An EBFM approach, encompassing all species, their relationships, and overall system dynamics including human behavior, is much more likely to lead to a sustainable fishery than the current single-species management concept. An EBFM approach will take into account biodiversity and environmental conservation of lake resources collectively, as well as improved livelihoods. To realize these, the following ought to be done: 1) Solve the problem of nutrient load into the lake, fueling eutrophication. However, this could be a long-term undertaking that needs the political will of the riparian nations. Nutrient enrichment in the lake is an enormous problem and much of the nutrients come into the lake from catchment activities and onshore activities. Tackling the problem requires a multiagency approach including the private sector alongside local, national and regional authorities responsible for agriculture and fisheries, urban planning, environment, water and sanitation. 2) Adapt to the current situation and improve fisheries within the gulf.

Although the gulf is eutrophic, ways can be devised to sustainably exploit fish in these biotopes. Scientists may design strategies on how communities can best fish in these waters while they engage governments and policy agencies for long term solutions. Given the current situation, eutrophication in the inner gulf has disenfranchised nearby communities; more so women who do not have the capability and ability to fish in the open lake. Large-scale changes in the ecology of the lake have had several implications for women in riparian households (Medard *et al*., 1996). It has proven difficult for them to take advantage of the economic opportunities that have arisen while their access to lake fisheries has been curtailed by both economic and social factors. From the findings of this study, most of the indigenous species like the catfishes (squeakers and *C. gariepinus*), lungfish, and cyprinids inhabit the inner gulf. Researchers can work with women and maximize the development of the inner gulf fishery targeting indigenous species (lower value commercially, but often high value nutritionally and culturally). Men typically go out into the deep waters in the open lake targeting Nile perch, which have high commercial value; but their nutritional value may sometimes be compromised by the very high-fat content, the requirement for refrigeration, and are targeted for the export market.

The accessible but eutrophic inner gulf can be utilized in the following ways, 1) take advantage of the fish that are there and exercise a judicious fishery, 2) practice alternative livelihoods near the shore of the lake (i.e., horticulture can utilize the nutrient-rich water from the lake or be used to refine catchment water before it enters the lake); 3) allow limited aquaculture in the eutrophic areas. The control of nutrient load from the catchment will benefit aquaculture, as the water quality in the gulf will improve; 4) diversify fish landing sites on the shore such that even those areas without fish, can benefit from landed fish caught elsewhere. For instance, fish caught in the open waters off Mfangano Island can be landed at Kisumu beaches so that communities around Kisumu benefit by getting fish. To keep fish fresh and avoid spoilage requires investment in cold storage facilities.

The biodiversity of organisms in an ecosystem is an indicator of environmental health, and how the environment is changing. It is also an indicator, which can be used to gauge if efforts toward reducing eutrophication in a water body are working. In Lake Victoria, biotopes with a thriving population of haplochromine cichlids are an indicator of a healthy environment. It is expected that with reduced eutrophication, biodiversity will increase, and in situations of increased eutrophication, biodiversity will decrease. Catchment afforestation, reduction in point source and non-point source pollution, and agricultural runoff, among other measures, can reduce nutrient load to the lake, thus minimizing eutrophication. Monitoring biodiversity is important as it provides a basis for evaluating the integrity of ecosystems, their responses to disturbances, and the success of actions taken to conserve or recover biodiversity. It is therefore important to greatly improve biodiversity monitoring in Lake Victoria, 1) to assure the availability of food for the Nile perch (are cichlids increasing or decreasing), 2) to assess if any new fishery opportunities can be exploited in the lake as native food fish (i.e., are *Bagrus docmak*, mormyrids, cyprinids, or other catfishes increasing in the lake), and 3) besides, biodiversity monitoring is an excellent regular guide to use for fishery management.

The synergies between biodiversity and fisheries need to be understood by both researchers and fisheries managers. Biodiversity enhances fisheries via recruitment, and fisheries enhance biodiversity once fisheries management regulations are in place and enforced. Whatever is done to enhance fisheries (i.e., use of minimum slot size and reduced eutrophication) will help biodiversity and vice versa. This is important in a place like Lake Victoria given its world-famous haplochromine radiation. The importance of this as a study system for the evolutionary process is a resource whose value is rarely, if ever explicitly reckoned into resource management.

Conservation focuses on 1) protecting species from extinction; 2) maintaining and restoring habitats, and 3) enhancing ecosystem services and protecting biological diversity. For a sustainable fishery in Lake Victoria, the habitats and ecosystems that shelter and feed the fish should be protected. For instance, if there are no haplochromines, *Caridina*, and other supportive fishes, then there will be no Nile perch in the lake. For the riparian communities, conservation measures include being sensitized to protect the wetlands. If communities clear the wetlands (papyrus) and then talk of managing eutrophication, it is counterproductive. The fringing papyrus wetlands trap and filter nutrients from the catchment, thus minimizing the nutrient load on the lake. As a conservation measure, there is a need to reduce the nutrient load on the lake to minimize eutrophication. Any measures instituted to remove eutrophication from the lake, should simultaneously ensure that the swamps and wetlands are protected. This would be an integral aspect of EBFM, bearing in mind that the aquatic ecosystem does not stop at the beach, but stretches to the catchment. What happens at the watershed affects the lake.

Regional bodies like the Lake Basin Development Authority (LBDA) should be proactive in fisheries management; for example, producing *Clarias* fingerlings and other native fishes to facilitate restocking water bodies in the basin for fisheries and aquaculture. There is a need for governments' reforms, emphasizing synergy in how research and management agencies work and embracing EBFM approach in the management of aquatic resources to minimize costs and maximize tangible results.

CHAPTER THREE: THE EFFECTS OF CAGE AQUACULTURE ON LIMNOLOGY AND FISH COMMUNITIES IN LAKE VICTORIA, KENYA.

3.1 Introduction

Lake Victoria, the world's largest tropical lake, has experienced rapid ecological changes due to the effects of introduced species, intensive fishery exploitation and cultural eutrophication (Kitchell *et al*., 1997). Despite the ecological changes, the Lake Victoria ecosystem remains a biodiversity hot spot whose endemic cichlid fish species flock is a global inspiration to students of macroevolution (Kaufman, 1992; Seehausen *et al*., 1997; Witte *et al*., 1992, 2007). Most fishe and some invertebrates are endemic to Lake Victoria and its surrounding satellite lakes. Other members of the biota are more widespread, either within the Nile headwaters or as members of the trans-Saharan assemblage. The lake has however changed largely attributable to the introduction of invasive species, uncontrolled resource exploitation, climate change, and resource use conflicts (Hooper *et al*., 2005; Nyamweya *et al*., 2020). Lake Victoria's ecosystem has progressively deteriorated since the early 1960s both in water quality and fish species diversity (Ochumba and Kibaara, 1989; Witte *et al*., 1992; Hecky *et al*., 1994; Verschuren *et al*., 2002; Stager *et al*., 2009; Sitoki *et al*., 2010; Aloo *et al*., 2017). A few introduced species have come to dominate the flora, and fauna of the lake (Acere, 1988; Ogutu-Ohwayo, 1990; Kaufman, 1992). The key drivers of this mass extinction are anthropogenic, chief among them cultural eutrophication, climate change, and exotic species introductions, both planned and unplanned (Witte *et al*., 2012; Nyamweya *et al*., 2020). Catchment degradation coupled with point source and non-point source pollution has contributed to lake water nutrient enrichment leading to water quality deterioration, especially in Winam Gulf, Kenya (Lung'ayia *et al*., 2001; Sitoki *et al*., 2012; Gikuma-Njuru *et al*., 2013). The invasive water hyacinth (*Eichhornia crassipes*) has thrived, especially in the eutrophic shallow inner bays of the lake (Gichuki *et al*., 2012; Mwamburi *et al*., 2020).

The lake's changing ecology coupled with overfishing has led to reductions in the capture fishery, as well as decline, and extinction within the endemic species flock (Ogutu-Ohwayo, 1990; Kaufman, 1992; Taabu-Munyaho *et al*., 2016; Nyamweya *et al*., 2020). Up to the late 1970s, the indigenous tilapiines *Oreochromis esculentus* and *O. variabilis* abounded and were among the principal food fishes, while the endemic haplochromine cichlids contributed up to 80% of the total catch landings in the fishery (Ogutu-Ohwayo, 1990). Later, the fishery became dominated by only three species, two of which were introduced to the lake: Nile perch (*Lates niloticus*) and Nile tilapia (*O. niloticus*). The third is a native shoaling pelagic minnow, "omena" (*Rastrineobola argentea)*. Total annual fish catches in Lake Victoria amount to one million tons, with 230,000 tons of landed Nile perch fueling an export fishery that generates substantial foreign revenue (LVFO, 2016).

With recently declining catches from capture fisheries, cage aquaculture was introduced in some parts of the lake to augment fish production, particularly to meet local market and food security needs. Cage aquaculture across the world is diverse in terms of the species farmed, farming intensity, and methods employed (FAO, 2006). Although people in high-income countries and most of the emerging economies of Southeast Asia have practiced cage culture for some time in marine and fresh waters (Beveridge and Muir, 1999), it is a relatively new industry across the wider African Great Lakes (AGLs). The number of cages in the Kenyan part of the lake is growing rapidly (Aura *et al*., 2018; Njiru *et al*., 2019; Hamilton *et al*., 2020), and cage fish farming as a livelihood has begun to offer a viable alternative to wild capture fisheries (Njiru *et al*., 2019). There has long been concern about cage farms as a driver of eutrophication, but cage farming has many effects, negative and positive. In Lake Victoria, there is a prospect that well-managed cage farms could act as jurisdictional and structural refugia from fishing pressure and natural predation, while also stimulating a periphyton-based benthic food web within a wider eutrophic, phytoplankton-based pelagic system. Given the extent and rapid expansion of cage farm aquaculture, it has the potential to help restore some portion of Lake Victoria's biodiversity and wild capture fishery value while supporting regional food security. Waste food can attract fish and increase fishing activities around the cages with a positive economic impact (FAO, 2006). Lake areas with cage farms have limited wild capture fishing and exploitative activity because the cage owners protect their farms against encroachment by fishermen. Cage owners employ guards to prevent poaching, thus conferring a level of protection on cage farm areas like that of a no-take marine reserve. Fishing activities in the surrounding waters remain unrestricted. In Lake Tanganyika and Australia's Murray-Darling Basin, the ecological performance of protected areas has been assessed by comparing it with that of nearby unprotected areas; species abundance and diversity were higher in protected areas and decreased with distance from it (Chessman, 2013; Sweke *et al*., 2016). However, related studies on cage farms' effects are scarce.

This study examined how open-lake cage farms influenced the surrounding environment and fish assemblage and assessed the implications of these effects for biodiversity conservation and natural resource management. It was hypothesized that there would be a higher abundance and diversity of fish species in the cage areas than in non-cage areas (control); a higher nutrient load in Winam Gulf than in the open waters of Lake Victoria, and an elevated nutrient load and higher turbidity at cage stations. Fish abundance and diversity between the cage and control areas were compared, and environmental variables were measured at the cages and control areas at four sites along a spatial gradient ranging from the inner Winam Gulf to the open lake. The results inform the global debate concerning cages as a source of nutrient enrichment, and as potential refugia in conserving fisheries resources in freshwater ecosystems.

3.2 Methods

3.2.1 Study site

The study was conducted in the Kenyan waters of Lake Victoria from November 2018 to July 2019. Sampling sites were located within Winam Gulf and the open lake (Figure 3-1). The gulf is shallow with a mean depth of 10 m, and it is 70 km long and 15 to 30 km wide. It connects to the main lake by the 5 km wide Rusinga Channel, through which a limited exchange of water with the main lake occurs (Calamari *et al.*, 1995). The gulf has undergone dramatic physicochemical and biological changes in the past five decades, including the irruption of Nile perch in the lake, increased eutrophication, deterioration of water quality, and invasion by water hyacinth (Ochumba and Kibaara, 1989; Sitoki *et al*., 2010; Taabu-Munyaho *et al*., 2016). These changes are associated with anthropogenic activities leading to higher nutrient loading within the gulf (Lowe-McConnell, 2009; Nyamweya *et al*., 2020). In contrast, the water quality in the open lake has remained relatively oligotrophic. The four sampling sites were selected, one each within the inner gulf (Dunga), mid gulf (Ndere), transition gulf (Naya), and open lake (Mfangano) (Figure 3-1). At each site, the cage and control stations were at least 1 km apart. Price et al. (2015) reported that nutrient enrichment of the near-field column is not detectable beyond 100 m of a farm when formulated feeds are used, and feed waste is minimized. In this study, the distance was extended to 1 km so that the controls were not affected by cage influence due to differences in cage farm management.

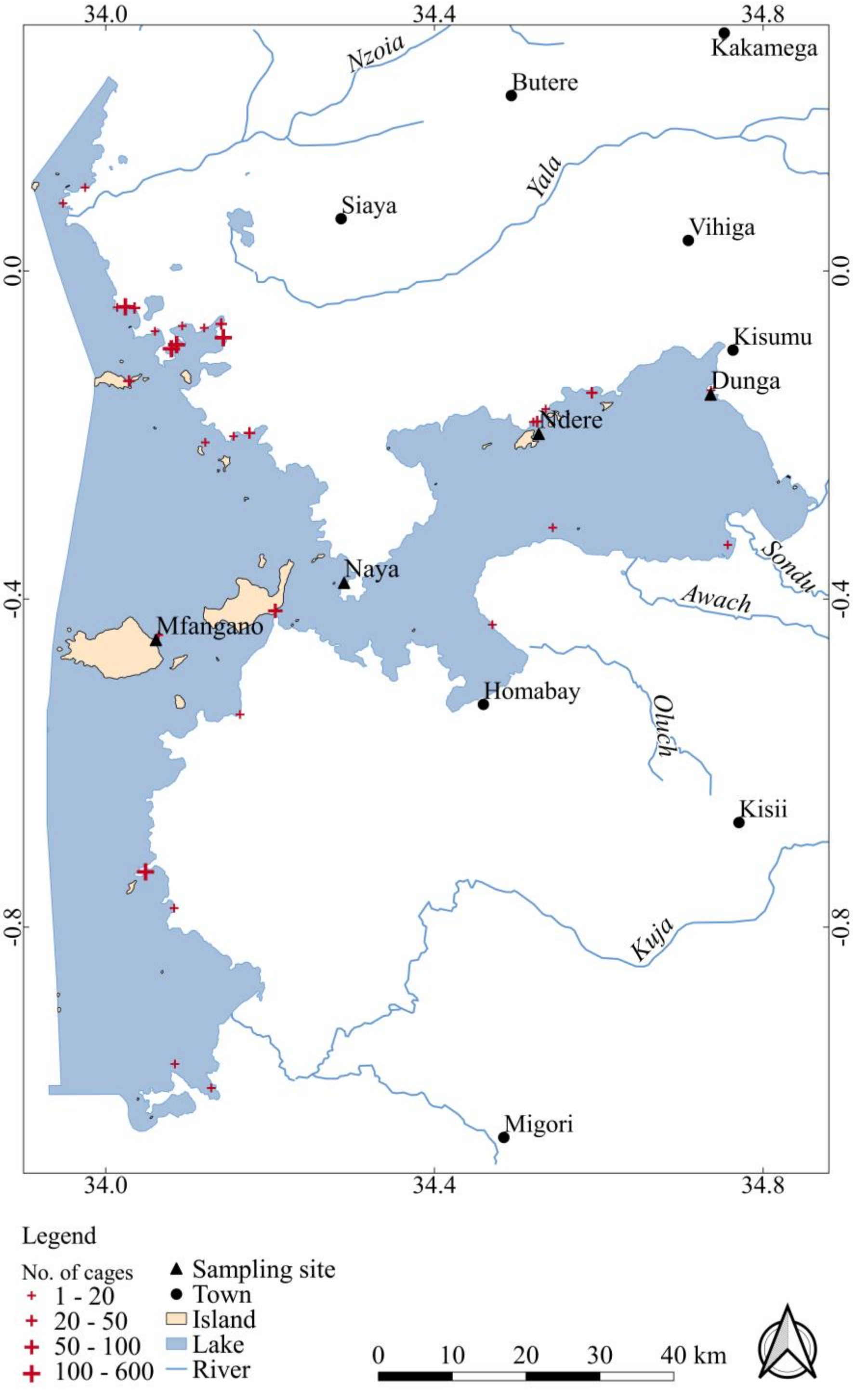


Figure 3-1. Location of sampling sites (cages and control stations) in Lake Victoria, Kenya. The four sampled sites were at Dunga, Ndere, Naya and Mfangano, arrayed along a limnological gradient from the inner gulf to the open waters.

3.2.2 Environmental parameters

Physicochemical parameters were determined *in situ* at 1 m depth using a multiparameter sonde (YSI Model 650–MDS-multi-parameter-YSI 6600 system). The parameters measured included: depth, pH, dissolved oxygen (DO), temperature, turbidity, conductivity, total dissolved solids (TDS), chlorophyll-a, alkalinity, and oxidation-reduction potential (ORP). Replicate water samples for nutrient analysis were taken at 1 m depth and fixed using sulfuric acid (H_2SO_4) and kept at 4°C until laboratory analysis and final quantification. The concentrations of the following nutrients: total nitrogen (TN), total phosphorous (TP), ammonium (NH_4^+), nitrates (NO_3^-), nitrites (NO_2^-), and silicon (SiO_2), were measured using standard methods (Wetzel and Likens, 1991; APHA, 2005).

3.2.3 Fish sampling

Fish samples were collected using gillnets following the Lake Victoria Fishery Organization’s (LVFO) Standard Operating Procedures (LVFO, 2005a) for all fish sampling. Guidelines on collecting and monitoring biological and ecological information of fishes also directed environmental characterization (LVFO, 2005b). Sampling for fish was done at depths between 2 m and 10 m using three replicates of monofilament gillnets (two fleets were set parallel and one fleet was set perpendicular to the shoreline). Six panels, each with a width of 1.37 m and 30 m in length (before mounting), were joined end to end to form one fleet 180 m in length. The mesh sizes of the panels ranged from 0.5” to 2.0” (inches) (i.e., 12.7mm to 50.8mm), at an interval of 0.25” (i.e., 0.5”, 0.75”, 1.0”. 1.25”, 1.75”, 2.0”). Nets of different mesh sizes were used to increase the variability of the sizes of fish and minimize sampling errors. The nets were set and hauled away after one hour. After hauling, all the fish samples (except haplochromines) were sorted and identified to species level according to (Greenwood, 1996; Trewavas, 1983; Witte and van Densen, 1995). The haplochromine cichlids were recorded as a group (*Haplochromis spp.*) due to the difficulty of immediate identification to species level in the field. Total catch, species, and wet weights of fish were recorded at each station. Some fish samples, particularly the haplochromines, were preserved for later taxonomic work and as reference material. A summary of the study design and analyses is as depicted in a conceptual framework (Figure 3-A1).

3.2.4 Statistical analyses

A Principal Components Analysis (PCA) was used to reduce the large dataset into fewer principal components (PCs) that represent large-scale patterns of limnology driven by highly correlated physicochemical, nutrient, and diversity parameters. Analysis of variance (ANOVA) tests were used to determine differences in PC scores (proxy variables for correlated patterns of limnology) and individual ecological parameters between sites (Dunga, Ndere, Naya, Mfangano) and station (cage and control). Tukey’s HSD Test was used to determine post-hoc differences for significant results. All statistical analyses were performed in RStudio version 1.3.1093 (RStudio Team, 2020).

The Shannon Diversity Index (H) was calculated as a composite measure of species diversity for each site and station, as follows:

$$H' = -\sum_{i=1}^{S} p_{i(\ln p_i)}$$

Where p_i is the proportion of individuals belonging to the *i*th species and *S* is the total number of species (Shannon and Weaver, 1963). Though the value of H gives an indicator of overall diversity, it can also be difficult to understand. It was supplemented with two other parameters: the simple number of species present (S), and the "evenness" of the community represented by an index (J), that (Pielou, 1969) proposed with the following equation:

$$J = \frac{H'}{\ln(S)}$$

Where *H'* is Shannon diversity index and S is the total number of species in a sample, across all samples. The resulting species evenness ranges from zero to one, with zero signifying low diversity (no evenness) and one, indicating high diversity (complete evenness).

3.3 Results

3.3.1 Spatial variation in limnology and diversity

PC1 and PC2 accounted for the majority of limnological variation (Figure 3-2; Figure 3-A4). A two-way ANOVA on PC1 and PC2 scores revealed significant differences between sites (PC1, F_{Site}=139.426, p<0.001; PC2, F_{Site}=10.675, p<0.001) but not between cage and control stations at any site. Thus, cage and control stations were grouped at each site for further analyses. Tukey's HSD tests revealed significant differences in PC1 scores for all comparisons except Ndere and Dunga, the two inner gulf sites (*p*=0 for all comparisons). Comparisons of PC2 scores were significant between Dunga-Naya (*p*<0.001) and Naya-Mfangano (*p*<0.001). PC1 (30.4%) represented nutrient loading, species diversity, and water clarity, while PC2 (9.4%) accounted for pH, temperature, and DO (Figure 3-A2). Dunga and Ndere are characterized by low water clarity, high overall non-haplochromine species diversity, and a high nutrient load, while the transitional Naya and open-lake Mfangano have progressively clearer water and lower nutrients. The PCA indicates a strong association of Dunga and Ndere with high electrical conductivity, turbidity, TDS, alkalinity, hardness, SiO_2, ORP, chlorophyll-a, TP, SRP, NH_4^+, and TN. Interestingly, Shannon diversity index (H) and evenness (J) for non-haplochromine species were positively correlated with nutrients and turbidity (Figure 3-A2).

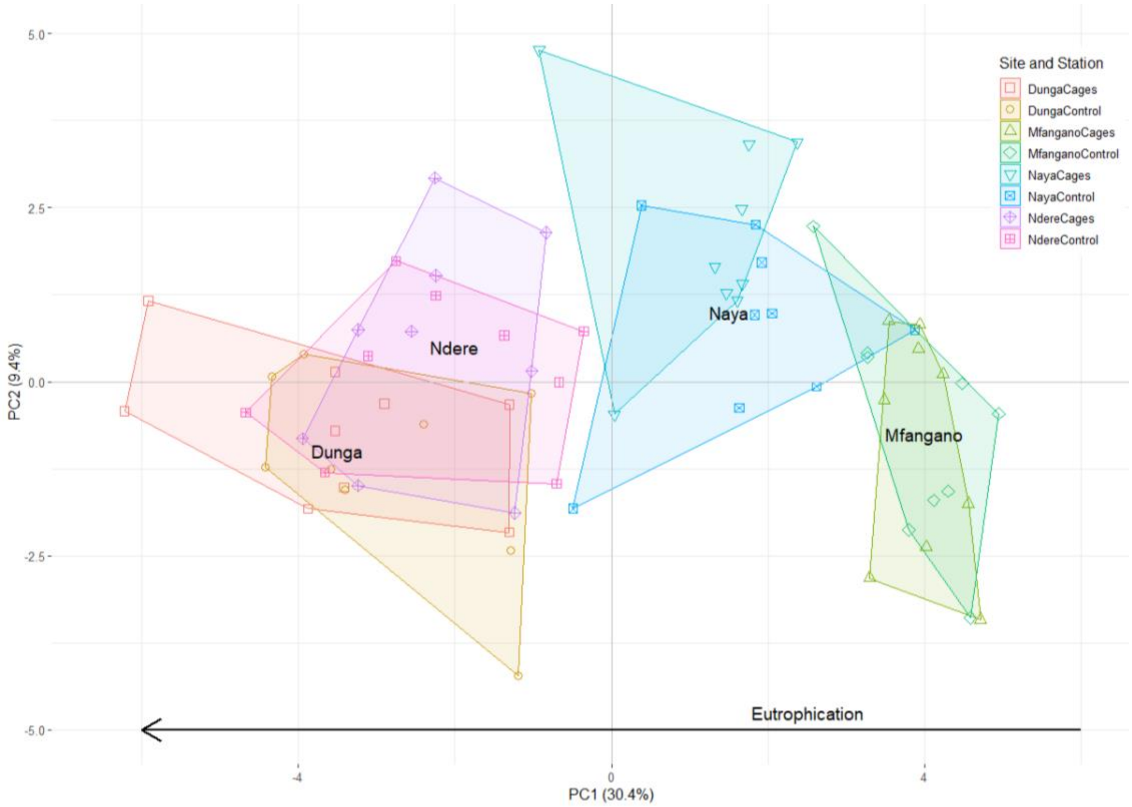


Figure 3-2. PCA biplot of all measured variables. PC1 accounts for nutrient loading, overall species diversity, and water clarity with low PC1 scores having high loading, high diversity, and low clarity. PC2 accounts for temperature, DO, and pH, reflecting seasonal variability. The PCA indicates a strong association of inner gulf sites (Dunga and Ndere) with high nutrient loading and turbidity.

3.3.2 Physicochemical parameters

Seasonal variability of physicochemical parameters was highest in the inner gulf and decreased towards the open lake (Figure 3-3). Variables associated with water transparency (turbidity, TDS, Secchi depth) indicated a steady increase in water clarity from the inner gulf to the open lake. The highest values for turbidity and TDS were recorded at Dunga and the lowest at Mfangano; Secchi depth showed a reverse trend and ranged from 2.65 ± 0.4 m at Mfangano to 0.38 ± 0.09 m at Dunga. The site had a significant effect on Secchi depth (F=305.7, *p*<0.001), and Tukey’s HSD Test revealed this was significant between all sites except Dunga and Ndere (p=0 for all significant comparisons). The site also had a significant effect on conductivity (F=80.82, p<0.001), alkalinity (F=40.48, p<0.001), and hardness (F=11.69, p<0.001), which followed the same spatial gradient as water clarity. Dunga had a lower pH than all other sites (F=12.22, p<0.001) (Tukey's HSD; p<0.001 for all comparisons); there was no variation among the other sites. Surface water temperature, DO, and ORP did not vary along the inner gulf-open lake gradient, and there were no significant differences between cage and control stations at each site.

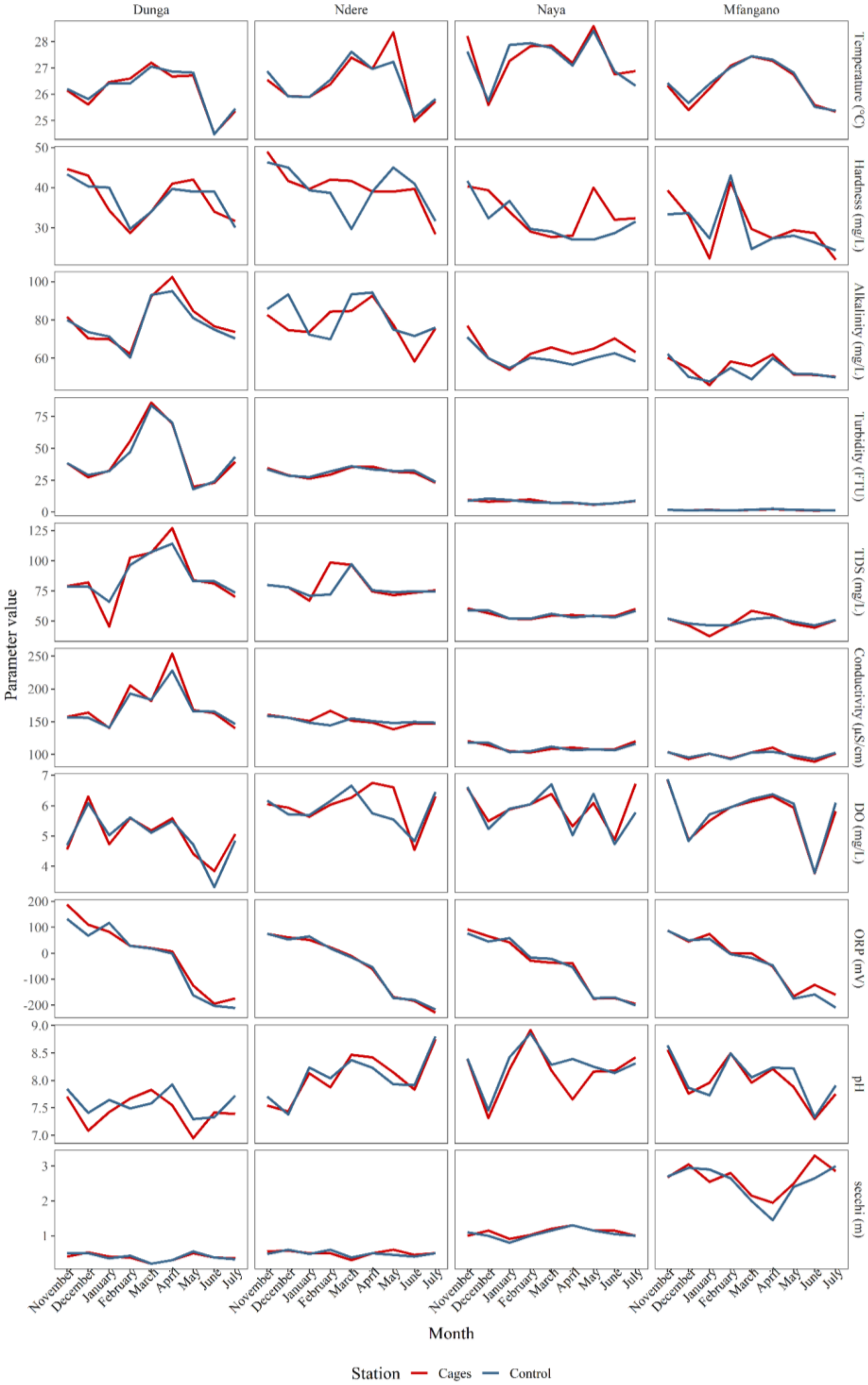


Figure 3-3. Temporal and spatial (site and station) variation in physiochemical water parameters in Lake Victoria, Kenya from November 2018 to July 2019. The highest values for turbidity and TDS were recorded in the inner gulf and lowest in the open waters; Secchi depth showed a reverse trend.

3.3.3 Nutrients and chlorophyll-α

Nutrient concentrations fluctuated greatly at Dunga and Ndere; both seasonal variability and loading decreased towards the open lake (Figure 3-4). Site had a significant effect on NO_3^- (F=11.47, $p<0.001$), NO_2^- (F=26.9, $p<0.001$), SRP (F=5.275, $p<0.01$), SiO_2 (F=24.71, $p<0.001$), NH_4^+ (F=4.783, $p<0.01$), and TP (F=12.23, $p<0.001$). All these parameters were highest at Dunga and Ndere, and Tukey's HSD Tests revealed significant differences between the open lake and inner gulf for all variables ($p<0.01$ for all variables) except SRP.

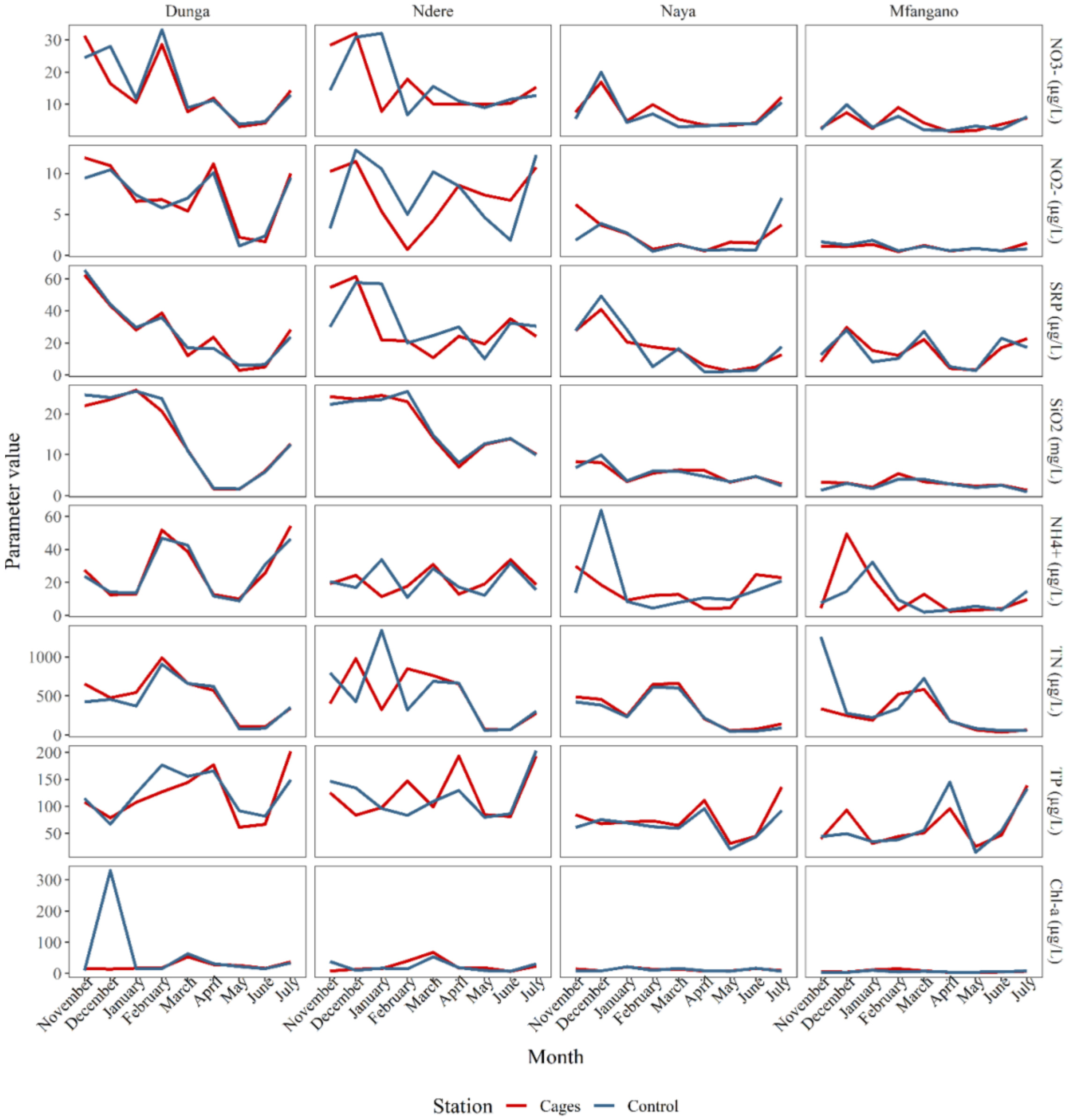


Figure 3-4. Temporal and spatial (site and station) variation in nutrient loading and chlorophyll-a in Lake Victoria, Kenya from November 2018 to July 2019. There was a spatial gradient in nutrient loading with significantly higher concentrations in the gulf than in the open lake. The temporal fluctuations in nutrient levels were more pronounced in the inner gulf than in the open waters.

The measure of phytoplankton biomass, represented as chlorophyll-a concentration, differed significantly between sites (F=3.168, *p*<0.05), though only between Mfangano and Dunga (Tukey HSD, $p<0.05$). At Ndere and Dunga, concentrations of chlorophyll-a peaked in March, while levels remained relatively constant throughout the year at Naya and Mfangano (Figure 3-4). Mean chlorophyll-a ranged from 59.74 ± 96.53 µg l^{-1} at Dunga to 6.07 ± 1.9 µg l^{-1} at Mfangano.

3.3.4 Fish biomass

Overall, a two-way ANOVA revealed cage stations had a significantly higher mean total monthly biomass than control stations, and there was no difference between sites ($F_{Station}=6.517$, $p<0.05$; $F_{Site}=0.499$, $p=0.684$) (Figure 3-5a). In total seventeen species (considering *Haplochromis* spp. as one group) were recorded, belonging to eight families (Table 3-A1).

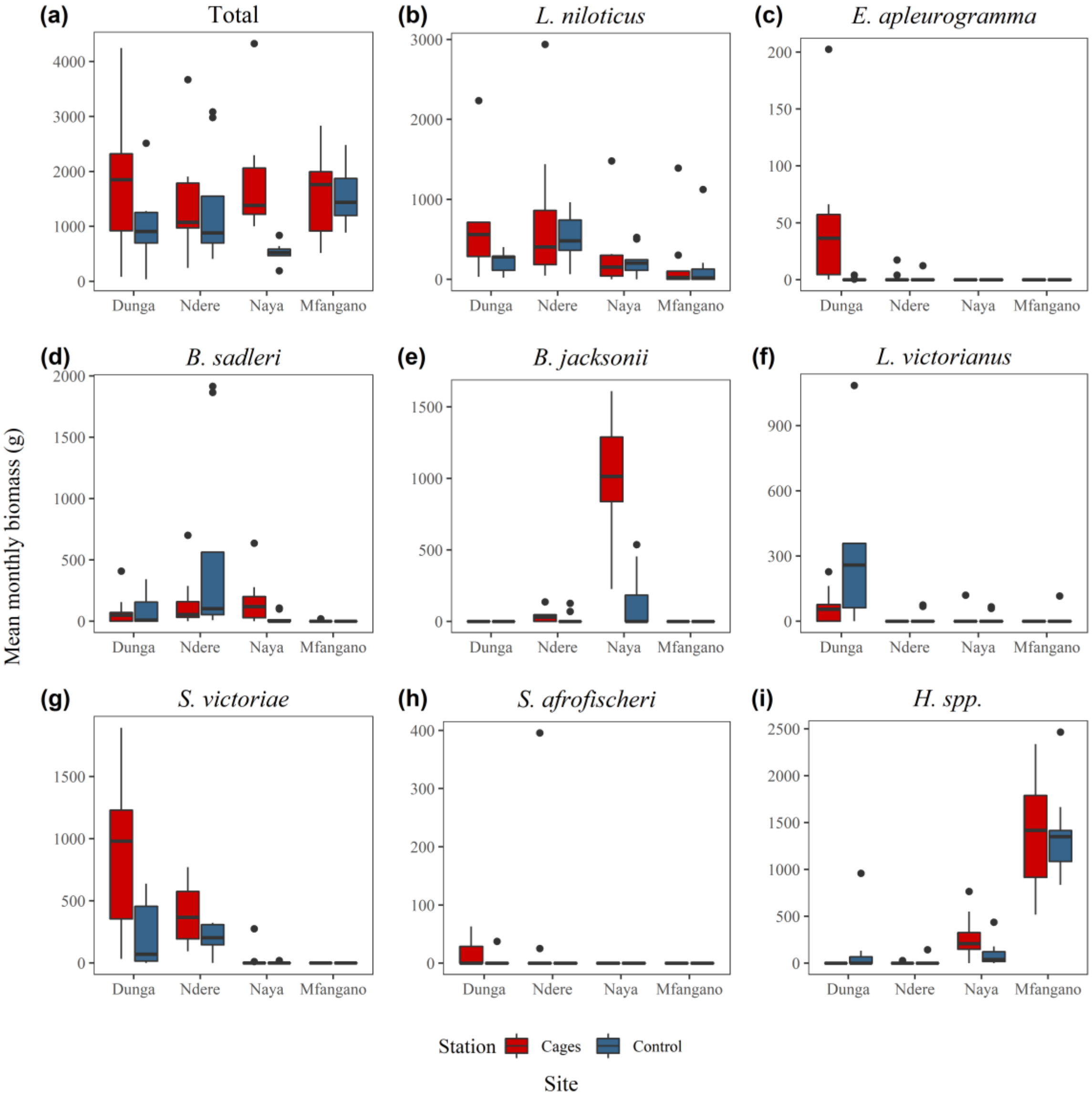


Figure 3-5a–i. Mean monthly biomass (in grams) of most abundant fish species caught near cage and control stations in Lake Victoria Kenya, from November 2018 to July 2019. Overall, the mean total monthly biomass near the cage stations was higher than control stations (3-5a). *Brycinus jacksonii* biomass was higher in the mid gulf (3-5e). *Synodontis victoriae* biomass was higher in the inner gulf than in the open waters (3-5g). *Haplochromis spp*. biomass was higher in open waters (3-5i).

For *L. niloticus*, there was no significant difference in biomass between cage or control stations at any site, though the biomass at Ndere was significantly higher than at Mfangano (F_{Site}=2.753, $p<0.05$; Tukey's HSD, $p<0.05$) (Figure 3-5b). The biomass of *Enteromius apleurogramma* was significantly higher at the Dunga cages than at any other site or station (Figure 3-5c). The highest *Brycinus sadleri* biomass was recorded at Ndere control (Figure 3-5d), though this was not significantly different from any other site or station. Mean *Brycinus jacksonii* biomass was significantly higher at the Naya cages than all other sites and stations, including the Naya control (F_{Site}=21.98, $p<0.001$; $F_{Station}$=13.92, $p<0.001$) (Tukey's HSD, $p<0.001$ for all comparisons) (Figure 3-5e). *Synodontis victoriae* biomass differed significantly between sites (F_{Site}=14.04, $p<0.001$) and stations ($F_{Station}$=10.64, $p<0.01$), with cage stations having higher mean biomass. There was no difference in *S. afrofischeri* biomass in any sites or stations. The highest *Haplochromis* spp. biomass was found at Mfangano (Figure 3-5i), which was significantly higher than all other sites (F_{Site}=76.347, $p<0.001$) with no difference between cage and control stations ($F_{Station}$=0.012, $p=0.911$). Other fish species recorded, though in low numbers or single specimens, included *O. niloticus, O. variabilis* (very rare), *Schilbe intermedius, Marcusenius plagiostoma, M. victoriae, Mormyrus kannume, Coptodon zillii, Protopterus aethiopicus* and *Enteromius profundus* (Table 3-A1).

3.3.5 Fish species diversity

Shannon diversity index was greatest at the most eutrophic sites, with a greater diversity of non-haplochromine species in the inner gulf than in the open lake

(F_{Site}=29.657, p<0.001; Tukey's HSD, p=0) and no difference between cage and control stations (Figure 3-6a). The same pattern was found for mean species number (F_{Site}=18.364, *p*<0.001); Tukey HSD, *p*=0) (Figure 3-6b) and evenness (F_{Site}=25.55, *p*<0.001; Tukey's HSD, *p*=0) (Figure 3-6c).

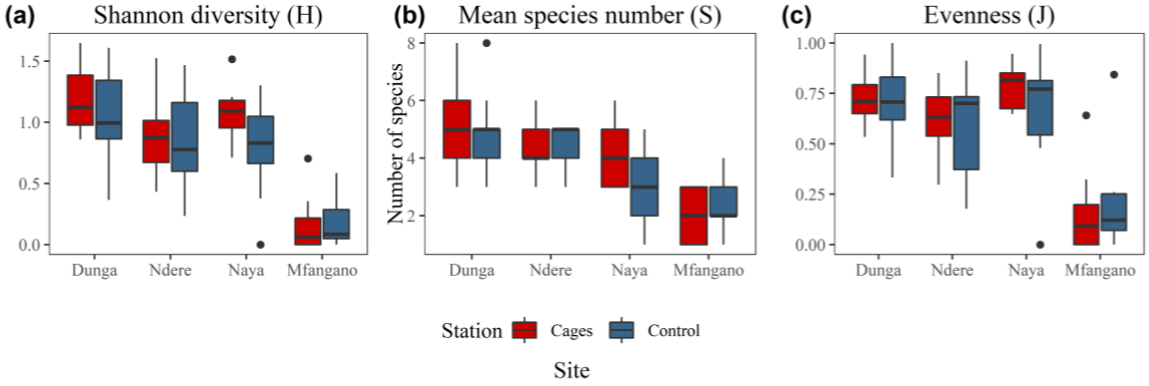


Figure 3-6a–c. Mean diversity indices for sampled sites and stations in Lake Victoria Kenya, from November 2018 to July 2019. Non-haplochromines showed greater diversity in the inner gulf than in open waters (3-6a). Evenness (J) and species number (S) had a similar pattern (3-6b, c).

3.4 Discussion

Results from this study confirm the existence of a strong limnological gradient in Winam Gulf, with the inner gulf holding highly eutrophic, turbid waters that progressively clear towards the open lake (Figure 3-2). Higher fish biomass (Figure 3-5a-i) and significantly greater diversity of non-haplochromine species were observed in the gulf than in the open lake (Figure 3-6a-c), and several species were found to be most abundant at cage stations or within the inner gulf (Figure 3-5b-i). The implications of these results are elucidated with respect to the future of cage aquaculture, biodiversity conservation, fisheries, and the marriage between them in Lake Victoria.

3.4.1 The limnological gradient in Winam Gulf

In this study, physicochemical parameters could vary spatially between cage and control stations, between inner and outer gulf stations, and temporally across the months of sampling. There was little evidence for differences between paired cage and control stations, but all sites were strongly affected by their position along the inner gulf to the open lake gradient. Water transparency was positively correlated with increasing distance from the inner gulf, while nutrient loading showed a reverse trend (Figure 3-2). This inner gulf-open lake limnological gradient is generally consistent with previous studies that have shown differences in nutrient concentrations between the shallow gulf and deep main lake (Ochumba and Kibaara, 1989; Lung'ayia *et al*., 2001; Gikuma-Njuru and Hecky, 2005; Sitoki *et al*., 2010; Juma *et al*., 2014; Kundu *et al*., 2017; Guya, 2019; Mwamburi *et al*., 2020; Nyamweya *et al*., 2020).

Spatial trends of physicochemical variables showed higher mean values of turbidity, conductivity, TDS, hardness, alkalinity, and silicates in the inner gulf. Water transparency showed an inverse trend with high mean values of light penetration in the open-lake at Mfangano cages (2.65 ± 0.4 m) and low mean values in the gulf at Dunga cages (0.38 ± 0.09 m). This is much lower than earlier mean values of 1.1–1.6 m reported in Winam Gulf (Gikuma-Njuru and Hecky, 2005). The high turbidity and low water clarity at Dunga and Ndere (Figure 3-2) are not surprising; the gulf has high suspended solids content following the short (October–December) and long rainy season of March–June in Kenya (Mwamburi *et al*., 2020). Much of the materials in the gulf are depositions from rivers draining into the lake from the catchment. The rivers transport materials from both anthropogenic activities and natural rock weathering and mineral dissolution processes in the watershed rocks (Nyamweya *et al*., 2020). Light limitation within the gulf (Gikuma-Njuru and Hecky, 2005) has been associated with limitation of primary production, and eventual dominance by planktonic cyanobacteria. Low turbidity in the open waters is attributed to the increased settling of deposited particulate matter and the dilution effect of the deep offshore waters (Mwamburi *et al*., 2020). Mean conductivity decreased from a high of 174.89 ± 33.75 μScm^{-1} at Dunga cages to 99.02 ± 6.33 μScm^{-1} at Mfangano cages; the higher mean values in the gulf are driven by terrestrial runoff and discharges from rivers. There was no spatial variation in DO concentration. However, there were temporal differences with low DO concentrations at all sites recorded in June. This coincides with a period of deep water column mixing experienced from June to July during which there is stratification breaking and hypoxic water from the lake bottom comes to the surface (Hecky *et al*., 1994). Surface water temperatures did not vary among the four sites, with a mean of 26.58 ± 0.44 °C for the entire gulf.

There was a spatial gradient in nutrient loading with significantly higher concentrations in the gulf than in the open lake (Figure 3-2, Figure 3-A2). However, no plausible evidence was found that suggests cage farms are directly adding to this load. The temporal fluctuations in nutrient levels were more pronounced in the inner gulf than in the open waters. This is explained by the inner gulf consisting of embayments and vast shallow littoral areas near river mouth discharges. These shallow sites within the gulfs, such as Ndere and Dunga, are more likely influenced by riverine inputs, urban activities, and other land-based runoff inputs than by effluent from cage farms. The higher chlorophyll-a concentrations in the inner gulf are a consequence of greater mixing in shallow inshore waters as well as proximity to terrigenous and riverine nutrient inputs. Many rivers entering the inner gulf bring in silt, waste, and other effluents from the catchment. These wastes increase turbidity in the inner gulf and decrease dissolved oxygen in the water column due to their biodegradation (Sitoki *et al*., 2010; Nyamweya *et al*., 2020). Water quality affects aquatic species abundance, composition, stability, productivity, and physiological condition (APHA, 2005). In the inner gulf (Ndere and Dunga), the cage stations had ambient water quality conditions of the surrounding water. This is because the limnology of the entire inner gulf is associated with high nutrients from anthropogenic inputs (Sitoki *et al*., 2012; Guya, 2019). The more eutrophic state, especially in the inner gulf, is a concern in the occurrence of algal blooms (cyanobacteria) which are a threat to aquatic ecosystem services, flora, and fauna. Lake circulation patterns drive major in-lake processes that cause the distribution of elements, nutrients, and organisms. Several studies have described lake characteristics as being dependent on the influences of rainfall and evaporation processes, leading to spatially homogenous conditions (MacIntyre *et al*., 2014). The net effects of the complex hydrodynamics in lakes determine the dominant processes and extent of nutrient re-mobilization, especially in shallow and intermediate water depths (5–10 m) of the gulf.

3.4.2 Spatial trends in fish biomass

Overall, cage stations had a significantly higher mean total monthly ichthyobiomass than controls, and there was no overall difference between sites. Despite the gulf being highly eutrophic, it held high biomass of non-haplochromine fishes. The high biomass of *L. niloticus* in the gulf would suggest either the fish use the inner gulf as a foraging or breeding ground. The abundance of the squeakers (*S. victoriae* and *S. afrofischeri*) was remarkably higher near the cages in the inner gulf, where they likely feed on periphyton that establishes on the cage nets and structures. The submerged cage structures and nets provide substrate for the establishment of periphyton, which creates food-rich microhabitats for fish to forage as they take shelter/refuge beneath the cages (Oakes and Pondella II, 2009). *B. sadleri* was most abundant at Ndere while *B. jacksonii* was most abundant at the Naya cages. The separation of these two very similar species (*B. jacksonii* reaches about twice the size of *B. sadleri*) is surprising from what is previously known; *B. sadleri* was found to occur in pelagic areas far from river mouths, whereas *B. jacksonii* were confined to the river mouths only (Ojuok, 2008). This would suggest the cage environment at Naya has river mouth-like conditions, and that attraction to the cages may be enhanced by abundant periphyton and shelter. *E. apleurogramma* and *L. victorianus*, two cyprinids, were most abundant at the Dunga cage and control, respectively (Figure 3-5c, f). These benthic feeders scrape material from submerged structures and substrates, likely benefiting from the periphyton and structure of the cages and eutrophic waters. Haplochromine biomass was significantly higher in the open lake and thus also related to high water transparency (Figure 3-2). In the early 1970s, the haplochromine spp. and other indigenous fishes comprised the major fishery in Winam Gulf (Wanjala and Marten, 1974). This is no longer the case. The low haplochromine biomass in the inner gulf, as reported in this study, should be a wake-up call on how rapidly changing ecology and degrading habitats can lead to species extirpation from a given area.

3.4.3 Fish species diversity

The Shannon diversity index indicated that fish species diversity for non-haplochromines was significantly higher in the inner gulf than in the open waters. Shannon diversity and evenness for non-haplochromine fishes were positively correlated with nutrients and turbidity (Figure 3-A2). Though highly eutrophic, the inner Winam Gulf is still a critical habitat for these diverse species. Most of these fish favor riverine and wetland habitats that serve as spawning and nursery areas. Given the anthropogenic inputs from the catchment into the rivers, plus wetland shrinkage due to encroachment, the inner gulf could be the only habitat available for fluvial fishes. This underscores the importance of the inner gulf as critical habitat for species of commercial, ecological, and social importance. The most abundant species recorded in the inner gulf at Dunga and Ndere were *L. niloticus* (Nile perch), *E. apleurogramma* (a barb), *B. sadleri* (a small tetra), *L. victorianus* (an endemic, potamodromous cyprinid), *S. afrofischeri* and *S. victoriae* (catfishes) (Table 3-A1).

Haplochromines were recorded separately as a group and were dominant in open water at Mfangano (Figure 3-5i). The haplochromine cichlids are extremely diverse ecologically; however, their modest overall morphological diversity, the prevalence of intraspecific variation, and the existence of many undescribed and previously unknown taxonomic entities (species, hybrids, local variants) make a rapid assignment of individuals to known taxa in the field a difficult and incomplete exercise (Witte *et al*., 2007). Therefore, the haplochromine cichlid flock was, for the purposes here, considered as a single unit. Viewed in this way, fish species diversity and richness were higher in the gulf than in the open lake, with no significant differences between cages and controls. However, the haplochromines found at Mfangano comprise multiple genera and trophic groups, which our diversity indices do not account for. The clear water of the open lake promotes trophic differentiation, species coexistence, sexual selection, and year-round spawning, indicating that the functional diversity of Mfangano is much greater than what is reported in our study (Seehausen *et al.*, 1997; Witte *et al.*, 2012).

It is worth noting that very few tilapiines (both introduced and indigenous) were recorded during this study. No single indigenous *O. esculentus* was recorded during the entire survey, and only two individuals of *O. variabilis* were recorded, at Mfangano. Few individuals of the introduced Nile tilapia (*O. niloticus*) were caught; its plummeting catches is a major reason for its prevalence in cage aquaculture in the lake.

3.4.4 Cage farms as a refugia

Fishing pressure in Lake Victoria is very high (Van der Knaap, 2013), whereas all forms of exploitation including fishing are prohibited around the cage areas, and cage owners actively restrict any encroachment by fishermen. The study found that these cage areas had higher total fish biomass than controls. *B. jacksonii* biomass was highest at the Naya cages and significantly higher than at the control (Tukey HSD, $p<0.001$) as well as at every other station at each site (Figure 3-5e). This suggests that in areas with high fishing pressure like Naya, cages could act as a refugium and foraging ground for at least some fishes. Other studies have documented that protected areas harbor higher fish diversity as compared to unprotected areas (Sahyoun *et al.*, 2013). Poor enforcement of fisheries regulations by local and national authorities can help explain the low fish biomass and diversity in a station like Naya control – an area not protected from exploitation by cage farmers. The use of prohibited fishing gear like beach seine nets and monofilaments was encountered in all sampled sites during the study, and in some places distanced from cage farms, gill net density can be so high as to impede free passage of a boat. Many nets are lost, and the use of illegal, unreported, and unregulated (IUUs) fishing and ghost gear are serious threats to sustainable fisheries, conservation, and food security.

3.4.5 The effect of cage farms on biodiversity conservation

Given the eutrophic status of Winam Gulf, it would be advisable to have low fish stocking densities in inner gulf cages and higher stocking densities in open lake cages. Sites with good water exchange can have higher stocking densities, while those with poor water exchange should use lower stocking densities (Beveridge and Muir, 1999). Cage aquaculture has associated environmental and ecological problems, and these must be considered critically at all stages from the initial planning to site selection, and finally as part of the regular monitoring for daily operation. In Lake Victoria, these concerns have been recently raised by cage farmers, conservationists, and fishermen, particularly regarding the potential negative effect on the critical export fishery and endemic biodiversity. Most importantly, this study’s findings suggest that the current state of cage aquaculture is not the major cause of eutrophication in Winam Gulf. Rather, terrestrial, and other sources are the major contributing factors; cage farms have no significantly higher nutrient enrichment or turbidity than the ambient conditions of control sites. Even at Mfangano, where deep water and fast dispersal due to wind and currents maintain oligotrophic conditions, the cage farms did not have a significant environmental signature. The capacity of the environment to assimilate nutrients varies greatly according to local conditions of depth, hydrography, and water exchange and sediment type (FAO, 2006). This gives promise to the expansion of cage aquaculture on Lake Victoria. Well-managed cage farms positioned in open, deep waters may contribute little to cultural eutrophication. However, the fact that eutrophication is already a serious problem in the lake, particularly in Winam Gulf, is not a reason to permit unregulated cage aquaculture. Cages should not be installed in areas that are known fish spawning grounds to avoid tampering with recruitment, or in areas that are prominent fishing grounds for capture fisheries. Doing so might redirect fishing pressure to limited areas, thus posing management challenges. However, if cages are well managed, they can act as refugia attracting diverse fish assemblages which can enhance biodiversity conservation and, potentially, the fishery. In Indian inland waters, submerged bamboo structures assisted the growth of periphyton on the submerged parts. This served as a refuge for feeding either by grazing on periphyton, micro-invertebrates and insects or by predation on smaller fishes that took shelter under refuge (Suresh, 2000). Such provisions have also been reported in Malawi (Banda *et al*., 2005). Taken together, the results suggest that cage farms positioned in the outer gulf and open lake areas (Naya and Mfangano) can act as refugia from fishing while supporting a periphyton-based food web without discernably contributing to eutrophication. In addition, the growth of cage aquaculture may take pressure off the wild capture fishery.

As cage aquaculture continues to expand in the region, there is a cumulative and eventually wider effect on the environment. Therefore, the need for continued coupled human and natural systems (CHANS) studies (Walker *et al*., 2004; Liu *et al.*, 2007) to provide regular monitoring, management guidelines for best cage practices, and the capability to recognize when limits are reached. Future studies should give particular attention to how the riparian community can be engaged in sustainable cage aquaculture, wild capture fisheries, and biodiversity conservation in the region to safeguard food security and livelihoods.

CHAPTER FOUR: CAGE AQUACULTURE AND LOCAL FISHERIES ADAPTATIONS IN LAKE VICTORIA: BIOPHYSICAL LIMITS, SOCIAL EQUITY AND ACCESS, AND TRADE-OFFS.

4.1 Introduction

Lake Victoria is one of the world’s largest tropical lakes, and one of its two largest inland fisheries, on par with Cambodia’s Tonle Sap. The fish it produces is an important source of food and employment for the region’s 45-plus million people. Fish landed from capture fisheries in Lake Victoria have dwindled due to overfishing, among other factors, whereas demand for fish protein has been on a gradual increase because of a burgeoning human population (FAO, 2016; LVFO, 2016). The per capita fish consumption in the Kenyan waters of Lake Victoria has fallen to < 5 kg/person/year (Wenaty *et al.*, 2018; KNBS, 2020), compared to a global average of 20 kg/person/year (FAO, 2016). For about a decade now, cage farms have been operating in the lake to augment fish production, a practice that is now exploding in an attempt to boost fish production. In terms of temperature and water quality, parts of Lake Victoria are suitable for Nile tilapia cage farming; and increased production is likely as new investors install cages on the lake and some existing farms add more cages to scale up production (Orina *et al.*, 2021). Therefore, cages as production units are contributing to food security, employment, and economic growth in the country. The advent of cage aquaculture has seen significant private-sector investments made in different aspects of aquaculture production including feed manufacture, seed and table fish production, processing and marketing facilities (Orina *et al.*, 2018). Unlike pond fish farming, cage aquaculture on the lake has brought a fundamental paradigm shift in the way fish farming has been done in the country, from subsistence pond fish farming to a business-oriented model of cage fish farming. In Kenya today, cage fish farming contributes significantly to the supply of Nile tilapia (*Oreochromis niloticus*) available in the local markets (Orina *et al*., 2021). However, cage aquaculture can have positive or negative environmental, biodiversity, and social-economic effects. As the number of cages in the lake is increasing, there are concerns about the sustainability of the undertaking (Hamilton *et al*., 2020).

Cage aquaculture has certain advantages over other methods of fish culture. These include high production per unit volume of water; relatively low investment per unit produce and potentially high profitability; the use of existing water bodies, thus reducing pressure on land; relatively low capital outlay requirements; ease of movement and relocation; and flexibility of management (El-Sayed, 2019; De Silva and Phillips, 2007). The production in cages and ease of harvest render the method useful both for flexible adaptation to market demands and for continuous supply. High stocking densities are possible; fish are easily observed facilitating intervention when necessary; harvest is simple and quick, and technological steps can be mechanized. An indirect advantage is that by utilizing existing natural waters, land areas of fish ponds can be used for other agricultural activities.

Cage aquaculture that is not well managed also comes with negative environmental concerns, such as the release of particulate and dissolved nutrients through uneaten waste feed, fecal matter, and excretory products (Masser, 2003). This can cause eutrophication and negatively affect the environment through anoxic conditions in sediments (due to organic enrichments) underlying the cages, thus changing invertebrate abundance and species composition (Ngupula and Kayanda, 2010). Moreover, eutrophication can impact the water column as well (Ngupula *et al.*, 2012). Additionally, farmed fish can escape and interact with other fish in the wild resulting in the spread of diseases and parasites, decreased genetic diversity (due to genetic dilution) and increased mortality of wild stocks (due to transferred diseases). Since in cage culture natural feed is partly or completely ruled out of the fish diet, a complete artificial feed of high protein content is required. This significantly increases the feeding expense in the net cost of the fish meat produced. Due to high stocking density, fish are susceptible to bacterial and parasitic infection and are more sensitive to the decrease in the dissolved oxygen (DO) content of water. This latter outcome may result in a lack of appetite and mortality in serious cases. When choosing the site, the foreseeable environmental stresses (pollution, oxygen depletion) should be considered.

Despite these challenges, good aquaculture practices should be employed in the development of this industry, and in how best to serve the lake community without eliminating other values and ecosystem services. It is therefore important to understand the linkages between the environment, biodiversity and social-economic activities of riparian human communities, both in terms of the effects of cage aquaculture on the environment and human well-being, and the effects of the environment and human activities on cage aquaculture. Building on the results of chapters 2 and 3 and the body of literature, this chapter addresses the following questions: 1) What are the areas suitable for cage aquaculture in Lake Victoria, Kenya?, 2) What are the biophysical limits and other limits that the cage aquaculture industry in Lake Victoria must stay within to preserve other values, services, and ecosystem integrity?, 3) What are the impacts on access and equity to fish as a resource (through either cage aquaculture or fisheries) by the local communities?, and 4) What are the trade-offs to ensure the sustainability of the systems (e.g., what is the cost of doing it wrongly or correctly, and why should cage operators listen)?. Lastly, drawing on these conclusions, recommendations are made to aid fisheries managers and policy makers on how best to manage cage aquaculture, fisheries and biodiversity for equitable and sustainable development of Lake Victoria and other freshwater bodies.

4.2 Suitable cage installation sites in Lake Victoria, Kenya

4.2.1 Major characteristics to consider for suitability

Choosing suitable sites for cage aquaculture in a natural water body requires careful consideration of water quality, water depth, and water currents, among other factors. Water quality must meet the requirements of the species (in terms of physicochemical parameters), and the expected change in water quality parameters during the growing season must be taken into account. For water depth, there should be good clearance (more than 2 m) below the bottom of the cage net and lake bottom sediments. Deeper water areas are preferable, for they offer greater clearance from the bottom and often better water circulation. Water currents are a crucial factor in cage farming. Though cage culture can be done successfully even in still water, some current (10–20 cm sec^{-1}) is beneficial for the oxygen supply to the fish and removal of wastes, ensuring adequate water exchange between the water inside and outside the cage. Too high a water velocity is disadvantageous because it can wash away large amounts of food and the fish are forced to swim occasioning energy waste; and the regular shape of the cage may be deformed by strong flow (decreasing the useful water volume inside the cage). It has been suggested that water velocity should not exceed 40 cm sec^{-1} (Váradi, 1984). The prevailing wind may have a good effect on water exchange by generating surface water current, but if it is too strong the cages need to be placed in a sheltered water area.

Bathymetry and GIS spatial analysis were used to determine suitable sites for cage installation in the Kenyan waters of Lake Victoria (Orina *et al.*, 2018; Hamilton *et al.*, 2020). Several characteristics were used to formulate suitability criteria that included: depth (shallow or deep), littoral areas, sheltered bays, open lake, protected breeding areas, fishing grounds, transport routes, water abstraction and pumping points, river mouths, areas prone to currents and wave action. Using suitability criteria, areas in the lake were designated as most suitable, suitable, less suitable, unsuitable, and constrained for cage installation (Orina *et al.*, 2018) (Figure 4-1). Based on optimal water quality and bathymetry, the area of the lake under the delineated categories was estimated as follows: most suitable (191.3 km^2 or 4.67%; 8–12 m), suitable (171.1 km^2 or 4.17%, 6–8 m), least suitable (227.2 km^2; 4–6 m and 2,394 km^2; > 12 m), unsuitable (984.5 km^2; 0–4 m), and constrained (i.e, protected fish breeding areas, 296 km^2) (Figure 4-1). Nearshore littoral areas of 0–4 m depth were categorized as unsuitable cage installation sites because of the impact from land-use activities and rivers; and it is here that most protected fish breeding grounds are. Depths of more than 12 m were also delineated, as unsuitable as they may be prone to strong currents. However, sturdy cages like high-density polyethylene (HDPE), with high volume and high fish stocking density may be installed in such areas but would suffer the disadvantage of the fish spending a lot of energy swimming against the currents, energy that would otherwise be used for growth. Depths of 4–6 m are considered least suitable because of nearness to shallow unsuitable areas and the potential for low dissolved oxygen (DO) due to poor water exchange, particularly at night. Areas with a depth of 6–12 m are regarded as most suitable. They are likely to be in the sweet spot for beneficial water current velocities, allowing high volume cages with high stocking density to be installed in these areas (Figure 4-1).

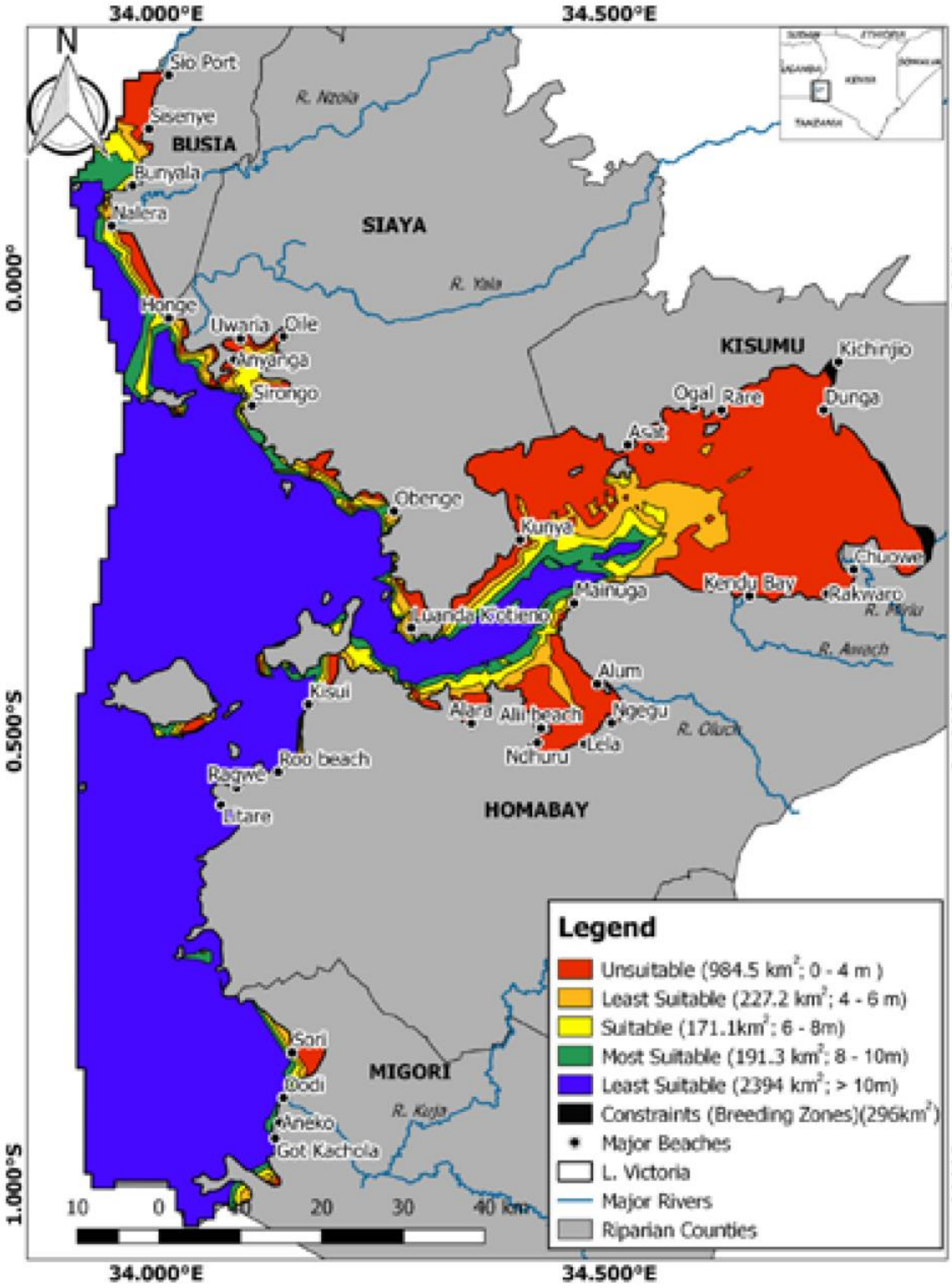


Figure 4-1. Cage aquaculture suitability map in Lake Victoria, Kenya (adapted from Orina *et al*., 2018).

4.2.2 Estimating potential annual fish production from cages in Lake Victoria, Kenya

Recent aerial drone surveys using GIS tools and satellite imagery technology estimated that there were at that time about 4,357 fish cages in operation. These covered an area of 62,132 m^2 or 0.0621 km^2 on the surface of Kenya's portion of Lake Victoria (Hamilton *et al*., 2020). The lake area suitable for cage culture was estimated as (171.10 km^2 + 191.30 km^2) which is about 362.40 km^2 or 8.84% of the available lake surface area (Kenya's segment of the lake accounts for about 7% of Lake Victoria surface area). If an area of 0.0621 km^2 can be occupied by 4,357 fish cages (assume an average size of a cage as 2 x 2 m), then an area of 362.40 km^2 will be occupied by 25,426,357 cages. Given a cage of size 2 x 2 x 2 m (8 m^3) with a stocking density of 40 fish/m^3 and a survival rate of 70%, and harvesting fish at an individual average weight of 350 g after 6 months growth cycle; then harvest from one cage will be 78.4 kg. Therefore, cage aquaculture production potential for the Kenyan portion of Lake Victoria is estimated at 1,993,426 metric tons annually (i.e., 25,426,357 cages x 78.4 kg per cage). Due to some limitations and capacity to invest, the estimated potential may not be fully utilized. However, should even one eighth of the potential area be put under cage aquaculture, that would be a production of about 250,000 metric tons annually (i.e., 1/8 of 1,993,426 tons annually). This is the equivalent of Nile perch production at its peak from the entire lake. From these estimates, the potential for aquaculture is big enough to compete with the entire Nile perch capture fishery in the lake. It should be emphasized here that the estimated production of 250,000 metric tons per annum is only from utilizing a small area of the Kenyan lake (about 8.84%, an area suitable for cage aquaculture).

This would be a sizable contribution to Kenya's aquaculture subsector, considering that 19,945 metric tons were realized from aquaculture production (Figure 4-2), and total fish production (capture fisheries and aquaculture) was 149,678 metric tons in the country in 2020 (Figure 4-3) (KNBS, 2021).

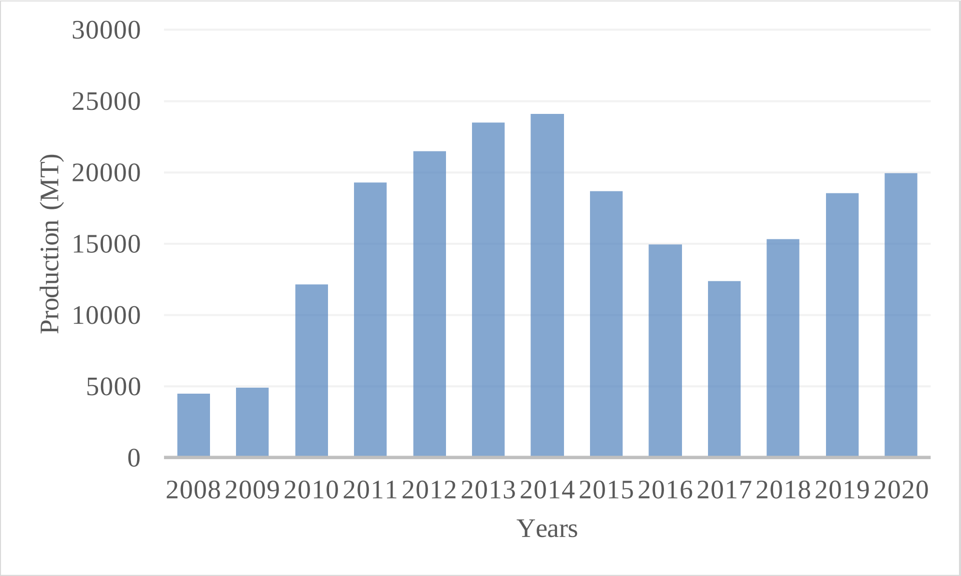


Figure 4-2. Aquaculture production (metric tons) in Kenya 2008 – 2020. Data source: Kenya National Bureau Statistics (KNBS, 2021)

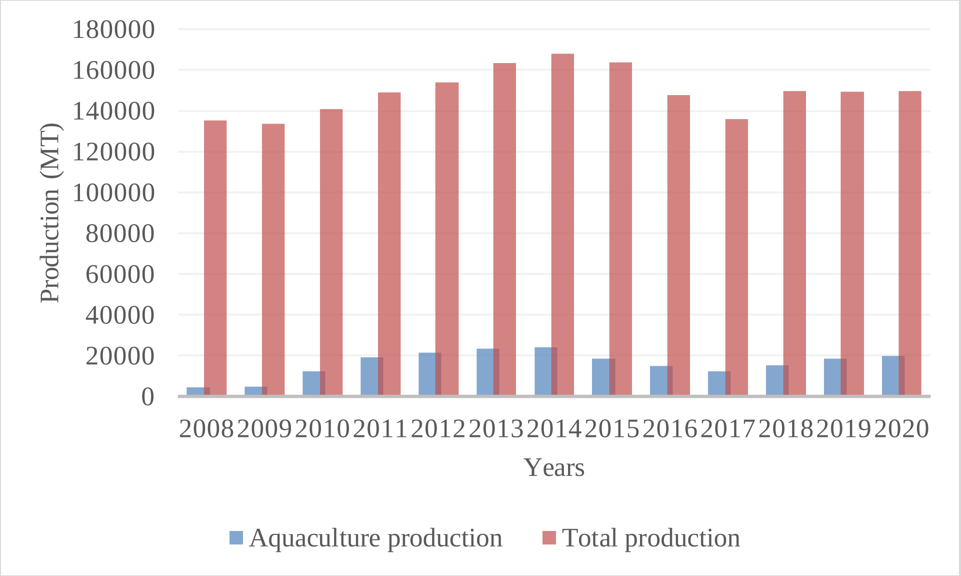


Figure 4-3. Total fish production (metric tons) in Kenya 2008 – 2020. Data source: Kenya National Bureau Statistics (KNBS, 2021)

The production from cages alone could greatly reduce the fish import deficit. In 2018, Kenya imported 32,717 metric tons of fish and fishery products worth KES 3.96 billion (USD 39.6 million). Of the fish and fish products imported that year, 16,966 metric tons, or 52% were Nile tilapia (KNBS, 2020), fish that could have been produced domestically. The large amount of imported tilapia poses challenges locally including quality assurance and price fluctuations hurting local producers and other participants in the aquaculture value chain.

An estimated area of 459 km^2 in the Kenyan portion of Lake Victoria is categorized as having constraints for cage culture. These include areas inaccessible due to the presence of water hyacinth, delimited fish breeding grounds, and mobile islands of macrophytes (mainly hippo grass intertwined with water hyacinth). In total, the area considered not suitable for cage aquaculture is approximately 3,737.5 km^2, representing

91.16% of the lake surface area (i.e., unsuitable sites of 984.5 km^2 or 24.1% and least suitable sites of 2,753.0 km^2 or 67.15%). This is a large area of the lake useful and available to support wild fishery and other ecosystem services (i.e., water extraction, recreation, navigation and transport, among others). Another factor to take into account while siting cages is lake upwelling. Lake Victoria exhibits annual cycles of thermo-stratification (September–May) and mixing (June–August). The lake also exhibits a seiche (internal wave) and underflow current that creates upwelling and downwelling spots (McIntyre *et al*., 2014; Nyamweya *et al.*, 2016). Cages should not be installed in such areas as upwelling brings bottom anoxic water to the surface that can lead to mass fish mortalities in the cages.

Despite the identification of the most suitable areas for open lake aquaculture, some cage farms in Lake Victoria did not take cognizance of these factors. Some cages were found to hav been installed near river mouths, navigation routes, fishing and breeding grounds, and other critical habitats for fish. Some were installed on areas prone to water hyacinth and floating islands (floating mats of papyrus). Most of the cages were found located relatively near the shoreline within 200 m (Aura *et al*., 2018); a factor attributable to high operation costs of accessing the open water regularly, insecurity from poaching, and fast-moving currents and wave action in the open lake. Studies have shown that poor cage siting leads to high fish mortalities and conflict with other lake water users. Therefore, cage aquaculture investors should adhere to the guidelines of good aquaculture practices (GAqP) that includes proper siting of cages for optimal production.

4.3 Biophysical limits of cage aquaculture

The rapid growth of cage aquaculture in Lake Victoria will, like many other agricultural investments run into formidable challenges. These include the often poor water quality in the lake, resource use conflict, theft, and infections (Masser, 2003). In addition, a lack of good aquaculture practices (GAqP) coupled with low water exchange in and out of cages and increasing water temperatures with climate change, are catalysts for diseases (FAO, 2007). Cage farms impact their environment, and the environment impacts what’s going on in the cages.

4.3.1 Environmental considerations - effect of cage fish farming on the environment

Cage aquaculture can negatively or sometimes even positively influence the lake’s biophysical environment. Like other anthropogenic activities, cage aquaculture produces wastes that, if not well managed can cause eutrophication. In intensive aquaculture (i.e., cage culture), much organic waste is produced in the form of particulate and or soluble substances (mainly the uneaten food and excreta). This increases biological oxygen demand, nitrates, and phosphates in receiving waters (Beveridge *et al*, 2013). If natural waters are not overloaded, then the added waste load can be recycled into the lake system; but Winam Gulf, which constitutes much of the Kenyan portion of Lake Victoria, is already highly eutrophic. The increased fertility of naturally oligotrophic waters can even bring positive effects on the local ecosystem (positive from a human perspective). This has happened in Lake Victoria, as is visible in the open waters around Mfangano Island, where lakewide eutrophication has enriched the abbreviated food chain that leads to the introduced Nile perch, Nile tilapia, the native minnow omena (*Rastrineobola argentea*), and *Caridina* shrimp. The smaller species have become super abundant, enhancing food availability for wild fish stocks. The risk of negative impacts of cage aquaculture wastes is greatest in enclosed waters with poor exchange rates, where excessive development of intensive aquaculture can lead to eutrophication and other ecosystem changes (i.e., algal blooms and low dissolved oxygen levels). Unfortunately, that is where many of the early cage farms have been going. The difficulties are site-specific and occur in slow-moving rivers, lakes and shallow bays, when the nutrient loading is far higher than the carrying capacity of the ecosystem, usually because of over-crowding or poor water exchange. Inner Winam Gulf is shallow and sheltered, as are other gulfs and embayments in Lake Victoria. Given that, Winam Gulf is already eutrophic; precautions should be taken not to install many cages in the gulf to safeguard against further water quality deterioration. However, there can probably be a few high-volume, low-density cages.

Eutrophication triggers different types of impacts, including primary physical, chemical, and biological effects on the environment, as well as secondary effects such as algal blooms, benthic impacts, biodiversity loss, and harm to sensitive habitats. Wastes emanating from fish farming can be put in three overlapping categories: 1) solid wastes, being mostly uneaten feed materials and feces; 2) soluble wastes, being the products of fish excretion and including reactive nitrogen species such as ammonia, and 3) chemical wastes, being medicines — such as antibiotics and anti-parasitic, disinfectants, antifoulants-such as tin or copper compounds formulated into coatings or paints. All can quickly become problematic in areas with low water exchange rates, especially against a historical background of cultural eutrophication.

4.3.1.1 Solid wastes

The main solid wastes from cage aquaculture are uneaten feed and fecal material. The quantity of these components will vary by species, food conversion ratio, food digestibility, type of feed (whether sinking or floating pellets), and the skills of the operator in matching feed availability to demand (Merican and Phillips, 1985). A significant amount of feed may not be eaten by farmed fish and goes into the environment, which can have significant impacts. Some of the feed can be in the form of dust that is too small to be ingested by the fish; the feed may get lost through overfeeding the fish, or if the fish pellets are the wrong size for the fish. These may be consumed by wild fish, and by benthic organisms, or broken down into nutrients by benthic assimilation. The unconsumed feed can have several effects both in the water column and on the bottom. Fish fecal matter constitutes a major and unavoidable form of nutrient enrichment affecting the environment. Contemporary fish feeds are made in a way to minimize the loss of nutrients that are expensive additives, by providing them in forms that can be easily assimilated by the fish (mainly protein). The nutrients that are not assimilated are excreted mainly as soluble wastes such as urea and ammonia, so the fecal matter consists mostly of carbon and inertia material (Merican and Phillips, 1985).

4.3.1.2 Soluble wastes

Soluble wastes, such as ammonia and urea, constitute a large part of the wastes released by cage farms. Like fecal matter, these are natural products produced by wild fish (Silvert, 1992). Soluble nutrients from the cages may constitute a risk of eutrophication. Consequences of eutrophication include increased abundance of micro-algae, killing of wild fish, farmed fish, or benthic organisms, and removal of oxygen from deep water (Black *et al*., 2002).

Nitrite-N (NO_2-N)

Nitrite is an intermediate in the process of nitrification and can be found in intensive aquaculture systems because large amounts of nitrogen are added in the form of manufactured feeds. The ideal and normal measurement of nitrite is zero in any aquatic system, and the desired optimal concentration of nitrite in water is less than 2.5 mg l^{-1} in aquaculture (Boyd and Tucker, 1998; Stone and Thomforde, 2004). At levels above optimal, nitrite oxidizes hemoglobin to methemoglobin in the blood, turning the blood and fish gills brown and hindering respiration by reducing blood oxygenation and potentially inducing tissue hypoxemia; a condition known as the “brown blood disease” (Lawson, 1995). It also damages the nervous system, liver, spleen and kidneys of fish; increasing pH, low dissolved oxygen and high ammonia can increase its toxicity (Devi *et al*., 2017).

Nitrate-N (NO_3-N)

Nitrate is a product of the nitrification process; i.e., the oxidation of NO_2 to NO_3 by the action of aerobic bacteria. Nitrate not taken up directly by aquatic plants is denitrified in anaerobic sediments (Furnas, 1992). Desired nitrate concentration for aquaculture is 0.2 to 10 mg l^{-1} (Boyd and Tucker, 1998). Higher concentrations of nitrate in drinking water are toxic (Umavathi *et al*., 2007). As stated by the Environmental Protection Agency (EPA), the maximum contaminant level (MCL) of nitrate concentration is 10 mg l^{-1} for drinking water (Self and Waskom, 2008). The fertilizers used on agricultural farms, through leaching and surface runoff into rivers during heavy rainfall also contribute to high levels of nitrate in receiving water bodies (Rao, 2011). The results from the previous chapters 2 and 3 show that affluent rivers bring in nutrients into Lake Victoria from the catchment agricultural activities contributing to high levels of nitrate in the inner Winam Gulf (Table 2-2).

Ammonia-N (NH_3-N)

Ammonia-N is the principal nitrogenous waste produced by aquatic animals via metabolism, and in fish, it is expelled across the gills (Cao *et al*., 2007). Ammonia is higher at fish culture sites because of farmed fish feces (Nyanti *et al*., 2012). It strongly influences the dynamics of dissolved oxygen in water. Safe concentrations of ammonia for freshwater fish are less than 0.05 mg l^{-1} (Lawson, 1995). Research indicates that high fish densities, along with the high feeding rates, often reduce dissolved oxygen and increase ammonia concentration in and around the cage, especially if there is no water movement through the cage nets (Karnatak and Kumar, 2014).

Phosphorus

Phosphorus is a limiting nutrient in tropical freshwater ecosystems contributing to production (Barik *et al*., 2001) and enters the aquatic environment from cage aquaculture through fish feed (Gavine *et al*., 1995). Many cages in an area can surpass the carrying capacity of the environment, which may result in problems caused by high concentrations of phosphorus (Mallasen *et al*., 2012). Santos *et al*. (2012) reported acceptable phosphorus levels to be 0.03 mg l^{-1} for Nile tilapia. Phosphorus has historically been recognized as a pollutant, as excess phosphorus along with nitrogen can cause eutrophication in water bodies. In Lake Victoria, mobilization of phosphorus is related to changing land use and urbanization. Deforestation, increasing population density, and intensity of land use results in increased runoff from land, accelerating sediments and nutrients downs tream into the lake and leading to the proliferation of blue-green algae (cyanobacteria), especially in Winam Gulf (Sitoki, *et al*., 2010, 2012).

Results from Chapters 2 and 3 show significant differences in nutrients between the inner gulf and open water sites ($p < 0.05$, Figure 2-3; Figure 3-4; Table 2-2), potentially attributable to the inner gulf as sheltered with less water circulation. In the inner Winam Gulf river mouth, the mean levels of phosphorus were 202.73 ± 3.03 ug l^{-1} while in the open lake it was 90.28 ± 42.45 ug l^{-1}. Although nutrient levels near the cages were not substantially elevated in this study, intensification of cages could increase levels in the surrounding water dangerously. Cage farms need to be careful to avoid practices that cause nutrient enrichment in the surrounding water column (Beveridge and Muir 1999, Beveridge *et al*., 2013).

4.3.1.3 Benthic effects

One early effect of nutrient enrichment around aquaculture cages is an increase in benthic productivity since there is more food to feed the benthic community. This condition can continue for a long time if the scale of enrichment is low. However, the amount of deposition under cage farms can be so high that benthic scavengers cannot process all of it, and some decompose through bacterial processes. This leads to reduced oxygen levels and increased sulfide concentrations to levels stressful for many bottom dwellers. Therefore, species can be driven out of an area, reducing local species diversity. At extreme levels, only a few species can persist, notably certain oligochaetes and polychaetes (which are often used as indicator species). In Lake Victoria, the benthos is currently dominated by gastropod and bivalve mollusks along with worms and anoxia-resistant insect larvae (Ngupula and Kayanda, 2010); but there are no data to indicate whether benthic productivity has increased because of eutrophication.

4.3.1.4 Chemical wastes

Three of the most commonly used classes of chemicals in fish farming are antibiotics, antiparasitics, and antifoulants. Though there are no reported cases of antibiotics use in Lake Victoria cage farms, clandestine antibiotic prophylaxis in fish feed mixes by some feed manufacturers or some fish farms is of particular concern. Where residues persist, low levels of antibiotic intake can stimulate resistance in human pathogens (Liu *et al*., 2017; Miranda *et al*., 2018; Cabello, 2019; Lulijwa *et al*., 2020). In general, limits have not been set for the concentrations of antibiotics permitted in the aquatic environment.

4.3.1.5 Water temperature

All chemical and biological processes in cage aquaculture are influenced by temperature. A range of temperatures from 26.06 to 31.97 °C is suitable for warm water fish culture (Boyd, 1982). High water temperatures can be experienced in areas of low water level like the shallow littoral areas of the lake, and temperature could be expected to decrease as depth increases. During the study, the average surface temperature in Lake Victoria was 27.02 °C, which is favorable for Nile tilapia culture.

4.3.1.6 Dissolved oxygen (DO) depletion

In a water body, dissolved oxygen (DO) is important in the production and support of life, as well as for the decomposition and decay of organic matter. DO concentrations in water chiefly depend upon temperature, dissolved salts, the velocity of wind, pollution load, photosynthetic activity, and respiration rate (Tamot *et al*., 2008). Oxygen is consumed in the vicinity of fish cages by fish, the release of organic compounds that decompose in the water column by chemical processes that use oxygen

(Biological Oxygen Demand, BOD), and by primary production (algae) and secondary production (zooplankton) that utilize additional nutrients released by aquaculture. The low DO at some aquaculture sites is mainly caused by the consumption of DO by microorganisms in the decomposition of organic matter (Yee *et al*., 2012).

DO affects the growth, distribution, behavior, and physiology of aquatic organisms. Oxygen depletion in water leads to poor feeding of fish, starvation, reduced growth, and exacerbated mortality, either directly or indirectly (Bhatnagar and Devi, 2013). Optimal DO levels depend on size, species and other environmental variables. Cultured fish should not be fed when DO concentrations are less than 3–4 mg l^{-1} (Boyd and Tucker, 1998). A minimum DO concentration of 5 mg l^{-1} is recommended for warm-water fish and 6 mg l^{-1} for cold-water species (Thomas *et al*., 1994). Fish can survive at low DO levels (1.4 – 4 mg l^{-1}), but have reduced feed intake, higher feed conversion ratios (FCRs), slower growth, stress, and increased susceptibility to disease. A mean surface DO concentration of 5.6 mg l^{-1} was recorded in Lake Victoria during this study (Figure 3-3) but given the eutrophic nature of the inner gulf, DO concentrations would be more constrained in the inner Winam Gulf than in the open lake waters.

4.3.1.7 pH

pH, which is defined as hydrogen ion concentration in water plays an important role in the productivity of an aquatic ecosystem. Hepher and Pruginin (1981) reported that a pH of 6.5 to 9.0 is good for fish culture. The pH may drop in fish cage culture because of waste deposits (Bekcan *et al*., 2001). Food decomposition and breathing release carbon dioxide, which reacts with water producing carbonic acid and hydrogen ions, increasing acidity (Mallasen *et al*., 2012). Yee *et al*. (2012) reported that low pH values corresponded with low dissolved oxygen and high BOD values due to oxygen consumption during the breakdown of organic matter from excess feed and fish waste. The slightly lower pH values are attributed to the respiration of aquatic animals and the decomposition of organic matter from uneaten feed and fish excrement.

4.3.1.8 Turbidity

In some instances, cage aquaculture may make water more turbid due to the release of particulate matter. Increased turbidity can reduce light penetration, which can in turn reduce primary production by phytoplankton and by benthic macrophytes, and possibly the feeding efficiency of visual predators. In Lake Victoria, turbidity and algal blooms are thought to have affected haplochromines because reduced visibility may have disrupted the visual cues used by spawning haplochromines. Water with a narrow spectral width may have constrained the functional diversity of color signals, limiting the numbers of species that could be sexually isolated, and thus increasing the frequency of intermediate phenotypes between sympatric forms (Seehausen *et al*., 1997). High turbid water is also known to clog fish gills resulting in death.

4.3.1.9 Disease transmission

In countries in Europe and Asia with a long history of fish farming, there are impacts from the release of disease organisms and the pharmaceuticals used to treat them into the water column. This is known to lead to disease transmission between farms and even to wild stocks, and the effects of antibiotics and other treatments on natural communities. Disease occurrence is one of the main challenges cited to hinder sustainable cage culture production, whose risks increase with the rise in intensification, as is observed in cage culture. Diseases affecting fish can be bacterial, viral, fungal and or parasitic. Various studies have established that high parasite loads (ectoparasites or endo-parasites) significantly contribute to decreased fish growth, mortalities, and market unacceptability, culminating in aquaculture losses. Generally, fish diseases in cages can be attributed to infections due to the introduction of infected fish, contamination by transportation containers, avian spread, intermediate host population rise, malnutrition, lack of seed traceability, and disease ambient conditions (Okaeme *et al*., 1990). To realize cage culture as an investment, it is imperative to ensure good aquaculture practices (GAqP) by all stakeholders. This can be achieved through the development and implementation of national and regional guidelines on GAqP to avoid losses and limit resource use conflicts in Lake Victoria.

4.3.1.10 Genetic erosion/or contamination

The Nile tilapia brooders used in hatcheries to produce fingerlings to stock in the cages are obtained from Lake Victoria or water bodies within the Lake Basin. However, there are concerns about genetic erosion or contamination if escapees from farmed fish mate with wild fish. Escapement therefore, raises important concerns about ecological and genetic impacts, both within and outside the native range of the species (Gross, 1998). Domestic fish are bred for traits that are not always optimal for survival in the wild, so if some escape they may pass over undesirable traits. As aquaculture expands to address issues of food security, there is a need to minimize the potential harm to wild fish genetic resources (FiGR) arising from aquaculture activities and future development (Lind *et al*, 2012).

4.3.1.11 Biodiversity

Aquaculture can affect local biodiversity in several ways. The harvest of fish to make fishmeal (protein source) in feed formulations can deplete the target fish, as has been the case with anchovies in Peru (Smith *et al*., 2011; Fréon *et al*., 2014). It can be argued that this is now in danger of happening with the sardine-like omena (*Rastineobola argentea*), in Lake Victoria. The harvest of fry and juveniles from the wild to stock in ponds, pens, and cages is still practiced for some marine species. Repeated fishing or harvesting of juveniles of certain species for stocking can drastically alter species composition by preventing some of them from being recruited into the reproductive population. An example of this potentially happening in Kenya involves juveniles of the native catfish *Clarias gariepinus*, which are used as bait for Nile perch. For a while, these were bred domestically by the Lake Basin Development Authority (LBDA). The movement of broodstock and fry within a country or between countries can significantly alter the genetic characteristics of local stocks of the same species due to inevitable escapees or stock enhancement practices. Likewise, the escape of cultured “alien” Nile tilapia (same as the genetic escape) from cages can have deleterious effects on biodiversity. On the other hand, aquaculture can enhance biodiversity through restocking and stock enhancement programs, as is the case of restocking depleted water bodies that have been overfished (Bell, 2004; Zhang *et al*., 2015). There is great potential for this in Lake Victoria in the form of restoration programs for vanishing, and often highly valued native species such as *Labeo victorianus* and the two native tilapiines, *Oreochromis esculentus* and *O. variabilis.* Aquaculture can also be used to stock communal water bodies like newly constructed dams. The strongest remaining populations of Lake Victoria Region’s endemic tilapiines are now limited to satellite lakes, impoundments, and reservoirs such as Tanzania’s Nyumba ya Mungu Reservoir and Kenya’s Yala Swamp lakes (Bailey *et al*., 1978; Denny *et al*., 1978; Kaufman and Ochumba, 1993; Kaufman *et al*., 1997; Mwanja *et al*., 2001; Goudswaard *et al*., 2002; Aloo, 2003; Outa *et al*., 2018).

4.3.1.12 Sensitive habitats and social totems

Cage installation, especially in sensitive ecological habitats, can have negative impacts. Organic wastes from improperly located fish cages can move down the water column and smother sensitive ecosystems. Such environmental effects include disturbances in wild fish breeding and spawning or nursery grounds. Freshwater marshes and wetlands that are often home or feeding grounds of fish, birds and other fauna and flora are potential areas that might be improperly used for aquaculture if there are no strict government controls (e.g., aquaculture finger-ponds).

The human riparian communities also regard some localities in the lake or on the shores of the lake, as sacred. Such places are totems for the local communities where they perform their social and spiritual rites. Unless well planned, aquaculture can contribute to the loss of these totem sites. Though there have been campaigns to create awareness of the importance of conserving fragile and critical habitats, these habitats are shrinking in and around Lake Victoria. Hence the need to keep sensitizing people on the deleterious use of critical habitats for aquaculture. There is also the need to develop appropriate policies and regulatory measures, especially mandatory environmental impact assessments, since fragile habitats should be identified and protected.

4.3.2 Physical structures

The cage nets, installation frameworks or platforms, and associated moorings change the environment by preventing and causing friction to water currents and changing current patterns. The cage installations can also interfere with other lake ecosystem services like lake transport, and fishing grounds, and bring about user conflicts.

4.4 The role of aquaculture and fisheries in human nutrition and food security

Globally, there has been significant growth in fisheries and aquaculture production (FAO, 2016; Naylor *et al.*, 2021). This growth has steadily increased the world’s annual per capita fish consumption, with FAO estimates indicating the 2015 average exceeded 20 kg (FAO, 2016). Other studies reveal that fish consumption has grown substantially in the last decades in Southeast Asia (from 13.1kg in 1961 to 33.6 kg in 2013), East Asia (10.8 kg to 39.2 kg), and North Africa (2.8 kg to 16.4 kg) (FAO, 2016; WFC, 2009). In contrast, fish consumption in sub-Saharan African (SSA) countries has stagnated on average at 8.6 kg (FAO, 2016; Naylor *et al*., 2021), while consumption in Kenya has declined from 6.0 kg in 2000 to 4.3 kg in 2018 (KNBS, 2020). This is slightly below the average fish and seafood consumption in the East African Community (EAC) of 4.7 kg per capita annually (Wenaty *et al*., 2018).

Fish is often regarded as a ‘rich food for the poor’ and the most inexpensive and accessible source of animal protein, providing many of the fundamental nutrients and calories that are necessary for mental and physical growth. Some studies have underscored the nutritional and health benefits linked with fish consumption, such as cognitive development and increased intelligence in children, and reduced risks of high blood pressure, cardiovascular disorders, and various forms of cancers (Can *et al*., 2015; Kris-Etherton, 2003). For these reasons, fish is recommended as an important component of a healthy meal (Birch *et al*., 2012), and the varied range of highly bioavailable micronutrients present makes fish an essential food product (FAO, 2017). Nevertheless, micronutrient deficiencies affect hundreds of millions of people, particularly children and women in developing countries (FAO, 2016). The dangers of micronutrient deficiencies are increased risks of perinatal and maternal mortality, growth retardation, child mortality, and cognitive deficits, and reduced immune function (Black *et al*., 2008).

In Kenya, the catches from freshwater bodies have dwindled over the years (LVFO, 2016; KNBS 2020; Nyamweya *et al*., 2020). Despite their proximity to the lake, people near Lake Victoria have had difficulties accessing fish as food. This paradox is a reality these riparian communities live with. The introduction of Nile perch did not only change the ecology of Lake Victoria, but it also changed access to fish as food and as a resource for riparian human communities. It shifted a fishery that was dominated by the indigenous tilapiines (*O. variabilis* and *O. esculentus*) and haplochromines, to one dominated by exotic species (Nile perch and Nile tilapia) and the local silver sardine-like fish omena. These transformations in Lake Victoria have had consequences for local communities. The Nile perch boom of the 1990s changed fisheries from a barter and local market trade fishery towards one increasingly shaped by global export market demands (Medard, 2019). Ole-Moiyoi (2017) evaluated consumption patterns of different types of proteins in Kenya and found that wild-caught, followed by pond fish, make up a large proportion of the total protein that is consumed by lower socioeconomic groups. This implies that for increasingly poor households, fish also becomes increasingly important to their total protein intake. Given that catches from the wild are declining, aquaculture can play a meaningful role in food security provision, especially to poor households in the community. This emphasizes the need to continue developing aquaculture for protein provision, especially in poor and vulnerable riparian communities.

The Nile tilapia farming in cages in Lake Victoria does not rake in such huge revenues, as do Nile perch fillets sold to the export markets. Even if the production of Nile tilapia from Kenya were to make a dent in the global export market, tilapia products from the Chinese market (low-value tilapia from China) undercut local producers. This is a blessing in disguise as low-value Nile tilapia is limited to markets for local communities. The total dollar value from Nile perch exports could be less than the public health costs averted by providing local people access to the affordable nutritional value of Nile tilapia. Seeing the lake through such a whole-system, the ecological economic lens is essential if one hopes to appreciate the real values and costs of lake-based activities.

Few people benefit from the Nile perch fishery (e.g., boat owners, factory owners, and fillet exporters). Fishermen and the local communities hardly derive any tangible benefits from the Nile perch fishery. The few people who benefit from the Nile perch fishery do not plow this value back into local communities. A fisher needs a boat and fishing gear, costing between US$800 to US$1,500. People who cannot afford this investment are employed as crew on larger boats that operate offshore. The owners of these vessels provide crew members with only the most basic needs, such as shelter and food (Onyango and Jentoft, 2010; Nunan *et al*., 2012). They determine when and what price to pay for fish, rendering fishers powerless and frustrated. With no alternative, they (fishers) accept what they are offered while striving to survive. Again, this has left the fisher folks in perpetual poverty as the boat and factory owners smile to the bank. Women in the Nile perch fishery in most cases are socially and economically marginalized, and their livelihoods contain risky and insecure components (Lwenya and Yongo, 2012; Medard, 2012; Nunan *et al*., 2012).

In contrast, cage aquaculture in Lake Victoria could be a game-changer in empowering women and the youth who are currently so disenfranchised from the capture fisheries industry; a severing of engagement that can have profound socioeconomic consequences. Cage aquaculture is directly contributing to fish production and supply while making a significant impact on job creation and economic growth. About 500 people are employed directly or indirectly in cage aquaculture production in the country (Orina *et al*., 2018). The technology uptake has also indirectly created income opportunities for over 4,000 people in rural and urban settings through the supply of cage construction materials, feed and seed, and in the distribution and retail of fish in various market outlets (Orina *et al*., 2021; Figure 4-A1). Women's roles are evident in seed production in hatcheries, grow-out (feeding, sampling, grading, harvesting), and overall farm supervision. They are also involved in processing, marketing, retailing, and other activities along the value chain (Figure 4-A1). This earns them income, provides nutrition, secures food security, and reduces poverty, thus improving their livelihoods and fulfilling the UN-SDGs. Cage aquaculture, goes hand-in-hand with strategies that aim to end poverty (SDG1), increase food production (SDG2), improve health (SDG3), gender equality (SDG5), economic growth (SDG8), life below water (SDG14), and life on land (SDG15). All of these good effects have room for prudent expansion in Kenya.

4.5 Trade-offs: Balancing Lake Victoria's ecosystem goods and services

Trade-offs among various ecosystems goods and services are common in the management of ecosystems, although rarely factored into decision-making. In Lake Victoria, there is overlapping ecosystem use for wild fisheries, cage aquaculture, and other ecosystems goods and services. The trade-offs in the activities in the lake can be assessed in the context of coupled human and natural systems (CHANS). CHANS explores ecosystem services by linking human food security and wild fisheries through physical and economic changes brought about by escalating cage aquaculture. The introduction of the Nile perch to Lake Victoria illustrates how profound and unpredictable trade-offs can be when management decisions are made without regard to how the ecosystem will respond. The Nile perch's introduction into the lake resulted in an economic boom but devastated the lake's biodiversity contributing to the extinction of some haplochromine cichlids (Ogutu-Ohwayo, 1990; Kaufman, 1992; Lowe-McConell, 2009).

Importantly, the local communities that had depended on the native fishes for decades did not benefit from the success of the Nile perch fishery, mainly because Nile perch and tilapia are caught by gear that local fishers could not afford and most of the catch is exported (Onyango and Jentoft, 2010; Medard, 2015). The Nile perch landings have since plummeted from the boom catch of the 1990s, now raising concerns even about the sustainability of the Nile perch fishery. Eutrophication and overfishing are major threats to the fishery and the stability of the entire aquatic ecosystem which has been drastically altered. Due to human activities, there is increased pressure on the catchment leading to deforestation, increased siltation, and eutrophication that, against a mounting backdrop of anthropogenic climate change, have in turn further unbalanced the precarious lake ecosystem.

In Lake Victoria, the increasing demand for fish and fisheries products and dwindling fish stocks are contributing to an increase in fisheries conflict that is exacerbated by the strong link between fisheries and food security. Major civil conflicts have occurred in some of the Lake Victoria basin countries leading to a large number of internally displaced persons (IDPs). Studies have shown that armed conflict that occurs away from fishing grounds may increase fish catch as a result of displaced populations and greater fishing effort (Sarah *et al*., 2019). In Lake Victoria there has been simmering conflict over who has a right to fish at Migingo Island, between Kenyan and Ugandan fishermen; potentially threatening an armed conflict between the two countries. Primarily illegal fishing, foreign fishing, weak governance, limits on access to fishing grounds, and criminal activities including piracy cause conflicts (Devlin *et al*., 2021).

To forestall conflicts and ensure the success of cage aquaculture in Lake Victoria, there should be an understanding of the linkages between aquaculture activities and the social, economic and institutional environment in which they operate. Cage aquaculture development should not only be a production focus but take into account the communities whose lives may be directly or indirectly affected by such development. Development activities should employ participatory approaches to research and development (Chambers *et al*., 1989; Scoones and Thompson, 1994). The crucial question to ask on the cages is who is participating and how, and whether these individuals are representative of the cross-section of community interests and the power of regulatory structures. Such issues are crucial considering that the lake supports a wide range of ecosystem services, e.g., fish breeding grounds, fisheries, drinking water, transport, community deities, or spiritual sites, among others. Other key questions to be addressed include issues of ownership, control, users and associated uses, and rights of use. In the Philippines, the development and expansion of pen farming of milkfish in Laguna De Bay led to severe constraints to the access of fishers to traditional fishing grounds and conflicts (Marte *et al.*, 2000). The different aspects of resource use and management can involve a wide spectrum of stakeholders, from rural landless poor individuals to government institutions. There is the potential for direct and physical resource use conflict, relating to space and access to, or competition for, water or inputs (Beveridge, 1984). In assessing the role and benefits of cage aquaculture from the lake as a resource, understanding these social dimensions is crucial.

Cage aquaculture can take pressure off wild capture fisheries by providing an alternative source of fish, acting as a tool to reduce demand for wild fish and thus tackling overfishing by reducing pressure on wild populations. With reduced fishing effort, wild fish populations can rebound, especially where aquaculture surpasses wild capture fisheries. In chapter 3, there was no significant proximal nutrient load associated with cages. However, considering that Lake Victoria has experienced shifts in ecology due to many point and nonpoint source anthropogenic impacts, the expanding cage industry should be closely monitored. Leadership and management must understand that although wastes and excreta from cages can have positive effects by providing nutrients and increasing primary productivity; increasing primary productivity is not generally the problem that needs to be solved in Lake Victoria. In excess, nutrients can be a source of pollution, degrading water quality and decreasing biodiversity. That is, for the most part, the current situation in the Kenyan waters of the lake.

4.6 Conclusions

In this study, we found high nutrient loading and low water clarity in the inner gulf than open lake, affirming the inshore-offshore gradient. The gradient had an influence on fish species distribution. Nile perch and haplochromines were abundant in less eutrophic open waters. Non-haplochromine cichlids and other native fishes were more abundant in the inner gulf. Size structure of Nile perch exhibited spatial variability, with smaller class individuals more in the gulf and larger sizes in the open lake. Juveniles fed exclusively on *C. nilotica* and larger Nile perch fed on admixture of fish and haplochromines.

However, we found little evidence that suggests cage farms are driving this gradient. At the current cage intensity in the lake, there was no evidence of nutrient load proximal to cages. Overall, mean total monthly biomass near the cages was higher than at control stations, suggesting cages act as refugium for some threatened endemic fish species. Fish species diversity and richness for non-haplochromines were higher in the gulf than in the open lake, underscoring the importance of the gulf as a critical habitat.

The estimated suitable area of about 362.40 km^2 (8.84 %) for cage aquaculture development in Lake Victoria Kenya, has a projected production potential of about 250,000 metric tons of Nile tilapia annually. If managed well, cage aquaculture can be a boon to food security and biodiversity conservation.

Cage aquaculture can significantly contribute to food security, women empowerment, and biodiversity conservation, which are part of the UN-SDGs. This study highlights synergies across the SDGs particularly, no poverty (SDG1), zero hunger

(SDG2), improved health (SDG3), gender equality (SDG5), economic growth (SDG8), life below water (SDG14), and life on land (SDG15) that can be achieved with the inclusion of carefully planned cage aquaculture.

4.7 Recommendations

Lake Victoria will continue to change, and it can be anticipated that there will be additional anthropogenic and environmental impacts. Nutrient loading will increase, making the lake increasingly eutrophic, with intense and prolonged deoxygenation of the water column leading to a reduction in fish catches and diminishing of the area suitable for cage aquaculture. Climate change is also emerging as a major environmental challenge in the 21st Century, becoming more severe with extremes of drought or floods. Recently (April–May 2020), communities along the shoreline were displaced by raging floods due to backflows from the lake following heavy rainfall.

To maintain sustainable aquaculture that can co-exist with fishery, while allowing recovery in biodiversity, the following is recommended:

Ecosystem-based management (EBM): Over the years, the management of the fisheries resource in Lake Victoria has used a single species model approach emphasizing overfishing as the major threat. There is a need for a paradigm shift towards an ecosystem-based fisheries management (EBFM) approach to the lake's fishery resources, and indeed, a comprehensive EBM approach to the management of human activities in the lake basin as a whole. The EBFM approach considers the fact that the lake fisheries are declining due to multiple stressors and factors including, overfishing, ecological alterations, biodiversity loss, catchment activities, climate change, inadequate information to inform management, and un-harmonized ways of managing the fisheries. For instance, Kenya has 7% of the lake’s surface area, but its many rivers contribute more of the surface water inflow into the lake as a whole. Many of the rivers traverse a wide catchment area under pressure from diverse anthropogenic activities. EBM further recognizes that whatever is happening in the catchment or basin affects the lake (all pollution from the catchment is dumped into the lake). EBFM is the domain of fishery managers and supporting science; but true EBM that looks after the entire relationship between society and the lake basin entails having inputs of all stakeholders (local community, administrators, fisheries managers and researchers) considered before formulating research programs and policies. The lake being a shared resource, an EBM approach should consider the entire watershed of the lake managed collectively as a way of ameliorating the deleterious effects on the lake. This is the way to address the reality that future impacts will affect the lake as a whole and not align with human jurisdictional boundaries, or even single user-groups, such as the fishery. In the management of lake resources, the Lake Victoria nations should choose which path to take, which decisions to make to limit or cut back nutrient load and overfishing, and how to increase monitoring and data collection. The EBM approach will ensure the lake ecosystem is maintained in a healthy, resilient and productive condition so that it can provide the services humans want and their needs — fisheries, and all the others as well.

Harmonized data collection: Researchers and fisheries managers at the local, national, and regional levels need to harmonize data collection and analysis, and reporting. Data should not be disparate; rather, data sets from each country should be seen as samples that enrich the sample size before analysis. There should be time-series data collection and information gathering, and all should be stored in harmonized formats for future use and reference across countries. Data collection and archiving, and information synthesis is a precursor to good policy formulation. Therefore, the riparian governments should invest in data collection, analysis, reporting, and archiving for success in this area. Capacity (both human and facilities) development should be continuous to match the research and management needs. The Lake Victoria Basin straddles five nations, and the lake itself, three. All must work together for any of this to make sense.

Formulating management measures: Given the spatial variations in population structure (e.g., of Nile perch and other fishes), in the lake, there is a need for spatial considerations when formulating management measures for the fishery and the lake at large. The lake is highly heterogeneous such that it can be considered as being composed of many small lakes.

Good Aquaculture Practices (GAqP): Aquaculture production cannot be decoupled from land use. Freshwater fish are raised on compound feed, which is made mainly from terrestrial but also marine ingredients. The inclusion of plant-based ingredients in aquaculture feeds has increased and this needs to continue. Where feeds still require some animal protein, this should come from insects rather than vertebrate animals. It is necessary to plan how much arable land will be available to produce plant-based feeds for aquaculture (i.e., soya, sunflower cake, palm oil, cotton seed cake, and others) to avoid conflicts between farming food crops or cash crops. This balance is necessary for aquaculture and fisheries to co-exist in Lake Victoria. In addition, according to suitability for siting, cage aquaculture can be operational only in about 8.8% of the lake surface area (Kenya portion) and the rest of 91.2% is available to fisheries and other ecosystem goods and services. As the Blue Economy under the Blue Growth initiative is exploited through cage culture, there is not only the need to sustainably manage the resource through sound stakeholder consultative policies but also enlighten investors on how their investment can transit their livelihoods from small scale to large scale market-size tilapia production levels. There should be safeguards put in place to ensure good aquaculture practices (GAqP) coupled with good governance. Regular monitoring of the cage environment should be part of GAqP.

Management plan policy: Policies enacted should regulate aquaculture production; make fish from aquaculture accessible, affordable and healthy; and involve community participation and ensure gender parity.

Institutional: In other instances, the obstacle to policy development or formulation is institutional. In rare cases, do resource managers or policy makers fully weigh the various trade-offs among ecosystem goods and services. In some cases, the barrier is a lack of information, especially with ecosystem services such as water quality, that have no cost or price tag. If such information is available, it may not include estimates of the economic costs and benefits of the trade-offs. Yet, particularly when considering changes that affect the livelihoods of all people, there is a need for institutions to see the bigger picture. Multidisciplinary and cross-sectoral approaches to these issues are necessary for better trade-offs determination. Governments should strengthen local, national and regional research and management institutions e.g., Lake Victoria Fisheries Organization (LVFO), Lake Victoria Basin Commission (LVBC), among others.

Community education: Since poverty can be both a cause and consequence of overfishing, poverty alleviation strategies and policies would need to work at both ends. A fishery commons (i.e., open access, as is the case of Lake Victoria) is in danger of collapse due to overuse and ecologically destructive fishing practices and requires urgent measures — but simply locking out the small-scale fishers — directly or indirectly — may not be the best answer. Rather, what is needed is a more comprehensive governance reform that both empowers communities and protects resources. In Lake Victoria, community education is key to sustainable exploitation of fish resources. There could be responsible exploitation if governments (local, national, and regional) aim to provide small-scale fishers with a broader set of opportunities, entitlements, and capabilities than they currently have. Education will make it easier for information to flow between the government and those they represent. It is worth noting that the kind of ideas put into regulatory policy and practice, would determine the outcomes for small-scale fishers. The policies should be robust enough in protecting resources while giving small-scale fishers and local people the justice they have so long deserved.

Monitoring: Cage aquaculture in Lake Victoria Kenya, is an industry at its infancy (occupies about 0.02 % of suitable area). As it expands and intensifies, there is a need for regular monitoring to guard against exceeding biophysical limits. Spatial planning can be used to comprehensively consider multiple uses and values of the lake. Planning decisions should leverage the best available information, and policies, regulations and laws should be developed and enacted to guide sustainable cage aquaculture development. A lakewide harmonized monitoring strategy should be developed and implemented.

APPENDIX

Family	Genus/Species
Alestidae	*Brycinus jacksonii*
Alestidae	*Brycinus sadleri*
Atyidae	*Caridina nilotica*$^{+}$
Bagridae	*Bagrus docmak*
Cichlidae	*Coptodon zillii*
Cichlidae	*Oreochromis leoucostictus*
Cichlidae	*Oreochromis niloticus*
Cichlidae	*Oreochromis variabilis*
Cichlidae	*Haplochromis spp.**
Clariidae	*Clarias gariepinus*
Clariidae	*Xenoclarias*
Cyprinidae	*Enteromius profundus*
Cyprinidae	*Labeo victorianus*
Cyprinidae	*Rastreneobola argentea*
Latidae	*Lates niloticus*
Mochokidae	*Synodontis afrofischeri*
Mochokidae	*Synodontis victoriae*
Mormyridae	*Mormyrus kannume*
Protopteridae	*Protopterus aethiopicus*
Schilbeidae	*Schilbe mystus*

$^{+}$The only species of shrimp in Lake Victoria

* Haplochromine cichlids recorded as a group (*Haplochromis spp.*) due to the difficulty of immediate identification to species level in the field.

Table 2-A1. Twenty species (considering *Haplochromis spp*. as one group) belonging to eleven families were recorded in Lake Victoria, Kenya during the gillnet survey in April/May 2017.

Family	**Genus/Species**
Alestidae	*Brycinus jacksonii*
Alestidae	*Brycinus sadleri*
Atyidae	*Caridina nilotica*[+]
Bagridae	*Bagrus docmak*
Cichlidae	*Oreochromis niloticus*
Cichlidae	*Haplochromis spp.**
Clariidae	*Clarias gariepinus*
Clariidae	*Xenoclarias*
Cyprinidae	*Enteromius profundus*
Cyprinidae	*Rastreneobola argentea*
Latidae	*Lates niloticus*
Mochokidae	*Synodontis victoriae*
Mormyridae	Mormyrus kannume
Protopteridae	*Protopterus aethiopicus*
Schilbeidae	*Schilbe mystus*

[+]The only species of shrimp in Lake Victoria
* Haplochromine cichlids recorded as a group (*Haplochromis spp.*) due to the difficulty of immediate identification to species level in the field.

Table 2-A2. Fifteen species (considering *Haplochromis spp.* as one group) belonging to eleven families were recorded in Lake Victoria, Kenya during the trawl survey in July/August 2017.

Date	**Female (cm TL)**	**Male (cm TL)**	**Region/lake**	**Source**
1979–1983	100	74	Winam Gulf	Asila & Ogari (1987)
1988–1989	110	60	Mwanza Gulf	Ligtvoet & Mkumbo (1990)
1985–1989	85	55	L. Victoria, Kenya	Ogari & Asila (1992)
1998–2001	76	54	Mwanza Gulf	Mkumbo (2002)
2004–2005	62	54	L. Victoria, Kenya	Njiru *et al.* (2008)
2017	85.5	61	L. Victoria, Kenya	This study

Table 2-A3. Total length (TL) cm of Nile perch (*Lates niloticus*) in Lake Victoria at 50% maturity.

Family	***Genus/species***
Alestidae	*Brycinus jacksonii*
Alestidae	*Brycinus sadleri*
Cichlidae	*Coptodon zillii*
Cichlidae	*Oreochromis variabilis*
Cichlidae	*Oreochromis niloticus*
Cichlidae	*Haplochromis spp.**
Cyprinidae	*Enteromius profundus*
Cyprinidae	*Enteromius apleurogramma*
Cyprinidae	*Labeo victorianus*
Latidae	*Lates niloticus*
Mochokidae	*Synodontis victoriae*
Mochokidae	*Synodontis afrofischeri*
Mormyridae	*Marcusenius victoriae*
Mormyridae	*Mormyrus kannume*
Mormyridae	*Marcusenius plagiostoma*
Protopteridae	*Protopterus aethiopicus*
Schilbeidae	*Schilbe intermedius*

* Haplochromine cichlids recorded as a group (*Haplochromis spp.*) due to the difficulty of immediate identification to species level in the field.

Table 3-A1. Seventeen species (considering *Haplochromis spp.* as one group) belonging to eight families were recorded in Lake Victoria, Kenya during the study period November 2018–July 2019.

Figure 1-A1. Nile tilapia (*Oreochromis niloticus*) cage aquaculture in Lake Victoria, Kenya. Some farms operate a battery of small cages, each 2 x 2 x 2 m (8 m^3). They are low volume/high stocking densities with a stocking density of 125 fish/m^3; while others operate high volume/low stocking density (97 fish/m^3) polyethylene (HDPE) floating fish cage culture systems of 20 m diameter (471m^3). The cages were stocked with Nile tilapia fingerlings (5–10 g) or with post-fingerlings (20–30 g) which are sourced from hatcheries within the Lake Victoria Basin. The stocking densities of fingerlings vary from farm to farm and depending on the size of cages.

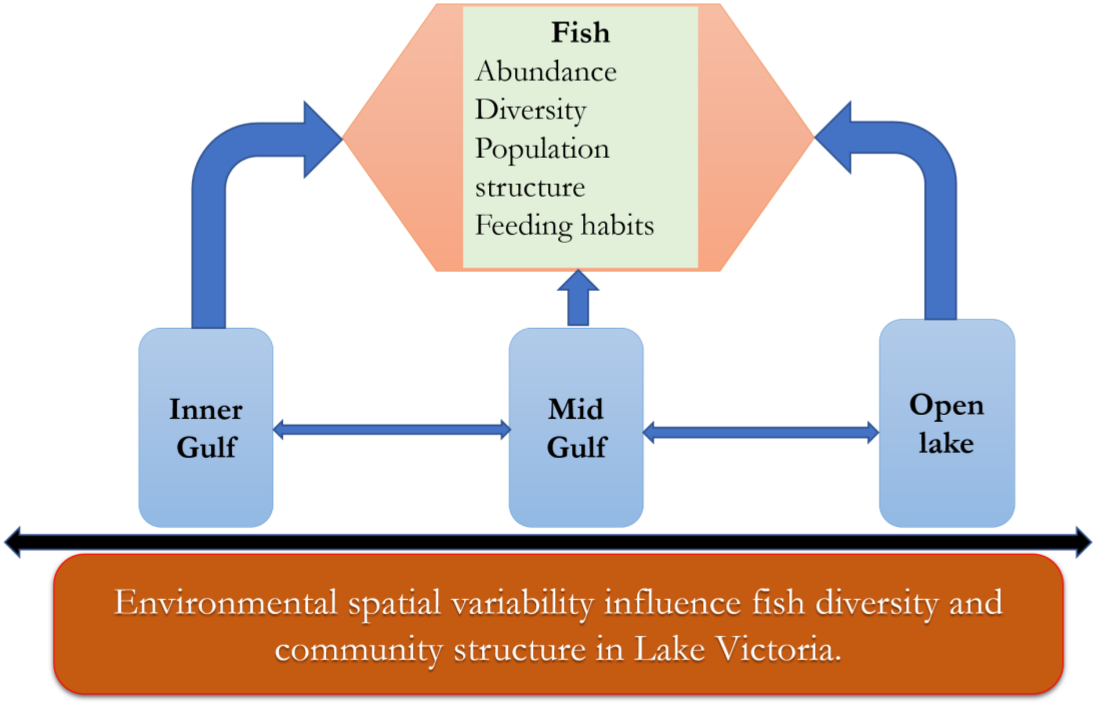


Figure 2-A1. Summary – Environmental spatial variability influence fish diversity and community structure in Lake Victoria

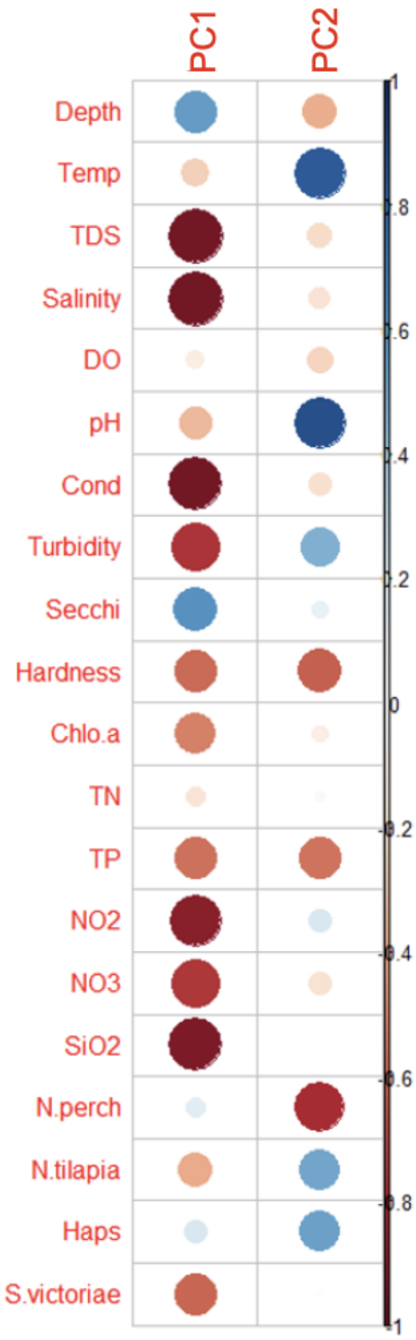


Figure 2-A2. Correlation plot between variables and the first two dimensions (PC1 and PC2). The red and blue dots correspond to negative and positive correlations, respectively. Larger dots with darker colors represent higher intensity correlations, and small dots with light colors correspond to lower intensity correlations.

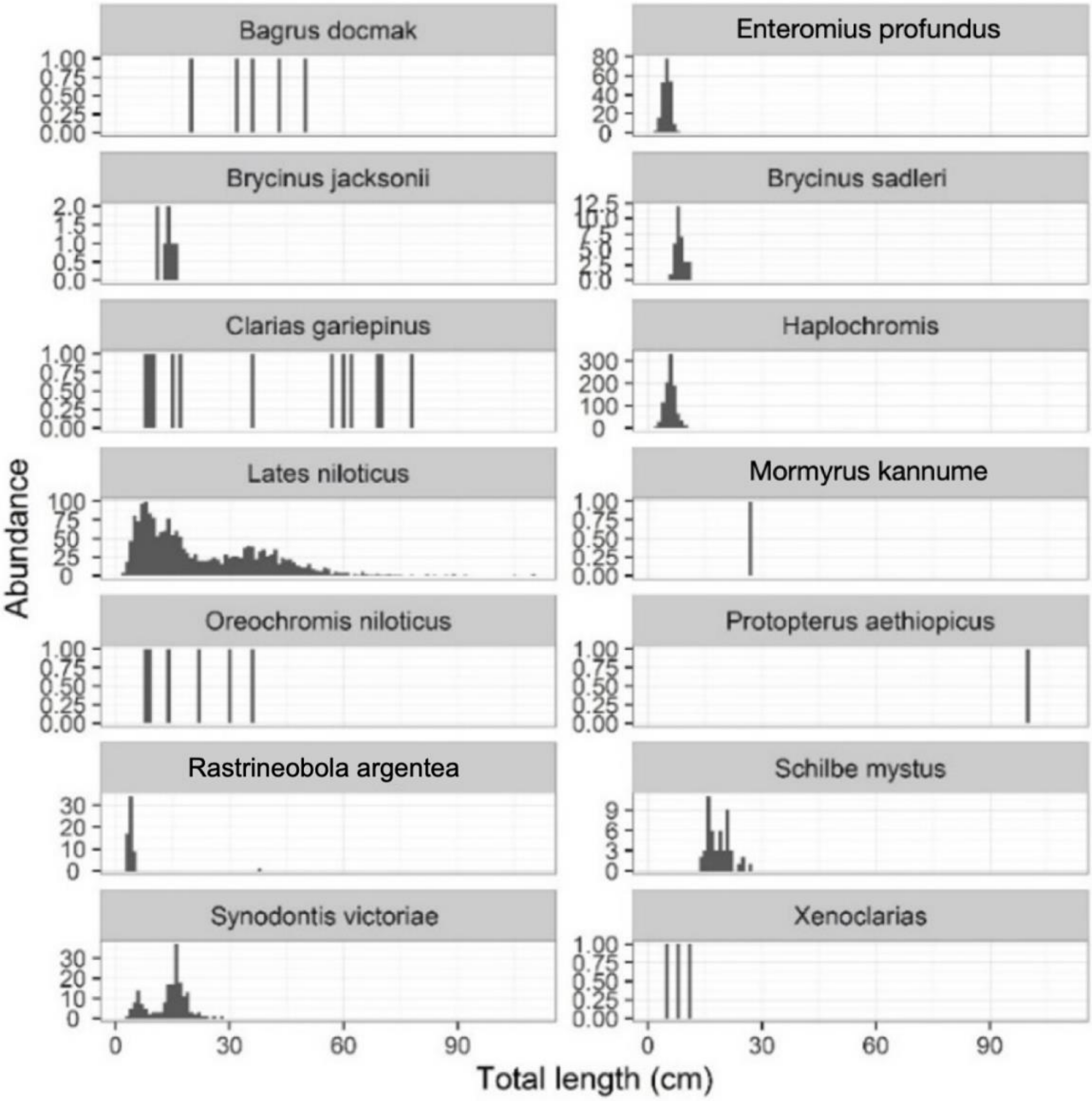


Figure 2-A3. Size structure of different fish species sampled during July 2017 bottom trawl survey in Lake Victoria, Kenya. *L. niloticus, C. gariepinus* and *P. aethiopicus* dominated the larger size classes, whereas the reminder of the species were of small sizes.

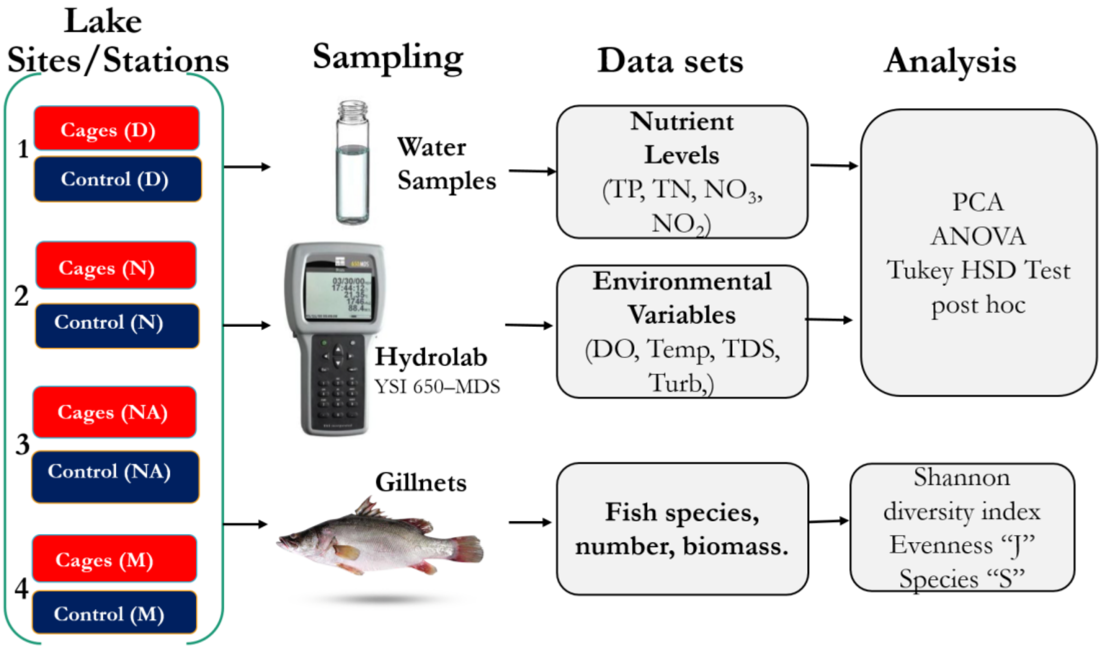


Figure 3-A1. A conceptual framework of the study design and analyses for environmental variables and fish assemblages at cages and controls in Lake Victoria, Kenya. The four study sites were arrayed along a limnological gradient from the inner gulf (D = Dunga, N = Ndere), mid gulf (NA = Naya) and open lake (M = Mfangano).

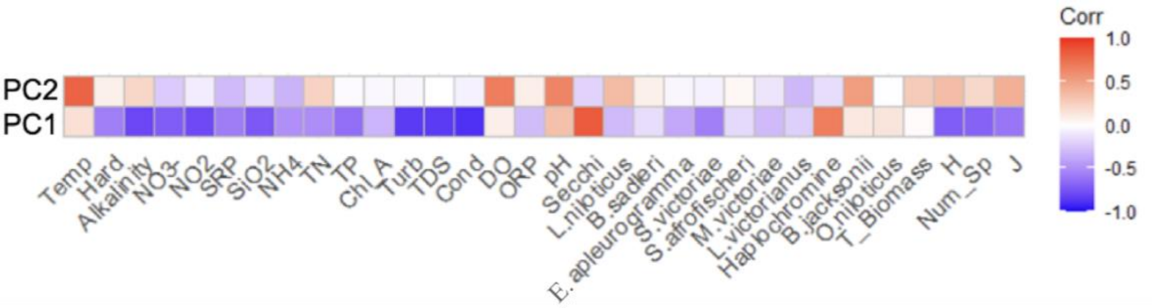


Figure 3-A2. Correlations between environmental variables and the first two principal components, contributing the most to variation in water quality among the inner gulf, mid gulf, transitional and open lake stations. The red and blue squares correspond to negative and positive correlations, respectively. Squares with darker colors represent higher intensity correlations, and squares with light colors correspond to lower intensity correlations.

Figure 3-A3. Some of the identified haplochromine cichlids caught in Lake Victoria, Kenya during the study period, November 2018 to July 2019.

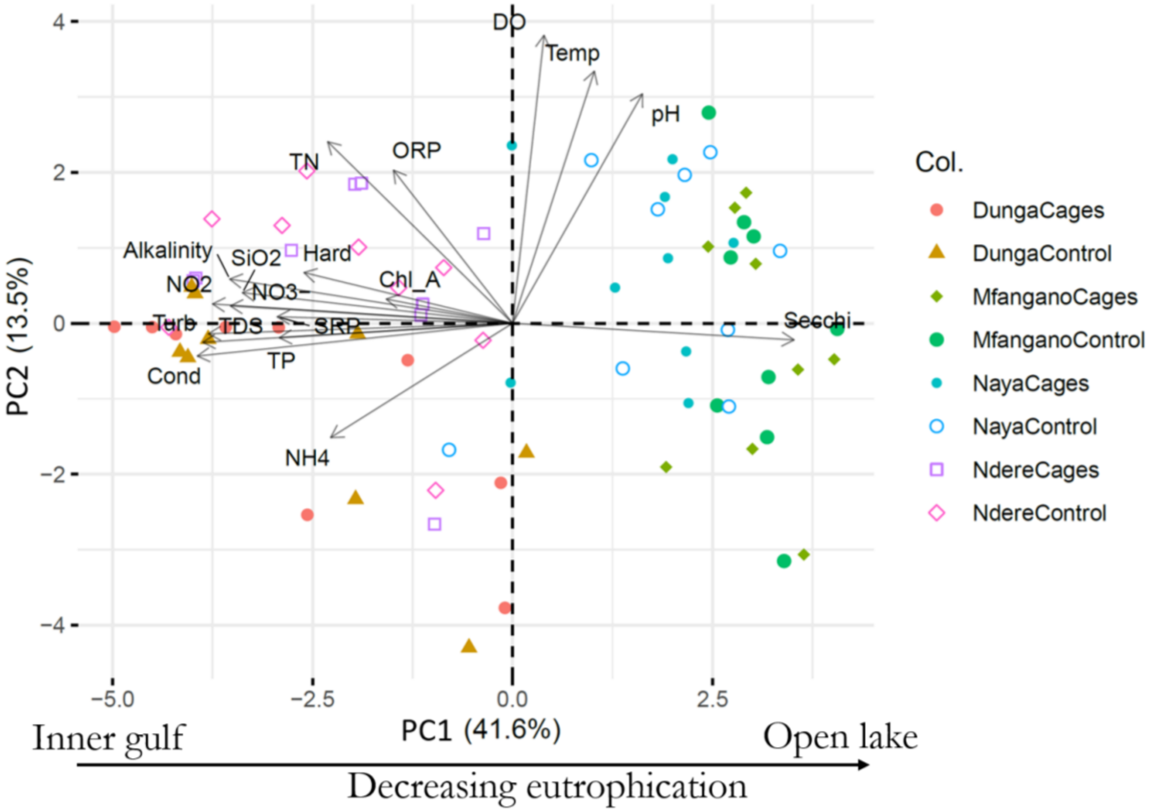
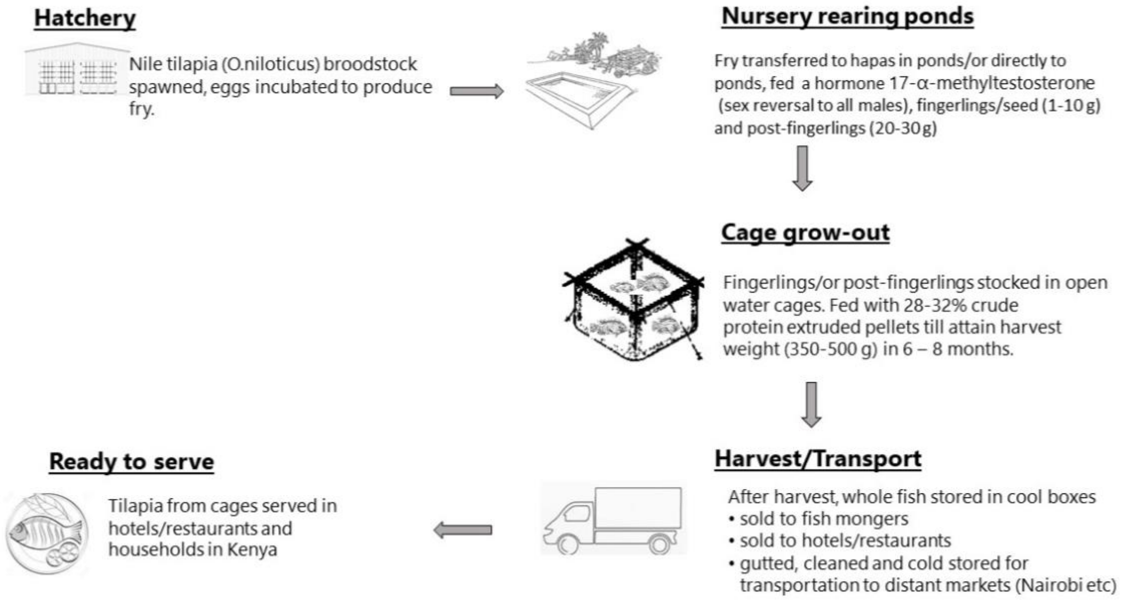


Figure 3-A4. PC1 & PC2 accounted for majority of limnological variations. The PCA indicates a strong positive correlation in the gulf sites between turbidity, total phosphorus (TP), total nitrogen (TN), total dissolved solids (TDS), and chlorophyll-a. Temperature, pH and DO were significantly and positively correlated and associated with open waters. Overall nutrients were significantly different in the gulf than the open lake and no significant differences between the cages and the controls.



Nile tilapia (O.niloticus) broodstock spawned, eggs incubated to produce fry.

Fry transferred to hapas in ponds/or directly to ponds, fed a hormone 17-α-methyltestosterone (sex reversal to all males), fingerlings/seed (1-10 g) and post-fingerlings (20-30 g)

Fingerlings/or post-fingerlings stocked in open water cages. Fed with 28-32% crude protein extruded pellets till attain harvest weight (350-500 g) in 6 – 8 months.

After harvest, whole fish stored in cool boxes
- sold to fish mongers
- sold to hotels/restaurants
- gutted, cleaned and cold stored for transportation to distant markets (Nairobi etc)

Tilapia from cages served in hotels/restaurants and households in Kenya

Figure 4-A1. Cage cultured Nile tilapia (*Oreochromis niloticus*) value chain – from egg to the table.

BIBLIOGRAPHY

Acere, T. O. (1988). The controversy over Nile perch, *Lates niloticus*, in Lake Victoria, East Africa. *Naga: The ICLARM Quarterly 11*(4), 3–5. https://hdl.handle.net/20.500.12348/3221

Achieng, A. P. (1990). The impact of the introduction of Nile perch, Lates niloticus (L.) on the fisheries of Lake Victoria. *Journal of Fish Biology*, *37*, 17–23.

Akintola, S. L., Brown, A., Bakare, A., Osowo, O. D., & Bello, B. O. (2013). Effects of hot smoking and sun drying processes on nutritional composition of giant tiger shrimp (Penaeus monodon, fabricius, 1798. *Polish Journal of Food and Nutrition Sciences*, *63*(4), 227–237.

Albright, T. (2004). The rise and fall of water hyacinth in Lake Victoria and the Kagera River Basin, 1989–2001. *Journal of Aquatic Plant Management, 42,* 73–84.

Aloo, P. A., Njiru, J., Balirwa, J. S., & Nyamweya, C. S. (2017). Impacts of Nile Perch, *Lates niloticus*, introduction on the ecology, economy and conservation of Lake Victoria, East Africa. *Lakes & Reservoirs: Research & Management*, *22*(4), 320–333.

Aloo, P. A. (2003). Biological diversity of the Yala Swamp lakes, with special emphasis on fish species composition, in relation to changes in the Lake Victoria Basin (Kenya): threats and conservation measures. *Biodiversity & Conservation*, *12*(5), 905–920.

APHA. (2005). Standard Methods for the Examination of Water and Wastewater, (21st edn). APHA-AWWA-WEF, Washington, DC.

APHA. (1985). American Public Health Association Standard Methods for the Examination of Water and Wastewater. Washington, D.C., APHA-AWWA-WEF, ISBN 0875530478.

Asila, A. A., & Ogari, J. (1988). Growth parameters and mortality rates of Nile perch (Lates niloticus) estimated from length-fequency data in the Nyanza Gulf (Lake Victoria). *FAO Fisheries Report (FAO)*.

Aura, C. M., Musa, S., Yongo, E., Okechi, J. K., Njiru, J. M., Ogari, Z., ... & Oucho, J. A. (2018). Integration of mapping and socio-economic status of cage culture: Towards balancing lake-use and culture fisheries in Lake Victoria, Kenya. *Aquaculture Research*, *49*(1), 532–545.

Bailey, R. G., Churchfield, S., Petr, T., & Pimm, R. (1978). The ecology of the fishes in Nyumba ya Mungu reservoir, Tanzania. *Biological Journal of the Linnean Society, 10*(1), 109–137.

Balirwa, J. S., Chapman, C. A., Chapman, L. J., Cowx, I. G., Geheb, K., Kaufman, L. E. S., ... & Witte, F. (2003). Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? *BioScience*, *53*(8), 703–715.

Balirwa, J. S. (1995). The Lake Victoria environment: its fisheries and wetlands—a review. *Wetlands Ecology and Management*, *3*(4), 209–224.

Balirwa, J. S. (1992). The evolution of the fishery of *Oreochromis niloticus* (Pisces: Cichlidae) in Lake Victoria. *Hydrobiologia*, *232*(1), 85–89.

Banda, M., Jamu, D., Njaya, F., Makuliwa, M., & Maluwa, A. (2005). *The chambo restoration strategic plan* (Vol. 71). WorldFish.

Barel, C. D., Dorit, R., Greenwood, P. H., Fryer, G., Hughes, N., Jackson, P. B. N., ... & Yamaoka, K. (1985). Destruction of fisheries in Africa's lakes. *Nature*, *315*(6014), 19–20.

Barik, S. K., Purushothaman, C. S., & Mohanty, A. N. (2001). Phosphatase activity with reference to bacteria and phosphorus in tropical freshwater aquaculture pond systems. *Aquaculture Research*, *32*(10), 819–832.

Bekcan, S., Pulatsü, S., Kirkagac, M. U., & Demir, N. (2001). Influence of trout cage culture on water quality, plankton and benthos Anatolian dam lake. *Israeli Journal of Aquaculture-Bamidgeh*, *53*, 20304.

Bell, J. (2004). Management of restocking and stock enhancement programs: the need for different approaches. *Stock enhancement and sea ranching: developments, pitfalls and opportunities*, 213–224. Blackwell Publishing.

Beveridge, M. C., Thilsted, S. H., Phillips, M. J., Metian, M., Troell, M., & Hall, S. J. (2013). Meeting the food and nutrition needs of the poor: the role of fish and the opportunities and challenges emerging from the rise of aquaculture. *Journal of Fish Biology*, *83*(4), 1067–1084.

Beveridge, M. C. M., & Muir, J. F. (1999). Environmental impacts and sustainability of cage culture in Southeast Asian lakes and reservoirs. *Fish and Fisheries of Lakes and Reservoirs in Southeast Asia and Africa*, 383–396. Westbury Publishing, Otely

Beveridge, M. C. (1984). *Cage and pen fish farming: Carrying capacity models and environmental impact* (No. 255-259). Food & Agriculture Organization

Bhatnagar, A., & Devi, P. (2013). Water quality guidelines for the management of pond fish culture. *International Journal of Environmental Sciences, 3*(6), 1980–2009.

Birch, D., Lawley, M., & Hamblin, D. (2012). Drivers and barriers to seafood consumption in Australia. *Journal of Consumer Marketing, 29*(1), 64–73.

Black, R. E., Allen, L. H., Bhutta, Z. A., Caulfield, L. E., De Onis, M., Ezzati, M., ... & Maternal and Child Undernutrition Study Group. (2008). Maternal and child undernutrition: global and regional exposures and health consequences. *The Lancet*, *371*(9608), 243–260.

Black, K. D., Cook, E. J., Jones, K. J., Kelly, M. S., Leakey, R. J., Nickell, T. D., ... & Willis, K. (2002). Review and synthesis of the environmental impacts of aquaculture. *Report for the Scottish Executive Central Research Unit* (http://www.scotland.gov.uk/cru/kd01/green/reia. pdf), 80.

Bootsma, H. A., & Hecky, R. E. (1993). Conservation of the African Great Lakes: a limnological perspective. *Conservation Biology, 7*(3), 644–656.

Boyd, C. E., & Tucker, C. S. (1998). Water quality requirements. In *Pond aquaculture water quality management* (pp. 87–153). Springer, Boston, MA.

Boyd, C. E. (1982). *Water quality management for pond fish culture*. Elsevier Scientific Publishing Co.

Brooks, J. L. (1950). Speciation in ancient lakes (concluded). *The Quarterly Review of Biology*, *25*(2), 131–176.

Bundy, A., & Pitcher, T. J. (1995). An analysis of species changes in Lake Victoria: did the Nile perch act alone? In *The impact of species changes in African lakes* (pp. 111–135). Springer, Dordrecht.

Burridge, L., Weis, J. S., Cabello, F., Pizarro, J., & Bostick, K. (2010). Chemical use in salmon aquaculture: a review of current practices and possible environmental effects. *Aquaculture, 306*(1–4), 7–23.

Cabello, F. C., & Godfrey, H. P. (2019). Salmon aquaculture, Piscirickettsia salmonis virulence, and One Health: Dealing with harmful synergies between heavy antimicrobial use and piscine and human health. *Aquaculture, 507*, 451–456.

Cadwalladr, D. A. (1965). The decline in the *Labeo victorianus* Blgr.(Pisces: Cyprinidae) fishery of Lake Victoria and an associated deterioration in some indigenous fishing methods in the Nzoia River, Kenya. *East African Agricultural and Forestry Journal*, *30*(3), 249–256.

Calamari, D., Akech, M. O., & Ochumba, P. B. O. (1995). Pollution of Winam Gulf, Lake Victoria, Kenya: A case study for preliminary risk assessment. *Lakes & Reservoirs: Research & Management*, *1*(2), 89–106.

Campbell, L. M., Hecky, R. E., Nyaundi, J., Muggide, R., & Dixon, D. G. (2003). Distribution and food-web transfer of mercury in Napoleon and Winam Gulfs, Lake Victoria, East Africa. *Journal of Great Lakes Research*, *29*, 267–282.

Can, M. F., Günlü, A., & Can, H. Y. (2015). Fish consumption preferences and factors influencing it. *Food Science and Technology*, *35*(2), 339–346.

Cao, L., Wang, W., Yang, Y., Yang, C., Yuan, Z., Xiong, S., & Diana, J. (2007). Environmental impact of aquaculture and countermeasures to aquaculture pollution in China. *Environmental Science and Pollution Research-International*, *14*(7), 452–462.

Chambers, R., & Thrupp, L. A. (Eds.). (1994). *Farmer first: farmer innovation and agricultural research*. Karthala Editions

Chapman, L. J., Chapman, C. A., Schofield, P. J., Olowo, J. P., Kaufman, L., Seehausen, O., & Ogutu-Ohwayo, R. (2003). Fish faunal resurgence in Lake Nabugabo, East Africa. *Conservation Biology*, *17*(2), 500–511.

Chessman, B. C. (2013). Do protected areas benefit freshwater species? A broad-scale assessment for fish in Australia's Murray–Darling Basin. *Journal of Applied Ecology*, *50*(4), 969–976.

Cornelissen, I. J. M., Van Zwieten, P. A. M., Peter, H. K., & Nagelkerke, L. (2015). Nile perch distribution in south-east Lake Victoria is more strongly driven by abiotic factors, than by prey densities. *Hydrobiologia*, *755*(1), 239–255.

Dadebo, E., Mengistou, S., & Gebre-Mariam, Z. (2005). Feeding habits of the Nile perch, *Lates niloticus* (l.)(Pisces: Centropomidae) in lake Chamo, Ethiopia. *SINET: Ethiopian Journal of Science*, *28*(1), 61–68.

Delmas R.A., Loudjani P., Podaire A. & Menaut J. (1991). Biomass burning in Africa. In: Levine J.S. (ed.) *Global Biomass Burning. Atmospheric, Climatic and Biospheric Implications.* The MIT Press, Cambridge, pp. 126–132.

Denny, P., Bowker, D. W., & Bailey, R. G. (1978). The importance of the littoral epiphyton as food for commercial fish in the recent African man-made lake, Nyumba ya Mungu reservoir, Tanzania. *Biological Journal of the Linnean Society*, *10*(1), 139–150.

De Silva, S. S., Phillips, M. J., De Silva, S. S., & Phillips, M. J. (2007). A review of cage aquaculture. *Cage Aquaculture: Regional Reviews and Global Overview*, *498*, 21.

Devi, P. A., Padmavathy, P., Aanand, S., & Aruljothi, K. (2017). Review on water quality parameters in freshwater cage fish culture. *International Journal of Applied Research*, *3*(5), 114–120.

Devlin, C., Glaser, S. M., Lambert, J. E., & Villegas, C. (2021). The causes and consequences of fisheries conflict around the Horn of Africa. *Journal of Peace Research*, 00223433211038476.

Downing, A. S., van Nes, E. H., Balirwa, J. S., Beuving, J., Bwathondi, P. O., Chapman, L. J., ... & Mooij, W. M. (2014). Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's ecosystem services. *Ecology and Society*, *19*(4).

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E., & Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, *10*(6), 522–538.

El-Sayed, A. F. M. (2019). *Tilapia culture*. Academic Press.

FAO. (2016). *The State of the World Fisheries and Aquaculture*. FAO, Rome. https://www.fao.org/3/i5555e/i5555e.pdf

FAO. (2007). *Cage Aquaculture. Regional Reviews and Global Overview*. FAO Fisheries Technical Paper 498 (241).

FAO. (2006). *Regional Technical Expert Workshop on Cage Culture in Africa. Entebbe, Uganda, 20–23 October 2004*. FAO Fisheries Proceedings, No. 6. Rome, FAO. 2006.

Fréon, P., Sueiro, J. C., Iriarte, F., Evar, O. F. M., Landa, Y., Mittaine, J. F., & Bouchon, M. (2014). Harvesting for food versus feed: A review of Peruvian fisheries in a global context. *Reviews in Fish Biology and Fisheries*, *24*(1), 381–398.

Fryer, G. (1974). East African Freshwater Fisheries Research Organisation, Annual Report for 1971. East African Community, Nairobi: 56 pp., 1973. *Environmental Conservation*, *1*(4), 315–315.

Fryer, G. (1961). Observations on the biology of the cichlid fish Tilapia variabilis Boulenger in the northern waters of Lake Victoria (East Africa). *Revue de Zoologie et de Botanique Africaines*, *64*(1–2), 1–33.

Fryer, G. (1959). Some aspects of evolution in Lake Nyasa. *Evolution*, 440–451.

Furnas, M. J. (1992). The behavior of nutrients in tropical aquatic ecosystems. *Pollution in Tropical Aquatic Systems*, *1*(1), 30–65.

Garrod, D. J. (1961). The history of the fishing industry of Lake Victoria, East Africa, in relation to the expansion of marketing facilities. *East African Agricultural and Forestry Journal*, *27*(2), 95–99.

Gavine, F. M., Phillips, M. J., & Murray, A. (1995). Influence of improved feed quality and food conversion ratios on phosphorus loadings from cage culture of rainbow trout, Oncorhynchus rnykiss (Walbaum), in freshwater lakes. *Aquaculture Research*, *26*(7), 483–495.

Giardino, C., Bresciani, M., Braga, F., Cazzaniga, I., De Keukelaere, L., Knaeps, E., & Brando, V. E. (2017). Bio-optical modeling of total suspended solids. In *Bio-optical modeling and remote sensing of inland waters* (pp. 129–156). Elsevier.

Gichuki, J., Omondi, R., Boera, P., Okorut, T., Matano, A. S., Jembe, T., & Ofulla, A. (2012). Water Hyacinth Eichhornia crassipes (Mart.) Solms-Laubach dynamics and succession in the Nyanza Gulf of Lake Victoria (East Africa): implications for water quality and biodiversity conservation. *The Scientific World Journal*, *2012*.

Gikuma-Njuru, P., Guildford, S. J., Hecky, R. E., & Kling, H. J. (2013). Strong spatial differentiation of N and P deficiency, primary productivity and community composition between Nyanza Gulf and Lake Victoria (Kenya, East Africa) and the implications for nutrient management. *Freshwater Biology*, *58*(11), 2237–2252.

Gikuma-Njuru, P., & Hecky, R. E. (2005). Nutrient concentrations in Nyanza Gulf, Lake Victoria, Kenya: light limits algal demand and abundance. *Hydrobiologia*, *534*(1), 131–140.

Glaser, S. M., Hendrix, C. S., Franck, B., Wedig, K., & Kaufman, L. (2019). Armed conflict and fisheries in the Lake Victoria basin. *Ecology and Society*, *24*(1).

Goldschmidt, T., Witte, F., & Wanink, J. (1993). Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology*, *7*(3), 686–700.

Goodrich, J. S., Sanderson, S. L., Batjakas, I. E., & Kaufman, L. S. (2000). Branchial arches of suspension–feeding Oreochromis esculentus: sieve or sticky filter? *Journal of Fish Biology*, *56*(4), 858–875.

Gophen, M., Ochumba, P. B. O., Pollingher, U., & Kaufman, L. S. (1993). Nile perch (Lates niloticus) invasion in Lake Victoria (East Africa). *Internationale*

Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, *25*(2), 856–859.

Goudswaard, K. P., Witte, F., & Katunzi, E. F. (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, P. C., Witte, F., & Katunzi, E. F. (2002). The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. *Journal of Fish Biology*, *60*(4), 838–856.

Goudswaard, P. C., & Witte, F. (1997). The catfish fauna of Lake Victoria after the Nile perch upsurge. *Environmental Biology of Fishes*, *49*(1), 21–43.

Graham, M. (1929). *The Victoria Nyanza and its Fisheries: A Report on the Fishing Survey of Lake Victoria, 1927–1928, and Appendices*. Crown Agents for the colonies. 225 p. London: Millbark.

Greenwood, P. H. (1966). *The fishes of Uganda* (2nd edition). The Uganda Society, Kampala.

Greenwood, P. H. (1951). Evolution of the African cichlid fishes: the Haplochromis species-flock in Lake Victoria. *Nature*, *167*(4236), 19–20.

Gross, M. R. (1998). One species with two biologies: Atlantic salmon (Salmo salar) in the wild and in aquaculture. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 131–144.

Guya, F. J. (2019). Intrinsic and extrinsic sources of phosphorus loading into the Nyando River, Kenya. *Lakes & Reservoirs: Research & Management*, *24*(4), 362–371.

Hamilton, S. E., Gallo, S. M., Krach, N., Nyamweya, C. S., Okechi, J. K., Aura, C. M., ... & Kaufman, L. (2020). The use of unmanned aircraft systems and high-resolution satellite imagery to monitor tilapia fish-cage aquaculture expansion in Lake Victoria, Kenya. *Bulletin of Marine Science*, *96*(1), 71–93.

Hamilton, H. A., Brod, E., Hanserud, O. S., Gracey, E. O., Vestrum, M. I., Bøen, A., ... & Brattebø, H. (2016). Investigating cross-sectoral synergies through integrated aquaculture, fisheries, and agriculture phosphorus assessments: A case study of Norway. *Journal of Industrial Ecology, 20*(4), 867–881.

Hao, W. M., & Liu, M. H. (1994). Spatial and temporal distribution of tropical biomass burning. *Global Biogeochemical Cycles*, *8*(4), 495-503.

Harrison, K., Crimmen, O., Travers, R., Maikweki, J., & Mutoro, D. (1989). Balancing the scales in Lake Victoria. *Biologist, 36*(4), 189–191.

Hecky, R. E., Mugidde, R., Ramlal, P. S., Talbot, M. R., & Kling, G. W. (2010). Multiple stressors cause rapid ecosystem change in Lake Victoria. *Freshwater Biology, 55,* 19–42.

Hecky, R. E., Bugenyi, F. W. B., Ochumba, P., Talling, J. F., Mugidde, R., Gophen, M., & Kaufman, L. (1994). Deoxygenation of the deep water of Lake Victoria, East Africa. *Limnology and Oceanography, 39*(6), 1476–1481.

Hecky, R. E. (1993). The eutrophication of lake Victoria. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 25*(1), 39–48.

Hepher B, Pruginin Y. (1981). *Commercial fish farming.* A Wiley Interscience Publication, New York.

Hooper, D. U., Chapin Iii, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35.

Hopson, A. J. (1972). *A study of the Nile perch (Lates niloticus (L.), Pisces: Centropomidae) in Lake Chad*. HM Stationery Office, London UK.

Hughes, N. F. (1992a). Growth and reproduction of the Nile perch, *Lates niloticus*, an introduced predator, in the Nyanza Gulf, Lake Victoria, East Africa. *Environmental Biology of Fishes*, *33*(3), 299–305.

Hughes, N. F. (1992b). Nile perch, Lates niloticus, predation on the freshwater prawn, Caridina nilotica, in the Nyanza Gulf, Lake Victoria, East Africa. *Environmental Biology of Fishes*, *33*(3), 307–309.

Hyslop, E. J.(1980). Stomach content analysis – a review of methods and their application. *Journal of Fish Biology*, *17,* 411429.

Jabiol, J., McKie, B. G., Bruder, A., Bernadet, C., Gessner, M. O., & Chauvet, E. (2013). Trophic complexity enhances ecosystem functioning in an aquatic detritus-based model system. *Journal of Animal Ecology*, *82*(5), 1042–1051.

Juma, D. W., Wang, H., & Li, F. (2014). Impacts of population growth and economic development on water quality of a lake: case study of Lake Victoria Kenya water. *Environmental Science and Pollution Research*, *21*(8), 5737–5746.

Kateregga, E., & Sterner, T. (2007). Indicators for an invasive species: Water hyacinths in Lake Victoria. *Ecological Indicators*, *7*(2), 362–370.

Katunzi, E. F. B., Van Densen, W. L. T., Wanink, J. H., & 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*(1), 121–133.

Kaufman, L. S., Chapman, L. J., & Chapman, C. A. (1997). Evolution in fast forward: haplochromine fishes of the Lake Victoria region. *Endeavour*, *21*(1), 23–30.

Kaufman, L., & Ochumba, P. (1993). Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in northern Lake Victoria. *Conservation Biology*, *7*(3), 719–730.

Kaufman, L. (1992). Catastrophic Change in Species-Rich Freshwater Ecosystems: The lessons of Lake Victoria. *BioScience*, *42*(11), 846–858.

Kishe-Machumu, M. A., van Rijssel, J. C., Wanink, J. H., & Witte, F. (2015). Differential recovery and spatial distribution pattern of haplochromine cichlids in the Mwanza Gulf of Lake Victoria. *Journal of Great Lakes Research*, *41*(2), 454–462.

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.

Kishe, M. A., & Machiwa, J. F. (2003). Distribution of heavy metals in sediments of Mwanza Gulf of Lake Victoria, Tanzania. *Environment International*, *28*(7), 619–625.

Kitaka, G. E. B. (1971). An instance of cyclonic upwelling in the southern offshore waters of Lake Victoria. *African Journal of Tropical Hydrobiology and Fisheries*, *1*(2), 85–92.

Kitchell, J. F., Schindler, D. E., Ogutu-Ohwayo, R., & Reinthal, P. N. (1997). The Nile perch in Lake Victoria: interactions between predation and fisheries. *Ecological Applications*, *7*(2), 653–664.

KNBS. (2021). Economic Survey. Nairobi: Kenya National Bureau of Statistics. https://www.knbs.or.ke/economic-survey-2021/

KNBS. (2020). Economic Survey. Nairobi: Kenya National Bureau of Statistics. https://www.knbs.or.ke/?wpdmpro=economic-survey-2020#

Kolding, J., Medard, M., Mkumbo, O., & Van Zwieten, P. A. M. (2014). Status, trends and management of the Lake Victoria fisheries. *Inland fisheries evolution and management—case studies from four continents. FAO Fisheries and Aquaculture Technical Paper*, *579*.

Kolding, J., & Skaalevik, A. (2010). Pasgear II Version 2.4. *University of Bergen. Bergen, Norway Lake Victoria Fisheries Research Project Phase II (LVFRP/TECH/01/16). Technical Document*, *16*.

Kudhongania, A. W., Ocenodongo, D. L., & Okaronon, J. O. (2019). Anthropogenic perturbations on the Lake Victoria ecosystem. In *The Limnology, Climatology and Paleoclimatology of the East African Lakes* (pp. 625–632). Routledge.

Kudhongania, A. W., & Chitamwebwa, D. B. (1995). Impact of environmental change, species introductions and ecological interactions on the fish stocks of Lake Victoria. In *The impact of Species changes in African lakes* (pp. 19–32). Springer, Dordrecht.

Kudhongania, A. W., Twongo, T., & Ogutu-Ohwayo, G. (1992). Impact of the Nile perch on the fisheries of Lakes Victoria and Kyoga. *Hydrobiologia*, *232*(1), 1–10.

Kudhongania, A. W., & Cordone, A. J. (1974). Batho-spatial distribution pattern and biomass estimate of the major demersal fishes in Lake Victoria. *African Journal of Tropical Hydrobiology and Fisheries*, *3*(1), 15–31.

Kundu, R., Aura, C. M., Nyamweya, C., Agembe, S., Sitoki, L., Lung'ayia, H. B., ... & Werimo, K. (2017). Changes in pollution indicators in Lake Victoria, Kenya and their implications for lake and catchment management. *Lakes & Reservoirs: Research & Management*, *22*(3), 199–214.

Lawson, T. B. (1995). Flow Estimation and Measurement. In *Fundamentals of Aquacultural Engineering* (pp. 133–156). Springer, Boston, MA.

Lehman, J. T. (1998). Role of climate in the modern condition of Lake Victoria. *Theoretical and Applied Climatology*, *61*(1), 29–37.

Lehman, J. T., Mbahinzireki, G. B., & Mwebaza-Ndawula, L. (1996). *Caridina nilotica* in Lake Victoria: abundance, biomass, and diel vertical migration. *Hydrobiologia*, *317*(3), 177–182.

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

Ligtvoet, W., Witte, F., Goldschmidt, T., Van Oijen, M. J. P., Wanink, J. H., & Goudswaard, P. C. (1991). Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology*, *42*(2–3), 214–232.

Lind, C. E., Brummett, R. E., & Ponzoni, R. W. (2012). Exploitation and conservation of fish genetic resources in Africa: issues and priorities for aquaculture development and research. *Reviews in Aquaculture*, *4*(3), 125–141.

Liu, X., Steele, J. C., & Meng, X. Z. (2017). Usage, residue, and human health risk of antibiotics in Chinese aquaculture: a review. *Environmental Pollution*, *223*, 161–169.

Liu, J., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., ... & Taylor, W. W. (2007). Complexity of coupled human and natural systems. *Science*, *317*(5844), 1513–1516.

Lowe-McConnell, R. (2009). Fisheries and cichlid evolution in the African Great Lakes: progress and problems. *Freshwater Reviews*, *2*(2), 131–151.

Lowe-McConnell, R. H. (1993). Fish faunas of the African Great Lakes: origins, diversity, and vulnerability. *Conservation Biology*, *7*(3), 634–643.

Lulijwa, R., Rupia, E. J., & Alfaro, A. C. (2020). Antibiotic use in aquaculture, policies and regulation, health and environmental risks: a review of the top 15 major producers. *Reviews in Aquaculture*, *12*(2), 640–663.

Lung'Ayia, H., Sitoki, L., & Kenyanya, M. (2001).The nutrient enrichment of Lake Victoria (Kenyan waters). *Hydrobiologia*, *458*(1), 75–82.

LVFO. (2017). *Lake Victoria Fisheries Organization*. *Lake Victoria (Kenya) Biennial Fisheries Survey National Report*. In Ministry of Agriculture, Livestock and Fisheries, Kenya.

LVFO (2016). *Technical Report: Stock Assessment Regional Working Group*. Jinja, Uganda: Lake Victoria Fisheries Organization, 17 pp.

LVFO. (2009). *Regional Status Report on Lake Victoria Bi-annual Frame Surveys between 2000 and 2008*. Unpublished official report of the LVFO, Jinja.

LVFO. (2005a). *The Standard Operating Procedures (SOPs) for gill net survey, East African Community.*

LVFO. (2005b). *The Standard Operating Procedures (SOPs) for collecting and monitoring biological and ecological information of the fishes, East African Community*.

Lwenya, C., & Yongo, E. (2012). The fisherman's wife: Vulnerabilities and strategies in the local economy; the case of Lake Victoria, Kenya. *Signs: Journal of Women in Culture and Society*, *37*(3), 566–573.

Maan, M. E., Seehausen, O. L. E., & Van Alphen, J. J. (2010). Female mating preferences and male coloration covary with water transparency in a Lake Victoria cichlid fish. *Biological Journal of the Linnean Society*, *99*(2), 398–406.

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.

MacIntyre, S. (2013). Climatic variability, mixing dynamics, and ecological consequences in the African Great Lakes. In *Climatic change and global warming of inland waters: Impacts and mitigation for ecosystems and societies.* (Pp. 311–336. Wiley.

Mallasen, M., de Barros, H. P., Traficante, D. P., & Camargo, A. L. S. (2012). Influence of a net cage tilapia culture on the water quality of the Nova Avanhandava reservoir, São Paulo State, Brazil. *Acta Scientiarum. Biological Sciences*, *34*(3), 289–296.

Marshall, B. E. (2018). Guilty as charged: Nile perch was the cause of the haplochromine decline in Lake Victoria. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(9), 1542–1559.

Marte, C. L., Cruz, P., & Flores, E. E. C. (2000). Recent developments in freshwater and marine cage aquaculture in the Philippines. In *Cage Aquaculture in Asia: Proceedings of the First International Symposium on Cage Aquaculture in Asia, 2–6 November 1999, Tungkang Marine Laboratory, Taiwan Fisheries Research Institute, Tungkang, Taiwan* (pp. 83–96). Asian Fisheries Society

Marten, G. G. (1979). Impact of fishing on the inshore fishery of Lake Victoria (East Africa). *Journal of the Fisheries Board of Canada*, *36*(8), 891–900.

Masser, M. P. (2003). Cage culture: site selection and water quality. *SRAC 161.* Oklahoma: Southern Regional Aquaculture Center. https://shareok.org/bitstream/handle/11244/319776/oksa_SRAC-0161_2003-02.pdf?sequence=1&isAllowed=y

Mbabazi, D., Ogutu-Ohwayo, R., Wandera, S. B., & Kiziito, Y. (2004). Fish species and trophic diversity of haplochromine cichlids in the Kyoga satellite lakes (Uganda). *African Journal of Ecology*, *42*(1), 59–68.

McGee, M. D., Borstein, S. R., Meier, J. I., Marques, D. A., Mwaiko, S., Taabu, A., ... & Seehausen, O. (2020). The ecological and genomic basis of explosive adaptive radiation. *Nature*, *586*(7827), 75–79.

McGee, M. D., Neches, R. Y., & Seehausen, O. (2016). Evaluating genomic divergence and parallelism in replicate ecomorphs from young and old cichlid adaptive radiations. *Molecular Ecology*, *25*(1), 260–268.

Medard, M., Van Dijk, H., & Hebinck, P. (2019). Competing for kayabo: gendered struggles for fish and livelihood on the shore of Lake Victoria. *Maritime Studies*, *18*(3), 321–333.

Medard, M. (2012). Relations between people, relations about things: gendered investment and the case of the Lake Victoria fishery, Tanzania. *Signs: Journal of Women in Culture and Society*, *37*(3), 555–566.

Medard, M., & Wilson, D. C. (1996). Changing economic problems for women in the Nile perch fishing communities on Lake Victoria. *Anthropologica*, 149–172.

Merican, Z. O., & Phillips, M. J. (1985). Solid waste production from rainbow trout, Salmo gairdneri Richardson, cage culture. *Aquaculture Research*, *16*(1), 55–69.

Miranda, C. D., Godoy, F. A., & Lee, M. R. (2018). Current status of the use of antibiotics and the antimicrobial resistance in the Chilean salmon farms. *Frontiers in Microbiology*, *9*, 1284.

Mkumbo, O. C., & Marshall, B. E. (2015). The Nile perch fishery of Lake Victoria: current status and management challenges. *Fisheries Management and Ecology*, *22*(1), 56–63.

Mkumbo, O. C., & Ligtvoet, W. (1992). Changes in the diet of Nile perch, Lates niloticus (L), in the Mwanza Gulf, Lake Victoria. *Hydrobiologia*, *232*(1), 79–83.

Mkumbo, O. C. (2002). *Assessment and management of Nile perch (Lates niloticus L.) stocks in the Tanzanian waters of Lake Victoria* (Doctoral dissertation, University of Hull).

Moreau, J., Ligtvoet, W., & Palomares, M. L. D. (1993). Trophic relationship in the fish community of Lake Victoria, Kenya, with emphasis on the impact of Nile perch (Lates niloticus). In *Trophic models of aquatic ecosystems. Center for Living Aquatic Resources Management Conference Proceedings* (Vol. 26, pp. 144–152).

Mugidde, R. (1993). The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *25*(2), 846–849.

Mwamburi, J., Basweti, G., Owili, M., Babu, J., & Wawiye, P. (2020). Spatio-temporal trends of nutrients and physico-chemical parameters on Lake Ecosystem and fisheries prior to onset of cage farming and re-opening of the Mbita passage in the

Nyanza Gulf of Lake Victoria. *Lakes & Reservoirs: Research & Management*, *25*(3), 292–313.

Mwanja, W. W., Armoudlian, A. S., Wandera, S. B., Kaufman, L., Wu, L., Booton, G. C., & Fuerst, P. A. (2001). The bounty of minor lakes: the role of small satellite water bodies in evolution and conservation of fishes in the Lake Victoria Region, East Africa. *Hydrobiologia*, *458*(1), 55–62.

Natugonza, V., Musinguzi, L., Kishe, M. A., Rijssel, J. C. V., Seehausen, O., & Ogutu-Ohwayo, R. (2021). The consequences of anthropogenic stressors on cichlid fish communities: revisiting Lakes Victoria, Kyoga, and Nabugabo. In *The behavior, ecology and evolution of cichlid fishes* (pp. 217–246). Springer, Dordrecht.

Naylor, R. L., Hardy, R. W., Buschmann, A. H., Bush, S. R., Cao, L., Klinger, D. H., ... & Troell, M. (2021). A 20-year retrospective review of global aquaculture. *Nature*, *591*(7851), 551–563.

Ngupula, G. W., Ezekiel, C. N., Kimirei, I. A., Mboni, E., & Kashindye, B. B. (2012). Physical and chemical characteristics of the Tanzanian inshore and offshore waters of Lake Victoria in 2005–2008. *African Journal of Aquatic Science*, *37*(3), 339–345.

Ngupula, G. W., & Kayanda, R. (2010). Benthic macrofauna community composition, abundance and distribution in the Tanzanian and Ugandan inshore and offshore waters of Lake Victoria. *African Journal of Aquatic Science*, *35*(2), 185–192.

Ngwala, J.J., 2014. Diet and feeding ecology of Nile Tilapia, *Oreochromis niloticus* and Nile Perch, *Lates niloticus* in protected and unprotected areas of Lake Victoria, Tanzania. *International Journal of Scientific and Technology Research*, 3: 11.

Njiru, J. M., Aura, C. M., & Okechi, J. K. (2019). Cage fish culture in Lake Victoria: A boon or a disaster in waiting? *Fisheries Management and Ecology*, *26*(5), 426–434.

Njiru, M., Nyamweya, C., Gichuki, J., Mugidde, R., Mkumbo, O., & Witte, F. (2012). Increase in anoxia in Lake Victoria and its effects on the fishery. *Anoxia*, 99–128.

Njiru, M., Kazungu, J., Ngugi, C. C., Gichuki, J., & Muhoozi, L. (2008). An overview of the current status of Lake Victoria fishery: Opportunities, challenges and management strategies. *Lakes & Reservoirs: Research & Management, 13*(1), 1–12.

Nunan, F., Luomba, J., Lwenya, C., Yongo, E., Odongkara, K., & Ntambi, B. (2012). Finding space for participation: fisherfolk mobility and co-management of Lake Victoria fisheries. *Environmental Management*, *50*(2), 204–216.

Nyamweya, C. S., Natugonza, V., Taabu-Munyaho, A., Aura, C. M., Njiru, J. M., Ongore, C., ... & Kayanda, R. (2020). A century of drastic change: Human-induced changes of Lake Victoria fisheries and ecology. *Fisheries Research, 230,* 105564.

Nyamweya, C. S., Sturludottir, E., Tomasson, T., Taabu-Munyaho, A., Njiru, M., & Stefansson, G. (2017). Prediction of Lake Victoria's response to varied fishing regimes using the Atlantis ecosystem model. *Fisheries Research*, *194,* 76–83.

Nyamweya, C., Desjardins, C., Sigurdsson, S., Tomasson, T., Taabu-Munyaho, A., Sitoki, L., & Stefansson, G. (2016). Simulation of Lake Victoria circulation patterns using the Regional Ocean modeling system (ROMS). *PLoS One*, *11*(3), e0151272.

Nyanti, L., Hii, K. M., Sow, A., Norhadi, I., & Ling, T. Y. (2012). Impacts of aquaculture at different depths and distances from cage culture sites in Batang Ai Hydroelectric Dam Reservoir, Sarawak, Malaysia. *World Applied Sciences Journal*, *19*(4), 451–456.

Oakes, C. T., & Pondella II, D. J. (2009). The value of a net-cage as a fish aggregating device in Southern California. *Journal of the World Aquaculture Society, 40(1),* 1-21

Ochumba, P. B. (1995). Limnological changes in Lake Victoria since the Nile perch introduction. In *The Impact of Species Changes in African Lakes* (pp. 33–43). Springer, Dordrecht.

Ochumba, P. B. (1990). Massive fish kills within the Nyanza Gulf of lake Victoria, Kenya. *Hydrobiologia*, *208*(1), 93–99.

Ochumba, P. B., & Kibaara, D. I. (1989). Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. *African Journal of Ecology*, *27*(1), 23–34.

Odada, E. O., Ochola, W. O., & Olago, D. O. (2009). Drivers of ecosystem change and their impacts on human well-being in Lake Victoria basin. *African Journal of Ecology*, *47*, 46-54.

Ogari, J., & Asila, A. (1990). The state of Lake Victoria fisheries, Kenya waters. *FAO Fisheries Report (FAO). no. 430.*

Ogari, J., & Dadzie, S. (1988). The food of the Nile perch, *Lates niloticus* (L.), after the disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). *Journal of Fish Biology*, *32*(4), 571–577.

Ogutu-Ohwayo, R. (1999). Deterioration in length–weight relationships of Nile perch, *Lates niloticus* L. in lakes Victoria, Kyoga and Nabugabo. *Hydrobiologia*, *403*, 81–86.

Ogutu-Ohwayo, R., Hecky, R. E., Cohen, A. S., & Kaufman, L. (1997). Human impacts on the African great lakes. *Environmental Biology of Fishes*, *50*(2), 117–131.

Ogutu-Ohwayo, R. (1995). Diversity and stability of fish stocks in Lakes Victoria, Kyoga and Nabugabo after establishment of introduced species. In *The impact of species changes in African lakes* (pp. 59–81). Springer, Dordrecht.

Ogutu-Ohwayo, R. (1994). Growth rates of juvenile Nile perch, Lates niloticus L. in lakes Victoria, Kyoga and Nabugabo. *African Journal of Tropical Hydrobiology and Fisheries*, *5*(2), 101–108.

Ogutu-Ohwayo, R., & Hecky, R. E. (1991). Fish introductions in Africa and some of their implications. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(S1), 8–12.

Ogutu-Ohwayo, R. (1990). The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes*, *27*(2), 81–96.

Ojuok, J. E. (2008). *Distribution, Status, and some aspects of the Biology of two Non-Cichlid Native Fishes of Lake Victoria, Kenya* [Lake Victoria Environmental Management Project (LVEMP)]. http://hdl.handle.net/11671/748.

Okaeme, A. N., Olufemi, B., & Amubode, F. (1999). A review of diseases associated with cage culture systems: diagnosis and control in small scale fish farming. In: *13th Annual conference of the Fisheries Society of Nigeria (FISON)*, pp. 92–96.

Okedi, J. (1970). A study of the fecundity of some mormyrid fishes from Lake Victoria. *East African Agricultural and Forestry Journal*, *35*(4), 436–442.

Okely, P., Imberger, J. R., & Antenucci, J. P. (2010). Processes affecting horizontal mixing and dispersion in Winam Gulf, Lake Victoria. *Limnology and Oceanography*, *55*(5), 1865–1880.

Okemwa, E. (1983). The Food of Nile Perch *Lates Niloticus* Linne:(Pisces: Centropomidae), in Relation to the Disappearance of Tilapia Spp in Nyanza Gulf of Lake Victoria. *East African Agricultural and Forestry Journal*, *49*(1–4), 21–26.

Ole-Moiyoi, L. K. (2017). *Fishing for answers: Can aquaculture transform food security in rural Kenya* (Doctoral dissertation, Stanford University).

Ongore, C. O., Aura, C. M., Ogari, Z., Njiru, J. M., & Nyamweya, C. S. (2018). Spatial-temporal dynamics of water hyacinth, *Eichhornia crassipes* (Mart.) and other macrophytes and their impact on fisheries in Lake Victoria, Kenya. *Journal of Great Lakes Research*, *44*(6), 1273–1280.

Onyango, P., & Jentoft, S. (2010). Assessing poverty in small-scale fisheries in Lake Victoria, Tanzania. *Fish and Fisheries*, *11*(3), 250–263.

Orina, P. S., Ogello, E., Kembenya, E., Githukia, C., Musa, S., Ombwa, V., ... & Okechi, J. K. (2018). State of Cage Culture in Lake Victoria, Kenya. Kenya Marine and Fisheries Research Institute. https://repository.maseno.ac.ke/bitstream/handle/123456789/2258/STATEOFCAGECULTUREformail%20%281%29.pdf?sequence=1&isAllowed=y

Orina, P., Ogello, E., Kembenya, E., Muthoni, C., Musa, S., Ombwa, V., ... & Karoza, S. (2021). The state of cage culture in Lake Victoria: A focus on sustainability, rural economic empowerment, and food security. *Aquatic Ecosystem Health & Management*, *24*(1), 56–63.

Outa, N. O., Yongo, E. O., Keyombe, J. L. A., Ogello, E. O., & Namwaya Wanjala, D. (2020). A review on the status of some major fish species in Lake Victoria and possible conservation strategies. *Lakes & Reservoirs: Research & Management*, *25*(1), 105–111.

Payne, I. (1987). A lake perched on piscine peril. *New Scientist*, *115*(1575), 50–54.

Pielou, E. (1969). *An Introduction to Mathematical Ecology*. New York, NY: Wiley Interscience.

Price, C., Black, K. D., Hargrave, B. T., & Morris Jr, J. A. (2015). Marine cage culture and the environment: effects on water quality and primary production. *Aquaculture Environment Interactions*, *6*(2), 151-174.

Pringle, R. M. (2005a). The origins of the Nile perch in Lake Victoria. *BioScience*, *55*(9), 780–787.

Pringle, R. M. (2005b). The Nile perch in Lake Victoria: local responses and adaptations. *Africa*, *75*(4), 510–538.

Rao, M. (2011). Impact of phosphorus on water quality. *Publication no. SL 275*, University of Florida, IFAD Extension.

Reddy, M. V. (Ed.). (2005). *Restoration and management of tropical eutrophic lakes*. CRC Press.

RStudio Team. (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. http://www.rstudio.com/

Sahyoun, R., Bussotti, S., Di Franco, A., Navone, A., Panzalis, P., & Guidetti, P. (2013). Protection effects on Mediterranean fish assemblages associated with different rocky habitats. *Journal of the Marine Biological Association of the United Kingdom*, *93*(2), 425–435.

Santos, D. M. S., Cruz, C. F., Pereira, D. P., Alves, L. M. C., & de Moraes, F. R. (2012). Microbiological water quality and gill histopathology of fish from fish farming in Itapecuru-Mirim County, Maranhão State. *Acta Scientiarum. Biological Sciences*, *34*(2), 199–205.

Schofield, P. J., & Chapman, L. J. (1999). Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. *Environmental Biology of Fishes*, *55*(4), 343–358.

Scoones, I., & Thompson, J. (1994). *Beyond farmer first: rural people's knowledge, agricultural research and extension practice*. Intermediate Technology Publications.

Seehausen, O., van Alphen, J.J.M., Witte, F. (2003). Implications of eutrophication for fish vision, behavioral ecology and species coexistence. In: Crisman TL, Chapman LJ, Chapman CA, Kaufman LS (eds). *Conservation, ecology, and management of African freshwaters*, University Press of Florida. pp 268–287.

Seehausen, O., Witte, F., Van Alphen, J. J. M., & Bouton, N. (1998). Direct mate choice maintains diversity among sympatric cichlids in Lake Victoria. *Journal of Fish Biology*, *53*, 37–55.

Seehausen, O., Van Alphen, J. J., & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, *277*(5333), 1808–1811.

Self, J. R., & Waskom, R. M. (2008). Nitrates in drinking water, no. 0.517. *Colorado State University Extension*.

Shannon, C. E., & Weaver, W. (1963). *The mathematical theory of communication*. University of Illinois Press.

Silsbe, G., & Hecky, R. (2008). Are the Lake Victoria fisheries threatened by exploitation or eutrophication? Towards an ecosystem-based approach to management. *The ecosystem approach to fisheries*, 309–354.

Silvert, W. (1992). Assessing environmental impacts of finfish aquaculture in marine waters. *Aquaculture*, *107*(1), 67–79.

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*(1), 109–122.

Sitoki, L., Gichuki, J., Ezekiel, C., Wanda, F., Mkumbo, O. C., & Marshall, B. E. (2010). The environment of Lake Victoria (East Africa): current status and historical changes. *International Review of Hydrobiology*, *95*(3), 209–223.

Smith, A. D., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., ... & Tam, J. (2011). Impacts of fishing low–trophic level species on marine ecosystems. *Science*, *333*(6046), 1147–1150.

Srivastava, D. S., & Bell, T. (2009). Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. *Ecology Letters*, *12*(10), 1016–1028.

Stager, J. C., Hecky, R. E., Grzesik, D., Cumming, B. F., & Kling, H. (2009). Diatom evidence for the timing and causes of eutrophication in Lake Victoria, East Africa. *Hydrobiologia*, *636*(1), 463–478.

Stone, N. M., & Thomforde, H. K. (2004). *Understanding your fish pond water analysis report* (pp. 1–4). Cooperative Extension Program, University of Arkansas at Pine Bluff, US Department of Agriculture and county governments cooperating.

Sun, X., Xie, L., Semazzi, F. H., & Liu, B. (2014). A numerical investigation of the precipitation over Lake Victoria basin using a coupled atmosphere-lake limited-area model. *Advances in Meteorology*, *2014*, 1–15.

Suresh, V. R. (2000). Floating islands: a unique fish aggregating method. *Naga, the ICLARM Quarterly*, *23*(1), 11–13.

Sweke, E. A., Assam, J. M., Chande, A. I., Mbonde, A. S., Mosha, M., & Mtui, A. (2016). Comparing the performance of protected and unprotected areas in conserving freshwater fish abundance and biodiversity in Lake Tanganyika, Tanzania. *International Journal of Ecology*, *2016*.

Taabu-Munyaho, A., Marshall, B. E., Tomasson, T., & Marteinsdottir, G. (2016). Nile perch and the transformation of Lake Victoria. *African Journal of Aquatic Science*, *41*(2), 127–142.

Taabu-Munyaho, A., Nyamweya, C. S., Sitoki, L., Kayanda, R., Everson, I., & Marteinsdóttir, G. (2014). Spatial and temporal variation in the distribution and density of pelagic fish species in Lake Victoria, East Africa. *Aquatic Ecosystem Health & Management*, *17*(1), 52–61.

Taabu, A. M., Steinarsson, B. A., & Hjörleifsson, E. (2005). Assessment of the status of the stock and fishery of Nile perch in Lake Victoria, Uganda. *Project report for United Nations University–Fisheries Training program* 54pp.

Talling, J.F.(1966). The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Internationale Revue der gesamten Hydrobiologie, 51*, 545–621.

Talling, J., & Talling, I. (1965). The chemical composition of African lake waters. *Internationale Revue der gesamten Hydrobiologie und Hydrographie, 50*(3), 421–463. https://doi.org/10.1002/iroh.19650500307

Tamatamah, R. A., Hecky, R. E., & Duthie, H. (2005). The atmospheric deposition of phosphorus in Lake Victoria (East Africa). *Biogeochemistry*, *73*(2), 325-344.

Tamot, P., & Mishra, R. (2007). Somdutt, 2008. Water quality monitoring of Halali reservoir with reference to cage aquaculture as a modern tool for obtaining enhanced fish production. *Proceedings of Taal*, 318–324.

Thomas, K. L., Lloyd, D., & Boddy, L. (1994). Effects of oxygen, pH and nitrate concentration on denitrification by Pseudomonas species. *FEMS Microbiology Letters*, *118*(1–2), 181–186.

Trewavas, E. (1983). *The tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia*. London (UK) British Museum (Natural History).

Tweddle, D., Ridgway, S., & Asila, A. (1999). The design of multimesh, multidepth gillnet fleets for use in the Lake Victoria Fisheries Research Project. LVFRP Technical Document, 06. http://hdl.handle.net/1834/7270

Umavathi, S., Logankumar, K., Subhashini, S., & Logaswamy, S. (2007). Studies on the nutrient content of Sulur pond in Coimbatore, Tamil Nadu. *Ecology, Environment and Conservation*, *13*(3), 501–504.

UNEP. (2006). Lake Victoria Basin Environment Outlook: Environment and Development. UNEP, Nairobi.

Váradi, L. (1984). Fish Culture Research Institute Szarvas, Hungary. *Inland Aquaculture Engineering: Lectures Presented at the ADCP Inter-regional Training Course in Inland Aquaculture Engineering, Budapest, 6 June–3 September 1983*, *21*, 343.

van der Knaap, M. (2013). Comparative analysis of fisheries restoration and public participation in Lake Victoria and Lake Tanganyika. *Aquatic Ecosystem Health & Management*, *16*(3), 279–287.

van der Meer, H. J., Van Rijssel, J. C., Wagenaar, L. C., & Witte, F. (2012). Photopic adaptations to a changing environment in two Lake Victoria cichlids. *Biological Journal of the Linnean Society*, *106*(2), 328–341.

van de Wolfshaar, K. E., HilleRisLambers, R., Goudswaard, K. P., Rijnsdorp, A. D., & Scheffer, M. (2014). Nile perch (Lates niloticus, L.) and cichlids (Haplochromis spp.) in Lake Victoria: could prey mortality promote invasion of its predator? *Theoretical Ecology*, *7*(3), 253–261.

van Oijen, M. J. P., & Witte, F. (1996). Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria. *Zoologische Verhandelingen*, *302*(1), 1–56.

van Rijssel, J. C., Hecky, R. E., Kishe-Machumu, M. A., Meijer, S. E., Pols, J., van Tienderen, K. M., ... & Witte, F. (2016). Climatic variability in combination with eutrophication drives adaptive responses in the gills of Lake Victoria cichlids. *Oecologia*, *182*(4), 1187–1201.

van Rijssel, J. C., Hoogwater, E. S., Kishe-Machumu, M. A., Reenen, E. V., Spits, K. V., van der Stelt, R. C., ... & Witte, F. (2015). Fast adaptive responses in the oral jaw of Lake Victoria cichlids. *Evolution*, *69*(1), 179–189.

van Rijssel, J. C., & Witte, F. (2013). Adaptive responses in resurgent Lake Victoria cichlids over the past 30 years. *Evolutionary Ecology*, *27*(2), 253–267.

van Zwieten, P. A., Kolding, J., Plank, M. J., Hecky, R. E., Bridgeman, T. B., MacIntyre, S., ... & Silsbe, G. M. (2016). The Nile perch invasion in Lake Victoria: cause or consequence of the haplochromine decline? *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(4), 622–643.

Vanni, M. J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, *33*(1), 341–370.

Verschuren, D., Johnson, T. C., Kling, H. J., Edgington, D. N., Leavitt, P. R., Brown, E. T., ... & Hecky, R. E. (2002). History and timing of human impact on Lake Victoria, East Africa. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1488), 289–294.

Vignesh, R., Karthikeyan, B. S., Periyasamy, N., & Devanathan, K. (2011). Antibiotics in aquaculture: an overview. *South Asian Journal of Experimental Biology*, *3*, 114–120.

Walker, B., Holling, C. S., Carpenter, S. R., & Kinzig, A. (2004). Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, *9*(2).

Wanink, J. H., Kashindye, J. J., Goudswaard, P. K., & Witte, F. (2001). Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine Rastrineobola argentea? *Freshwater Biology*, *46*(1), 75–85.

Wanjala, B., & Marten, G. (1974). Survey of the Lake Victoria fishery in Kenya. *EAFFRO Annual Report*, 81–85.

Welcomme, R. L. (1968). Observations on the biology of the introduced species of Tilapia in Lake Victoria. *Revue de Zoologie et de Botanique Africaines*, *76*(3–4), 249–279.

Welcomme, R. L. (1967). The relationship between fecundity and fertility in the mouthbrooding cichlid fish Tilapia leucosticta. *Journal of Zoology*, *151*(4), 453–468.

Wenaty, A., Mabiki, F., Chove, B., & Mdegela, R. (2018). Fish consumers preferences, quantities of fish consumed and factors affecting fish eating habits: A case of Lake Victoria in Tanzania. *International Journal of Fisheries and Aquatic Studies*, *6*(6), 247–252.

Western, D. (2001). Human-modified ecosystems and future evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(10), 5458–5465.

Wetzel, R. G. (2001). *Limnology: lake and river ecosystems*. Gulf Professional Publishing.

Wetzel, R. G., & Likens, G. E. (1991). Inorganic nutrients: nitrogen, phosphorus, and other nutrients. In *Limnological analyses* (pp. 81–105). Springer, New York, NY.

WFC. (2009). Fish Supply and Food Security for Africa. World Fish Center, Penang.

Wilson, D. C. (1993). Fisheries Management on Lake Victoria, Tanzania. In *Annual Meeting of the African Studies Association, Rutgers University, New Brunswick, NJ, December* (pp. 4–7).

Wilson, J. R., Ajuonu, O., Center, T. D., Hill, M. P., Julien, M. H., Katagira, F. F., ... & Van, T. (2007). The decline of water hyacinth on Lake Victoria was due to biological control by *Neochetina spp*. *Aquatic Botany*, *87*(1), 90–93.

Williams, A. E., & Hecky, R. E. (2005). Invasive Aquatic Weeds and Eutrophication: The Case of Water Hyacinth in Lake Victoria: 1 and Robert E. Hecky2. In

Restoration and management of tropical eutrophic lakes (pp. 211–250). CRC Press.

Witte, F., Seehausen, O., Wanink, J. H., Kishe-Machumu, M. A., Rensing, M., & Goldschmidt, T. (2013). Cichlid species diversity in naturally and anthropogenically turbid habitats of Lake Victoria, East Africa. *Aquatic Sciences*, *75*(2), 169–183.

Witte, F., Silsbe, G. M., Hecky, R. E., Goudswaard, P. C., Guildford, S. J., Kishe-Machumu, M. A., & Wanink, J. H. (2012). Did the loss of phytoplanktivorous fish contribute to algal blooms in the Mwanza Gulf of Lake Victoria? *Hydrobiologia*, *679*(1), 283–296.

Witte, F., Welten, M., Heemskerk, M., Van der Stap, I., Ham, L., Rutjes, H., & Wanink, J. (2008). Major morphological changes in a Lake Victoria cichlid fish within two decades. *Biological Journal of the Linnean Society*, *94*(1), 41–52.

Witte, F., Wanink, J. H., Kishe-Machumu, M., Mkumbo, O. C., Goudswaard, P. C., & Seehausen, O. (2007). Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria. *Aquatic Ecosystem Health & Management*, *10*(4), 416–433.

Witte, F., & van Densen, W. L. (eds.) (1995). *Fish stocks and fisheries of Lake Victoria. A handbook for field observations*. Cardigan: Samura.

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), 1–28.

Yee, L. T., Paka, D. D., Nyanti, L., Ismail, N., & Emang, J. J. (2012). Water quality at Batang Ai hydroelectric reservoir (Sarawak, Malaysia) and implications for aquaculture. *International Journal of Applied Science and Technology*, *2*(6), 23–30.

Yongo, E., Outa, N., Kito, K., & Matsushita, Y. (2018). Studies on the biology of Nile tilapia (*Oreochromis niloticus*) in Lake Victoria, Kenya: in light of intense fishing pressure. *African Journal of Aquatic Science*, *43*(2), 195–198.

Zhang, L., Song, X., Hamel, J. F., & Mercier, A. (2015). Aquaculture, stock enhancement, and restocking. In *Developments in Aquaculture and Fisheries Science*, *39*, 289–322.

CURRICULUM VITAE

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