Understanding the Impacts of Changes in Water Inflow on the Fishes of Lake Turkana, Kenya

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Abstract of Dissertation

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Lake Turkana, Kenya is an understudied desert lake that receives over 90% of its inflow from the Omo River in Ethiopia. The volume and patterns of inflow from this river influence the lake's chemistry and productivity, as well as the availability of habitat and the breeding migrations of its fishes. Lake Turkana is at the precipice of large-scale changes in ecological function due to climate change and economic development along the Omo River, including the construction of massive dams and irrigation projects. Upstream development will reduce the volume of water entering the lake and dampen the lake's ecologically crucial seasonal flood pulse. These changes will almost certainly impact the lake's fisheries at a time when they are becoming increasingly important to local livelihoods and national food security. This dissertation considers how the lake's fish communities, which have not been well studied since the 1980's, will respond to upstream development. Using data from satellite altimetry and local fisheries organizations, this study showed that water levels and their fluctuations are key drivers of fisheries productivity in the system. Using geographic information systems, water levels were shown to alter the distribution of habitat types and seasonal flood pulses to determine the extent of productive dynamic littoral habitat in the lake. Stable isotope analysis and a breeding vulnerability index for the top fishery species in the system showed that while some species of economic importance are ecologically flexible (e.g. *Oreochromis niloticus. Lates niloticus*), others (e.g. *Tilapia zillii, Labeo horie*) are highly sensitive to changes in habitat availability and food web structure. Lastly, a synthesis of published food web models for African lakes showed that altering the magnitude of water level fluctuations of these lakes has implications for their productivity, fish diversity, and the complexity, efficiency and connectivity of their food webs. Taken together, these studies suggest that upstream development will have extensive negative consequences for Lake Turkana and its fisheries. Although recommendations are made regarding minimizing impacts to the lake, more research must be conducted to comprehensively inform water resource management in the region.

Dedication Page

To my friends, family, and mentors.

I would have never made it this far without your love and support.

Asante Sana, Tasha.

Frontispiece

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Chapter 1: Background and Introduction

This dissertation provides an in-depth study of factors affecting the fish communities and fisheries of Lake Turkana, Kenya. The findings reported in this dissertation are timely, as the region surrounding the lake is expected to undergo rapid economic development during this decade. The lake, which has not been well studied since the 1980's, will be subject to large-scale ecological changes due to several of the development projects underway. The environmental mitigation measures for the planned development projects have little scientific basis. Key questions remain regarding the ecology of the lake's fishes and their sensitivity to changes in environmental conditions.

Inland fisheries provide over 93% of the fish catch in Kenya, but only 5% of these catches originate from Lake Turkana. Regardless, Lake Turkana's fisheries provide an alternative livelihood and important source of protein in the poverty-stricken Turkana District. To place Lake Turkana in a broader context, this chapter provides a brief overview of inland fisheries in Africa and threats to these fisheries. This overview is followed by more specific information on Lake Turkana, its fisheries, and development projects in the region. The chapter concludes with a brief description of the dissertation chapters to follow.

African Lake Fisheries: Importance and Threats

Inland fisheries account for approximately one-third of all capture fisheries production in Africa and employ over half of the continent's fishers (de Graaf and Garibaldi 2014, FAO 2014). These fisheries catch 2.7 million metric tons of fish annually, valued at nearly 6.3 billion dollars, and are particularly important sources of income in regions surrounding the African Great Lakes and large rivers (FAO 2014). For example, in countries surrounding Lake Victoria, fisheries account for 3-5% of gross domestic product (GDP; Ogutu-Ohwayo and Balirwa 2004). Fish are also a vital source of protein and nutrients, particularly in the most poverty-stricken regions of Africa (Welcomme et al. 2010, Belton and Thilsted 2014, Youn et al. 2014). Demand for fish products is therefore likely to increase concurrent with the continent's rapidly growing human population (Gerland et al. 2014). It has been predicted that fish supply will not be able to meet demand in Africa over the next decade (FAO 2014). Inland fisheries are likely to play an even more important role in developing countries than currently recognized, as FAO reported statistics on these fisheries are widely regarded as underestimates (Welcomme et al. 2010, Youn et al. 2014, Bartley et al. 2015).

The overall yield from Africa's inland fisheries has increased steadily (Figure 1.1). Yet, many of the continent's individual inland fisheries are in decline (e.g. Nile perch fishery in Lake Victoria; Ogello et al. 2013). Recent increases in the continent's total inland fisheries yield are most likely the result of the emergence of new fisheries (Jul-Larsen and van Zweitin 2002), improvements in the reporting of catch statistics, and the inclusion of stocked fishes in catch statistics (Bartley et al. 2015). African inland fisheries are subject to a number of threats, among the most important of which are pollution, overfishing, invasive species, and changes to hydrological cycles (Ogutu-Ohwayo and Balirwa 2004, Welcomme et al. 2010, Yuon et al. 2014, Bartley et al. 2015). Many of these fisheries are subject to several impacts that interact in complex ways and therefore need to be managed in an ecosystem-based context (Pikitch et al. 2004, Kolding et al. 2008).

Although pollution, overfishing and invasive species are often cited as the major threats to African inland fisheries, the importance of water level regimes has only recently gained attention (e.g. Leira and Cantonati 2008, Wantzen et al. 2008, Kolding and van Zweitin 2012, Youn et al. 2014). Absolute water level and intra- and inter-annual water level fluctuations (WLF) are now widely accepted as central factors structuring African lakes (Karenge and Kolding 1995, Jul-Larsen et al. 2003, Wantzen et al. 2008, Kolding and van Zwieten 2012). In particular, WLF influence the productivity and species diversity of lakes and the breeding success of their fauna.

Seasonal pulses of water often carry external nutrients to lakes from rivers or surrounding terrestrial ecosystems (Wantzen et al. 2008), and are particularly important to the productivity of shallow lakes. The aquatic/terrestrial transition zone (ATTZ) is the portion of the lake that fluctuates between wet and dry conditions dependent on seasonal WLF (Wanzten et al. 2008). These zones are highly productive ecosystem components due to the resuspension of nutrient-rich organic matter by rising waters. Water inflow also influences the internal mixing of nutrients in deep, stratified lakes (Zohary and Ostrovsky 2011).

The breeding movements of tropical freshwater fishes are often structured around seasonal WLF (Lowe-McConnel 1987). This phenomenon is common in tropical systems due to a lack of seasonal variability in temperature and day length. Water level fluctuations also alter habitat availability, complexity and quality. Depending on the form and structure of the lake, relatively small changes in water levels can lead to large variations in littoral habitat size (Wantzen et al. 2008). Habitat changes can in turn influence the breeding success of fauna, including fishes. Water level fluctuations also influence the quality of littoral habitat through their control on the extent of the ATTZ, substrate availability (Wilcox and Meeker 1992, Hill et al. 1998) and the coverage and diversity of shoreline vegetation (e.g. Van Geest et al. 2005, Zohary and Ostrovsky 2011).

Humans are profoundly altering hydrological cycles from local to global scales through the construction of impoundments, the extraction of water, and climate change (Nilsson et al. 2005, Döll et al. 2009, Haddelend et al. 2014). In many cases, these factors act synergistically and lead to greater water stress (Palmer et al. 2008). Africa is considered one of the most vulnerable continents to climate change (Boko et al. 2007). The continent is also likely to undergo growth in dam construction in the coming decades (Zarfl et al. 2015). Climate change and extractive water uses, including irrigation, are likely to intensify WLF, while dams are likely to dampen these fluctuations (Poff et al. 2007, Döll et al. 2009, Stocker et al. 2014, Haddelend et al. 2014). The ability to predict WLF is likely to decrease in Africa, particularly due to increased precipitation variability resulting from climate change (e.g. Dai et al. 2004, Tadross et al. 2005). Acting in concert, these effects have the ability to considerably alter the WLF regimes of Africa's freshwater ecosystems.

Lake Turkana Fisheries: Importance and Threats

Lake Turkana, Kenya, is the world's largest permanent desert lake (Kolding 1992). The lake is endoheric, with <250 mm of rain annually and evaporative water loss balancing the inflow of river water, over 90% of which comes from the Omo River. The system is characterized by large climate-driven WLF, and has thus been called an "amplifier lake"

(Johnson and Malala 2009). While greater in magnitude, Lake Turkana's long-term fluctuations coincide temporally with those of other African lakes (Butzer 1971, Verschuren et al. 2000, Johnson and Malala 2009). Water level fluctuated approximately 20 m over the 20th century (Odada et al. 2003), decreasing from a high of 381 masl in the late 1880's to a low of 361 masl in the late 1990's. Seasonal water inflow cycles result in intra-annual fluctuations of 1-1.5 m (Kolding 1992)**.** Lake Turkana has been spared from many of the threats that plague other African lakes (e.g. pollution, overfishing, and invasive species introductions), largely due to its remote and inhospitable nature. However, compared with other large African lakes, it is likely to experience the greatest changes to its hydrological cycle due to future development patterns.

Upstream development along the Omo River, the lake's "umbilical cord" (Kolding 1992), has included building dams to support hydroelectric power generation (the Gilgel Gibe Dams) and large irrigation schemes. The reservoir of the Gibe III Dam began filling in February, 2015; Gibe III will be the largest hydropower project in Africa and the fourth largest in the world, towering nearly 60 m taller than the Three Gorges Dam in China. In addition to lowering Lake Turkana's water levels during reservoir filling, the dam will drastically reduce the magnitude of the lake's flood cycle (Avery 2010). Although an artificial flood has been planned for this dam area, it has little scientific basis. For example, the duration of this flood will be only ten days, much shorter than the lake's natural flood pulse. Futhermore, the planned artificial floods for the Gibe I dam, a much smaller dam in the Gibe Dam series, have yet to be released. This raises doubts that Gibe III's artificial floods will actually be implemented (Avery 2012).

Downstream of the Gibe III Dam, land is being cleared for sugarcane and cotton plantations, which will eventually cover over 200,000 hectares. Much of this land was previously within the Omo and Mago national parks and Tama preserve, which were re-demarcated for these plantations (Avery 2012). The associated large-scale irrigation schemes will consume substantial portions of the Omo River's flow and could lead to lake level declines on the order of 20 m in a lake only 30 m deep on average (Avery 2012). The magnitude of these threats can be illustrated by the fear that Lake Turkana will become "East Africa's Aral Sea". The Aral Sea is a prime example of a freshwater system in which antropogenic changes to the hydrologial cycle were ecologically and economically disastrous (IR 2013).

There are close to 60 documented fish species in Lake Turkana, 10 of which are endemic. It is likely that there are additional species in the lake yet to be described (FishStat 2015). The Lake Turkana fish community will be subjected to two phases of hydrological change, which will have profound impacts. Initially, reduction in the lake's flood pulse will lead to degradation of littoral habits and diminished breeding cues. These changes will lead to declines in the abundance of species that breed and feed in the lake's littoral habitats and in the Omo River, the impacts of which are likely to cascade throughout the food web. Pelagic low-trophic level species are also likely to undergo population declines during this phase. These declines will result from a reduction in nutrient inputs from the Omo River. The species that survive changes during the first few years of upstream development will face more extreme water level declines and associated increases in salinity and alkalinity.

A decline in the lake's fish populations will have severe ecological and socioeconomic implications. Many of the 350 species of aquatic and terrestrial birds identified in the region, which is considered an "Important Bird Area" by BirdLife International (BirdLife International 2015), are reliant on fish for their diet. Similarly, the lake is home to one of the world's largest populations of the Nile crocodile, *Crocodylus niloticus*, which has a diet that consists nearly exclusively of the Nile tilapia, *Oreochromis niloticus* (Kolding 1993). Lake Turkana is also thought to be the “cradle of mankind” due to the large quantity of early hominid fossils that have been found in the region (e.g. Joordens 2011). Fishing is likely to have been a major source of food for people surrounding the lake over its geological history, particularly during periods of high lake stand (Owen et al. 1982, Garcin et al. 2012, Wright et al. 2015). The ecological and anthropological value of Lake Turkana has been formally recognized by its designation as a UNESCO World Heritage Site.

Turkana is Kenya’s poorest and most remote county. Over 70% of its population is reliant on food aid (USAID 2014, Rembold et al. 2014). Although the tribes currently living around Lake Turkana are traditionally pastoralists (with the exception of the El Molo tribe), fishing provides an important alternative livelihood, particularly during periods of drought (Watson and van Binsbergen 2008ab, Yongo et al. 2010, Carr 2012). The fisheries of Lake Turkana also have the potential to contribute to national GDP and food security. As of 1962, Lake Turkana was considered the “last great lake remaining in Africa with its fish population in a pristine, natural condition” (Mann 1962: page 10). The lake continues to be one of the least exploited of the large African lakes (Kolding and van Zweitin 2012). For example, the portion of Lake Victoria that lies within Kenya is half the size of Lake Turkana, yet supports a higher density of fishermen (Yongo et al. 2010). There is some evidence of increased interest in Lake Turkana’s fisheries by the Kenyan Government, given declines other Kenyan inland fisheries (KMFRI 2007).

Dissertation Objectives

The objective of this dissertation is to further understand Lake Turkana fish communities and fisheries and predict how they will be impacted by changes to the lake’s hydrological cycles. Lake Turkana is immensely understudied, which makes predicting its response to impending upstream development a difficult task. There have been only four major research expeditions studying the lake and its fauna: the Cambridge University Expedition of 1930-1931 (Worthington 1936), the Lake Turkana Project of 1972-1975 (Hopson 1982), the Lake Turkana Limnological Study of 1985-1988 (Kallqvist et al. 1988) and the Turkana Fisheries Study (Kolding 1989). The most recent comprehensive review on Lake Turkana was published over 20 years ago (Kolding 1992).

Avery (2010, 2012) and Velpuri and Senay (2012) have predicted the hydrological impacts of upstream development on Lake Turkana, and note the need for research on the lake’s resources to be considered in an ecological context. Throughout this dissertation, a variety of methodological approaches were employed to begin to fill this knowledge gap. These approaches include literature and data synthesis, modelling, and stable isotope sample collection and processing.

Chapter 2 of this dissertation provides an overview of Lake Turkana’s hydrology, physiochemical characteristics, and its flora and fauna based on an extensive literature review. This chapter also delves into the ecosystem services provided by the lake and the development project in the region that threatens these services. In Chapter 3, the history of the lake’s fishery is discussed in more detail, with a focus on understanding the relationship between hydrological cycles and fisheries production throughout the 1990’s and 2000’s. In discussing these links, Chapter 3 provides insight into how changes to Omo River inflow will influence the lake’s fishery. To further understand the link between fisheries and water level regimes, Chapter 3 also explores the implications of changing water levels for fish habitat availability and quality. This analysis relies on geographic information systems (GIS) modelling based on recently collected bathymetry data (Davidson and Smith 2011, Syracuse University 2011).

In Chapters 4 and 5, the structure of the lake's food web and the trophic sensitivity of its key fishery species are described as determined by stable isotope analysis. Chapter 4 gives a general overview of the structure of the lake's food web, determines the level of functional redundancy in the system, and explores ontogenetic dietary shifts among the lake's fishes. Chapter 5 focuses on seven "key" fish species, chosen both to represent different trophic guilds, and to their economic importance and ubiquitous nature in the system. These species are ranked in terms of their sensitivity to changing hydrological cycles based on their breeding and feeding habits, which were determined from stable isotope analysis and literature synthesis.

Chapter 6 takes a broader perspective of the relationship between water level regimes and ecosystem functioning. This chapter synthesizes information on the ecological attributes (primary production, species diversity, food web complexity and connectivity, etc.) of thirteen African lakes and reservoirs using published Ecopath models and explores how these attributes are related to annual and seasonal WLF. It aims to answer the question "What large-scale ecological changes occur when humans increase or decrease the WLF of African lakes"?

The last chapter of this dissertation, Chapter 7, reviews the findings of Chapters 2-6 and and discusses their implications for the future of the lake and its fisheries. The ultimate goal of this dissertation is to assist in improving management of the lake's resources in the face of future threats. Chapter 7 therefore provides guidance on priorities for future research and for minimizing the impacts of upstream development on the lake given the current state of scientific knowledge.

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Figures

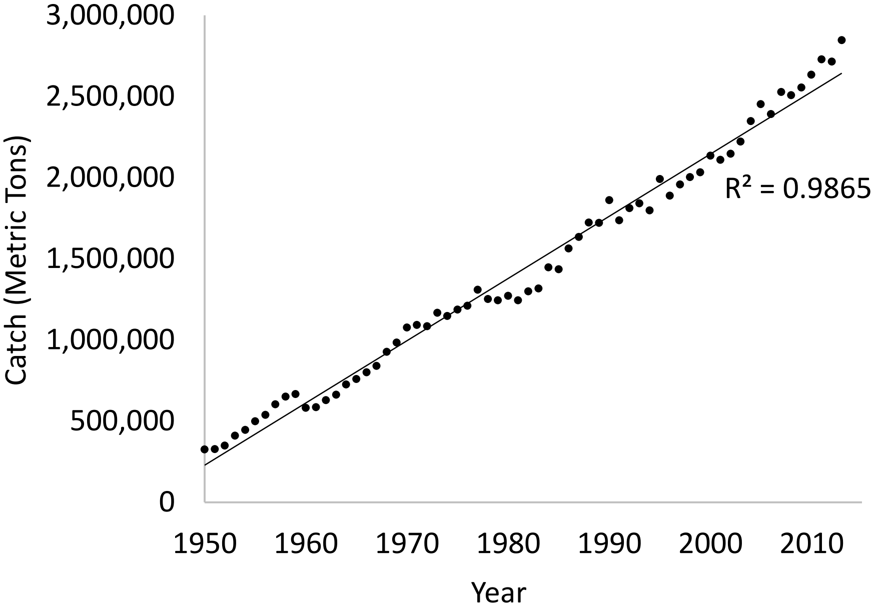

Figure 1.1: Total yield of inland fisheries in Africa, shown in metric tons. The continent's inland fisheries yield has increased continuously since the 1950's, but some of this increase may be due to better reporting of catch statistics or to the inclusion of stocked fishes in catch statistics. FAO FishStat (2015).

Chapter 2: Lake Turkana, the World's Largest Permanent Desert Lake

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Introduction

Lake Turkana is a unique ecosystem, distinguished as the world's largest permanent desert lake and largest alkaline water body. Of the East African Rift Valley Lakes, Lake Turkana is the most remote (Johnson and Malala 2009), and the last of the world's great lakes to be studied (Hopson 1982). The lake occupies an arid region in East Africa and lies largely within northwestern Kenya, but extends northward into southwestern Ethiopia (Figure 2.1). The lake's catchment basin covers an area of approximately 130,860 km^2. With a surface area of about 7,560 km^2, the lake is 260 km long and has an average width of 30km. The lake's mean depth is 31 m, with a maximum depth of 114 m.

Lake Turkana is fed by three major rivers: the Omo, Turkwel and Kerio. The Omo River, which flows continuously and is fed by precipitation from the Ethiopian Highlands, accounts for more than 90% of the lake's freshwater influx and acts as the lake's "umbilical cord" (Kolding 1992; Avery 2010). The Turkwel and Kerio Rivers provide intermittent freshwater inputs (Ricketts and Johnson 1996). Owing to the Turkwel dam, river discharge is regulated and is perennial, but sometimes all of the water percolates through the riverbed and is lost before reaching the lake (Avery 2012). The Turkana area has been called the "cradle of mankind" due to the preponderance of early hominid fossils that have been found in the region (e.g. Joordens 2011). Its national and global archaeological importance led to the creation of Sibiloi National Park in 1973. A few years later, in 1978, UNESCO listed Mount Kulal as a Biosphere Zone. In 1983 and 1985 the Central and South Island National Parks were formed, and together with Sibiloi these were designated a UNESCO World Heritage Site in 1997. The lake is widely known as the "Jade Sea", because of its remarkable, almost incandescent color caused by the blue-green phytoplankton present on its surface.

Physical and Chemical Characteristics of Lake Turkana

Hydrology

Despite its large size, Lake Turkana is a highly pulsed, variable system as a result of its endorheic drainage basin, arid surroundings, and its strong dependence on one river for the majority of its inflow. As a result, the lake is sometimes called an "amplifier lake" (i.e. it "amplifies" changes in climate (Street-Perrot and Roberts 1983). The water budget of the lake is balanced between river inflows, groundwater exchanges, and evaporation losses (Avery 2010). The surface area of the lake, which receives less than 200 mmyr^{-1} of rainfall, is 5.7% of its drainage area (Avery 2012). An estimated mean evaporation rate of 2.5 m year^{-1} (Kolding 1989) requires an inflow compensation of about 600 m^{3}s^{-1} or 19 km^{3}year^{-1} to maintain the lake's water balance. The Omo River's drainage basin makes up 56.6% of the lake's total drainage area, but the river contributes approximately 90% of the lake's inflow (Avery 2012). As a result, the lake's water level fluctuations are almost entirely caused by variations in rainfall over the Ethiopian highlands. At its present size, the lake has a relatively long residence time of about 12.5 years (Kolding 1992).

Data on historical and current water levels of Lake Turkana were provided by the Kenya Marine Fisheries Research Institute (KMFRI) and obtained from TOPEX/Poseidon and other satellite records (Avery 2010, 2012; Crétaux et al. 2011). The highest lake level in recent history was recorded in the late 1800's, when levels were approximately 15 meters higher than the Hopson zero datum of 365.4 meters above sea level (masl; Hopson 1982, Avery 2012). Between the late 1800's and mid 1900's, the lake level dropped approximately 20 meters (Avery 2012). The lake level rose 5-10 meters in the 1970's and 1980's and then decreased again to current levels by 1990. Over the past 25 years the lake level has fluctuated between 360 and 365masl, and has at times reached levels at which the lake's most productive fisheries area, Ferguson's Gulf, becomes dry (Avery 2012). Ferguson's Gulf dries up when the lake level is 3.1 meters lower than the Hopson zero datum, which happened most recently from 1993-1998, 2003-2008, and in 2010 and 2012 (Figure 2.2). Within a given year the lake level varies 1-1.5 meters with the highest annual water levels generally occurring from September through December (Figure 2.3).

Geochemistry (Water Quality & Nutrients)

Lake Turkana has average conductivity levels of 3,500 $uScm^{-1}$, making it a "high ion" or "Class II" lake (Talling and Talling 1965). Due to its closed-basin nature, the conductivity of the lake has been increasing by approximately 0.45 $\mu Scm^{-1}yr^{-1}$ (Hopson 1982). Current salinity levels are 2.5 (Odada et al. 2003), with the system moving toward the limit of 3 defining true saline lakes. Lake Turkana is also the world's largest alkaline lake, with a pH range of 8.6-9.5 (Cohen 1986). The annual surface temperature ranges between 27.2–29.4^{o}C, and bottom temperatures vary only 1.0^{o}C, from 25.4-26.4^{o}C. Turbidity levels are high in Lake Turkana and the euphotic zone extends to only 6m in the open lake (Källqvist et al. 1988). The lake is known for its strong southeasterly winds, which create surface water currents to the northwest and deep reverse bottom water currents (Hopson 1982). Due to these currents and the lake's relatively shallow nature, the lake is well mixed and the water is generally well-oxygenated at all depths (Källqvist et al. 1988), with oxygen levels of $\geq$5 mgl^{-1} observed at all stations in a recent study (KMFRI 2007).

Lake Turkana is highly dependent on riverine nutrient inputs (Hopson 1982, Källqvist et al.1988). The most recent lakewide study found low levels of biologically available nitrogen, with nitrate levels below 100 μgl^{-1} and ammonia levels below 40 μgl^{-1} throughout the lake, and phosphorus levels of 2.2-2.4 mgl^{-1} (Källqvist et al. 1988). Recent measurements indicate much higher total nitrogen levels of 6-520 mgl^{-1} and total phosphorus levels of 0.5-140 mgl^{-1} in some regions of the lake (KMFRI 2008). Although nitrogen levels are higher than they were in the past, the N:P ratio for the lake water is still lower than the Redfield Ratio, suggesting nitrogen limitation. Although the N:P ratio of the Omo River's water is unknown, patterns of primary productivity in the lake suggests that the nutrient inputs from the river are essential (Tebbs et al. 2014). In acting as its primary source of freshwater, the Omo River's inflow also alters the lake's salinity. Salinity increases during years of low inflow, due to evaporative concentration of salts, and shows a north to south increasing gradient during periods of spate (Källqvist et al. 1988).

Inflow from the Omo River also influences turbidity and light availability in Lake Turkana. Sediment plumes extend up to 100 km into the lake following flood influxes from the river (Yuretich and Cerling 1983). Typical of tropical lake ecosystems, Lake Turkana exhibits relatively little seasonal variation in water temperature and day-length (Lowe-McConnell 1987). Instead, periods of high inflow from the Omo River and the resultant changes in the lake's turbidity act as signals for the lake's fishes to move into shallow areas or rivers to breed (Hopson 1982). The volume of the river's inflow, which controls the lake's water levels, also influences the availability and distribution of different habitat types.

Lake Turkana Ecology

Diversity of Wetland Ecosystems

The most notable wetland ecosystem in Lake Turkana is the Omo Delta. Other notable wetland ecosystems within the lake include Ferguson's Gulf, Central Island National Park, and the mouths of the Kerio and Turkwel rivers (Figure 2.1). In addition, the lake margins host many smaller but important wetlands, in some cases physically separate from the lake.

i) Omo Delta Wetland

The Omo Delta is located at the northern tip of Lake Turkana. The delta has a complex pattern of waterways that show large fluctuations in size (Olago and Odada 2007). During the early 1970's the Omo Delta was entirely contained within the boundary of Ethiopia. The delta increased by 500 km^2 between mid-1980's and late 1990's (Haack and Messina 1997). By the mid-2000's, the front edge of the delta had moved approximately 12 km to the south and had crossed over the Ethiopian border into Kenya. Over this time, the area of wetland vegetation increased nearly 300%, from 117 km^2 to 334 km^2. Delta expansion probably resulted from reduced lake levels and increases in sediment inflow, a consequence of anthropogenic influences on the river's watershed that have led to deforestation, including overgrazing and clearing of land for agriculture (Haack and Messina 1997; Ayalew 2009; Avery 2010).

There is a unique pattern of succession taking place within the lake, with wetland vegetation largely replacing previously water-covered regions during periods of lower water, but reversing when the lake rises again, as it did in 2015, and these vegetated areas become inundated. While an increase in faunal biodiversity in new delta areas has been noted, the expansion of the delta has also attracted humans, possibly fueling the recent increase in human-wildlife conflicts (Olago and Odada 2007). The expansion of the delta southwards has also increased conflicts between Ethiopian and Kenyan tribes, as Ethiopian tribes have migrated south into Kenya to continue fishing in the lake.

The Omo Delta and fringing riverine wetlands are characterized by dense macrophytic vegetation, dominated by *Potamogeton* spp., and the emergent grasses *Paspalidium geminatum* and *Sporobolus spicatus*, which occur in shallow areas. Several submerged plants, including *Ceratophyllum demersum*, *Hydrocotyle* sp., and floating plants, including *Lemna gibba*, *Nymphaea* spp., and *Ottelia ulvifolia*, have been recorded in the area (Hughes and Hughes 1992). Besides the ubiquitous acacia tree (*Acacia tortilis*) that dominates the landscape, there is the gingerbread palm tree (*Hyphaene thebaica*), whose oval fruit is edible, and the doum palm (*Hyphaene coriacea*), used for making rafts locally. The presence and imminent impact of the noxious invasive water hyacinth (*Eichhornia crassipes)* is of great concern to many conservationists, though it may not survive in the semi saline lake.

Though the Omo Delta and the fringing riverine wetlands may well be considered part of the broader Lake Turkana, they are home to some unique species that are rarely found in the lake proper. These include several species of Mormyrids (Freshwater elephantfish): *Mormyrus longirostris, Marcusenius victoriae, Marcusenius macrolepidotus, Mormyrus anguilloides, Mormyrus kannume, Marcusenius stanleyanus, Hyperopisus bebe,* and unidentified *Mormyrus* sp;

Arapaimidae (*Heterotis niloticus*) – the African Arowana; Gymnarchidae (*Gymnarchus niloticus*) – the African Knife-fish (an electric fish), and Polyteridae (*Polytepterus senegalis*). Together with the riverine fish species, the delta hosts representatives of more than 15 different fish families (Ojwang et al. 2011). Other species found within the delta include Nile crocodile *(Crocodilus niloticus)* (average of 8 individuals/km^{-1} along the river channel), several rare and endemic species of invertebrates, reptiles and amphibians, and over 128 avian species (Ojwang et al. 2011).

ii) Kerio/Turkwel deltas

These two smaller deltas differ greatly from each other and are associated with the seasonal Kerio and Turkwel Rivers (Figure 2.1). The Kerio River runs parallel to the primary direction of the wind in the region, so its mouth is situated on a low energy shoreline. It is also protected from the direct north-south wave action that arises when winds change direction and has consequently developed a dense mass of riverine-associated macrophytes. The Turkwel River, on the other hand, drains directly into the part of the bay facing the strong SE winds for which the lake is known. As a result, rooted macrophytes have failed to take hold along the banks and there is little permanent vegetation except for the invasive thorny shrubs of *Prosopis juliflora*.

iii) Ferguson’s Gulf

Ferguson’s Gulf is the most important tilapia habitat in Lake Turkana, especially for the indigenous species *Oreochromis niloticus*. The gulf, which is approximately midway down the lake’s western shoreline east of Kalokol, is protected from the open lake’s wave action and direct mixing by the Longech/Namukuse spit. The relatively calm waters of the gulf support a different phytoplankton community from the rest of the lake, with primary production rates up to three orders of magnitude higher than the open waters (Källqvist et al. 1988). The gulf generally experiences annual water level fluctuations of 0.5 to 1.5m, but has also dried completely three times in the past 25 years (Figure 2.2). Intensive fishing activities conducted using small mesh beach seines, set gillnets and purse seines are rampant in the area. The fishery is characterized by boom and bust cycles that are largely dependent on the Omo River’s flooding cycles. The invasive shrub, *P. julifora*, heavily covers the shores of the Gulf. Its thick interlocking thorny canopy blocks access to previously important fishing grounds and certain landing beaches.

iv) Sibiloi/Koobi Fora protected area

Sibiloi National Park, which was designated a Protected Area under Kenyan law in 1973, covers 1570 km² along the northeastern shores of Lake Turkana. The shoreline within the park is approximately 90 km long and is characterized by several spits, muddy shorelines, inlets, seasonal river mouths and, in some areas, lush growth of submerged and rooted macrophytes (e.g. *Potamogeton pectinatus*). Sibiloi Bay and Allia Bay are shallow regions near the park headquarters that boast the largest submerged beds of rooted aquatic macrophytes of Lake Turkana proper. Another important wetland habitat in Sibiloi National Park is Koobi Fora, which lies directly east of North Island, midway between the southern and northern ends of the park. The wetland areas of the park, which are devoid of fishing activities other than some sports fishing and poaching, support the highest fish biomass in Lake Turkana. Furthermore, experimental fishing within Sibiloi National Park resulted in catches of individuals larger than those caught with the same fishing gear in highly fished areas, such as those surrounding Ferguson’s Gulf (KMFRI 2008).

v) Other protected areas of the lake

In 1978, UNESCO listed Mt. Kulal and the southern lake area, including South Island, in its Biosphere Reserves Directory. In 1983, South Island was made into a national park in its own right, followed in 1985 by Central Island. At the south end of the lake there is a crater lake and some small lakes that are hydraulically connected to the lake proper. At Loyangalani, on the south-eastern shore, an oasis of potable springs and doum palms is the focal point for the largest human settlement on the eastern shores of the lake. Another oasis, situated not far north of Loyangalani, is the main water source for the El Molo tribe. Similar spring-fed oases on the western lake shores at Eliye and Lobolo provide valuable sources of potable water to the local population. These springs are crucially important, as the main lake water itself is too high in fluoride for safe consumption (Avery 2010, 2012). Central Island is especially interesting as it includes three distinct lakes within the main lake, each with different salinity, and each providing a distinct habitat for birds in particular, including lesser flamingos.

Lake Turkana Biodiversity

Phytoplankton diversity is relatively low in Lake Turkana. The phytoplankton community is dominated by the blue-green algae *Microcystis aeruginosa* and the green alga *Botryococcus braunii.* The total annual photosynthetic plankton primary production was estimated at ca. 2 kg O_2/m^2/year from 1985-1988 (Källqvist et al. 1988). The zooplankton community includes copepods, cladocerans and protozoans, whose total production has been estimated at 216,000 – 540,000 metric tons of dry weight per year (Hopson 1982). There are records of 50 species of benthic organisms, dominated by ostracods and insects, within the lake and Omo Delta (Cohen 1986).

Lake Turkana is home to at least 60 fish species, 10 of which are endemic (FishStat 2015). For the most part, the species found in Lake Turkana can be found elsewhere in Nilo-Sudan lake and river systems. The number of fish species in the lake is low when compared to other African lake and river ecosystems, except for Lake Albert, which has a similar fish composition and diversity. Many of the more diverse lake systems, which host hundreds of species dominated by cichlids, are older and deeper than Lake Turkana (Lowe-McConnell 1987). Endemic species of fish include small zooplanktivores (e.g., *Brycinus minutus, Brycinus ferox*) that form a unique mid-water scattering layer in the lake, a smaller and more pelagic species of *Lates* (*L. longispinus)* and cichlids (e.g., *Haplochromis turkanae, Hemichromis exsul).* Unlike in Lake Victoria and some other African Lakes, the Nile tilapia (*Oreochromis niloticus*) and Nile perch (*Lates niloticus*) are native to Lake Turkana and in fact are the highest valued species in the lake's commercial fishery.

Lake Turkana supports over 350 native and migratory bird species, making it an "Important Birdlife Area" (UNESCO 2015). The lake also hosts the world's largest remaining population of Nile crocodile (*Crocodilus niloticus*) and contains protected breeding grounds for this species and for hippopotamuses and several venomous snakes (UNESCO 2015). Mammals sighted in the park areas and their environs include Grevy's (*Equus grevyi*) and Burchell's zebra (*Equus quagga burchellii*), Grant's gazelle (*Nanger granti*), Beisa oryx (*Oryx beisa*), topi (*Damaliscus korrigum*), greater kudu (*Tragelaphus strepsiceros***)**, hippopotamus (*Hippopotamus amphibious*), lion (*Panthera leo*; IUCN Red List status - Vulnerable), cheetah (*Acinonyx jubatus*; Vulnerable), leopard (*Panthera pardus*), striped hyaena (*Hyaena hyaena*), wild dog (*Lyacon pictus*; Endangered) and silver-backed jackal (*Canis mesomelas*). Giraffe are now extinct in the Park. There are also four species of endemic reptiles in the region, including three species of frogs (*Bufo chappuisi, B. turkanae* and *Phrynobatrachus zavattarii*) and the endemic Turkana mud turtle (*Pelusios broadleyi;* Vulnerable).

Lake Turkana Conservation

Ecosystem Services

Lake Turkana and its fringing floodplain wetlands provide a host of hydrologic, ecological, economic, and socio-economic services. These services include providing water for domestic and livestock use, water for energy (hydroelectric power) and agricultural uses, habitat for fisheries, forage for livestock, fuel, building materials, natural food products, climate moderating effects, and significant opportunities for ecotourism and preservation of cultural values. Important sites for tourism include Sibiloi National Park and the geologically active Central Island, which hosts the magnificent Crocodile, Flamingo and Tilapia Lakes. Lake Turkana, the Omo and Turkwel rivers and associated springs are permanent water sources used by thousands of people, hence forming important lifelines in the region for millennia, perhaps dating back to the dawn of humankind.

Fishing has taken place on Lake Turkana for at least 10,000 years, with catches used primarily for local consumption until the emergence of the commercial fishery in the 1940's (Owen et al. 1982); see Figure 2.4. Although Lake Turkana may have the potential to increase food security in a region where reliance on food aid is ubiquitous, the sustainability of the fishery has not been extensively studied. Pastoralism has been the preferred livelihood of people surrounding the lake for the last few thousand years, but fishing provides an important alternative and a "safety net" livelihood in the region (Kaijage and Nyagah 2010). Currently, one of the largest obstacles faced by the Lake Turkana fishery is post-harvest losses (e.g. fish spoilage) which can be as high as 50%. These post-harvest losses are largely the result of fish handling and preservation techniques surrounding the lake, which are heavily reliant on sun-drying (KMFRI 2007).

Riparian Communities

Lake Turkana is abutted by Turkana County on its western side and Marsabit County on its eastern side, with some of the lake's southernmost regions crossing into Samburu County. The Turkana tribe dominates Turkana County, but minor tribes that have migrated to the lake from other regions are also present. Marsabit County has a more diverse group of tribes, including the Dasanech, the Gabbra, the Rendille, the Samburu, the El Molo and the Turkana (Kaijage and Nyagah 2010). Nearly 100,000 members of at least eight distinct indigenous ethnic groups are heavily reliant on flood-recessional farming along the Omo River (Richter et al. 2010) while about 250,000 people of various ethnicities are dependent on fishing within the lake basin.

Conservation Status and Management

Lake Turkana resources are shared by Kenya and Ethiopia. The region is rich in natural resources and hosts unique endemic species. Even though parts of the lake and lower Omo Delta have been zoned as an international biosphere reserve, the protected areas are facing an immense threat from human activities. In spite of the apparent threats, however, there is no management plan in place to guide resource use in the region. Recent efforts to develop wildlife and fisheries management plans by Kenya Wildlife Services (KWS), National Museums of Kenya (NMK) and the State Department of Fisheries, Kenya, are worth accelerating. Otherwise the prevailing scenario of uncoordinated Lake Turkana resource management will ultimately compromise ecosystem services with drastic negative implications for development, poverty alleviation, and adaptation towards anticipated long-term environmental changes.

The natural resources and human populations within the Omo Delta, which is an "oasis" in the region, fits four of the criteria required for designation as a Ramsar Site and would benefit from being recognized as such (BirdLife International 2015). Other management efforts to consider include the establishment of a Lake Turkana-Omo Delta Transboundary Resource Management Committee, with members drawn from focal point ministries in Kenya and Ethiopia. Conservation and use of the World Heritage archaeological sites are needed to recognize and safeguard the region's cultural heritage and to create development opportunities.

Threats and Future Challenges

Human activities in the Lake Turkana basin have accelerated the rate of ecological change and increased threats to existing natural resources. The Lake Turkana region is currently experiencing unprecedented growth in several sectors. Oil was discovered in the region in 2012 and oil drilling operations led to a 500% increase in the population of some towns from 2012-2014. The largest wind farm in Africa, which will be located along the northeastern shores of the lake, is set to be commissioned in 2018 (LTWP 2015). Lake Turkana will also be along the direct route of the Lamu Port and Lamu-Southern Sudan-Ethiopia Transport Corridor (Bulzomi et al. 2014). Though these development projects are likely to benefit the people of the Lake Turkana region in some respects, such as improved access to roads and electricity, they will also foster rapid population growth and additional stress on natural resources. In addition to development within Kenya, the Omo River is the site of several development projects that are likely to have the largest immediate impact on Lake Turkana and its ability to provide ecosystem services.

Two dams (Gibe I and Gibe II) have been constructed along the Omo River, a third dam is under construction (Gibe III), and there are plans to build two additional dams in the future (Gibe IV and V) (See Figure 2.1). Gibe III will be 240 m high and produce 6,400 GWh/yr of energy (EEPCO 2009). The filling of its reservoir, which will store 11,750 m^3 of water, will lead to a reduction of 2 m in Lake Turkana's water level (Avery 2010, 2012; Velpuri and Senay 2012). Gibe IV's resevoir would require a similar volume of water to fill (Avery 2012).

A minimum environmental flow and an artificial 10-day flood has been proposed for Gibe III, but it is unknown whether a flood of this duration and size will be sufficient to sustain the ecological functioning of the lake (Avery 2012). Although a reduction in flooding is touted as a benefit by some (e.g. the Ethiopian Electric Power Corporation, EEPCO 2009), the resultant dampening of Lake Turkana's water level fluctuations is of great ecological concern, given the importance of intra-annual fluctuations to the control of fish productvity in African lakes (e.g. Kolding and van Zwieten 2012). The amplitude of the controlled lake level fluctuations, assuming the environmental floods proposed by EEPCO 2009 are implemented, will be 0.4 m less than the amplitude of the lake's natural fluctuations.

Associated with the Gilgel Gibe dams are thousands of hectares of sugar cane and cotton plantations and their irrigation infrastructure. Currently 150,000 hectares are being developed along the Omo River as part of the Kuraz Sugar Project; planting began in February 2013 (Ethiopian Sugar Corporation 2015). The Ethiopian Government plans to increase sugar production within Ethiopia from 300,000 tons in 2009/2010 to 2.25 million tons by mid-2015 (Ethiopian Sugar Corporation 2015). Additional land concessions have been awarded, mainly for cotton production. A total of 445,000 hectares of commercial agricultural development is planned, of which 135,285 hectares have been excised from Omo and Mago National Parks and Tama Wildlife Reserve (Avery 2012).

The Kuraz sugar scheme alone will use at least 30% of the Omo River's flow (Avery 2012). With the development of other irrigation schemes, water removal from the river can only increase, which means the inflow to the lake will diminish. If there is a 33.5% reduction in Omo River input to Lake Turkana, the lake will drop 13 m, and its volume will be reduced to 59% of its otherwise sustainable volume. If there is a 52% reduction in Omo inflow, the lake will fall 22 m, and over half the lake's volume will be lost. A drop of as little as 10 meters in lake level would reduce the lake’s size from 7,560 km^2 to 5,900 km^2 and the lake’s volume from 238 km^3 to 170 km^3 (Avery 2012). Changes in the lake’s water levels will also lead to changes in the shape of the lake’s shorelines, which will be the most prominent in the wetland areas shown in Figure 2.1 (Omo Delta, Ferguson’s Gulf, Allia Bay of Sibiloi National Park, and at the Turkwel and Kerio Deltas; Avery 2010, 2012; Velpuri and Senay 2012). Changes in the annual volume and patterns of water inflow from the Omo River will impact a variety of important parameters in Lake Turkana, including turbidity, salinity, productivity, and habitat availability. These changes will interact to influence the feeding, breeding, movement and ultimately the population levels of fishes in the lake and therefore the lake’s fisheries. The Gilgel Gibe Dams and irrigation schemes under construction will also have impacts beyond water inflow changes. For example, eutrophication caused by increased nutrient loads from fertilization of upstream crops or changes in turbidity due to further deforestation along the Omo River may also alter the Lake Turkana ecosystem.

Lastly, the Lake Turkana region, which is already known for its environmental sensitivity, will be subject to more extreme climate conditions as a result of global climate change (e.g. Bishaw 2012). Greater efforts are needed to forecast hydrodynamic and ecological responses to climate change in the region. It is also important to understand and to strengthen local adaptation not only to improve local conditions but also to avoid destabilization of the region due conflicts driven by resource scarcity (e.g. Vidal 2015).

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Figures

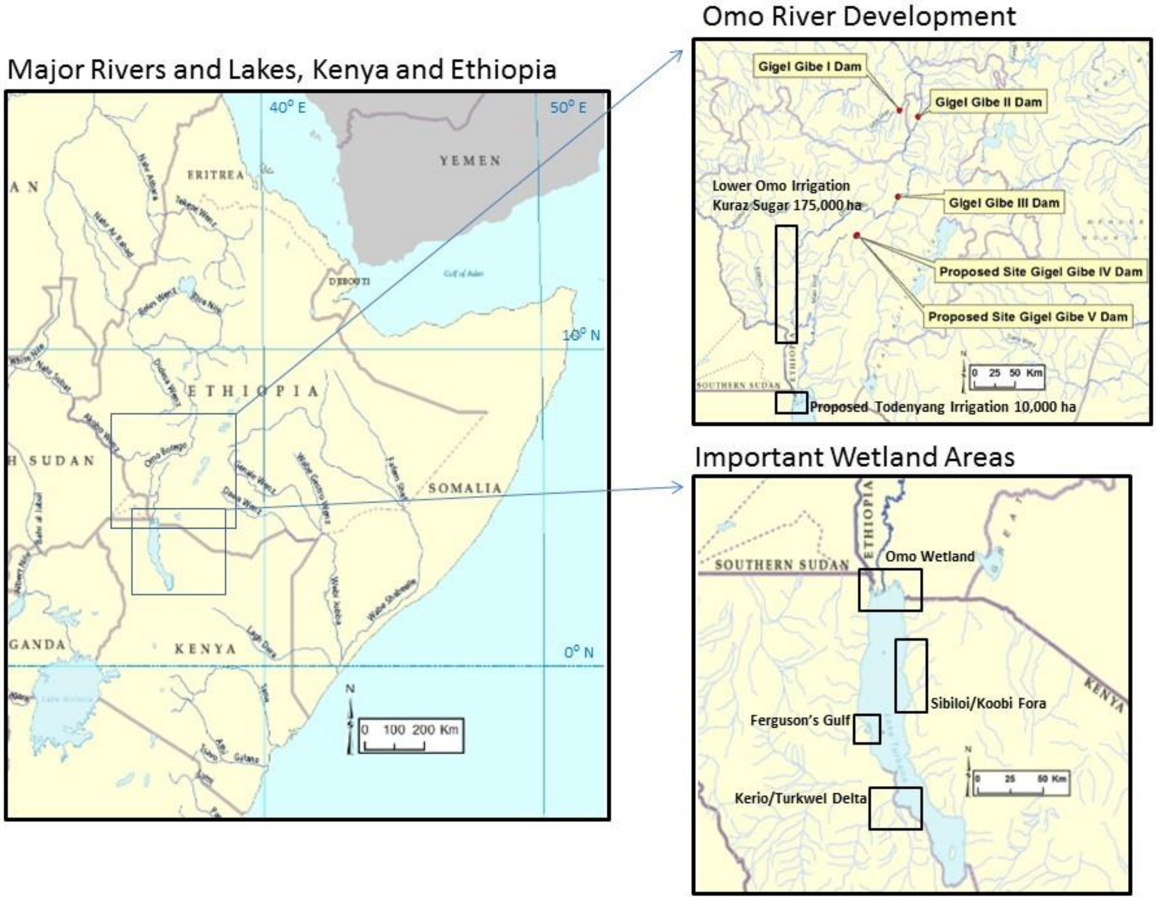

Figure 2.1: Map of Kenya and Ethiopia water systems showing Lake Turkana and important areas mentioned in the text.

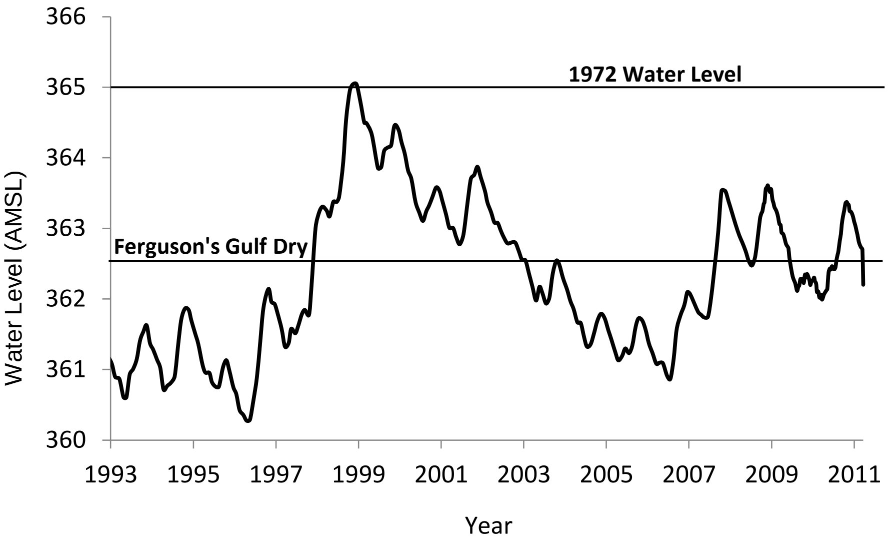

Figure 2.2: Satellite altimetry data (Crétaux et al. 2011) showing Lake Turkana water levels from 1993-2011. The top line represents the 1972 water level and the second line represents the water level at which Ferguson's Gulf, the Lake's most productive area, dries up (Hopson 1982; Avery 2010).

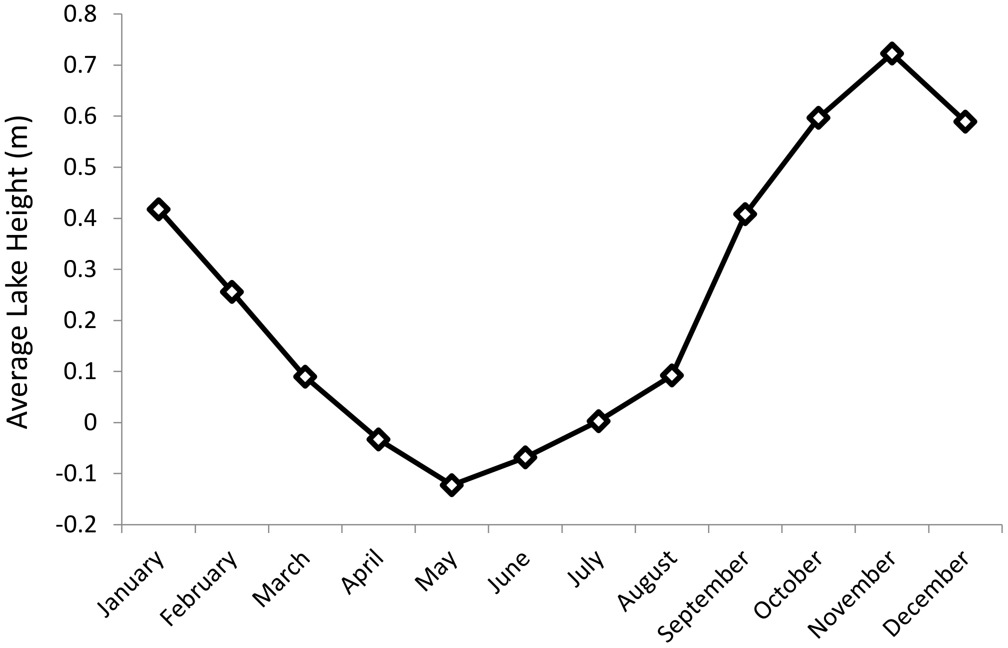

Figure 2.3: Average monthly water levels (years 1993-2013) relative to a 9-year average as measured by satellite altimetry from the USDA Global Lakes and Reservoirs database. Lake Turkana generally has intra-annual fluctuations of 1-1.5 meters.

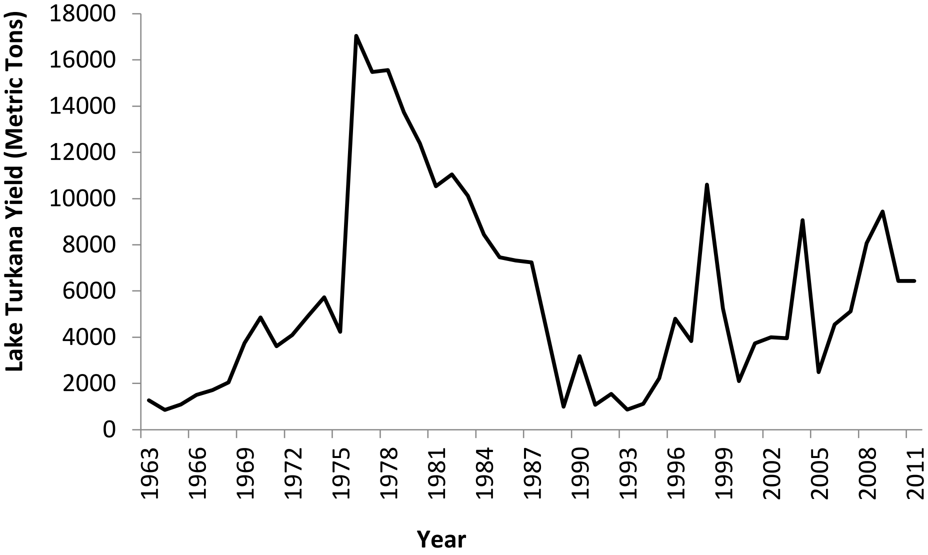

Figure 2.4: Fisheries yield for Lake Turkana in metric tons, 1963-2011.

Chapter 3: Reconciling Fisheries and Water Level Fluctuations in the World's Largest Desert Lake

Introduction

Lake Turkana, Kenya is the world's largest permanent desert lake and Africa's fourth largest lake by volume. While approximately 93% of the fisheries yield in Kenya originates from freshwater bodies, Lake Turkana has only contributed 5% of the total freshwater yield over the past decade (KNBS 2015). The remoteness of lake, it's choppy waters due to strong winds, the high parasite loads of its fishes (KMFRI 2007, Moravec et al. 2009), and the livelihood preferences of tribes living in the watershed (Yongo et al. 2010) have all contributed to limiting fisheries growth. Even at present production levels, however, the lake's fisheries provide a valuable protein source and an alternative livelihood in an area with chronic food security challenges, with nearly 75% of the population reliant on food aid for sustenance (Snyder 2006).

Concerns regarding reduced yield from Lake Victoria (e.g. Njiru et al. 2008, Ogello et al. 2013, Legros and Luomba 2011), which is home to Kenya's most productive inshore fisheries, have prompted the Kenyan Government to increase their focus on expanding Lake Turkana's fisheries over the past decade (KMFRI 2007). For example, Beach Management Units (BMUs) which bring together stakeholders and government organizations to co-manage the lake's fisheries, have been established on Lake Turkana to support fisheries growth. In Kenya, the implementation of BMUs began with Lake Victoria, where they have been met with limited success (Obiero et al. 2015). In addition, non-profit organizations have provided substantial financial support for fisheries development, primarily by donating boats and fishing nets (e.g. Watson and van Binsbergen 2008ab, Yongo et al. 2010).

Lake Turkana is also surrounded by a growing human population. Turkana County, located on Lake Turkana's western side, is where most of the lake's fisheries are concentrated. This country is dominated by the Turkana tribe and had a population of 855,399 people according to the Census report of 2009, with a per capita growth rate of 0.65% (KNBS 2015). Marsabit County, on the lake's eastern side, has a more diverse but smaller population made of up several tribes, including the Daasanech, Gabbra, Rendile, Samburu, El Molo and Turkana tribes. This county had 91,166 residents in 2009 and a per capita growth rate of 1.55% (KNBS 2015).

The Turkanas are a traditional pastoral community with strong cultural attachment to cattle as an indicator of wealth and social status (Pavitt 1997). The impact of frequent droughts, increasing insecurity and cattle rustling, and famine has led to partial or complete reliance on fishing as an alternative livelihood (Notenbaert et al. 2007, Watson and van Binsbergen 2008ab, Omolo 2010, Yongo et al. 2010). Livestock carrying capacity is highly linked to environmental variability in the region and therefore varies with climatic conditions (Vetaas and Kolding 1991). Regardless, it's likely that the region's livestock population is too large for the land to support (Watson and van Binsbergen 2008ab). If sustainably exploited, Lake Turkana's fisheries could improve the welfare of locals and contribute considerably to national gross domestic product (GDP).

Potential growth of Lake Turkana's fisheries coincides with the construction of major development projects in the region. For instance, the Lake Turkana Wind Power Project is constructing 365 wind turbines in lower Marsabit County, expected to begin functioning in 2018 (LTWP 2015), and there are several companies in the region exploiting recently discovered rich oil reserves (Imana 2013). These development projects require the building of roads and infrastructure that could improve access to Lake Turkana and make it a more attractive option for fisheries investments. Of most relevance to the lake's fisheries is a series of development projects along its major riverine water source, the Omo River, Ethiopia (Avery 2012, Gownaris et al. 2015). Lake Turkana is an endorheic lake with no surface outlet. Lake level therefore represents a balance between riverine inflow and high rates of evaporation over the lake. The Omo River makes up only 56.6% of the lake's drainage basin but contributes 90% of the lake's inflow, with the remaining inflow coming from ephemeral rivers (i.e. the Turkwel and Kerio rivers) and local precipitation, which amounts to less than 250 mm/year (Avery 2012). Lake Turkana's closed-basin nature, arid surroundings, and strong dependence on one inflowing river make it a highly pulsed, variable system (e.g. Butzer 1971, Street-Perrot and Roberts 1983).

Despite its relatively deep nature in the central northern and southern basins, variations in Lake Turkana's biological productivity are strongly driven by riverine nutrient inputs, rather than by mixing or atmospheric deposition (Hopson 1982, Kallqvist et al. 1988, Kolding 1992). As a result, primary productivity decreases along a north-south gradient in the lake (Hopson 1982, Liti et al. 1991, Kallqvist et al. 1988, KMFRI 2008). Inflow from the Omo River also influences other chemical and physical characteristics and determines the timing of important biological events among the lake's fish populations (Hopson 1982, Kolding 1992, Ojwang et al. 2010, Gownaris et al. 2015). Lastly, the magnitude of Omo River flow entering the lake alters the distribution and availability of lake habitats and the extent of the lake's aquatic terrestrial transition zone (ATTZ), the highly productive region of a lake that is covered by water only during the flood pulse (Junk et al. 1989, Wantzen et al. 2008).

Changes in lake level and their fluctuations have resulted in “booms” and "busts" of some Lake Turkana fish populations in the past (Kolding 1993a, Kolding 1995). The catch per unit effort (CPUE) of the lake's fisheries was shown to vary significantly with the previous year's lake level between 1972 and 1988, with higher lake levels leading to increased CPUE (Kolding 1992). Over geological time scales, the species composition of the lake's fisheries has changed based on its water level status, with a predominance of large species during high lake stands and small species during low lake stands (Wright et al. 2015). Furthemore, rates of primary production, which are positively correlated with fish production in lakes (Melack 1976, Downing et al. 1990), are linked to riverine inputs of nutrients in Lake Turkana. These findings are not unique to this system. Water level variables, including absolute lake level and intra and inter-annual fluctuations, are widely accepted as central factors structuring lake ecosystems and their fisheries (Jul-Larsen et al. 2003ab, Kummu and Varis 2007, Leira and Cantonati 2008, Wantzen et al. 2008, Kolding and van Zwieten 2012, Kolding et al. *in press*).

Development along the Omo River includes a series of five dams (the Gilgel-Gibe dams) and over 200,000 hectares of sugarcane and cotton plantations in the lower Omo Valley. The recently commissioned Gilgel Gibe III dam will lead to a reduction in of 2 m in lake level during the period of reservoir filling (which began in January 2015) and substantial dampening of the lake's seasonal flood cycle (Avery 2010, Velpuri and Senay 2012). If the planned 10-day artificial floods are released from the dam (in August/September; flows of approximately 1600 m^3/sec at Lake Turkana), the lake's seasonal fluctuations would decline from 1.1 m to 0.7 m (Avery 2012). Extraction of water for downstream plantations and associated irrigation will lead to further reductions in lake level. These irrigation operations will require 33.5% of the Omo

River's annual flow assuming a moderate irrigation efficiency of 70%, and as much as 43.9% of the river's flow at low irrigation efficiencies of 45% (Avery 2012). Water demands for these known irrigation projects translate to lake level declines of 13-22 m (Avery 2012).

Due to Lake Turkana's close connection with the Omo River, development projects altering the river's flow are highly likely to impact the lake's ecological functioning and fisheries productivity. The ecology of Lake Turkana has not been comprehensively studied since the 1980's. Considerable research effort is therefore necessary before the potential impacts of upstream development can be understood. For example, Avery (2012) and Velpuri and Senary (2012) note the need for work that considers their hydrological predictions in an ecological context. To do this, this study briefly reviews the evolution of and changes to the lake's fisheries since the seminal works conducted on the system and re-visits the roles that variations in fishing effort (number of fishermen, fishing vessels, nets or hooks) and water level have played in the productivity of the lake's fisheries. To further examine the influence of changing water inflow patterns, a geographic information system (ArcGIS 10.3) model was developed to simulate habitat availability in the lake at different water levels and to determine the relationship between the seasonal flood pulse and extent of the lake's ATTZ.

Methods

Potential Drivers of Fisheries

This study's description of Lake Turkana's fisheries relies heavily on earlier work conducted on the system, particularly that of Hopson (1982) and Kolding (1989), and on fisheries catch and effort data collected by State Department of Fisheries under Kenya's Ministry of Agriculture, Livestock and Fisheries (MoALF) from 1963-2014. Collection of fisheries data by MoALF focuses primarily on the western side of the lake, where the majority of fishing occurs. Lake Turkana fisheries data used in this study included fisheries yield and value data from 1993-2014 and fishing effort data (number of fishermen, fishing vessels, nets and hooks) for 1993-2007. Data on species composition of yield (1960-2011; 17 years) were available for selected years only.

Data on the lake's absolute water levels and fluctuations were collected from the USDA Global Lakes and Reservoirs Database (TOPEX/Poseidon satellite 1992-2003, Jason-1 satellite 2002-2009, OSTM satellite 2008-2015; USDA 2015). Throughout this study, water levels will be given in meters above sea level (masl), while depths and decline magnitudes will be given in meters (m). Water level values published by the USDA are relative to the satellite's reference datum for the system, which was calculated to be 362.87 masl with an accuracy of ±10 cm. Water level for a given year (WL_Y) was measured as the average water level of all records for that year, which are taken by satellite approximately every 10 days, and is meant to represent the general status (i.e. high or low stand) of the lake's water level at a given time. The change in water level from one year to the next (WL_Δ) was calculated as $WL_Y - WL_{Y-1}$ and signifies whether the lake is in an increasing or decreasing phase. Intra-annual fluctuation was calculated as the standard deviation in both water levels (WL_{stdev}) and amplitude (WL_{amp}, i.e. WL_{max}-WL_{min}) for a given year and provides a measure of the strength of the flood pulse. The variables WL_{stdev} and WL_{amp} were highly correlated ($r^2=0.91$, $p<0.001$), so only WL_{amp} was used for linear model creation.

A suite of multivariate linear regression models was developed to relate yield from Lake Turkana's fisheries to both fishing effort variables (numbers of fishers, hooks, net and vessels) and hydrological variables (water level, inter-annual fluctuations, intra-annual fluctuations). Prior to model creation, the relationship between each hydrological variable and yield were tested for potential time lags with a cross-correlation function (maximum lag of 5 years). Time lags have played important roles in similar analyses (e.g. Kolding 1995, Jul-Larsen et al. 2003ab), as strong year classes resulting from optimal hydrological conditions do not immediately enter the fishery. Models pertaining to effort variables were restricted to the time frame of 1993-2007, which were the years for which effort data were available. Two sets of models were created for the water level variables, one to coincide with the effort variable model (1993-2007) and one that covered the full time frame of data availability for these variables (1993-2014). Models were created using all relevant variables and their two-way interaction terms, then simplified to the most parsimonious model based on the Akaike's information criterion (AIC; Akaike 1972, Aho et al. 2014).

To better illustrate the impact of hydrological variables on fisheries yield, several predictions were made using the most parsimonious 1993-2014 model (Table 3.1). Six prediction scenarios assumed the approximate water level of January, 2015 (365 masl), when the Gilgel Gibe III reservoir began filling, and six assumed a WL_Y approximately 2 m lower. Due to uncertainties in the influence of upstream development on WL_Δ, two scenarios were created that represented, respectively, the positive and negative of the average absolute value of WL_Δ for 1993-2014. The three alternate scenarios for WL_{amp} were 1) maintenance of the lake's natural seasonal fluctuations (0.12 m), 2) predicted seasonal fluctuations based on the planned artificial flood for Gibe III (0.7m; Avery 2012), and 3) complete loss of the flood pulse (0.0m), assuming no artificial flood release (Table 3.1).

Bathymetry Data

Bathymetry data used in this study were from geophysical surveys of Lake Turkana undertaken by Fugro Survey Africa LTD (4°22'N to 2°51'N) and by Syracuse University (2°51'N to 2°25'N) for Tullow Oil from June-October 2011 (Davidson and Smith 2011, Syracuse University 2011). The spheroid and datum used by both studies were World Geodetic System 1984, with a local projection of Universal Transverse Mercator Zone 36 North. The lake vertical datum was confirmed using a Precise Point Positioning (PPP) GPS system, Fugro's SkyFix-XP, then reduced to an elevation of 364 masl using the 2008 Earth Gravitational Model (EGM2008; Pavlis et al. 2008). This datum was later adjusted to 366.5 masl to coincide with the Government of Kenya's control points and historic topographic maps.

Fugro Survey Africa LTD conducted depth measurements using a dual frequency (33 and 210 kHz) single beam echo sounder (SBES) transducer interfaced with a Simrad EA400 topside recording unit and Starfix.Seis software (Davidson and Smith 2011). These SBES readings were verified by comparing against a depth to the seabed using a pole lowered into the water and a tape measure at a depth of approximately 2 m, resulting in an acceptable error of ±15 cm. These readings were also verified against the stand-alone echo sounder unit on the Fugro Survey Africa LTD vessel. East to west grid lines were initially conducted at 1 km (4°22'N to 4°00'N) but were increased to 2 km (4°00'N to 3°30'N) then 3 km (3°30'N to 2°51'N) due to time constraints. Grid lines in the north to south direction were conducted at intervals of 5 km. Data collection by Syracuse University was conducted using a Knudsen 320 B/P SBES transducer interfaced with Sounder Suite acquisition software along East to West grid lines of approximately 2 km (2°51'N to 2°25'N). Bathymetry data collected by Fugro Survey Africa LTD and Syracuse University were combined and interpolated by employing a parabolic kriging function with a cell size of 30 m and a search radius of 3200 m in Starfix.Seis software.

Habitat Modelling

Hopson (1982) used beach seining and trawling to characterize four fish communities in Lake Turkana based on depth zone: a littoral community (shoreline to 4 m deep), an inshore demersal community, an offshore demersal community, and an offshore pelagic community. In this study, habitat availability was assessed for two depth zones, littoral (>0 m to ≤4 m) and non-littoral (>4 m), as the demarcation between inshore and offshore communities depends on time of day and turbidity (Hopson 1982). Habitat in Lake Turkana also varies along a north-south gradient. The lake lies in two grabens and is often broken into four sectors, the North, Central, Turkwel and South Sectors (Table 3.2). Differences in bathymetry, exposure to the lake's strong southeasterly winds, and proximity to inflowing rivers influence the shoreline features, primary productivity, turbidity, and conductivity of the four sectors (Table 3.2).

To simulate lake level declines from 0-50 m (366.5 masl to 316.5 masl), a model was created in ArcGIS 10.3 and run for each sector of the lake by sequentially decreasing each pixel by a depth of 1m. For each lake level decline scenario, the surface area and volume of total, littoral, and non-littoral habitat were assessed by sector. Surface area for a given sector and/or depth zone was calculated by multiplying the number of pixels by the pixel area, 0.25 m^2, then summing. The surface area of each pixel was multiplied by the pixel's depth to calculate pixel volume. Pixel volumes were summed to calculate the total volume within a given sector and/or depth zone for each lake level decline scenario.

To further place habitat changes in the context of the lake's fishery, human population density in the year 2012 was examined within each of the lake's sectors. Due to the uniformly low population density along the lake's eastern shores (KNBS 2015), this analysis focused on the western shore population. Estimates of population density were made using LandScan (2012), which provides population count data for pixels of approximately 1 km^2 (30 arc-second resolution). Within each sector, the LandScan dataset was clipped to include only those pixels within 10 km (Euclidean distance) of the lake's shoreline. The minimum, maximum, mean ± s.d., and mode of the population density and the number of pixels with a population density of >20 persons/km^2 within each sector were then calculated.

Bathymetry data for Lake Turkana were also used to determine the influence of changing WL_{amp} on the availability of ATTZ habitat. The extent of the ATTZ was determined by finding the total area that was dry during WL_{min} (pixel depth of less than 0 m) but wet during WL_{max} (pixel depth of greater than 0 m) using the ArcGIS model described above. Changes to the ATTZ were calculated: 1) historically for the years with available water level data (1993-2014) and 2) for potential future WL_{amp} scenarios. For future scenarios, a mean lake level of 363.34 masl was used, based on an assumed 2 m decline from the average January 2015 water level (365.34 masl) post-reservoir filling. A baseline WL_{amp} of 1.12 m was determined based on the water level data compiled for 1993-2014. The percent of WL_{amp} due to declining water level (WL_{min}) was calculated and found to be 41.7% (average trough of -0.467 m, average pulse of +0.656 m). The WL_{amp} was sequentially decreased by 10% of the original WL_{amp} and then the WL_{min} determined, resulting in ten scenarios. The WL_{max} for each scenario was determined by adding the WL_{amp} to the WL_{min}. The area of the ATTZ was then calculated following the methods described above. These scenarios, based on one possible future WL_{Y}, were meant to illustrate the relationship between WL_{amp} and the extent of the ATTZ at a constant average water level. It is important to note, however, that the extent of the ATTZ will change based on future WL_Y in addition to future WL_{amp}.

Results

Fisheries Drivers

The reported yield of Lake Turkana's fisheries have fluctuated greatly since the early 1990's. Annual yields from 1993-2014 ranged from approximately 900 to 11,000 metric tons, averaging close to 5,000 metric tons (Figure 3.2). Ferguson's Gulf, a 10 km^2 lagoon, has primary production rates that are three orders of magnitude greater than the open lake and is the lake's most productive fisheries area for tilapia (Kolding 1993a). The gulf dries up at lake levels below 362.3 masl. Though low yield coincided with the drying of Ferguson's Gulf in some years (e.g. 1993-1995 and 2006-2007), other cases of low yield occurred when Ferguson's Gulf was inundated (e.g. 2000-2003, 2012-2014).

Species composition of catches changed considerably over the period of 1960 to 1980, from being dominated by the large potamodromous *Citharinus citharus* and *Distichodus niloticus* to mainly lacustrine *Oreochromis niloticus* and other tilapia species, *Lates niloticus* and *Labeo horie*, but has remained similar since the 1980's (Figure 3.3). Apart from the number of hooks used, all effort variables increased from 1993-2007, with a particularly rapid increase in effort after the year 2000 (Figure 3.2). Both the number of fisherman (r^2=0.92, $p<1\cdot10^{-7}$) and number of vessels (r^2=0.79, $p<0.00001$) increased linearly over this time period. The number of fisherman had a positive significant correlation with the number of vessels (r^2=0.85, $p<0.001$) and the number of nets (r^2=0.41, $p<0.01$), but not with the number of hooks. The average number of fisherman each year from 1993-2007 was 4,797, using on average 385 vessels, 6,187 nets and 13,300 hooks. Each fisherman caught an average of 1.09 tons of fish annually from 1993-2007.

The WL_Y generally increased from 1993-1999, decreased from 2000-2006, then increased again from 2006-2014, with minimum (362 masl) and maximum (365 masl) values in 1995 and 1999, respectively (Figure 3.2). Half of the years showed positive WL_Δs, with the greatest being approximately 2 m, and the other half showed negative WL_Δs, with a minimum of approximately -1 m. Lake level seasonality for 1993-2014 indicates that water level was at its lowest point in June and peaked in November (Figure 3.4). The average WL_{amp} for 1993-2014 was 1.12 m, within the 1 to 1.5 m seasonal variation noted elsewhere for this system (e.g. Avery 2012, Figure 3.2). The seasonal flood cycle has been greatly altered in 2015 by the commissioning of Gilgel Gibe III during the month of January, with no evident flood pulse yet to be seen (Figure 3.4).

The most parsimonious model for yield versus effort variables contained all four effort variables and 4 interaction terms (Table 3.3). This model, however, did not produce a significant fit (r^2=0.75, p=0.43), indicating that none of the effort variables recorded are robust predictors of yield in Lake Turkana. The cross correlation function determined the relationship between WL_Y and yield to be strongest at lags of 0 and 1 years. The relationship between yield and other water level variables was strongest with no lag. As WL_{Y-1} is a direct result of two other variables, WL_Y and WL_Δ, it was not included in the model. The most parsimonious model for yield and water level variables for the 1993-2007 time frame retained WL_Y, WL_Δ, WL_{amp} and one interaction term (r^2= 0.74, p=0.005; Table 3.3). This interaction terms made good ecological sense, as the influence of rising water level (WL_Δ) will differ depending on whether the lake is at a low or high stand (WL_Y). The extended water level variable and yield data (1993-2014) resulted in the same variable lags and a similar parsimonious model to that resulting from the 1993-2007 data. The most parsimonious model for this time frame included all water level variables and one interaction term, but with a weaker fit than the 1993-2007 model (r^2= 0.52, p= 0.01; Table 3.3). In both the 1993-2007 and 1993-2014 models, water level fluctuation variables (WL_{Δ}, WL_{amp}) were stronger drivers than was absolute water level (WL_Y).

Model predictions for most scenarios, except for those with a WL_{amp} of 0.0 m, fell within the range of yields reported for 1993-2014 (Table 3.1). These predictions suggest collapse or near collapse of the Lake Turkana fishery in the case of no seasonal flood pulse to the system. As suggested by the interaction term included in this model, the influence of WL_{Δ} on fisheries yield is dependent on WL_Y (Table 3.1).

Habitat Modeling

Using the bathymetry data described above, the total lake area at the zero datum of 366.5 masl is 6,837 km^2, with a volume of 236 km^3. The following description gives an overview of the results of lake level simulations produced by the GIS model. These changes are discussed in terms of lake level decline in reference to the zero datum of 366.5 masl. A decline of 25 m is used as a benchmark throughout these descriptions, as this approximates the maximum decline predicted by Avery (2012) given the current development agenda.

At a decline of 25 m in lake level, the model created here shows a decrease of 58% in lake surface area and 40% in lake volume (Figure 3.5). These declines would occur largely in the lake's non-littoral (≤4 m) habitats. Conversely, littoral surface area and volume would nearly double as lake level declines up to 21 m, but then begin to slowly decrease as lake level recedes further. The overall ratio of surface area to volume (SA:V) of the lake would increase as lake level declined, from 29 at a 0m decline to 43 at a 25 m decline (Figure 3.6). This increase would steepen at lake level declines >25m, reaching a SAV of 75 at a lake level decline of 50 m.

Predicted changes in surface area and volume vary greatly by sector based on differences in bathymetry (Figure 3.5). The most drastic changes would occur in the North Sector, in which surface area and volume would decline 85% and 97% respectively under a 25 m lake level decline scenario. The Turkwel Sector would also decrease considerably, by over 51% in area and 85% in volume at this level of decline. At lake level declines >42 m, the North Sector would disappear completely and the Turkwel Sector would be greatly reduced and consist largely (80% by surface area) of littoral habitat. Drastic declines in the extent of the Turkwel Sector would lead to the separation of the system into two smaller lakes, which would occupy what are now the Central and South Sectors, respectively.

Due to their greater depth and steeper bathymetry, declines in the Central and South Sectors would be less severe. The Central Sector would decrease by 32% in surface area and by 55% in volume and the South Sector by 13% in surface area and by 47% in volume at lake level declines of 25 m (Figure 3.5). As seen for the lake overall, the area of littoral habitat would increase within each sector at lake level declines up to 20 m, but begin to decrease beyond declines of 20 m in the North and Central Sectors and 30 m in the Turkwel Sector. The surface area to volume ratio would increase in all sectors with lake level decline, but most notably in the North Sector, where it would increase from 61 to 335 for the 25 m decline scenario.

The average human population density on the lake's eastern shores in 2012 was low, with 73% of pixels having a population of zero and an additional 17% of pixels having a population of only one (Table 3.4). On the lake's western shores, the average population density was lowest surrounding the South Sector and highest surrounding the Turkwel Sector (Table 3.4). The highest density pixels within 10 km of the lake's western shoreline were found in the Central Sector. The Turkwel Sector, however, had the highest proportion of pixels with a population density of >20 persons/km^2 (39%) among the four sectors (Table 3.4).

The extent of the ATTZ varied from 42.48 km^2 in 2000 to 157.50 km^2 in 1998, with a mean of 83.53 km^2. For the years 1993-2014, there was a strong significant positive correlation between WL_{amp} and the extent of the ATTZ ($r^2=0.86$, $p<1x10^{-9}$; Figure 3.7a). The future scenarios model shows a linear decrease in the extent of the ATTZ with a decrease in WL_{amp} ($r^2=0.998$, $p<1x10^{-9}$; Figure 3.7b). ATTZ for these future scenarios ranges from 83.72 km^2 at 100% WL_{amp} to 8.7 0km^2 at 10% WL_{amp}.

Discussion

Fisheries Trends and Drivers

Lake Turkana is located in a region undergoing rapid development in several sectors. This study highlights the trade-offs associated with three sectors existing in the context of transboundary management in the region: hydropower, large-scale irrigation agriculture, and fisheries. As seen for the 1970's and 1980's (Kolding 1992), significant links were found between Lake Turkana's hydrology and fisheries catch for the years 1993-2014 in this study. Water level fluctuations were the strongest drivers among the hydrological parameters studied (Table 3.3), as also seen in Lake Kariba (Karenge and Kolding 1995), and are currently undergoing change due to the upstream construction of dams. Although it is impossible to predict the exact hydrological scenarios that Lake Turkana will face in the coming years, the scenarios tested here suggest that a reduction or loss of seasonal water level fluctuations could lead to strong reduction or collapse of the fishery, even if water levels decline only 2 m (Table 3.1).

Research on other African lakes has shown that, in many cases, fisheries catch is more strongly related to hydrological variables than to fishing effort (Jul-Larsen et al. 2003ab, Kolding and van Zwieten 2012). Lake Turkana appears to follow this pattern. Fishing effort does not significantly predict yield (Figure 3.2) and there is little anecdotal support that catch is driven by fishing effort in this system. In spite of nearly linear increase in effort, Lake Turkana's fisheries yield showed nearly cyclical fluctuations between 1993-2014, with peaks of 9,000-10,000 metric tons occurring approximately every five years, in 1999, 2004, and 2009, respectively (Figure 3.2).

These findings are in agreement with historical declines in Lake Turkana's fish stocks (Figure 3.3), which have largely been linked to changes in hydrology rather than to fishing pressure. The lake's water levels declined rapidly from the end of the 1970's to the end of the 1980's, leading to changes in the structure of the lake's food web (Kolding 1993b) and contributing to the population declines of several fish species (Kolding 1995, Muška et al. 2012). Populations of two of the lake's initial commercially important potamodromous species, *C. citharinus* and *D. niloticus,* collapsed early, possibly due to a combination of overfishing and falling water levels (Kolding 1995; Figure 3.3). The open water fishes *H. forskalli*, *A. baremoze* and *Brycinus spp.* also showed heavy declines during this period (Kolding 1993b, Kolding 1995, Muška et al. 2012). These declines could not be linked to fishing, however, as there was no pelagic fishery in the lake during that time. Pelagic fishes, particularly small zooplanktivorous species and their predators, have been noted as highly climate sensitive in several other African lakes (Tweddle and Lewis 1990, Sarch and Allison 2001, Plisnier 1997, van Zwieten et al. 2013, Kolding et al. *in press*).

Hydrology influences the fisheries productivity of Lake Turkana through mechanisms related to fish population size (food availability, habitat availability, and breeding cues) and catchability (e.g. tilapia catchability highest during falling water level; Kolding 1993a). The time lags between lake level and catch in this study coincide with the age at maturity of the top fishery species in Lake Turkana, which range from 6-10 months (*O. niloticus*) to 3-4 years (*L. niloticus*), suggesting that higher lake levels lead to larger year classes among these species. The degree to which changing hydrological regimes would influence the abundance of commercially important species will depend on their biology and ecology. For example, *L. niloticus* has a large dietary niche and breeds year round within the open lake, while *L. horie* is a potamodromous species reliant on seasonal breeding cues and has a more restricted diet (Gownaris et al. 2015). The breeding success of potamodromous species in particular is likely to be strongly influenced by intra-annual water level fluctuations. Although an artificial flood release has been planned for Gibe III, it is unknown whether a flood of this duration and size will be sufficient to sustain the ecological functioning of the lake. The likelihood of this artificial flood being implemented is questionable, as planned compensation flows have yet to be released from Gilgel Gibe I and flooding would damage the plantations being constructed downstream (Avery 2012).

Habitat Availability and Distribution

Habitat availability, distribution, and quality are a key consideration in maintaining the fisheries productivity of Lake Turkana due to their influence on: 1) the size of fishable habitat, 2) the location of fishable habitat in relation to human populations, 3) fish breeding habitat and predatory refuge for juveniles, and 4) nutrient and food availability. The availability and distribution of habitat in Lake Turkana is dependent on lake level and will consequently be impacted by lake level decline (Figure 3.5). Declines in lake level would also increase the Lake Turkana's SA:V and therefore evaporative volume (Figure 3.6). Due to the extremely arid climate in which the lake is situated, evaporation rates are high (2.3-2.8 m /yr, Kolding 1992) and account for the majority of water lost from the system (Avery 2012). An increase in the SA:V of Lake Turkana would create a positive feedback loop in which water level declines due to upstream development result in increased evaporative loss and further declines in water level.

Littoral habitat extent is of particular interest in the case of Lake Turkana, as nearly all fishing takes place here. The most common types of fishing gear are gillnets and beach seine nets, both generally limited to shallow inshore habitats (Hopson 1982, Kolding 1989, Yongo et al. 2010). The habitat model created here shows that, at lake level declines up to 25 m, Lake Turkana's littoral habitat would increase (Figure 3.5). Without seasonal fluctuations, however, this increase in habitat coverage would come at the expense of habitat quality. An increase in static littoral habitat as water levels decline would be coupled with a decrease in dynamic littoral habitat, the ATTZ, due to a dampened flood pulse (Figure 3.7). Systems with a fluctuating ATTZ are more productive than stable ones (Welcomme and Halls 2001, Wantzen et al. 2008, Kolding and van Zwieten 2012), and species that breed and feed within the ATTZ have higher growth rates and lower mortality rates than those that feed in the main water body, known as the "flood-pulse advantage" (Bayley 1991). With removal of the flood pulse, littoral habitats would likely stagnate and exhibit conditions harmful to fish populations, including low oxygen levels, forcing them into deeper waters, increasing predation pressure and reducing catchability (Kolding 1993a).

Water level fluctuations also influence the composition, diversity, and abundance of shoreline vegetation (e,g, Wilcox and Meeker 1992, Keddy and Fraser 2000, Fischer and Ohl 2005, Van Geest et al. 2005ab, Leira and Cantonati 2008). Lake Turkana's natural average inter-annual (WL_{Δ}; 0.46±0.48) and intra-annual water level fluctuations (WL_{amp}; 1.12±0.40) fall within the range of those most conducive to supporting healthy shoreline vegetation communities (Hill et al. 1998). Thus, altering the magnitude of these fluctuations would likely reduce vegetated habitat. The lake's native vegetation is already threatened by the invasive woody plant *Prosopis julifloria,* which would gain a competitive advantage at reduced seasonal variability in water level (Mwangi and Swallow 2005). Therefore, while reducing water levels would lead to an increase in overall littoral habitat, the quality of this habitat for fish production would be considerably diminished by a reduction in the flood pulse.

Lake level decline would also lead to a widespread loss of the open water habitat in the lake. Although less critical than the case of littoral habitat loss due to its greater volume, decreases in the pelagic habitat would limit the carrying capacity of species that live or breed there. Some of the lake's top and most valuable fishery species, including *L. niloticus,* either breed or have life history stages that depend on the lake's deeper waters (Hopson 1982, KMFRI 2008). The greatest potential for increased yield from the system is the inclusion of open water fish stocks, which may become possible with increased fisheries investments in the region. As such, the highest estimates of MSY for the system are those that include the lake's small pelagic fishes, which require open water habitat and are sensitive to changes in nutrient inflow (i.e. *Brycinus* and *Alestes spp*.; Table 3.5). Fisheries focused on small fishes, many of which are for pelagic species (e.g. "Kapenta" fishery in Lakes Tanganyika, Kariba, and Kivu; the "Dagaa" fishery in Lake Victoria; the "Ragoogi" fishery in Lake Albert) are the most productive among African inland fisheries and make up a large proportion of the catch where they are present (Mubamba 1992, Sarch and Allison 2001, Legros and Luomba 2011, Kirema-Mukasa 2012, Kolding et al. *in press*). It is also important to note that the majority of the lake's endemic species are found below the 10-m contour, so declines in inshore and offshore habitats would have ecological consequences for these species (Hopson 1982).

In addition to habitat availability, two important factors controlling the productivity of fish species in Lake Turkana are the nutrient-rich, turbid waters entering the North Sector from the Omo River and the strong southeasterly winds blowing from the South Sector (Table 3.2). Due to the elongated nature of the lake, the influence of these factors differs by sector and it is therefore important to consider habitat changes in this context. The productive and relatively sheltered North Sector, where lagoonal habitats are common, would be the most affected by lake level decline and will essentially dry up at declines of ≥25 m (Figure 3.5). The Turkwel sector would begin to disappear at declines of ≥40 m, which would result in two smaller lakes, existing in the current Central and South Sectors. The lake's South Sector would be the least and last affected by strong a lake level decline, due to its depth. However, it is also the least productive habitat due to its distance from the Omo River's nutrient rich inflow and may experience drastic increase in salinity if it becomes disconnected from the rest of the lake. This sector's rocky coastline, exposure to high winds, and lack of lagoonal habitats will further limit its potential as a productive fishing area (Table 3.2).

The impact of habitat changes and their distribution on the fisheries of Lake Turkana is also dependent on where human populations have settled around the lake. While population densities along the lake's eastern shores are uniformly low, densities along the lake's western shores vary among the four sectors described above. The South Sector, which will be least influenced by water level declines, is also the least populated (Table 3.4, Figure 3.5). In contrast, population density is highest along the Turkwel Sector, which will be heavily impacted by water level declines due to its shallow nature (Table 3.4; Figure 3.5). Widespread movement of human populations surrounding the lake following hydrological changes is possible. Such movements are particularly likely if water level declines are extreme enough to lead to the loss of the North and Turkwel Sectors of the lake (Figure 3.5). The North Sector lies close to the conflict-stricken Illemi triangle (Oba 1992) and, at high water levels, crosses into Ethiopia. Conflict over fishing rights in the Omo delta has worsened over the past decade and is exacerbated by low lake levels (Kine and Achalei 2011, Johannes et al. 2015, Wright et al. 2015). Some locals warn that resource scarcity will turn Lake Turkana into an "endless battlefield" (Vidal 2015). This problem may be intensified if the discovery of oil and growth in other sectors in the region leads to an increase in human settlement.

The Future of Lake Turkana's Fisheries

The future of Lake Turkana's fisheries looks bleak given the current development agenda on the Omo River and the effect of that development on water level fluctuations. These concerns have been raised elsewhere (see Avery 2012, Muška et al. 2012), yet little has been done to study or mitigate the impending impacts on the system. Monitoring of the ecological status of Lake Turkana and management of its fishery must be strengthened during this time of change. For example, the average recorded catch of around 1 tons per fisherman annually from 1993-2007 (Figure 3.2) is very low when compared to other African lakes (average of catch of 3 tons/fisherman/year; Kolding and van Zwieten 2012) and suggests that the lake's reported catches may be an underestimate. The lake's fisheries are therefore likely to be undervalued, which downplays their importance when considering development trade-offs. Another example is the grouping of several ecologically distinct species by the fishery statistics (e.g. Gownaris et al. 2015), which may lead to misleading conclusions regarding the health of various fish stocks in the system.

This study supports previous studies in suggesting that of utmost importance to Lake Turkana's fisheries is maintaining the system's natural flood cycle via the release of an artificial flood of ecologically appropriate timing, volume, and duration from the Gilgel Gibe dams (Table 3.1, Table 3.3; Figure 3.7). To do so, artificial floods should lead to seasonal increases in water level of approximately 1-1.5 m during July-November (Figure 3.4). Maintaining natural levels of flood disturbance is a recommendation for any hydro-engineering project (IFC 2015), but the presence of irrigation infrastructure downstream of the Gilgel Gibe dams make the likelihood of adherence to natural flooding regimes along the Omo River questionable. Although lake level declines of some magnitude are highly likely due to irrigation needs upstream, these declines must be minimized to keep the lake alive. In particular, declines of >25 m will represent a tipping point in the system due to the shallow bathymetry of the North and Turkwel Sectors. Irrigation developments beyond those already planned, which on its own could lead to declines of this magnitude, will therefore irrevocably harm the lake and its fisheries.

Conclusions

The results of this study suggest in line with previous work that the productivity of Lake Turkana's fisheries is heavily linked to the volume and annual patterns of water inflow from the Omo River, Ethiopia. These linkages result from the influence of hydrology on fish habitat and food availability, breeding cues and catchability. Though water level decline will initially lead to an increase in the coverage of littoral habitat, this habitat will be degraded due to the loss of productive newly inundated areas (the ATTZ). Water level decline will also lead to a reduction in open water habitat and productivity. If water level declines are extreme, the system will eventually separate into two smaller lakes with drastically altered physiochemical characteristics. These changes will limit the capacity of the lake’s fisheries at a time of increased local and national dependence. If the impacts on the lake and its fishery are to be minimized, efforts must be made to manage upstream development so to maintain natural inflows to Lake Turkana, particularly during the lake’s flood season in July-November.

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Figures

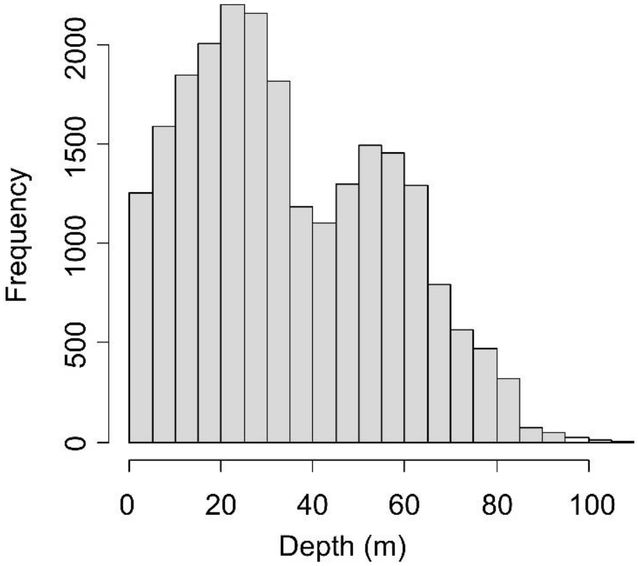


Figure 3.1: Lake Turkana depth distribution displayed as a histogram of pixel depth, measured in meters.

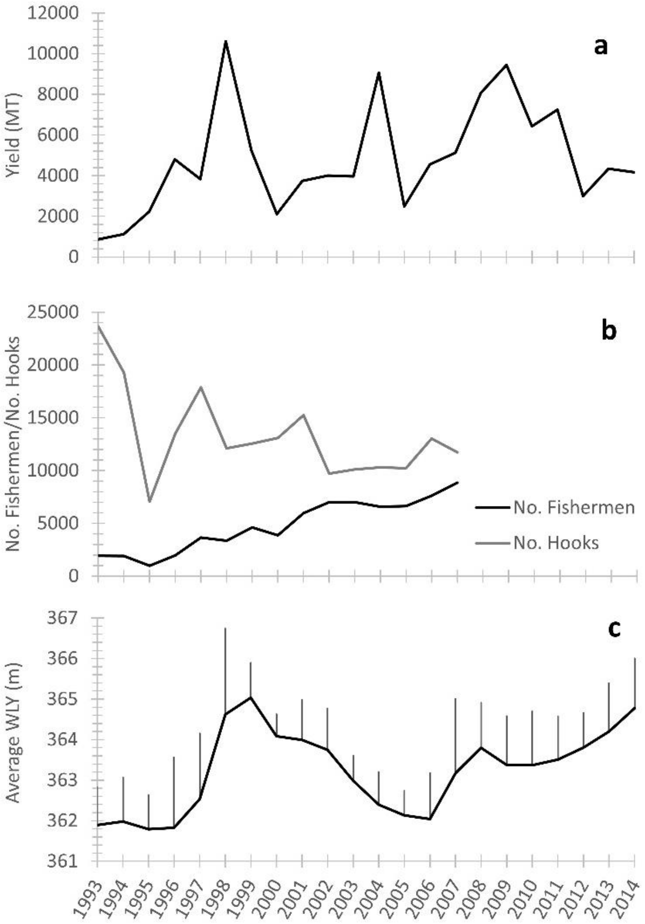


Figure 3.2: Trends in Lake Turkana's fisheries and hydrological variables.

d. Yield from the Lake Turkana fishery for 1993-2014. Data collected by the Kenyan Ministry of Fisheries and Agriculture.
e. Effort in terms of number of fishermen and number of hooks in the Lake Turkana Fishery for 1993-2007. Data collected by the Kenyan Ministry of Fisheries and Agriculture.
f. Average annual water level, WLY, in meters for the Lake Turkana Fisheries from 1993-2014. Vertical bars signify the seasonal amplitude for a given year. Satellite data collected from the United Stated Department of Agriculture Global Lakes and Reservoirs Database.

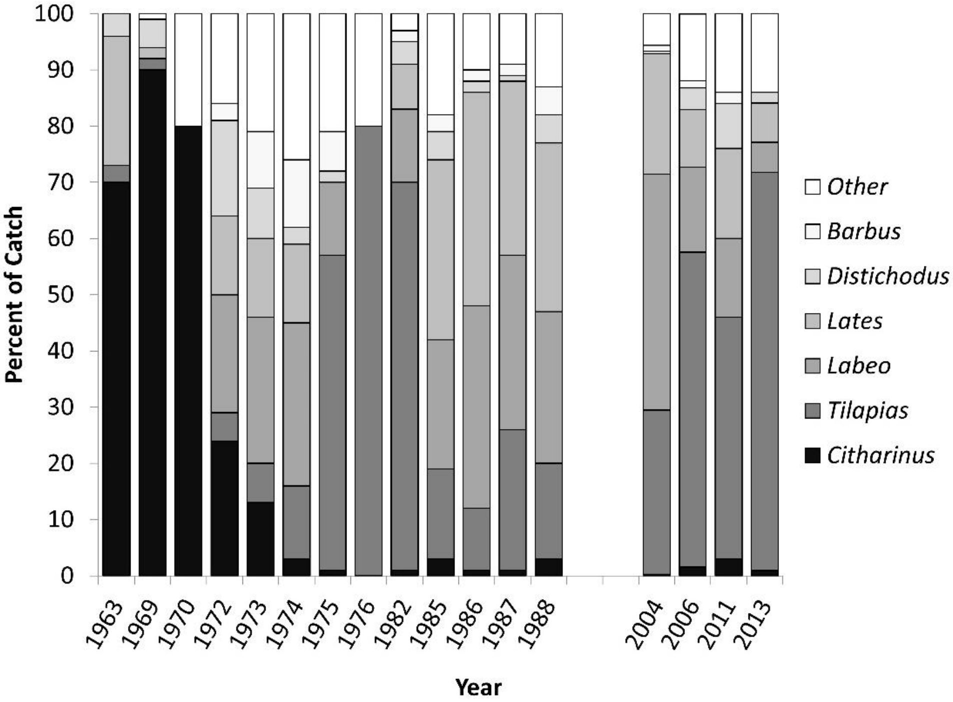


Figure 3.3: Species catch composition for the Lake Turkana fishery (available years). Data for 1963-1988 are taken from Kolding (1995), with some years excluded due to a high percentage of unspecified catches. Data for 2004 from MoLFD (2008). Data for 2006, 2011 and 2013 are taken from KNBS (2012, 2013, and 2014, respectively). Data on catch composition are not available for most years after 1989.

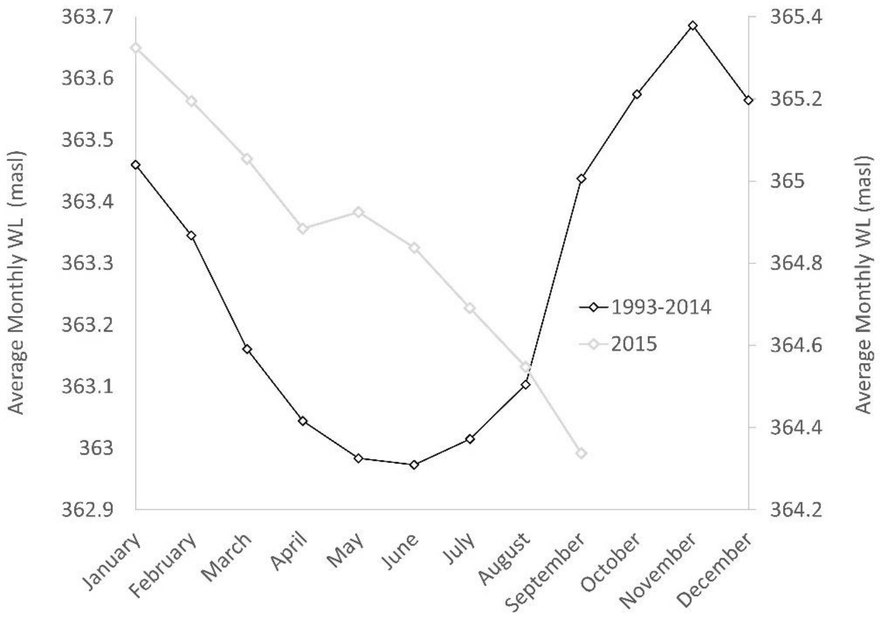


Figure 3.4: Lake Turkana mean monthly water levels in meters above sea level averaged by month across years for 1993-2014 and by month through September for 2015. Seasonal fluctuations play a key role in controlling the biology of the lake's fishes and will be considerably dampened by the construction of the Gibe dams along the Omo River. Satellite data are compiled from the United States Department of Agriculture Global Lakes and Reservoirs Database at a 10 day temporal resolution.

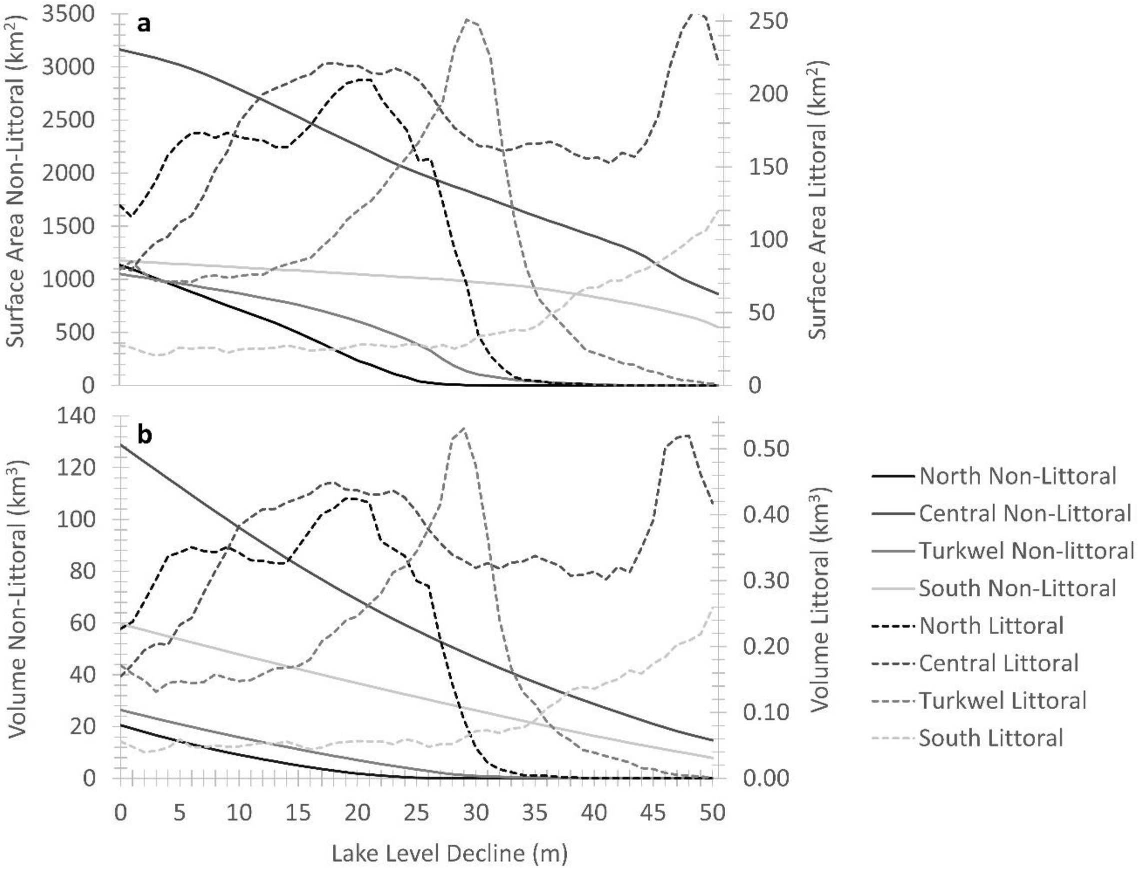


Figure 3.5: Surface area (3.5a) and volume (3.5b) along lake level declines of 0-50 meters (366.5-316.5 meters above sea level), shown by habitat type within each of Lake Turkana's four sectors. Littoral habitat is defined as habitat that is ≤4 meters in depth.

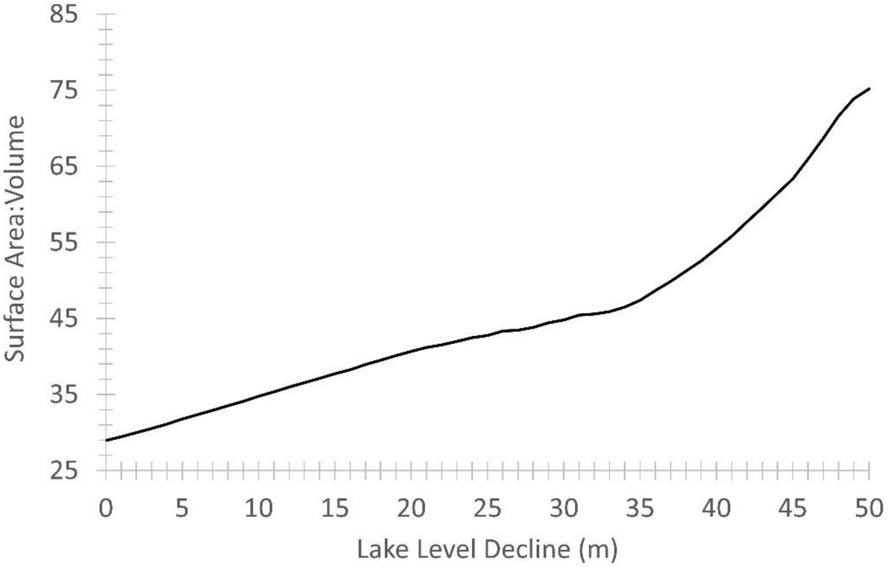


Figure 3.6: Change in the surface area to volume ratio of Lake Turkana along lake level declines of 0-50 meters (366.5-316.5 meters above sea level).

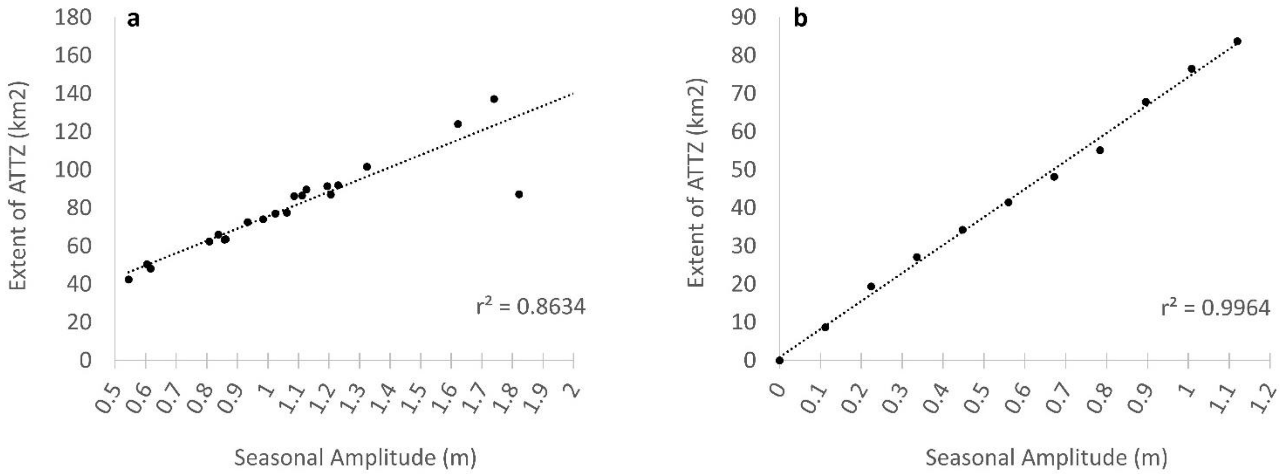
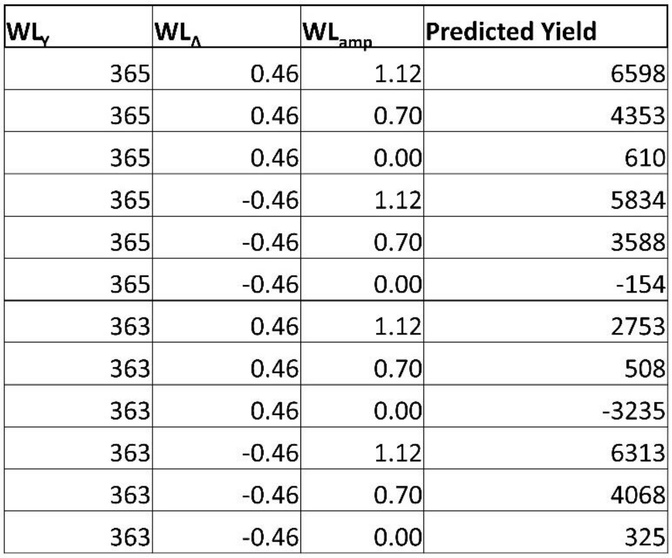


Figure 3.7: Relationships between seasonal amplitude and the extent of the aquatic terrestrial transition zone, defined as the area covered by water only during the seasonal flood pulse. Relationships were determined for the time period studied, 1993-2014 (3.7a), and for potential future scenarios (3.7b), determined by sequentially decreasing seasonal amplitude by 10% at a constant average water level of 363.34 meters above sea level. Satellite data used to calculate seasonal amplitude are compiled from the United States Department of Agriculture Global Lakes and Reservoirs Database at a 10 day temporal resolution.

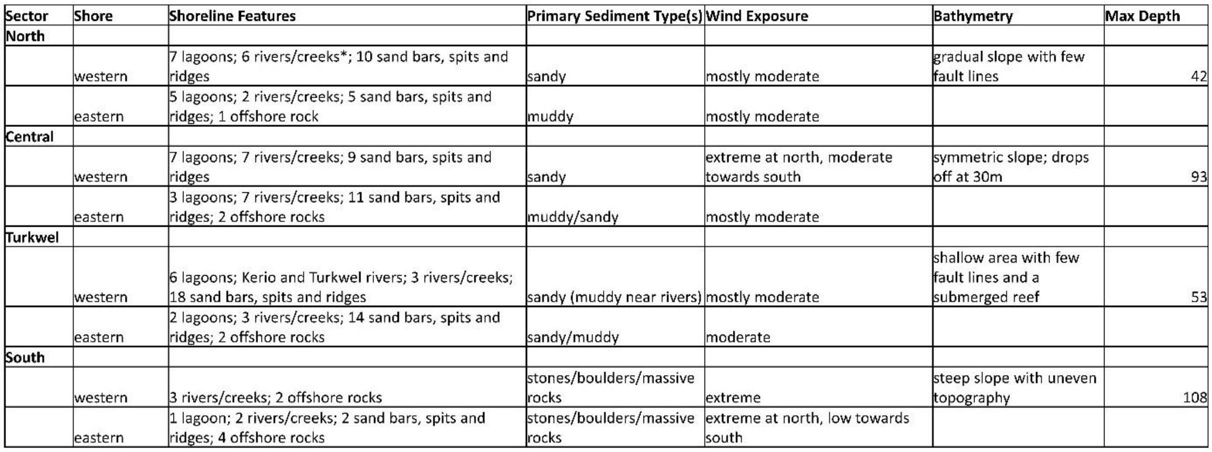
Tables

Table 3.1: Scenarios for Future Lake Turkana Hydrological Regimes and Predicted Fisheries Catch.



WL_{γ}	WL_{Λ}	WL_{amp}	Predicted Yield
365	0.46	1.12	6598
365	0.46	0.70	4353
365	0.46	0.00	610
365	-0.46	1.12	5834
365	-0.46	0.70	3588
365	-0.46	0.00	-154
363	0.46	1.12	2753
363	0.46	0.70	508
363	0.46	0.00	-3235
363	-0.46	1.12	6313
363	-0.46	0.70	4068
363	-0.46	0.00	325

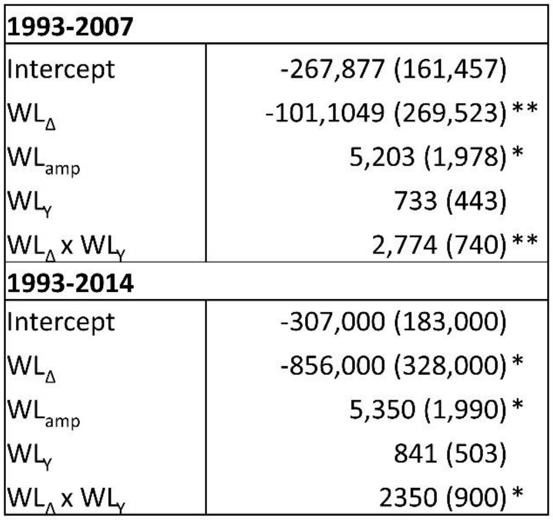
Table 3.2: Characteristics of the Four Sectors of Lake Turkana. Summarized from Hopson (1982).



Sector	Shore	Shoreline Features	Primary Sediment Type(s)	Wind Exposure	Bathymetry	Max Depth
North						
	western	7 lagoons; 6 rivers/creeks*; 10 sand bars, spits and ridges	sandy	mostly moderate	gradual slope with few fault lines	42
	eastern	5 lagoons; 2 rivers/creeks; 5 sand bars, spits and ridges; 1 offshore rock	muddy	mostly moderate		
Central						
	western	7 lagoons; 7 rivers/creeks; 9 sand bars, spits and ridges	sandy	extreme at north, moderate towards south	symmetric slope; drops off at 30m	93
	eastern	3 lagoons; 7 rivers/creeks; 11 sand bars, spits and ridges; 2 offshore rocks	muddy/sandy	mostly moderate		
Turkwel						
	western	6 lagoons; Kerio and Turkwel rivers; 3 rivers/creeks; 18 sand bars, spits and ridges	sandy (muddy near rivers)	mostly moderate	shallow area with few fault lines and a submerged reef	53
	eastern	2 lagoons; 3 rivers/creeks; 14 sand bars, spits and ridges; 2 offshore rocks	sandy/muddy	moderate		
South						
	western	3 rivers/creeks; 2 offshore rocks	stones/boulders/massive rocks	extreme	steep slope with uneven topography	108
	eastern	1 lagoon; 2 rivers/creeks; 2 sand bars, spits and ridges; 4 offshore rocks	stones/boulders/massive rocks	extreme at north, low towards south		

* p<0.05
** p<0.01

Table 3.3: Parameters Included in the Most Parsimonious Linear Models Relating Lake Turkana Water Level Variables to Fisheries Yield for 1993-2007 and for 1993-2014.



1993-2007	
Intercept	-267,877 (161,457)
WL_{Δ}	-101,1049 (269,523) **
WL_{amp}	5,203 (1,978) *
WL_{Y}	733 (443)
WL_{Δ} x WL_{Y}	2,774 (740) **
1993-2014	
Intercept	-307,000 (183,000)
WL_{Δ}	-856,000 (328,000) *
WL_{amp}	5,350 (1,990) *
WL_{Y}	841 (503)
WL_{Δ} x WL_{Y}	2350 (900) *

Table 3.4: Population Parameters of Lake Turkana's Four Sectors. All Parameters are expressed as Persons/km^2. Mode is Calculated Based from Pixels with a Population of >0.

	Max	**Mean**	**SD**	**Mode**	**Percent ≥20**
North Sector	160	11.76	13.88	12	13.63
Central Sector	1442	12.33	53.97	5	14.30
Turkwel Sector	74	14.92	15.15	21	38.80
South Sector	20	1.22	2.09	1	0.17
Eastern Shore	1793	1.84	38.14	2340	0.35

Table 3.5: Various Estimates of Maximum Sustainable Yield (MSY) for Lake Turkana

Reference	**MSY Estimate (tons/yr)**
Rhodes 1966	50,000-160,000
Coche and Balarin 1982	20,000-30,000
Hopson 1982	37,000
Hopson 1982b [1]	560,000
Kallqvist 1989	15,000-30,000
Kallqvist 1989b [2]	22,000
KMFRI 2008	88,404
Mbogo 2010	37,000

[1]- Includes capture of small pelagic fishes.

[2]- Based on the relationship between primary production and fish production described by Melack (1976).

Chapter 4: Lake Turkana Food Web Structure and Trophodynamics

Background and Objectives

The food web of Lake Turkana hasn't been comprehensively studied since the 1970's, when Hopson (1982) conducted in-depth gut content analyses for the lake's fishes. Using data from this and other studies (Bayley 1977, Hopson 1982, Kallqvist et al. 1988), Kolding (1993a) found that the open water food web of Lake Turkana changed drastically between 1973 and 1987. The principal change to the food web was a reduction in the populations of small pelagic fishes, linked in part to water level declines between the early 1970's and late 1980's, which subsequently altered the diet of piscivores. Given that the changes documented by Kolding (1993a) occurred in a little over a decade, it is unlikely that the data collected by Hopson (1982) over forty years ago still provides an accurate portrayal of the Lake Turkana food web.

The toolbox available to food web ecologists has also grown considerably since the 1970's. Stable isotope analysis in particular has become ubiquitous in the field (Layman et al. 2012, Middelburg 2014). Unlike gut content analysis, stable isotope analysis can be conducted on individuals with empty stomachs, provides a measure of which diet items are digested rather than ingested, and integrates diet over time periods ranging from days to years, depending on the metabolic activity of the tissue sampled (Peterson and Fry 1987, Dalerum and Angerbjörn 2005, Buchheister and Latour 2010). Among other things, stable isotopes can provide information on the overall food web structure and energy sources of a given ecosystem. At the species level, stable isotopes can be used to estimate trophic level, quantify dietary niche, and identify ontogenetic changes (Layman et al. 2012).

The two stable isotopes employed in this study are ^{13}C and ^{15}N. The ^{13}C and ^{15}N values of animal tissues are both dependent on diet, but ^{15}N shows strong trophic fractionation and ^{13}C does not (Peterson and Fry 1987). Trophic fractionation occurs because light isotopes of nitrogen are preferentially excreted by consumers, causing a sequential increase in $^{15}N/^{14}N$ ratios with trophic level. Stable nitrogen isotopes are therefore useful in understanding the trophic structure of an ecosystem (Vander Zanden et al. 1999, Vander Zanden and Rasmussen 1999, Post 2002). Stable carbon isotopes vary among primary producers, particularly those with different carbon fixation systems, but change little with trophic level ($\leq 1‰$; DeNiro and Epstein 1977). They can therefore be used to study the carbon sources fueling the food web. In general, littoral and benthic consumers have significantly more enriched $\delta^{13}C$ values than do pelagic consumers (France 1995).

The Lake Turkana food web is likely to have changed over the past forty years, and will be undergoing further change over the next decade. Several development projects are occurring in the Lake Turkana watershed, including along the Omo River, Ethiopia. The Omo River provides 90% of Lake Turkana's freshwater inflow. This river is the site of large-scale irrigations schemes and a series of five dams, both of which will alter the volume and annual patterns of freshwater entering Lake Turkana. Given Lake Turkana's high dependence on the Omo River, changes to the river's inflow will influence the lake's productivity, turbidity, salinity, habitat distribution and the breeding success of its fishes. These changes will ultimately alter the structure of the lake's food web. The purpose of this study was to employ stable isotope analysis to create an updated understanding of the Lake Turkana food web. In particular, this study relied on $\delta^{15}N$ and $\delta^{13}C$ signatures of species in the lake to answer the following questions:

1. What is the structure of the lake's food web and where do the lake's fishes fit within this food web? This portion of the study relies on traditional statistical approaches to stable isotope data, including the creation of bi-plots to examine food web structure and linear models to test for ontogenetic dietary changes among Lake Turkana's fishes. Additionally, clustering analysis is used to demarcate the system's trophic guilds. The motivation for this portion of the study is to develop "baseline" knowledge of the lake's food web prior to the impacts of upstream development.
2. To what extent does energy production in littoral habitats fuel production in non-littoral habitats? This portion of the study relies on the use of isotopic baseline data to trace energy flow throughout Lake Turkana. It is motivated by impending changes to the quantity and quality of the lake's littoral habitat. Previous observations suggest that many of the lake's pelagic piscivores move into shallow areas of the lake to feed (Kolding 1993b) and that littoral habitats often play a disproportionately large role in lake production (Wanzten et al. 2008).
3. What is the degree of functional redundancy in the Lake Turkana food web? This portion of the study relies on using stable isotope data to quantify species' trophic niches (Newsome et al. 2007, Jackson et al. 2011). The question is motivated by the hypothesized link between functional redundancy and increased ecosystem resilience (e.g. Walker 1992, Micheli et al. 2014). Resilience in this study is defined *sensu* Walker (1992) as "the capacity of an ecosystem to maintain its characteristic patterns and rates of processes".

Lake Turkana's Food Web

Lake Turkana has a relatively low phytoplankton diversity and low levels of primary production, which is limited in this system by turbidity and biologically available nitrogen (Hopson 1982, Kallqvist et al. 1988). *Microcystis aruginosa* (blue-green alga) is one of the lake's dominant phytoplankton species, but cannot be digested by many of its fauna. The high abundance of detrivorous zooplankton, ciliates feeding on bacteria, detritus feeding prawns and benthic feeding fish point to the importance of a detritus-based food web in the lake's open waters (Kolding 1993a).

There are approximately sixty recognized fish species in Lake Turkana, ten of which are endemic (Table 4.1). The assumed diets of the fishes examined in this chapter can be found in Table 4.2 (based on Hopson 1982). These dietary data suggest that the lake's fishes can be grouped into five trophic guilds: 1) Detritivores, 2) Macrophyte herbivores, 3) Filter feeders, 4) Mesocarnivores, and 5) Piscivores.

Two endemic species of *Brycinus* and the species *Alestes baremoze* were the lake's most important zooplanktivores in the 1970's. These species also formed the greatest biomass in the lake's open waters (Hopson 1982). Small pelagic fishes in Lake Turkana act as the lake's trophic link between zooplankton and piscivorous fishes (Kolding 1993a, Muška et al. 2012). For example, gut content analyses have shown that small pelagic fishes comprise 60% of the *Lates niloticus* diet and 99% of the *Hydrocynus forskallii* diet (Hopson 1982). The biomass of small pelagic fishes in the lake decrease fivefold between the 1970's and 1980's, leading to declines the biomass of *H. forskallii* (Kolding 1993a).

Tilapia make up a large portion of the biomass in shallow habitats, particularly those that are sheltered. Piscivores often move into littoral habitats to feed on tilapia and juveniles of other fish species (Kolding 1993b). *Oreochromis niloticus* acts as an especially important trophic link, as it is the only species in the system capable of digesting *Microcystis aeruginosa*. In addition to *Brycinus* and *Alestes spp.*, a large proportion of the *L. niloticus* diet (~20%) is comprised of *O. niloticus* (Hopson 1982).

Brief Description of Stable Isotope Studies on Other African Lakes

Lake Victoria is Africa's largest lake and undergone extreme ecological change over the last several decades due to overfishing, invasive species introductions, and eutrophication (Kolding et al. 2008). Several scientists have employed stable isotope analysis to understand the lake's food web and its response to these changes. Lake Victoria has a relatively short food web with highly variable baseline signatures that differ based on site (Campbell et al. 2003, Ojwang et al. 2004). The δ^{13}C values of the lakes fishes range from -14‰ to -20‰ at inshore sites and -17‰ to -27.8‰ at littoral gulf sites, with δ^{15}N ranges of 4‰ to 10‰ and 5.9‰ to 11.8‰ respectively. *Oreochromis niloticus* feeds on low trophic levels in the system, while *L. niloticus* occupies the highest trophic level and acts as an opportunistic feeder (Campbell et al. 2003, Ojwang et al. 2010). Both species feed at high trophic levels at larger sizes (Campbell et al. 2003). Zooplanktivorous fishes have a surprisingly high δ^{15}N in this system, suggesting complex feeding interactions within the lake's zooplankton community (Campbell et al. 2003). The presence of omnivory and functional redundancy within Lake Victoria's food web are thought to act as stabilizing agents against perturbation (Ojwang et al. 2010).

Located north of Lake Victoria is Lake Kyoga, a shallow lake complex in Uganda. Baseline signatures and food web structure vary greatly among sites in the lake complex. For example, the range of average δ^{13}C values for the fishes at the Bukungu site is -14.11‰ to -18.84‰, while the range of values for the same fishes at the Iyingo site is -15.43‰ to -23.21‰ (Schwartz et al. 2006, Mbabazi et al. 2010). At most sites, however, *O. niloticus* has the lowest average δ^{15}N and *L. niloticus* the highest average δ^{15}N of the fish community (Schwartz et al. 2006, Mbabazi et al. 2010). As in Lake Victoria, *L. niloticus* feeds at higher trophic levels as it grows in size in Lake Kyoga. This voracious predator also impacts the diversity and food web length of systems within the Lake Kyoga complex (Schwartz et al. 2006).

Located west of Lake Kyoga is Lake Albert, which is Africa's 7th largest lake and has a mean depth of 25m. The δ^{13}C values of most fishes in this system are restricted to -18‰ to -22‰ (tilapias shown signatures of -14‰ to -16‰), indicating a common carbon source. Similarly, most fish δ^{15}N values in the system are restricted to the range of 8‰ to 12‰ (tilapias show signatures of 3‰ to 6‰). The four tilapiine species in the ecosystem (*Tilapia zillii, Oreochromis leucostictus, Sarotherodon galilaeus* and *O. niloticus*) form the base of the consumer food web and have overlapping, generalist diets (Campbell et al. 2005). Unlike Lake Kyoga and Lake Victoria, *H. forskallii* is the top predator in Lake Albert. The two species of *Lates* in the lake, *Lates macrophthalmus* (endemic) and *L. niloticus*, have different habitat ranges but similar δ^{15}N and δ^{13}C values. Both *Lates spp.* fed on higher trophic levels at larger sizes. As seen for zooplanktivores in Lake Victoria, *Brycinus nurse* had higher δ^{15}N values than many of the lake's piscivores, likely due to feeding on a carnivorous zooplankton (e.g. *Mesocyclops spp.*). The fact that the δ^{15}N values of *B. nurse* were higher than those of some piscivores (excluding *H. forskallii*) suggests that pelagic food chains do not play an important role in the diet of large piscivorous fishes in Lake Albert (Campbell et al. 2005).

Methods

Sample Collection and Processing

All field sample collection was conducted with minimal discomfort to the animals of study. The methodology used was reviewed and approved by Stony Brook's Institutional Animal Care and Use Committee (Project 262729). Permits were obtained (NCST/RRI/12/1/BS011/99) to conduct field work in Kenya through the National Council for Science and Technology (now known as the National Commission of Science, Technology and Innovation-NACOSTI). Several local organizations, including the Kenya Marine and Fisheries Research Institute, collaborated on this study and helped to minimize any potential negative impacts of field sampling.

Stable isotope sample collection occurred between 2008 and 2013, with sample sites varying by year. Sampling sites were chosen to represent different habitat types in Lake Turkana, including latitudinal differences in habitat (e.g. Nachukui to Central Island), heavily fished (e.g. Ferguson's Gulf) versus unfished (e.g. Sibiloi) habitats, littoral (<5m; Napasinyang, Ferguson's Gulf, Sibiloi, and Nachukui) and pelagic habitats (Central Island and Northern Island), phytoplankton (e.g. Ferguson's Gulf) and macrophyte (e.g. Sibiloi) dominated habitats, and a spectrum of low conductivity (e.g. North Island) to high conductivity (e.g. Ferguson's Gulf) habitats (Figure 4.1). Fishes at each sampling site were collected using gill nets. At each site, up to 10 individuals of each fish species, representing the full size range collected, were sampled. A small piece of epaxial muscle tissue was removed from each individual and placed in the sun until fully dry (average air temperature of 31-33^{0}C, arid conditions), then stored in a cryovial until processing.

Samples were homogenized using a mortar and pestle cleaned with 70% ethanol. They were then then weighed to the nearest thousandth of a milligram and analyzed for C:N, δ^{15}N, and δ^{13}C using a GV Instruments IsoPrime isotope ratio mass spectrometer. All isotope values were calibrated to the international standards Vienna Pee Dee belemnite for carbon and atmospheric air for nitrogen. To determine intra-sample variability, one duplicate sample was run per every 10 unique samples. A total of 150 pairs of duplicates were analyzed and showed good agreement for δ^{13}C (average absolute difference of 0.07±0.11‰) and δ^{15}N (average absolute difference of 0.27±0.31‰). Additionally, an internal laboratory standard sample was run alternating between glycine and peptone for every 10 unique samples to test for machine accuracy. Both standards have been carefully calibrated using traditional methods (Dumas combustion, dual inlet IRMS) and have been calibrated to IAEA standards N1 and N2 for nitrogen, and NBS 20, 21 and 22 for carbon. The average observed values of glycine were -33.96±0.07‰ for δ^{13}C and 10.76±0.11‰ for δ^{15}N (n=86) and agreed well with the expected values for this standard of -34.00‰ for δ^{13}C and 10.73‰ for δ^{15}N (average absolute difference of 0.06±0.04‰ for δ^{13}C and of 0.04±0.07‰ for δ^{15}N). The average observed values of peptone were -14.76±0.07‰ for δ^{13}C and 7.30±0.13‰ for δ^{15}N (n=72) and agreed well with the expected values for this standard of -14.73‰ for δ^{13}C and 7.40‰ for δ^{15}N (average absolute difference of 0.06± 0.04‰ for δ^{13}C and of 0.11±0.07‰ for δ^{15}N).

Lipid Extraction

Lipid extraction is sometimes necessary prior to stable isotope analysis due to the depleted and variable nature of lipid δ^{13}C signatures (McConnaughey and McRoy 1979, DeNiro and Epstein 1977, Post 2002, Sotiropoulos et al. 2004). However, this process is widely debated in the stable isotope literature, particularly as it may also impact the δ^{15}N value of a sample. In general, aquatic stable isotope samples with C:N<3.5 have low lipid concentrations (<5%) and are not altered much by lipid extraction (Logan et al. 2008). Our samples had an average C:N of 3.11±0.22, with only 3% of samples exceeding a C:N of 3.5.

To ensure that untreated δ^{13}C values provided reliable estimates for the fishes studied, a preliminary lipid extraction study was conducted. A random subset of 38 samples were chosen and analyzed pre- and post-lipid extraction, using a variation of the methods described in Folch et al. (1957) and Hussey et al. (2011). For comparison purposes, a sub-sample of each individual pre-lipid extraction (bulk sub-sample) also analyzed. The results of this preliminary test were interpreted by determining whether $\Delta\delta^{13}$C for the 38 samples correlated with their C:N ratio. The $\Delta\delta^{13}$C was defined as $\Delta\delta^{13}C = \left(\frac{\left(\delta^{13}C_B - \delta^{13}C_{LE}\right)}{\delta^{13}C_B}\right) * 100$, or the percent change in the sample's isotope signature, where $\delta^{13}C_B$ represents the isotope signature of the bulk sub-sample and $\delta^{13}C_{LE}$ represents the isotope signature of the lipid extracted sub-sample. If $\Delta\delta^{13}$C resulted from the loss of lipids alone, a positive correlation would be expected because lipids do not contain nitrogen, so C:N is correlated with the lipid content of a tissue. The $\Delta\delta^{15}$N, defined in the same manner as $\Delta\delta^{13}$C, was also calculated to determine if this isotope's signature was impacted by the lipid extraction procedure.

Neither $\Delta\delta^{13}$C (r^2= 0.02, p=0.44) nor $\Delta\delta^{15}$N (r^2=0.02, p=0.44) showed a significant positive correlation with C:N. Changes in the two isotopes were, however, positively correlated with each other (r^2=0.62, p<0.0001). Furthermore, for most samples the absolute value of $\Delta\delta^{15}$N (average of 13.89±17.17%) was greater than the absolute value of $\Delta\delta^{13}$C (5.10±5.12%) and both isotopes showed large standard deviations. Due to a low C:N among the samples, the lack of a consistent relationship between $\Delta\delta^{13}$C and C:N, and the impact of lipid extraction on $\Delta\delta^{15}$N , uncorrected δ^{13}C signatures were used for the remainder of the study.

Data Analysis

Tracing energy flow within an ecosystem using stable isotope analysis requires that habitats can be differentiated based on isotope signature. In particular, this study is interested in tracing the flow of energy from littoral to non-littoral habitats in Lake Turkana. Time-averaged δ^{13}C and δ^{15}N data collected for the lake's phytoplankton were used to calculate the lake's isotopic baseline. Plankton samples were collected in four size fractions (<20µm, 20-90µm, 90-250µm, >250µm) at all sites in 2011-2012 using nylon filters. Plankton material was rinsed onto pre-combusted GFF filters using deionized water and dried the filters in the sun. A combination of ANOVA and Tukey's Post-Hoc tests were used to compare baseline isotope signatures across size classes and sites. These tests, in addition to all subsequent statistical tests discussed, were conducted in R version 2.15.1 (R Core Development Team 2013). The plankton species composition of preserved (2% Bouin's solution) water samples was examined using a FlowCAM.

To supplement phytoplankton baseline data, samples of aquatic vegetation were collected where possible. Of the sites sampled, hippograss (*E. stagnina*) dominates in Ferguson's Gulf but can also be found in Sibiloi, the perennial herb *Typha domingensis* is found only at Napasinyang, and the macrophyte *Potamogeton* spp. is found only at Sibiloi. The collection of benthic invertebrates using benthic cores was largely unsuccessful in all years. A large number of aquatic insect samples were collected in 2012 and 2013 using D-nets with 500µm mesh screens.

Ontogenetic dietary changes were examined for each fish species using linear models. The δ^{15}N signatures of each species were also compared to their expected trophic levels as listed on FishBase (Table 4.2). Food web structure among the lake's fishes was examined in three ways: 1) using the means of species' δ^{13}C and δ^{15}N signatures and bi-plots of these means, 2) creating scatterplots of all individual δ^{13}C and δ^{15}N signatures, and 3) testing whether the lake's fishes fit within expected trophic guilds.

Trophic guild predictions were tested using a *k*-means clustering analysis. In this analysis, *k* clusters are created so that each observation belongs to a cluster that minimizes its distance to that cluster's centroid. A *k* value of five was chosen to represent the five expected trophic guilds: 1) Detritivores, 2) Macrophyte herbivores, 3) Filter feeders, 4) Mesocarnivores, and 5) Piscivores. These analyses were exploratory in nature, as variation in isotope signatures and sample size varied greatly among the species studied and were likely to have influenced cluster distribution. The most frequent cluster within which individuals of a species fell (cluster mode) was used as that species final cluster number. The species composition of each cluster was then compared to the predictions of trophic guild composition.

Functional redundancy within the Lake Turkana food web was examined using the standard ellipse function in the Stable Isotope Analysis in R (SIAR) package, known as Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al. 2011, R Core Development Team 2013). The standard ellipse area, SEAc, for a given species is based on its δ^{15}N /δ^{13}C covariance matrix and includes approximately 40% of its data cloud (Jackson et al. 2011). Specifically, the SIAR package was used calculate the percent overlap between each species' ellipse and those of other fishes.

Results and Interpretation

Phytoplankton baseline signatures for δ^{13}C (F=6.88, p=0.01) and δ^{15}N (F=12.81, p<0.0001) in the <20µm size class differed significantly from all other plankton size classes (Tukey's post-hoc test, Figure 4.2). All size classes were dominated by *M. aeruginosa* varying from single cells to large colonies, which would explain the similar isotopic signatures observed for all sizes classes >20µm. The presence of non-photosynthetic bacteria may explain the significantly different signature for the <20µm size class. Baseline signatures for δ^{13}C differed among sites (F=4.28, p<0.01), but δ^{15}N signatures did not (F=0.70, p=0.60). Tukey's post-hoc test showed that the significant difference in δ^{13}C was driven by the difference in signature between grassy areas of Ferguson's Gulf and the open lake. Hippograss baseline signatures differed significantly between Sibiloi and Ferguson's Gulf in δ^{13}C (F=8.5, p<0.01) but not in δ^{15}N (F=2.3, p=0.15).

The aquatic insects sampled represent two main feeding groups: herbivore/detritivores (*Caridina spp., Micronecta spp*., and larvae of the orders Diptera and Ephemeroptera), and predators (larvae of the order Odonata and of the families Hemiptera, Nepidae and Notonectidae). Stable isotope value ranges are wide but comparable for herbivore/detritivore insects and for predatory insects (Figure 4.3). Herbivore/detritivore insects from Lake Turkana show δ^{15}N values of 0.77‰ to 6.59‰ and δ^{13}C values of -22.93‰ to -15.78‰. Similarly, Lake Turkana's predatory insects show δ^{15}N values of 0.6‰ to 6.13‰ and δ^{13}C values of -20.34‰ to -15.6‰.

The stable isotope analyses conducted for Lake Turkana suggest that this system has an overall food web structure similar to that of Lake Albert (Figure 4.3, Figure 4.4). The ranges of

$\delta^{13}C$ values and $\delta^{15}N$ values seen for Lake Turkana approximate those of Lake Albert, and in most cases have the same end members (Campbell et al. 2003), but differ from those of Lakes Victoria and Kyoga (Campbell et al. 2005, Schwartz et al. 2006, Mbabazi et al. 2010). Over half of the species studied show significant ontogenetic trends in their $\delta^{13}C$ or $\delta^{15}N$ signatures (Table 4.2). The most common ontogenetic trend is for species to feed at lower trophic levels and in more littoral or benthic habitats as they grow (Table 4.2).

The $\delta^{13}C$ of the majority of Lake Turkana's fishes fell within the range of -16‰ to -22‰ (Figure 4.4). *Tilapia zillii,* a species known to feed on macrophytes, has the most enriched average $\delta^{13}C$ value, with the benthic algivore *Citharis citharinus* showing the most depleted average $\delta^{13}C$ value (Figure 4.3). Generally, benthic consumers are assumed to have more enriched carbon signatures than pelagic consumers (France 1995). The depleted carbon signature for *C. citharinus* is therefore unexpected.

The $\delta^{15}N$ range among the lake's fishes is large, with individuals exhibiting values from 2‰ to 16‰ (Figure 4.5). Species trophic levels could not be calculated using $\delta^{15}N$ given the lack of an accurate isotopic baseline for the sites sampled. There is, however, a significant correlation between each species' average $\delta^{15}N$ value and their trophic level as recorded on FishBase ($r^2=0.54$, $p<0.001$). Therefore, $\delta^{15}N$ will be discussed as a proxy for trophic level.

Several cichlid species have the lowest $\delta^{15}N$ values in the system (*O. niloticus, T. zillii, S. galilaeus, Haplochromis spp.*). These species also have among the most enriched $\delta^{13}C$ values, corresponding to their littoral feeding habits (Figure 4.4). *Oreochromis niloticus* shows the strongest ontogenetic changes of the three tilapia species, feeding in more pelagic habitats and on higher trophic levels as it grows (Table 4.2). Some of the largest *O. niloticus* individuals sampled had $\delta^{15}N$ signatures of >10‰ and are likely to be feeding on aquatic insects.

One unique trait of Lake Turkana is that two catfish species (*Schilbe uranoscopus* and *Bagrus bayad),* rather than *L. niloticus* or *H. forskallii*, have the highest average $\delta^{15}N$ values in the system (Figure 4.4). These high $\delta^{15}N$ signatures are consistent with their assumed diet of fish and prawns (Hopson 1982). Both species feed increasingly in enriched $\delta^{13}C$ habitats (e.g. littoral or benthic habitats) as they grow. *Lates niloticus*, another piscivore in the system, has considerably lower (~2‰) $\delta^{15}N$ values than *S. uranoscopus* and *B. bayad* (Figure 4.4). This species' ontogenetic changes suggest it has a varied diet of pelagic and littoral fishes at small sizes. At larger sizes, *L. niloticus* has isotope signatures consistent with a diet of low-trophic, littoral fishes (Table 4.2).

Hydrocynus forskallii is still one of Lake Turkana's top predators, with the third highest $\delta^{15}N$ signature in the system (Figure 4.4). This species' $\delta^{13}C$ signature suggest that it feeds on a relatively depleted carbon source, which is likely to consist largely of *Brycinus spp*. The difference between the average $\delta^{15}N$ of *Brycinus nurse* and of *H. forskallii* in Lake Turkana approximates the often used average fractionation factor of 3.4‰ (Post 2002). *Hydrocynus forskallii* seems to rely on small pelagic fishes throughout its life, as it shows no clear ontogenetic shifts (Table 4.2).

As in Lakes Albert and Victoria (Campbell et al. 2003, Campbell et al. 2005), Lake Turkana's small pelagic fishes have higher $\delta^{15}N$ values than predicted based on the assumption of a zooplanktivorous diet (Hopson 1982). The lake's open water zooplankton community is dominated by detritivores (Kolding 1993a). The high $\delta^{15}N$ values of the lake's small pelagic fishes may therefore be propagating up from the detritus, and ultimately from *S. schall*. *Synodontis schall's* interlocking pectoral spines are an excellent defense against predators, leaving this species with a low predation mortality (Kolding 1993a). As a result, a large portion of the *S. schall* biomass in the system may eventually wind up in the detritus, raising its $\delta^{15}N$ value.

The clustering analysis did not show a direct relationship with the trophic guilds predicted based on Hopson (1982), but there was some correspondence with these guilds (Figure 4.5). Of the originally proposed trophic guilds, a combination of filter feeding and mesocarnivory seems to be the most common feeding strategy (Table 4.2). Fishes using one or both of these feeding strategies are found in all five trophic clusters.

Both proposed macrophye herbivores in the system (*T. zillii, Alestes dentex*) fall within one cluster (Cluster 5). Of the five trophic clusters, Cluster 5 has the lowest $\delta^{15}N$ values and most enriched $\delta^{13}C$ values (Table 4.2, Figure 4.5). Similarly, all of the lake's proposed piscivores (*L. niloticus, H. forskallii, Bagrus bayad, Schile uranoscopus,* and *Chrysicthys auratus*) are grouped within one cluster (Cluster 2). Cluster 2 has the highest average $\delta^{15}N$ value of the five clusters and also includes fishes that consumed benthic invertebrates (Table 4.2, Figure 4.5). The lake's proposed detritivores and benthic algivores (*Labeo horie, S. galilaeus, C. citharinus*) are found within the cluster with the most depleted $\delta^{13}C$ signatures (Cluster 1; Table 4.2, Figure 4.5). One of the five trophic clusters is represented by just one species. The *O. niloticus* cluster (Cluster 4) showed $\delta^{15}N$ and $\delta^{13}C$ signatures consistent with a littoral, low trophic level diet. The lake's second smallest cluster by species number (Cluster 3) consists of two species, *A. baremoze* and *Chelaethiops bibie*, which share insects as a major diet item (Table 4.2, Figure 4.5).

Approximately 64% of species pair show no overlap in their isotope ellipses (Table 4.3). Where overlap does exist, it is often low (31.04±28.10%). A few species pairs, however, have extremely high overlap (Table 4.3). The ellipse of *Leptocypris niloticus*, for example, is 100% within those of *Distichodus niloticus* and *L. horie*. High overlap is also present for *S. uranoscopus* and *H. forskallii*, for *A. baremoze* and *D. niloticus*, and for *B. bynni* and *L. niloticus*. Among the fishes studied, *Synodontis schall* has the highest occurrence of moderate to high (>50%) overlap with other species (Table 4.3).

Overlap was low to moderate among the lake's littoral cichlids and among its pelagic zooplanktivores (Table 4.3). Based on data collected by Hopson (1982), Lévêque (1997) suggests that the zooplanktivores of Lake Turkana partition resource by exhibiting: 1) species' specific preferences for prey size, 2) vertical and horizontal zonation of feeding, mediated by diel migrations, and 3) differences in ontogenetic patterns. As discussed above, littoral cichlids and pelagic zooplanktivores both act as important trophic links in the lake. These results suggest that functional redundancy is low in the system, including among species that act as important conduits of energy from low to high trophic levels.

The most striking difference between the food web structure of Lake Turkana and that of the other African lakes discussed above is the negative relationship between the $\delta^{13}C$ values and $\delta^{15}N$ values of all individuals sampled (Figure 4.5; $r^2=0.39$, $p<0.0001$). Most ecosystems for which isotope studies have been conducted exhibit a positive relationship between $\delta^{13}C$ values and $\delta^{15}N$ values (Post 2002), given that both isotopes fractionate with trophic level (though $\delta^{13}C$ to a much lesser extent). This expected positive relationship was seen for Lake Albert, Lake Victoria and some sites in the Lake Kyoga complex (Campbell et al. 2003, Campbell et al. 2005, Schwartz et al. 2006, Mbabazi et al. 2010). There are two potential explanations for the unexpected relationship seen for Lake Turkana. First is the unexpectedly high $\delta^{15}N$ values of the lake's small pelagic fishes. However, $\delta^{15}N$ values were also unexpectedly high in Lakes Albert and Victoria and these systems showed the expected position relationship between $\delta^{13}C$ and $\delta^{15}N$. Another possible explanation is that production in the lake's littoral habitats plays an important role throughout the Lake Turkana food web, “pulling” the food web towards more enriched $\delta^{13}C$ values.

Conclusions

Lake Turkana’s food web hasn’t been well studied since the 1980’s and wasn’t examined using stable isotope analysis prior to this study. The system is set to undergo large-scale changes over the coming decade, as upstream dams lead to a diminished flood pulse and irrigation schemes to lowered lake level. The findings of this study suggest several generalizations that can be made about the Lake Turkana food web regarding its resilience to change. First, functional redundancy is moderate to low and there is no clear demarcation of trophic guilds in the system. With the exception of a few instances of high overlap, the system lacks a functional “insurance policy” in the face of species loss. Second, many of the lake’s species switch between feeding in pelagic habitats and in littoral habitats depending on their size. As a result, these species will be impacted by potential changes to both habitat types over their life cycle. Lastly, trends between $\delta^{13}C$ values and $\delta^{15}N$ values in the system suggest the importance of a depleted source of ^{13}C to the overall food web. Although baseline signatures could not be differentiated based on the phytoplankton samples collected, this depleted signature is likely to represent energy production in littoral habitats. Altering littoral habitat is therefore likely to have implications for the lake’s food web as a whole.

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Figures

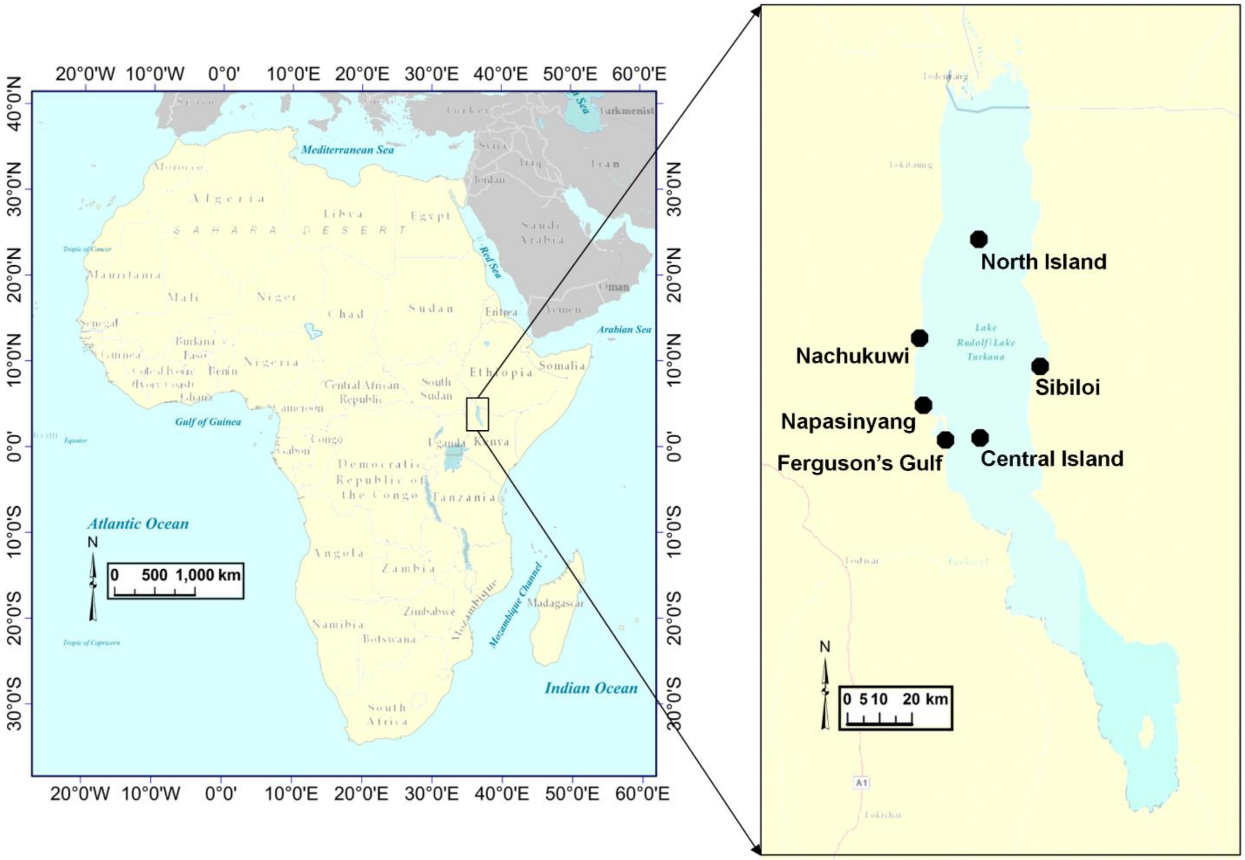


Figure 4.1: Map of Africa with an inset of Lake Turkana showing the study's six sampling sites.

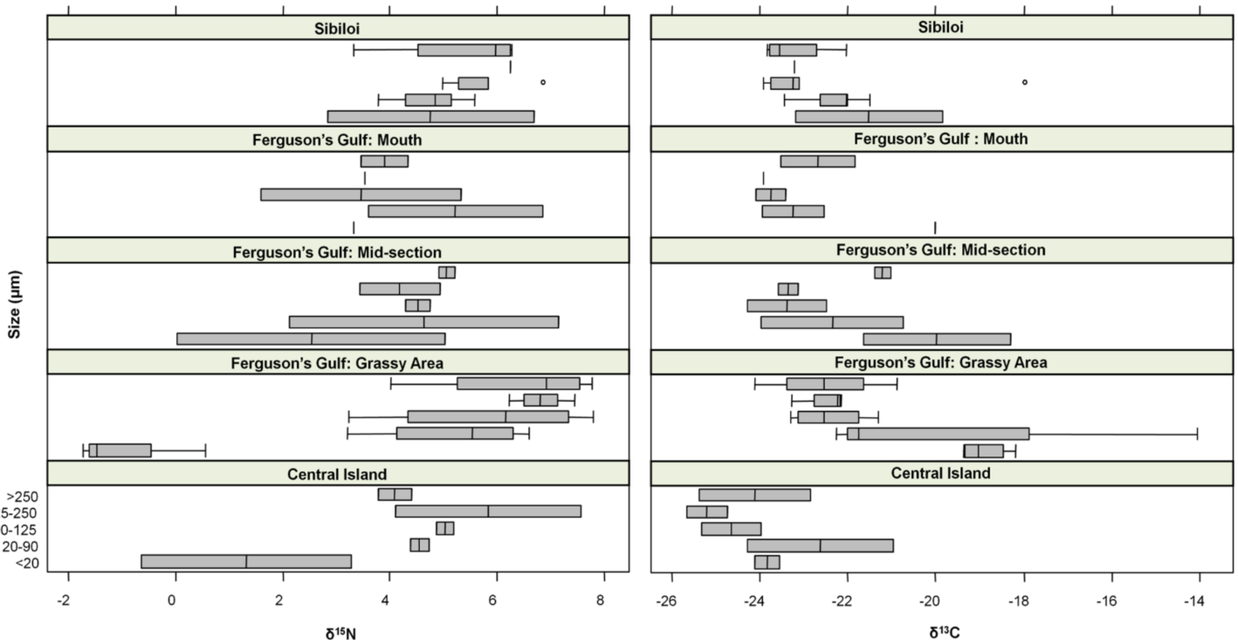


Figure 4.2: Box plot of phytoplankton baseline isotope signatures at the study's six sampling sites. Plankton samples were collected in five size fractions at each sampling site. Significant differences were found between the <20μm size class and all other size classes for $\delta^{13}C$ and $\delta^{15}N$. Significant differences were found between the grassy gulf and open lake sites for $\delta^{13}C$.

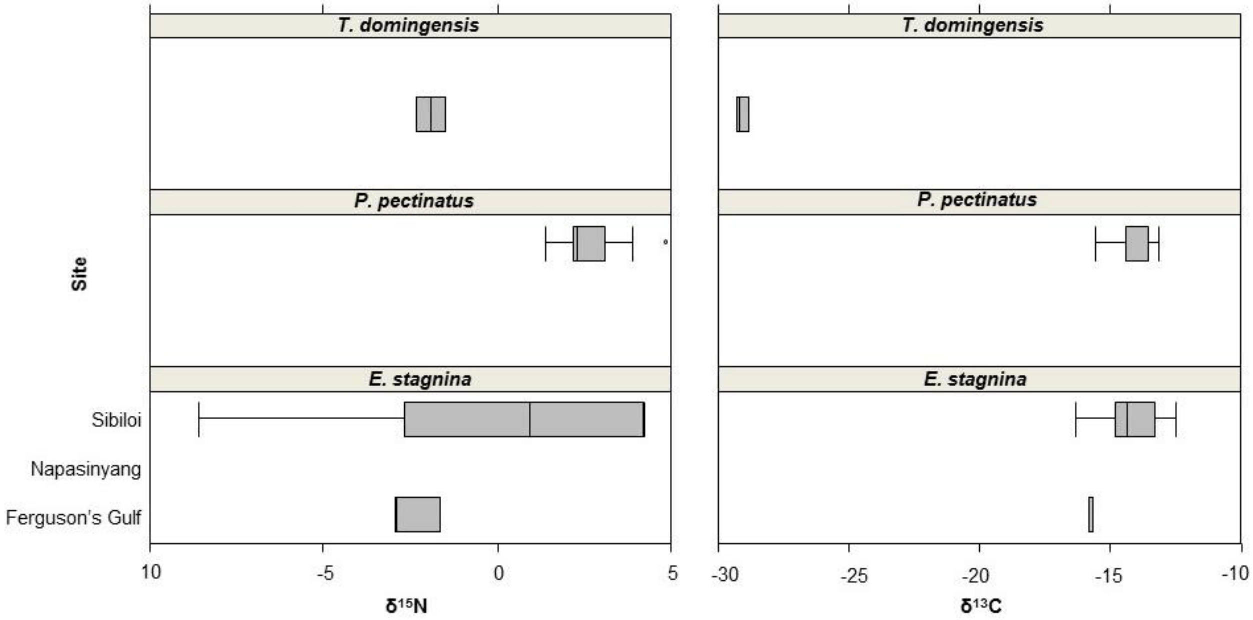


Figure 4.3: Box plot of attached primary producer isotope signatures at three of the study's littoral sites. Hippograss, *Echinochloa stagnina*, was the only species found at multiple sites. There was no significant difference in the signature of *Echinochloa stagnina* between Sibiloi and Ferguson's Gulf.

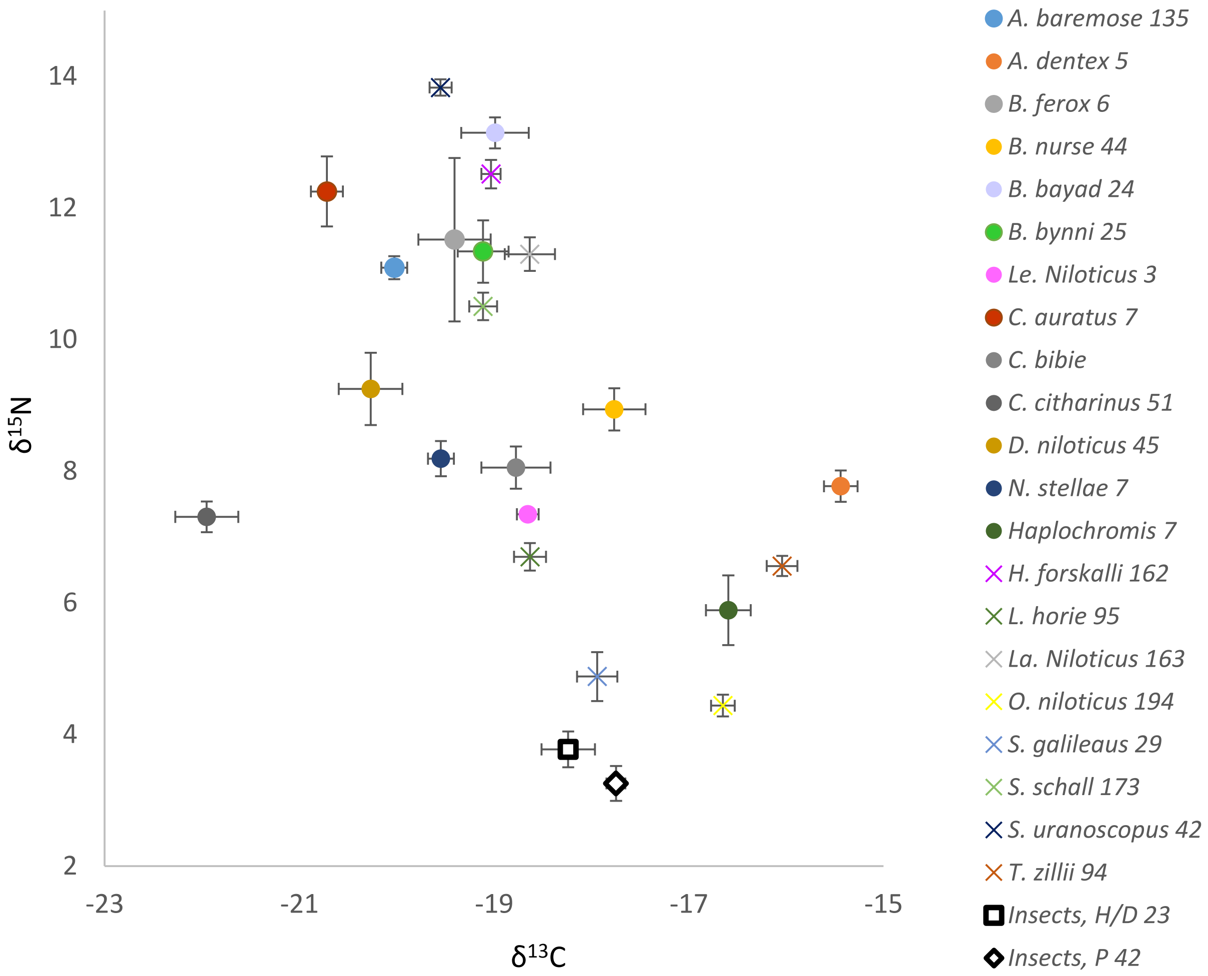


Figure 4.4: Stable isotope bi-plot showing the average δ^{15}N and δ^{13}C signatures of fishes and insects from Lake Turkana, Kenya. Signatures were averaged across sites and years, so represent all individuals of a given species sampled. Horizontal and vertical bars represent the standard errors of δ^{13}C signatures and δ^{15}N signatures, respectively.

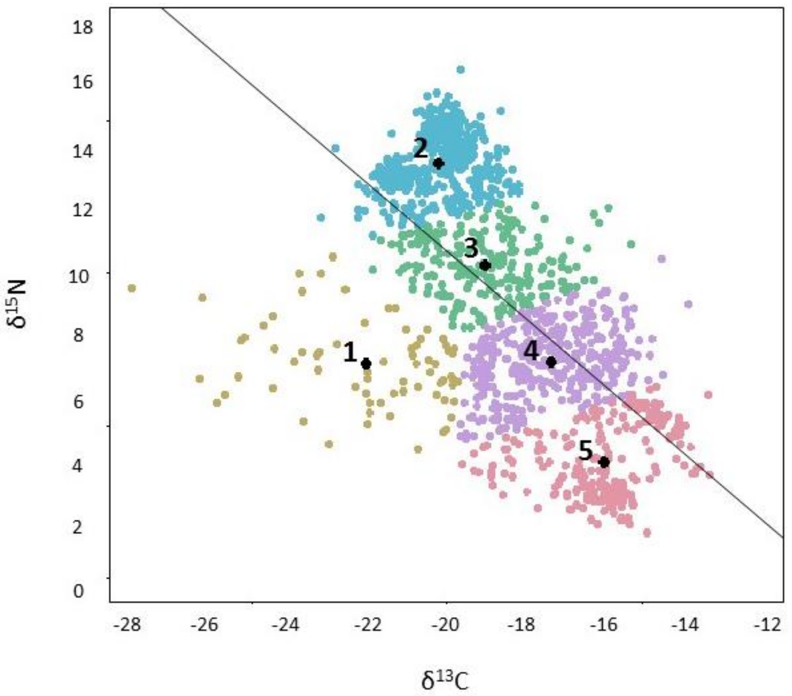
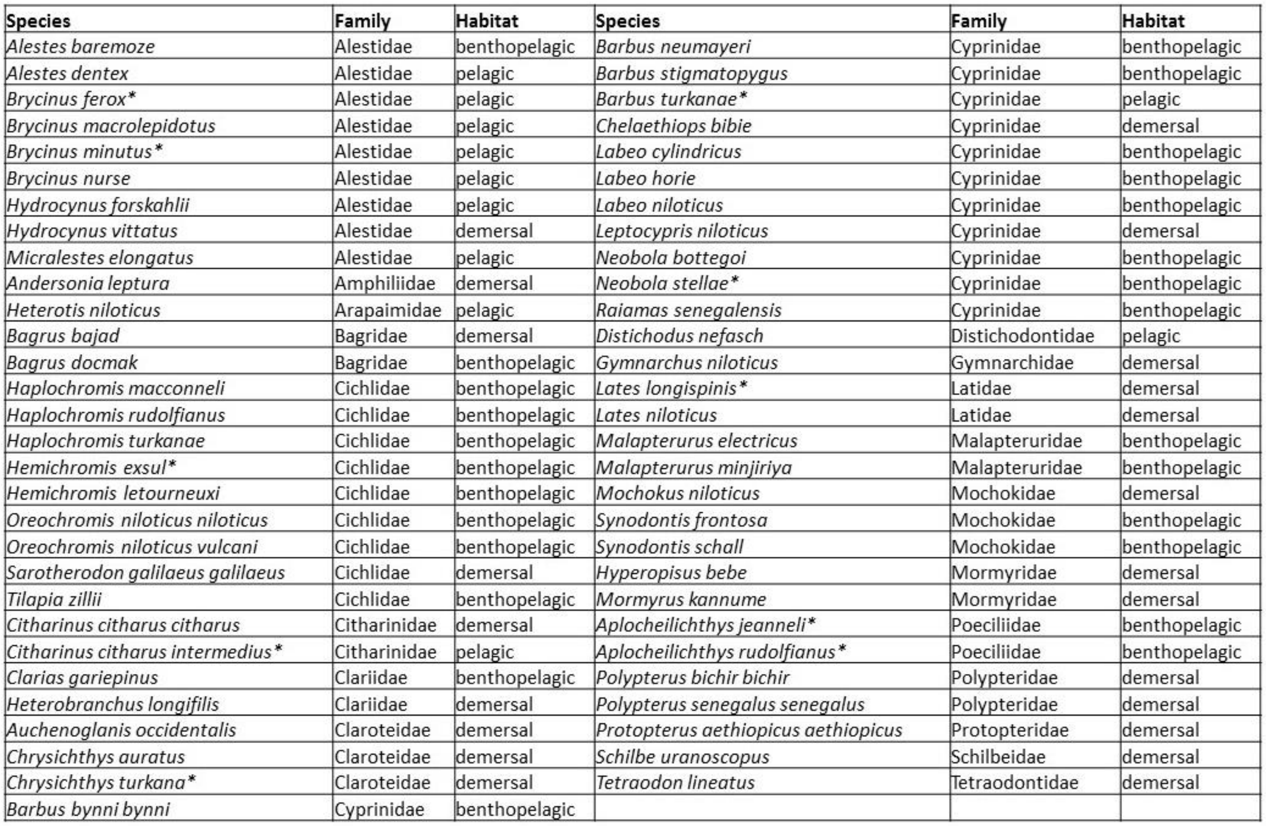


Figure 4.5: Stable isotope scatterplot showing the δ15N and δ13C signatures of all fishes sampled. The δ15N signatures of the lake's fishes were negatively correlated with their δ13C signatures. Colors represent the lake's five trophic clusters, which were calculated using k-means. Each cluster is labeled with its cluster number and with a dot that represents its mean.

Tables

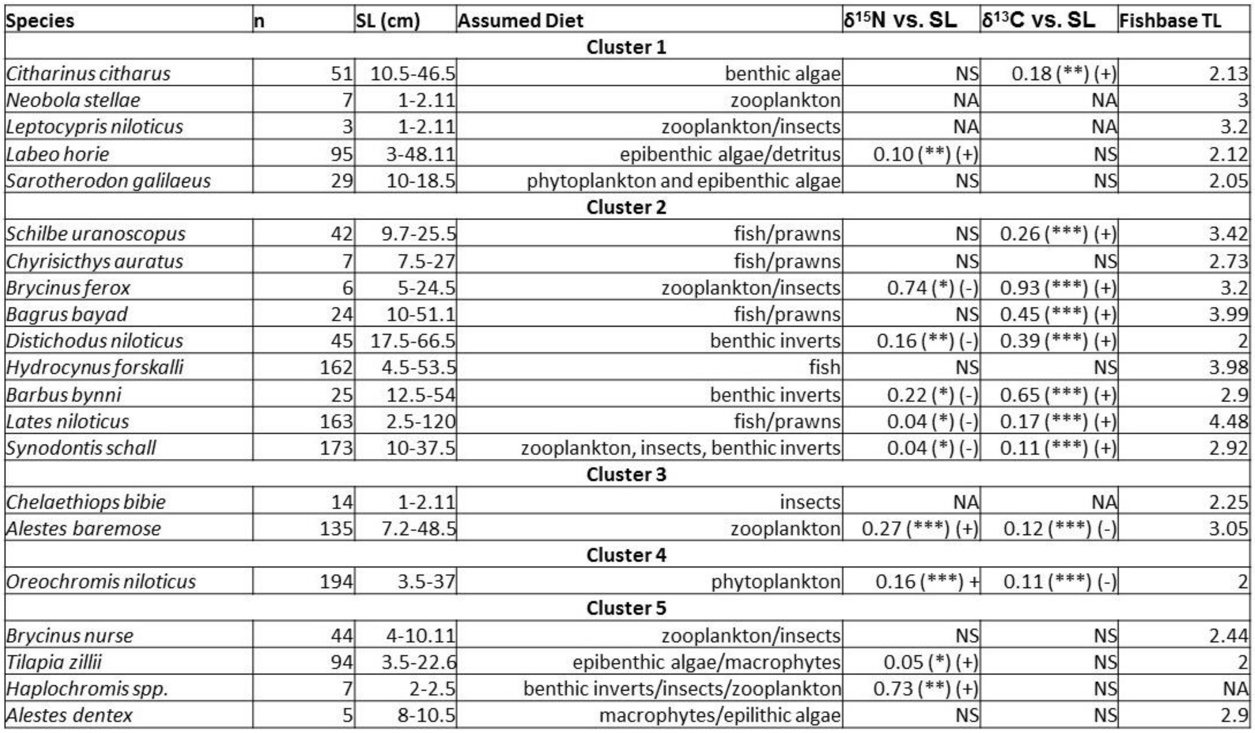
Table 4.1: Fish Species of Lake Turkana Recognized on FishBase



Species	Family	Habitat	Species	Family	Habitat
Alestes baremoze	Alestidae	benthopelagic	*Barbus neumayeri*	Cyprinidae	benthopelagic
Alestes dentex	Alestidae	pelagic	*Barbus stigmatopygus*	Cyprinidae	benthopelagic
*Brycinus ferox**	Alestidae	pelagic	*Barbus turkanae**	Cyprinidae	pelagic
Brycinus macrolepidotus	Alestidae	pelagic	*Chelaethiops bibie*	Cyprinidae	demersal
*Brycinus minutus**	Alestidae	pelagic	*Labeo cylindricus*	Cyprinidae	benthopelagic
Brycinus nurse	Alestidae	pelagic	*Labeo horie*	Cyprinidae	benthopelagic
Hydrocynus forskahlii	Alestidae	pelagic	*Labeo niloticus*	Cyprinidae	benthopelagic
Hydrocynus vittatus	Alestidae	demersal	*Leptocypris niloticus*	Cyprinidae	demersal
Micralestes elongatus	Alestidae	pelagic	*Neobola bottegoi*	Cyprinidae	benthopelagic
Andersonia leptura	Amphiliidae	demersal	*Neobola stellae**	Cyprinidae	benthopelagic
Heterotis niloticus	Arapaimidae	pelagic	*Raiamas senegalensis*	Cyprinidae	benthopelagic
Bagrus bajad	Bagridae	demersal	*Distichodus nefasch*	Distichodontidae	pelagic
Bagrus docmak	Bagridae	benthopelagic	*Gymnarchus niloticus*	Gymnarchidae	demersal
Haplochromis macconneli	Cichlidae	benthopelagic	*Lates longispinis**	Latidae	demersal
Haplochromis rudolfianus	Cichlidae	benthopelagic	*Lates niloticus*	Latidae	demersal
Haplochromis turkanae	Cichlidae	benthopelagic	*Malapterurus electricus*	Malapteruridae	benthopelagic
*Hemichromis exsul**	Cichlidae	benthopelagic	*Malapterurus minjiriya*	Malapteruridae	benthopelagic
Hemichromis letourneuxi	Cichlidae	benthopelagic	*Mochokus niloticus*	Mochokidae	demersal
Oreochromis niloticus niloticus	Cichlidae	benthopelagic	*Synodontis frontosa*	Mochokidae	benthopelagic
Oreochromis niloticus vulcani	Cichlidae	benthopelagic	*Synodontis schall*	Mochokidae	benthopelagic
Sarotherodon galilaeus galilaeus	Cichlidae	demersal	*Hyperopisus bebe*	Mormyridae	demersal
Tilapia zillii	Cichlidae	benthopelagic	*Mormyrus kannume*	Mormyridae	demersal
Citharinus citharus citharus	Citharinidae	demersal	*Aplocheilichthys jeanneli**	Poeciliidae	benthopelagic
*Citharinus citharus intermedius**	Citharinidae	pelagic	*Aplocheilichthys rudolfianus**	Poeciliidae	benthopelagic
Clarias gariepinus	Clariidae	benthopelagic	*Polypterus bichir bichir*	Polypteridae	demersal
Heterobranchus longifilis	Clariidae	demersal	*Polypterus senegalus senegalus*	Polypteridae	demersal
Auchenoglanis occidentalis	Claroteidae	demersal	*Protopterus aethiopicus aethiopicus*	Protopteridae	demersal
Chrysichthys auratus	Claroteidae	demersal	*Schilbe uranoscopus*	Schilbeidae	demersal
*Chrysichthys turkana**	Claroteidae	demersal	*Tetraodon lineatus*	Tetraodontidae	demersal
Barbus bynni bynni	Cyprinidae	benthopelagic			

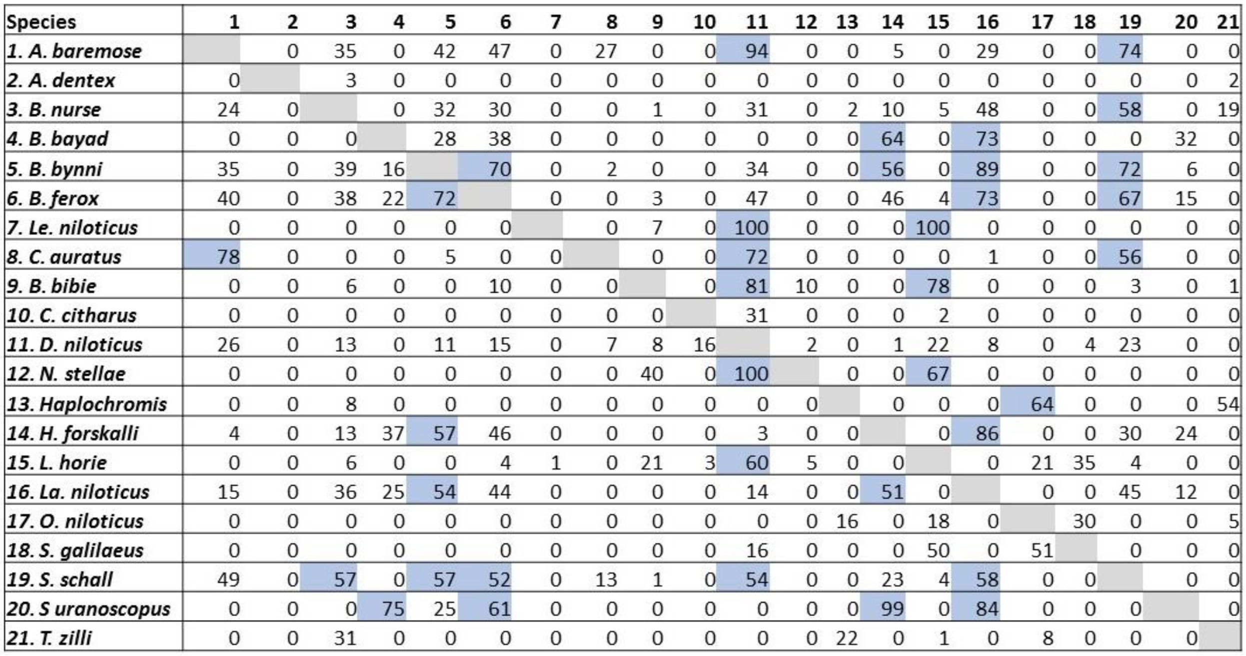
*endemic species

Table 4.2: Feeding Strategies and Ontogenetic Trends of Lake Turkana's Fishes



Species	n	SL (cm)	Assumed Diet	δ^{15}N vs. SL	δ^{13}C vs. SL	Fishbase TL
Cluster 1						
Citharinus citharus	51	10.5-46.5	benthic algae	NS	0.18 (**) (+)	2.13
Neobola stellae	7	1-2.11	zooplankton	NA	NA	3
Leptocypris niloticus	3	1-2.11	zooplankton/insects	NA	NA	3.2
Labeo horie	95	3-48.11	epibenthic algae/detritus	0.10 (**) (+)	NS	2.12
Sarotherodon galilaeus	29	10-18.5	phytoplankton and epibenthic algae	NS	NS	2.05
Cluster 2						
Schilbe uranoscopus	42	9.7-25.5	fish/prawns	NS	0.26 (***) (+)	3.42
Chyrisicthys auratus	7	7.5-27	fish/prawns	NS	NS	2.73
Brycinus ferox	6	5-24.5	zooplankton/insects	0.74 (*) (-)	0.93 (***) (+)	3.2
Bagrus bayad	24	10-51.1	fish/prawns	NS	0.45 (***) (+)	3.99
Distichodus niloticus	45	17.5-66.5	benthic inverts	0.16 (**) (-)	0.39 (***) (+)	2
Hydrocynus forskalli	162	4.5-53.5	fish	NS	NS	3.98
Barbus bynni	25	12.5-54	benthic inverts	0.22 (*) (-)	0.65 (***) (+)	2.9
Lates niloticus	163	2.5-120	fish/prawns	0.04 (*) (-)	0.17 (***) (+)	4.48
Synodontis schall	173	10-37.5	zooplankton, insects, benthic inverts	0.04 (*) (-)	0.11 (***) (+)	2.92
Cluster 3						
Chelaethiops bibie	14	1-2.11	insects	NA	NA	2.25
Alestes baremose	135	7.2-48.5	zooplankton	0.27 (***) (+)	0.12 (***) (-)	3.05
Cluster 4						
Oreochromis niloticus	194	3.5-37	phytoplankton	0.16 (***) +	0.11 (***) (-)	2
Cluster 5						
Brycinus nurse	44	4-10.11	zooplankton/insects	NS	NS	2.44
Tilapia zillii	94	3.5-22.6	epibenthic algae/macrophytes	0.05 (*) (+)	NS	2
Haplochromis spp.	7	2-2.5	benthic inverts/insects/zooplankton	0.73 (**) (+)	NS	NA
Alestes dentex	5	8-10.5	macrophytes/epilithic algae	NS	NS	2.9

Table 4.3: Percent Trophic Overlap among Lake Turkana's Fishes. Blue Boxes Represent Cases of High Overlap.



Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. A. baremose		0	35	0	42	47	0	27	0	0	94	0	0	5	0	29	0	0	74	0	0
2. A. dentex	0		3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
3. B. nurse	24	0		0	32	30	0	0	1	0	31	0	2	10	5	48	0	0	58	0	19
4. B. bayad	0	0	0		28	38	0	0	0	0	0	0	0	64	0	73	0	0	0	32	0
5. B. bynni	35	0	39	16		70	0	2	0	0	34	0	0	56	0	89	0	0	72	6	0
6. B. ferox	40	0	38	22	72		0	0	3	0	47	0	0	46	4	73	0	0	67	15	0
7. Le. niloticus	0	0	0	0	0	0		0	7	0	100	0	0	0	100	0	0	0	0	0	0
8. C. auratus	78	0	0	0	5	0	0		0	0	72	0	0	0	0	1	0	0	56	0	0
9. B. bibie	0	0	6	0	0	10	0	0		0	81	10	0	0	78	0	0	0	3	0	1
10. C. citharus	0	0	0	0	0	0	0	0	0		31	0	0	0	2	0	0	0	0	0	0
11. D. niloticus	26	0	13	0	11	15	0	7	8	16		2	0	1	22	8	0	4	23	0	0
12. N. stellae	0	0	0	0	0	0	0	0	40	0	100		0	0	67	0	0	0	0	0	0
13. Haplochromis	0	0	8	0	0	0	0	0	0	0	0	0		0	0	0	64	0	0	0	54
14. H. forskalli	4	0	13	37	57	46	0	0	0	0	3	0	0		0	86	0	0	30	24	0
15. L. horie	0	0	6	0	0	4	1	0	21	3	60	5	0	0		0	21	35	4	0	0
16. La. niloticus	15	0	36	25	54	44	0	0	0	0	14	0	0	51	0		0	0	45	12	0
17. O. niloticus	0	0	0	0	0	0	0	0	0	0	0	0	16	0	18	0		30	0	0	5
18. S. galilaeus	0	0	0	0	0	0	0	0	0	0	16	0	0	0	50	0	51		0	0	0
19. S. schall	49	0	57	0	57	52	0	13	1	0	54	0	0	23	4	58	0	0		0	0
20. S uranoscopus	0	0	0	75	25	61	0	0	0	0	0	0	0	99	0	84	0	0	0		0
21. T. zilli	0	0	31	0	0	0	0	0	0	0	0	0	22	0	1	0	8	0	0	0	

Chapter 5: Predicting Species' Vulnerability in a Massively Perturbed System: The Fishes of Lake Turkana, Kenya

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Introduction

Lake Turkana is an understudied rift valley lake located in northwestern Kenya that straddles the Ethiopian border. With a surface area of about 6,750 km^2, it is Africa's fourth largest lake and the world's largest permanent desert lake (Kolding 1993). Numerous tribes depend increasingly upon the lake's fishery due to the unsustainable nature of their traditional livelihood of pastoralism in this arid region (Kaijage and Nyagah 2010, Yongo et al. 2010). Lake Turkana is also a haven for wildlife, supporting over 350 native and migratory bird species and the world's largest remaining population of the Nile crocodile. Owing to the faunal diversity and paleoanthropological importance of the region, also known as the "cradle of mankind" (Joordens 2011), it has been named as a UNESCO World Heritage Site.

The Lake Turkana ecosystem is currently at the cusp of large-scale changes in ecological function due to multiple economic activities. These include building dams for hydroelectric power generation (the Gibe Dams) and large irrigation schemes along the Omo River, which supplies 90% of the lake's water and has been called the lake's "umbilical cord" (Kolding 1992). The Gibe III Dam, the resevoir of which began filling in February, 2015, will be the largest hydropower project in Africa and the fourth largest in the world. In addition to lowering Lake Turkana's water levels during reservoir filling, the dam will drastically reduce the magnitude of the lake's flood cycle and therefore will likely impact the timing and success of fish breeding and migration (Lowe-McConnell 1987, Avery 2012). In addition to the Gibe Dams, over 6,400 hectares of land were cleared for sugarcane and cotton plantations in the lower Omo Valley as of April 2014 (HRW 2014). Diversion dams, roads, survey lines, and other irrigation infrastructure are also being constructed (HRW 2014). When operational, these plantations will cover over 200,000 hectares. The associated large-scale irrigation schemes will consume substantial portions of the Omo River's flow and could lead to lake level declines on the order of 20 meters in a lake only 30 meters deep on average (Avery 2012). Flow reduction can impact fish communities by eliminating spawning and nursery areas in the watershed and by altering food web dynamics through changes in species composition and basic limnological function. Due to these impending threats, Lake Turkana is currently under consideration as a World Heritage Site in Danger by the United Nations Environmental Program.

Changing climate conditions have not been considered throughout the planning of the hydropower and irrigation projects discussed above, but will influence their degree of impact on the Lake Turkana ecosystem (Velpuri and Senay 2012). In general, climate projections for Ethiopia suggest higher temperatures in the late 21st century as compared to the late 20th century and lower levels of precipitation (Cline 2007). Precipitation in the Omo Gibe basin specifically is predicted to decrease during the long rainy season and increase during the short rainy season and dry season (Cheung et al. 2008, Bishaw 2012).

The Lake Turkana fish community will be subjected to two phases of profound impact due to upstream development and climate change. Initially, as littoral breeding habits are degraded and flood pulse breeding cues diminish, species dependent upon these attributes will decline in abundance, with likely knock-on impacts to the lake food web as a whole. The overall productivity of the system will also change during this stage, as Lake Turkana is a nitrogen-limited lake and is heavily dependent on nutrient inputs from the Omo River (Hopson 1982, Street-Perrott and Roberts 1983, Kallqvist et al. 1988, Jul-Larsen 2003, KMFRI 2008). In the second wave of impacts, species resilient to the initial changes will face increasing salinity and alkalinity as the lake's volume declines further. These physiochemical changes will alter species composition at multiple trophic levels (Wood and Talling 1988, Verschuren et al. 2000). Here the likely impacts of changes in water inflow on seven key species in the Lake Turkana fish community (*Alestes baremoze, Hydrocynus forskallii, Labeo horie, Lates niloticus, Oreochromis niloticus, Synodontis schall,* and *Tilapia zillii*) are projected based on their dietary niches and breeding vulnerabilities.

The species in this study were chosen based on the following criteria: 1) dominant species in the ecosystem, 2) species with economic and/or ecological importance, and 3) species representing different trophic guilds based on morphological differences (Table 5.1). Economic importance was gauged by the contribution of each species to fisheries catch using species composition data from previous studies spanning several years: 1960-1988 (Kolding 1989; some years excluded due to a high percentage of unspecified catches), 2004 (MoFLD 2008), 2005 (KNBS 2012), and 2011 (KMFRI pers. comm.). Records of fisheries catch were more consistent during the 1960's-1980's because of the Turkana Fishermen's Cooperative Society, which collapsed in 1989 (MoFLD 2008). Ecological importance (top predators, trophic links, etc.) was gleaned from studies on the ecosystem conducted in the 1970's and 1980's (Hopson 1982, MoFLD 2008) and on the role of these species in other ecosystems.

On average, the species studied constituted 65.8% of the total fisheries catch from 1960-2011 (selected years) and 81% of the total fisheries catch in 2011. The catch listed for *O. niloticus* is that of all tilapia species in the lake combined (*O. niloticus, T. zillii,* and *Sarotherodon galilaeus*). Based on the species composition of heavily fished areas such as Ferguson's Gulf, *O. niloticus* is likely to make up the majority of this catch (Hopson 1982). The overall increase in the contribution of these species to the fishery is primarily due to declines in the catch of *Citharinus citharus* and *Distochodus niloticus* over the 1960-2011 time period. *C. citharus* and *D. niloticus* were important fishery species in the 1970's but their populations collapsed by the 1980's (Kolding 1995).

Two of the most important fishery species by volume, *L. niloticus* and *O. niloticus*, are also the most valuable. The swim bladder of *L. niloticus* is a particularly coveted item and, at 166 ksh/kg, is worth more than five times that of bulk *L. niloticus* and *O. niloticus* (KMFRI 2008). Tilapia are targeted in shallow areas using seine nets and are a particularly important fishery resource during high production "boom" years. For example, Ferguson's Gulf, with an area of only 10km^2, yielded 16,000 tons of tilapia at its peak in 1976.

Although not all of the study species made up a large portion of catch (e.g. *A. baremoze, S. schall*), all play important ecological roles in Lake Turkana and, based on their morphological adapatations and previous research, are trophically disparate from each other. *Oreochromis niloticus* and *T. zillii* both possess deep bodies that accommodate long guts associated with an herbivorous diet, whilst *T. zillii* possesses tricuspid teeth unique among the tilapias, which allows it to consume macrophytic vegetation and to scrape epilithic algae (Hopson 1982, Ribble 1982, Trewavas 1982, Kramer and Bryant 1995, Wagner et al. 2009). Tilapiines are the most widely distributed group of non-native fishes (Canonico et al. 2005), including established populations of four exotic species in Lake Victoria. *Oreochromis niloticus* is native to Lake Turkana where it plays important ecological and economic roles. It is the only species in the lake that can both concentrate and digest the blue-green algae *Microcystis aeruginosa*, one of the lake's dominant phytoplankton species. Thus it links and transfers the otherwise wasted (from a fisheries standpoint) energy (i.e. primary production) to higher trophic levels (Hopson 1982, Kallqvist et al. 1988, Lu et al. 2006). While not distinguished from *O. niloticus* in Lake Turkana's fishery, *T. zillii* is likely to prove distinct in terms of its resilience to perturbation due to its trophic dependence on macrophytic vegetation.

Alestes baremoze, along with other species of *Alestes* and *Brycinus* spp. is thought to act as an important conduit of energy from zooplankton to piscivorous fishes in Lake Turkana (Hopson 1982). This species exhibits the hallmark body and caudal form of a midwater swimmer, and the small mouth of a zooplanktivore (Hopson 1982). *Synodontis schall* and *L. horie* have morphological characteristics consistent with a benthivorous diet, including barbels and a sub-terminal mouth. While *S. schall*'s buccal jaw possesses teeth that are sometimes employed to crush the shells of benthic invertebrates, like all cypriniforms, *L. horie* lacks buccal dentition (there are dentigerous pharyngeal jawplates) exhibiting instead a highly folded buccophayngeal membrane that facilitates the efficient entrapment of detrital particles (Girgis 1952, Hopson 1982). The pelagic food web of Lake Turkana is largely detritus-based and the lake is home to several detritivorous fish species (Kolding 1993). *L. horie* was chosen to represent the detritivore fish group due to its importance to the lake's fishery. As an ecological generalist (Araoye 1999, Laléyé et al. 2006, Dadebo et al. 2012, Akombo et al. 2014), *S. schall* may play an important role in Lake Turkana by expanding into portions of the food web vacated by the decline of other species. Lake Turkana harbors a unique midwater scattering layer of endemic characoids (*Brycinus* spp) that have shown population declines linked to reduced lake level (Kolding 1993, Hopson 1982, Muška et al. 2012). It is possible that *S. schall* has expanded its distribution to assume some of their role in the food web, an idea supported by the dominance of this species in recent gill net surveys of the open waters, and by the persistence of this species during the population declines of *Brycinus* spp. in the 1970's-1980's (Machena et al. 1993). *Synodontis schall* may also be a food web "dead end", as it is not readily consumed by other species due to its elongate, locking dorsal and pectoral spines (Kolding 1993, Hopson 1982, Machena et al. 1993).

L. niloticus is a top predator in many African Lake ecosystems, including in Lake Victoria where it is an invasive species that contributed to the decimation of native cichlid populations (Goldschmidt et al. 1993, Campbell et al. 2003, Schwartz et al. 2006, Mbabazi et al. 2010). *L. niloticus* has been found to impact diversity and food web length in the Lake Kyoga ecosystem and may also exert important top down control in Lake Turkana (Mbabazi et al. 2010). *H. forskallii*, a highly piscivorous apex predator in Lake Albert, the African Lake with the most similar fish assemblage to Lake Turkana, likely plays a similar role in this ecosystem (Campbell et al. 2005). *Lates niloticus* and *H. forskallii* exhibit different morphological attributes indicative of a predatory lifestyle. In the case of *L. niloticus*, a large gape size allows for the consumption of prey items up to 50% of their body length (Hopson 1982) and the presence of a tapetum lucidum enhances hunting in low light conditions (Somiya 1980). *Hydocynus forskallii*, while lacking a large gape, has interlocking razor-like teeth that allow it to tear prey items and an elongate body to allow for fast swimming to pursue prey (Hopson 1982, Paugy and Schaefer 2007).

There has been growing interest in using dietary position and breadth as measured by stable isotopes to explore trophic niche relationships and the ecological niche concept (Bolnick et al. 2003, Bearhop et al. 2004, Layman et al. 2007, Newsome et al. 2007, Jackson et al. 2011, Syväranta et al. 2013). Stable isotope analysis confers benefits over gut content analysis because it provides a measure of what is digested rather than ingested and integrates diet over time periods ranging from days to years, depending on the metabolic activity of the tissue sampled (Tieszen et al. 1983, Peterson and Fry 1987, Vander Zanden et al. 1997, Dalerum and Angerbjörn 2005, Buchheister and Latour 2010). Particularly useful are several quantitative measures developed and refined over the last several years that allow researchers to compare trophic diversity among populations and communities using stable isotope data (Layman et al. 2007, Jackson et al. 2011, Layman et al. 2012, Syväranta et al. 2013, Grant et al. 2014).

In this study, stable isotopes were used to measure the degree of intraspecific diet variation, as populations of specialist species (small ecological niche) are expected to be more vulnerable to perturbation than populations of generalist species (large ecological niche) (Levins 1968). Disproportionate declines in specialist species have been documented for a suite of taxa worldwide, from fungi to mammals (Julliard et al. 2004, Munday 2004, Rooney et al. 2004, Van der Veken et al. 2004, Devictor et al. 2008, Wilson et al. 2008, Nordén et al. 2013, Pimm et al. 2014, Weiner et al. 2014). Fossil records show that specialist species are more likely to go extinct than are generalist species over geological time scales (McKinney 1997, Clavel et al. 2010). When specialist species decline, they are replaced by a relatively small number of generalist species, lowering biodiversity via “taxonomic homogenization” (McKinney and Lockwood 1999, Fisher and Owens 1004, Olden and Rooney 2006). Although the ecological niche by definition is “n-dimensional”, the isotopic niche width, a measure of dietary niche breadth, is a useful proxy for understanding ecological niche where δ^{13}C and δ^{15}N represent environmental and trophic axes, respectively (Hutchinson 1978, Newsome et al. 2007, Jackson et al. 2011). Other factors can influence isotopic variance (Cummings et al. 2012), but a large isotopic niche may indicate a generalist population of specialists (Type B generalism; Bearhop et al. 2004) and variation in isotopic signature is correlated with intraspecific trophic diversity as measured by gut content analysis (Araújo and Gonzaga 2007).

To consider how water inflow changes will influence the breeding success of the species studied, a breeding vulnerability index was developed that combines species-specific information on flood pulse dependence and breeding habitat (Hopson 1982). In tropical and neotropical freshwater systems, it is a common phenomenon for fishes to show breeding peaks that coincide with periods of flooding (Lowe-McConnell 1987, Bøgh et al. 2003, Agostinho et al. 2004, Agostinho et al. 2008, Ojuok et al. 2008). Given likely changes in the flooding regime of Lake Turkana, the degree to which its fishes depend on the flood pulse as a breeding cue will influence their vulnerability. As lake level declines, habitat availability will also be altered, with the most immediate impacts occurring on the lake’s rocky eastern shores, which harbor extensive macrophyte beds, and in the Omo Delta region (Velpuri and Senay 2012). Breeding habitat preference is therefore another important component of breeding vulnerability.

Strong evolutionary specialization and differences in gut contents among the species studied lead to the following hypotheses regarding the dietary niches of the species studied: 1) dietary niches will not be significantly different in size and 2) dietary niches will occupy different places in isotopic space and therefore show low overlap. In testing these hypotheses, the goal of this study is to develop a better understanding of the relative dietary niche breadths of these seven key species. From these data and an understanding of the breeding vulnerability of the species studied, some inferences can be made regarding the effects of greatly reduced flow from the Omo River, with implications for the lake's fishery. Although the ecological implications of intraspecific diet variation for populations, particularly in terms of fitness and adaptability, have been noted elsewhere (Bolnick et al. 2011), this is the first study to use intraspecific diet variation as a predictor of response to perturbation, as well as the first study to apply these measures to the Lake Turkana ecosystem. The results of this study serve as a robust initial prediction of how Lake Turkana's fish community will be altered by upstream development.

Methods

All field sample collection was conducted with minimal discomfort to the animals of study. Sampling methodology was reviewed and approved by Stony Brook's Institutional Animal Care and Use Committee (Project 262729). A research permit was obtained (NCST/RRI/12/1/BS011/99) to conduct field work in Kenya, through the National Council for Science and Technology (now known as the National Commission of Science, Technology and Innovation-NACOSTI). Furthermore, collaborations with several local organizations, including the Kenya Marine and Fisheries Research Institute, helped to minimize potential negative impacts of the research.

Fish samples were collected from Lake Turkana, Kenya, using gill nets at various sites between 2008 and 2012. With each net set, 10 individuals of every species were sampled to obtain a representative size range. A small piece of epaxial muscle tissue was removed from each individual and placed in the sun until fully dry (average air temperature of 31-33^{0}C, arid conditions), then stored in a cryovial until processing.

Sample sites varied from year to year due to inter-tribal conflict in some areas during later years. In 2008, sampling occurred in May and December, respectively. In May 2008, three sites were sampled: open waters near North Island at depths of approximately 30m, open waters near Central Island at depths of approximately 30m, and a littoral site, Nachukui. In December 2008, two bays in Sibiloi National Park, located on the eastern shores of the lake were sampled. Shallow areas within the confines of Sibiloi National Park are protected from fishing. harbor the largest macrophyte beds (dominated by *Potamogeton* spp.) in the lake proper, and function as an important nursery habitat (KMFRI 2010). Sampling was not again feasible until March and December of 2011. In March 2011, sampling occurred in Napasinyang, an ephemeral river mouth on the western shore of the lake. In December 2011, sampling took place in two bays in Sibiloi National Park and at the mouth of Ferguson's Gulf. Ferguson's Gulf is the lake's most productive fishing area and an important breeding habitat, particularly for *O. niloticus*. Anecdotal evidence suggests that predatory fishes (including *H. forskallii* and *L. niloticus*) frequently move into the gulf to feed on juvenile fishes. The final sampling trip took place in July of 2012, when three areas of Ferguson's Gulf (the mouth of the Gulf, a grassy area of the Gulf and a mid-section of the Gulf), two bays in Sibiloi, and open waters near Central Island were sampled. The grassy area of Ferguson's Gulf is dominated by hippograss, *Echinochloa stagnina*, rather than by submerged macrophytes. Sampling sites were chosen to represent different habitat types in Lake Turkana, including latitudinal differences in habitat (e.g.

Nachukui to Central Island), heavily fished (e.g. Ferguson's Gulf) versus unfished (e.g. Sibiloi) habitats, littoral (<5m; Napasinyang, Ferguson's Gulf, Sibiloi, and Nachukui) and pelagic habitats (Central Island and North Island), phytoplankton (e.g. Ferguson's Gulf) and macrophyte (e.g. Sibiloi) dominated habitats, and a spectrum of low salinity (e.g. North Island) to high salinity (e.g. Ferguson's Gulf) habitats (Figure 5.1).

Samples were homogenized with a mortar and pestle and cleaned using 70% ethanol. Samples were then weighed to the nearest thousandth of a milligram and analyzed for C:N, δ^{15}N, and δ^{13}C using a GV Instruments IsoPrime isotope ratio mass spectrometer. Isotope values were calibrated to the international standards Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. To determine intra-sample variability, one duplicate sample was run per every 10 unique samples. An internal laboratory standard sample was also run alternating between glycine and peptone for every 10 unique samples to test for machine accuracy. Both standards were carefully calibrated using traditional methods (Dumas combustion, dual inlet IRMS) and were calibrated to IAEA standards N1 and N2 for nitrogen, and NBS 20, 21 and 22 for carbon. The average observed values of glycine were -33.95±0.06‰ for δ^{13}C and 10.77±0.13‰ for δ^{15}N (n=36) and agreed well with the expected values for this standard of -34.00‰ for δ^{13}C and 10.73‰ for δ^{15}N (average absolute difference of 0.07± 0.05‰ for δ^{13}C and of 0.10±0.10‰ for δ^{15}N). The average observed values of peptone were -14.75±0.07‰ for δ^{13}C and 7.28±0.13‰ for δ^{15}N (n=39) and agreed well with the expected values for this standard of -14.73‰ for δ^{13}C and 7.40‰ for δ^{15}N (average absolute difference of 0.06± 0.05‰ for δ^{13}C and of 0.15±0.10‰ for δ^{15}N). A total of 57 pairs of duplicates were analyzed and showed good agreement for δ^{13}C (average absolute difference of 0.06±0.06‰) and δ^{15}N (average absolute difference of 0.24±0.19‰).

Lipid extraction is a necessity in some SIA studies (Gu et al. 1997, Post 2002, Sotiropoulos et al. 2004) because lipids tend to show depleted and variable δ^{13}C values as compared to the rest of the organism (DeNiro and Epstein 1977, McConnaughey and McRoy 1979). However, the process of removing lipids can also impact the δ^{15}N value of a sample (DeNiro and Epstein 1977, Murry et al. 2006). To circumvent this issue, several mathematical lipid correction models have been created that rely on the relationship between C:N and the change in δ^{13}C due to lipid removal (McConnaughey and McRoy 1979, Post 2007, Logan et al. 2008, Sweeting et al. 2006). In general, aquatic stable isotope samples with C:N<3.5 have low lipid concentrations (<5%) and are not altered much by lipid extraction (Logan et al. 2008). Samples had an average C:N of 3.05±0.23‰, with only six samples exceeding a C:N of 3.5. To ensure that the use of uncorrected δ^{13}C values was valid, a preliminary lipid extraction study was conducted.

A random subset of 28 samples were chosen to analyze pre- and post-lipid extraction, using a variation of the methods described in (Folch et al. 1957) and (Hussey et al. 2011). For each sub-sample, 2-5 mg (depending on sample size) were placed into a cryovial, which was then filled with a 2:1 chloroform:methanol solution. Samples were vortexed then placed in a 30°C water bath for 24 hours. On the second day of the procedure, the cryovials were centrifuged for 5 minutes and the supernatant was decanted. This procedure was conducted twice for each sample to ensure that lipids were completely removed. Samples were then dried under a fume hood for 48 hours before being processed for SIA. For comparison purposes, a sub-sample of each individual pre-lipid extraction (bulk sub-sample) also analyzed.

The results of this preliminary test were interpreted by determining whether $\Delta\delta^{13}$C for the 38 samples correlated with their C:N ratio. The $\Delta\delta^{13}$C was defined as

$$\Delta\delta^{13}C = \left(\frac{\left(\delta^{13}C_B - \delta^{13}C_{LE}\right)}{\delta^{13}C_B} \right) * 100$$, or the percent change in the sample's isotope signature, where $\delta^{13}C_B$ represents the isotope signature of the bulk sub-sample and $\delta^{13}C_{LE}$ represents the isotope signature of the lipid extracted sub-sample. If $\Delta\delta^{13}C$ resulted from the loss of lipids alone, a positive correlation would be expected because lipids do not contain nitrogen, so C:N is correlated with the lipid content of a tissue. The $\Delta\delta^{15}N$, defined in the same manner as $\Delta\delta^{13}C$, was also calculated to determine if this isotope's signature was impacted by the lipid extraction procedure.

Neither $\Delta\delta^{13}C$ ($r^2= 0.02$, $p=0.44$) nor $\Delta\delta^{15}N$ ($r^2=0.02$, $p=0.44$) showed a significant positive correlation with C:N. Changes in the two isotopes were, however, positively correlated with each other ($r^2=0.62$, $p<0.0001$). Furthermore, for most samples the absolute value of $\Delta\delta^{15}N$ (average of 13.89±17.17%) was greater than the absolute value of $\Delta\delta^{13}C$ (5.10±5.12%) and both isotopes showed large standard deviations. Due to a low C:N among the samples, the lack of a consistent relationship between $\Delta\delta^{13}C$ and C:N, and the impact of lipid extraction on $\Delta\delta^{15}N$, uncorrected $\delta^{13}C$ signatures were used for the remainder of the study.

Trophic Diversity and Overlap

The standard ellipse function in the Stable Isotope Analysis in R (SIAR) package, known as Stable Isotope Bayesian Ellipses in R (SIBER) was used to address questions regarding isotopic niche (Jackson et al. 2011, R Core Development Team 2013). The standard ellipse area, SEA, uses the $\delta^{15}N$ /$\delta^{13}C$ covariance matrix and is akin to standard deviation for univariate data (Jackson et al. 2011). This ellipse includes approximately 40% of the data cloud and can be taken to represent a core isotopic niche. To reduce the influence of small sample sizes, a correction is made to the SEA value (i.e. using a correction of n-2 rather than n-1 for estimates of variance and covariance due to the use of two-dimensional data), resulting in SEA_c (Jackson et al. 2011). Hereafter, SEA_c will be referred to as the isotopic niche. A Monte-Carlo simulation built into SIAR is used to produce a range of possible values for the isotopic niche area of each species and to account for uncertainty in the data. The mean from this simulation will be referred to as SEA_B. These Bayesian estimates were used to calculate the probability that one species' isotopic niche was greater than another species'. Information on ellipse size and location was used to calculate the percent overlap between two given isotopic niches.

The SIAR package can also be used to calculate Layman's Metrics (Layman et al. 2007). Layman's Metrics were developed to compare communities or populations in terms of trophic diversity and include estimates of isotopic niche (Convex Hull- Hull) and measures of dispersion in isotope space (Centroid Distance- CD; Mean Nearest Neighbor Distance- MNND; Standard Deviation of Nearest Neighbor Distance- SDNND). Due to the sample size dependent nature of these metrics (Schwartz et al. 2006, Mbabazi et al. 2010), they were bootstrapped (R=1005) for the minimum sample size among the species studied (n=50; minimum sample size was for *T. zillii*, where n=55). For each metric, the average resulting from the bootstrapping exercise was recorded, with bootstrapped parameters indicated by the subscript "b".

Tissue Comparisons for *Synodontis schall*

Sample collection in 2008-2012 suggested that *S. schall* had several different color morphs in Lake Turkana. To better understand the trophodynamics of this species, two sample types (spine and muscle) were collected in 2013, using the same sampling methods described above for 2008-2012. For each individual, information was recorded on the degree of spotting (no spots, small spots, large spots) and coloration (light coloration, black coloration). Spines are less metabolically active than are muscles, leading to differences in turnover and fractionation rates (Tieszen et al. 1983, Vander Zanden et al. 2015). Comparing isotopic signatures of samples with different turnover rates can aid in determining whether the population of interest is a specialist, Type A generalist (generalist population where individuals are generalists), or Type B generalist (generalist population where individuals are specialists but consume different diet items) (Bearhop et al. 2004). While the average isotopic signature may be the same, isotopic signature variability is greater for slow turnover tissues than for fast turnover tissues if the population consists of Type A generalists, but this variability is consistent across time scales for Type B generalists (Bearhop et al. 2004). The variance in isotopic signature for the two sample types were compared using the F-test for equality of two variances. Isotopic signatures were also compared among individuals of different coloration and spotting patterns using ANOVA. These tests, in addition to all subsequent statistical tests discussed, were conducted in R version 2.15.1 (R Core Development Team 2013).

Baseline Signature Variability

To better understand variability in baseline isotope signatures, plankton samples were collected in four size fractions (<20µm, 20-90µm, 90-250µm, >250µm) at all sites in 2011 and 2012 using nylon filters. Plankton material was rinsed onto pre-combusted GFF filters using deionized water, which were dried in the sun. Baseline isotope signatures were compared across size classes and sites using ANOVA and Tukey's Post-Hoc test. A water sample was collected in association with each plankton isotope sample and preserved using a 2% Bouin's solution. Upon return to Stony Brook University, 0.1 ml of each sample was gently mixed then analyzed for community composition using a FlowCAM.

Phytoplankton are often inadequate baseline organisms, given their large spatial and temporal variability in isotopic signature (Cabana and Rasmussen 1996, France 1995, Vander Zanden and Rasmussen 1999). Filter feeders, grazers and other primary consumers can act as effective baseline organisms because they integrate primary producer signatures over longer time periods and larger spatial extents (Post 2002). Lake Turkana, however, has a "depauperate" invertebrate fauna and therefore lacks ubiquitous and appropriate baseline primary consumers (Cohen 1986). An alternative approach is to supplement baseline signatures derived from phytoplankton with baseline signatures derived from attached primary producers (e.g. macrophytes). Though attached primary producers are found in some areas of Lake Turkana, they vary from site to site and are not found at all sites. Of the sites sampled, hippograss (*E. stagnina*) dominates in Ferguson's Gulf but can also be found in Sibiloi, the perennial herb *Typha domingensis* is found only at Napasinyang, and the macrophyte *Potamogeton* spp. is found only at Sibiloi.

The issue of suboptimal baseline signatures and their influence on variability at higher trophic levels was addressed in several ways. First, samples of attached vegetation were collected at shallow water sites. Significant differences in isotopic signature were tested for using ANOVA and Tukey's Post-Hoc test when the same species was found at more than one site. Second, several exploratory analyses were conducted to better understand how baseline signatures may have impacted the size of the isotopic niches of the species studied. Size-corrected linear models (i.e. on the residuals resulting from size-signature regressions) were created for each species to determine what proportion of the remaining variability in their isotope signature was related to site, year, and their interaction terms. The use of size-corrected models allowed for the exploration of the influence of baseline variability without the confounding factor of differences in the size range of a species across sites and years (e.g. *O. niloticus* sampled in Ferguson's Gulf were much smaller on average than those sampled in Sibiloi). If baseline differences were large and influential, the variability described by these factors would be high and relatively consistent across species. Conversely, if the amount of variability described by these factors was inconsistent across species, this variability is more likely the result of differences in prey items consumed across space and time.

The relationship between the variability described by these factors was also compared for the two isotopes studied. If variability attributed to site, year and their interaction terms resulted primarily from baseline differences, a positive relationship between the variability described for δ^{13}C and δ^{15}N would be expected. Lastly, the relationship between the number of unique sites at which each species was sampled and their isotopic niche size was determined. Unique sites were defined as any combination of site and year for which >5 (10% of the smallest sample size) individuals of a species were sampled. If spatial or temporal baseline differences played a major role in determining the overall variability of a species' isotopic signatures and therefore the size of their isotopic niche, a positive relationship between the number of unique sites and isotopic niche size would be expected.

Breeding Vulnerability Index

To consider the intraspecific trophic diversity results in the context of breeding vulnerability, an index was developed based on the breeding behaviors of Lake Turkana's fishes (Hopson 1982). This index is a summation of the scores for two factors, flood pulse dependence and breeding habitat (Table 5.2). Under the habitat factor, species breeding in pelagic habitats are expected to be least impacted during the first phase of impacts to the lake, while those breeding in the Omo River or Omo Delta exclusively will be the most strongly impacted. Species capable of spawning in ephemeral rivers, including the Kerio and Turkwell Rivers, should not be as highly impacted as those spawning solely in the Omo River.

Among the species breeding in shallow areas, those that breed on the sandy, gently sloped western shores of the lake will be less impacted by water level declines than those that breed on the rocky, steep sloped eastern shores. Littoral habitat throughout the lake will be heavily degraded by reduced water level fluctuations. These fluctuations promote the maintenance of aquatic vegetation, which acts as important predatory refuge for juvenile fishes, and determine the extent of the aquatic-terrestrial transition zone (ATTZ). The ATTZ is the highly productive region of a lake that is covered by water only during the flood pulse (Junk et al. 1989, Wantzen et al. 2008). Systems with an active ATTZ are more productive than stable systems (Welcomme and Halls 2001, Wantzen et al. 2008), and species that feed within the ATTZ have higher growth rates than those that feed in the main water body (Bayley 1991).

Under the flood pulse factor, species that only breed during periods of spate (annual flood period of June-October) will be most vulnerable to changes in the Omo River's flood regime, species that show strong breeding peaks during periods of spate will be moderately vulnerable, and species that show weak breeding peaks during periods of spate or consistent breeding year-round will be least vulnerable (Table 5.2). Partial scores were sometimes assigned within factors (e.g. if a species has two sub-populations that each breed in a different habitat). The overall breeding vulnerability index score ranges from 0 (low vulnerability) to 4 (high vulnerability).

Results

Trophic Diversity and Overlap

Among the fish species studied, $\delta^{13}C$ ranged from -26.35‰ (*L. niloticus*) to -13.59‰ (*T. zillii*) and $\delta^{15}N$ ranged from 1.53‰ (*O. niloticus*) to 16.71‰ (*H. forskallii*). The means of $\delta^{13}C$ and $\delta^{15}N$ values were largely consistent with the end members for the ranges of these signatures, with *A. baremoze* exhibiting the lowest average $\delta^{13}C$ and *T. zillii* the highest. *O. niloticus* showed the lowest average $\delta^{15}N$ and *H. forskallii* the highest (Table 5.3).

There was a significant positive correlation between the sample size of each species and both their niche volume (Convex Hull; $r^2=0.83$, $p<0.005$) and centroid distances ($r^2=0.60$, $p<0.05$). MNND had a significant negative correlation with sample size ($r^2=0.40$, $p<0.005$), while there was no significant relationship between sdMNND and sample size. Once bootstrapped, the dependence of these metrics on sample size largely disappeared, with positive and borderline significant correlations for CD_b ($r^2=0.59$, $p=0.045$) and $Hull_b$ ($r^2=0.57$, $p=0.049$). SEA_c, showed no significant relationship with sample size ($r^2=0.33$, $p=0.18$).

SEA_c varied by a factor of two for the species studied and was smallest for characids (*H. forskallii* and *A. baremoze*) and *T. zillii* and largest for *O. niloticus* and *L. niloticus* (Table 5.3, Figure 5.2). There was good agreement between SEA_c and SEA_B for each species studied (Figure 5.3). Confidence in the relative sizes of the isotopic niches was high (Table 5.4); i.e. when comparing species with the smallest isotopic niches (*A. baremoze, H. forskallii,* and *T. zillii*) to those with the largest (*O. niloticus* and *L. niloticus*), probabilities were always >0.95 (Table 5.4). The results for bootstrapped Layman's Metrics were in agreement with the results from SIBER (Table 5.3). In general, species with the largest SEA_B also had the largest $Hull_b$ (with the exception of *H. forskallii*) and the highest values for the measures of dispersion CD_b, $MNND_b$, and $sdMNND_b$

The average eccentricity of the ellipses representing the isotopic niches was 0.87 ± 0.07, showing strong deviation from a perfectly circular shape. For all species, ellipse length was greater along the $\delta^{15}N$ axis than along the $\delta^{13}C$ axis. The only species with eccentricities below the average were *T. zillii* (0.75) and *L. horie* (0.81), suggesting that carbon source plays a more important role in the isotopic niche size of these species than the others studied. To account for the fact that larger variability along the $\delta^{15}N$ axis could be due to a substantially larger average fractionation factor for this isotope relative to $\delta^{13}C$ (McKinney and Lockwood 1999), the ellipse for each species was re-calculated using standardized values via the standard score method (i.e. z scores). The eccentricity trends were the same for the standardized ellipses, with an average of 0.88 ± 0.04 and with *L. horie* (0.79) and *T. zillii* (0.87) showing the smallest eccentricities.

The overlap between isotopic niches can be used as an indicator of functional redundancy, resource partitioning, or competition among species in an ecosystem (Jackson and Britton 2013, Olin et al. 2013, Ryan et al. 2013). Functional redundancy was not expected to be prominent among the species studied, as these species were selected to represent the full suite of feeding strategies used by the fishes of Lake Turkana (Table 5.1). However, if a large portion of the isotopic niche of one species overlaps with multiple species from varying trophic guilds, omnivory is indicated.

The median percent overlap between any one species and another was low for *A. baremoze* (1.15%), *H. forskallii* (1.33%), *L. horie* (2.10%), and *O. niloticus* (1.09%). Median percent overlap was slightly higher for *T. zillii* (6.23%) and highest for *L. niloticus* (10.63%) and *S. schall* (14.81%). Most species overlapped to some extent with three (*A. baremoze, H.*

forskallii, L. horie, and *O. niloticus*) or four (*T. zillii* and *L. niloticus*) of the other six species studied, whereas *S. schall* overlapped with all other six species. To further explore the overlap between *S. schall* and the other species studied, an aggregate isotopic niche was calculated (i.e. including all data from the species studied except for *S. schall*). The aggregate isotopic niche was large (SEA_c= 17.51), as might be expected due to the aggregation of several trophic guilds, and 97% of the isotopic niche of *S. schall* lay within this aggregate niche.

Tissue Comparisons for *Synodontis schall*

Muscle and spine samples for *S. schall* differed significantly in their $\delta^{15}N$ and $\delta^{13}C$ signatures (Table 4.5; $\delta^{13}C$: F=185.9, $p<0.0001$; $\delta^{15}N$: F=11.99, $p<0.001$), possibly due to differences in fractionation factor dependent on tissue type. The variance in $\delta^{15}N$ did not differ significantly between the two tissue types (F=1.30, p=0.27), while variance in $\delta^{13}C$ did (F=2.56, $p<0.0001$). Isotopic signatures were not significantly different among individuals of differing spotting patterns (Table 4.5; $\delta^{13}C$: F=0.431, p=0.65; $\delta^{15}N$: F=1.10, p=0.34), but were among individuals of different coloration (Table 4.5; $\delta^{13}C$: F=47.94, $p<0.0001$; $\delta^{15}N$: F=57.07, $p<0.0001$). The sample size was considerably lower for individuals of dark coloration (n=10) than for those of light coloration (n=62), but individuals of dark coloration had consistently lower $\delta^{15}N$ values and more enriched $\delta^{13}C$ values than did individuals of light coloration (Table 4.5).

Baseline Signature Variability

Phytoplankton baseline signatures for $\delta^{13}C$ (F=6.88, $p<0.05$) and $\delta^{15}N$ (F=12.81, $p<0.0001$) in the <20μm size class differed significantly from all other plankton size classes respectively (Tukey's Post-Hoc test, Figure 5.4). All size classes were dominated by *M. aeruginosa* varying from single cells to large colonies, which would explain the similar isotopic signatures observed for all sizes classes >20μm. The presence of non-photosynthetic bacteria may explain the significantly different signature for the <20μm size class. Baseline signatures for $\delta^{13}C$ differed among sites (F=4.28, $p<0.01$), but $\delta^{15}N$ signatures did not (F=0.70, p=0.60). Tukey's Post-Hoc test showed that the significant difference in $\delta^{13}C$ was driven by the difference in signature between grassy areas of Ferguson's Gulf and the open lake. There was no significant difference in hippograss baseline signatures between Sibiloi and Ferguson's Gulf (Figure 5.5).

The number of unique sites varied from four (*A. baremoze*) to eight (*H. forskallii* and *L. horie*) per species. The variability in any one isotopic signature ($\delta^{13}C$ or $\delta^{15}N$) described by site, year and their interaction terms ranged from 2.3% (*T. zillii* $\delta^{15}N$) to 66.6% (*L. horie* $\delta^{15}N$) (Figure 5.6). There was no significant relationship between the variability described in $\delta^{13}C$ and the variability described in $\delta^{15}N$ for each species. Similarly, there was no significant relationship between the number of unique sites and the isotopic niche size of each species (Figure 5.7.; r^2=0.15, p=0.39).

Breeding Vulnerability Index

In Lake Turkana, *A. baremoze* and *L. horie* breed exclusively during the flood pulse (Flood Pulse Factor=2), whereas *H. forskallii* and *O. niloticus* breed year-round but show marked breeding peaks during the flood pulse (Flood Pulse Factor=1; Hopson 1982). *Lates niloticus, S. schall and T. zillii* show consistent breeding year-round or weak breeding peaks during the flood pulse (Flood Pulse Factor=0). The species studied showed a wide range of breeding habitat preferences. *L. niloticus* breeds in the lake's pelagic habitats (Habitat Factor=0).

Of the lake's littoral breeders, *O. niloticus* prefers sandy breeding sites, which are concentrated on the lake's western shores (Habitat Factor=1), and *T. zillii* prefers rocky or macrophyte-dominated breeding sites, which are concentrated on the lake's eastern shores (Habitat Factor=2). Though *L. horie* and *S. schall* breed in all inflowing river mouths (Habitat Factor=1), *A. baremoze* breeds only in the Omo River and its Delta (Habitat Factor=2). *H. forskallii* is thought to have two sub-populations, one that breeds in the lake's pelagic habitats and one that breeds in inflowing river mouths (Habitat Factor=0.5; Hopson 1982). The overall breeding vulnerability index ranged from 0 (*L. niloticus*) to 4 (*A. baremoze*). In general, species with high trophic diversity also showed low breeding vulnerability while those with low trophic diversity also showed high breeding vulnerability (Figure 5.8).

Discussion

Lake Turkana is a system expected to undergo substantial changes in the next decade due to the impact of upstream development projects and global climate change on the volume and patterns of inflow from the Omo River. The methodology employed allowed for a relatively inexpensive and quick way of developing an initial understanding of dietary position and niche breadth for key fishes of Lake Turkana. The initial expectations regarding the dietary niche breadth of these species were structured around their trophic ecomorphology. Based on these expectations, the isotopic niches of the species studied were postulated to be (1) similar in size but (2) non-overlapping. The first hypothesis can be rejected based on the SIBER results, as isotopic niche size varied by a factor of two among the species studied. Isotopic niches for *L. niloticus* and *O. niloticus* were the largest, significantly larger than the smallest exhibited by *A. baremoze, H. forskallii* and *T. zillii*. *L. horie* and *S. schall* had mid-range isotopic niches, with lower certainty regarding relative niche size based on Bayesian interference. The degree of trophic diversity as measured by SIBER was confirmed by Layman's metrics (Hull_b and measures of dispersion). Although previous work has hypothesized that high trophic level species may be more likely to exhibit intraspecific variation (Araújo and Gonzaga 2007, Matthews et al. 2010), this was not the case here among the seven species studied.

The apparent discrepancy between ecomorphology and feeding behavior, and in particular the presence of morphological specialists behaving as generalists, is not a phenomenon unique to this system. This mismatch, especially common in teleost fishes, is referred to as "Liem's Paradox" and was first noted in east African lake cichlid fish populations (Liem 1980, 1990, Bootsma et al. 1996, Robinson and Wilson 1998, Binning et al. 2009, 2010). In "Liem's Paradox" structural feeding specializations invoke minimal functional limitations, permitting morphologically specialized taxa to feed on whatever is most advantageous when food resources are abundant and as specialists when the most desirable food resources are scarce (Wiens 1977, Binning et al. 2009). In tropical freshwater systems it is the flood cycle, rather than seasonality in any strict sense (as at high latitude), that controls food resource availability. This study is likely to have accurately captured the magnitude of each species' intraspecific diet variation, as sampling occurred during periods of low lake level (i.e. resource scarcity) and high lake level (i.e. resource abundance) at both seasonal and inter-annual scales.

The SIBER results supported the second hypothesis regarding the spacing of the key species' dietary niches in isotopic space. Except for *S. schall*, which overlapped with all other species, the species in this study showed little trophic overlap and are quite distinct in trophic function in Lake Turkana. High overlap between *S. schall* and the isotopic signatures of the other species studied indicate an omnivorous diet and a catholic behavioral repertoire for this species. The presence of omnivory within the Lake Turkana *S. schall* population was also supported by comparisons between spine and muscle isotope signatures. Variance in δ^{13}C for this species is significantly greater at short time scales (muscle) than it is at longer time scales (spine), indicating a Type A generalist population. The species' isotope signatures do, however, also hint at the presence of some Type B generalism. Certain sub-groups of *S. schall* (e.g. individuals of dark coloration) may have a different diet than do others, feeding on more enriched carbon and lower trophic levels than the rest of the population.

In isotopic space, there was distinct separation between pelagic and littoral species. *A. baremoze* and *H. forskallii* were end members representing the pelagic food web, showing the highest δ^{15}N values (possibly due to a longer food web in the lake's open waters), but the lowest δ^{13}C values, indicative of pelagic food sources (France 1995). In contrast, *T. zillii* and *O. niloticus* had low δ^{15}N values and the highest δ^{13}C values, placing them as secondary consumers in the lake's littoral food web. *T. zillii* had the highest δ^{13}C values, consistent with a diet predominantly consisting of macrophytes. The benthivores *S. schall* and *L. horie*, while not overlapping much, fell somewhere in the middle of the isotopic space. *L. niloticus*' niche also fell between the pelagic and littoral end members, suggesting a mix of prey from both habitats, but also surprisingly low in trophic level given its piscivorous reputation. Relative positions of these species in isotopic space were largely in agreement with stable isotope work conducted on other African Lake ecosystems (Campbell et al. 2003, 2005, Schwartz et al. 2006, Mbabazi et al. 2010, Ojwang et al. 2010).

Variability in the isotopic baseline propagates up food webs and must be considered in understanding variability at higher trophic levels (Bearhop et al. 2004, Semmens et al. 2009, Cummings et al. 2012). Although there are no appropriate primary consumer baseline organisms in Lake Turkana (Post 2002), the results from the primary producer baseline organisms suggest no significant difference in signatures across sites. Furthermore, factors relating to baseline differences (i.e. site and year) did not describe a consistent amount of variability among the species studied or between the isotopes studied for each species. Bearhop et al. (2004) describe four factors that have a large influence on intraspecific variability in isotope signature: the range and evenness of prey items consumed, the trophic level of these prey items, and the geographic range in which a species forages. If spatial differences in baseline signature are a key component of the variability in isotopic signature of the species studied, species that were sampled at a greater number of unique sites would have larger isotopic niches on average (Bearhop et al. 2004). The present study, however, showed no significant relationship between the number of unique sites sampled and the isotopic niche size of the species studied, suggesting that differences in the first three factors (range, evenness and trophic level of prey items consumed) have a stronger influence on intraspecific isotopic variability in Lake Turkana.

The conclusions reached regarding the relative diet variability of the species studied are also corroborated by previous research on Lake Turkana and other systems. *A. baremoze* and *H. forskallii* were among the more specialized feeders in recent research on Lake Albert, the African Lake with the closest fish assemblage to Lake Turkana (Campbell et al. 2005). Similarly, *T. zillii* is one of the most specialized feeders among the tilapias (Hopson 1982), and in Lake Turkana it has a strong preference for rocky littoral habitats with macrophytic vegetation (Lowe-McConnell 1987, Hopson 1982, Trewavas 1982). Of the less specialized species, *L. horie*'s diet has not been extensively studied but past research on Lake Turkana suggests that it is relatively omnivorous (Hopson 1982), feeding on benthic items including detritus and ostracod shells, a diet consistent with this species' position in isotopic space in this study. *S. schall* showed high morphological variation in Lake Turkana, consumed a variety of prey items in a recent gut content study (KMFRI 2008), and has been noted as an omnivore in other systems (Araoye 1999, Laléyé et al. 2006, Dadebo et al. 2012, Akombo et al. 2014). It is also the only *Synodontis* species in Lake Turkana proper (*S. frontosa* is confined to the Omo River and its delta), so it does not have competition from other members of the genus that are better suited for open water feeding (Hopson 1982). *L. niloticus* has a wide range of isotope values in other African lakes and has been shown to prey-switch in some systems, suggesting that it is an opportunistic feeder (Mkumbo and Ligtvoet 1992, Campbell et al. 2005, Post 2007, Matthews et al. 2010, Ojwang et al. 2010). Similarly, *O. niloticus* is known to be a particularly plastic species in ecosystems worldwide, capable of withstanding high environmental fluctuations and extreme breadth in both its fundamental and realized trophic niche (Lowe-McConnell 1987).

To better predict how these species will respond to changes in the ecosystem, intraspecific trophic diversity results were considered in the context of breeding vulnerability. Interestingly, the most vulnerable species based on diet (i.e. small isotopic niche, low intraspecific trophic diversity) also tended to have high breeding vulnerabilities (Figure 5.8). With, two strikes against them, *A. baremoze, H. forskallii, L. horie,* and *T. zillii* are predicted to be the most vulnerable to population declines in the face of changes to Lake Turkana. These predictions are largely in agreement with historical changes in the lake, as *A. baremoze* and *H. forskallii* both showed sharp population declines when lake levels dropped between the 1970's and 1980's. *L. horie* did not show similar declines, but a reduced catch of juveniles did suggest recruitment failure (Kolding 1995). *L. niloticus* and *O. niloticus* are expected to fare better than the other species studied, at least during the first phase of changes to Lake Turkana. These species both have low breeding vulnerability and high intraspecific trophic diversity (i.e. extralimital feeding adaptations, large isotopic niche), and have been highly successful invasive species in other systems, suggesting a general hardiness and ecological flexibility. *Synodontis schall* is grouped with the more resilient species in this ecosystem, based on its low breeding vulnerability and highly overlapping isotopic niche, consistent with an omnivorous diet. Although this species breeds primarily in inflowing rivers, it is not dependent solely on the Omo River and there is some evidence that it may also breed in shallow, sandy habitats within the lake proper (Hopson 1982). There was no evidence for population declines in *L. niloticus* or *S. schall* during the lake level declines of the 1970's-1980's (Kolding 1995).

In some ways, it is promising that *O. niloticus* and *L. niloticus* are among the less vulnerable species in Lake Turkana. Together, their multiple size classes can fill out a complete, if depauperate, fish food web. They are also highly desirable fisheries resources, and are the most valuable and heavily exploited species in the growing Lake Turkana fishery. In contrast, *L. horie* is the third largest fishery on Lake Turkana but based upon the results of this study will be among the most sensitive to imminent changes in the ecosystem, with implications for food security and quality. *T. zillii* should be treated separately from *O. niloticus* in the fishery, as this study suggests that the two species play different ecological roles in Lake Turkana. *T. zillii* will also be far less resilient to perturbation than *O. niloticus* and should be managed accordingly. Fishermen should be able to separate these species quickly in the field, given highly visible differences in morphology and coloration.

Past researchers have advocated for growth in the lake's offshore fishery, which would focus on *H. forskallii* and *A. baremoze* (Hopson 1982). It is unlikely that these two species will be able to withstand the combined effects of lake level decline and increased fishing pressure, given historic declines in their populations that occurred without the added impacts of fishing (Kolding 1995). The development of a fishery for these species in Lake Turkana may therefore be ill-advised. *S. schall* was among the more resilient species in this study and is one of the most abundant fish species in the Lake Turkana ecosystem (Hopson 1982, Muška et al. 2012). Dietary studies suggest little predation pressure on *S. schall* due to its formidable morphological defense of interlocking pectoral spines, so this species may act as a food web "dead end" (Kolding 1993, Hopson 1982, Machena et al. 1993). As earlier suggested by Kolding (1995), there may be potential for sustainably increasing fishing pressure on this species. However, an expanded fishery for *S. schall* would require careful monitoring, development, and enforcement of measures to limit the bycatch of more sensitive species.

In general, there is a lack of enforcement of fisheries regulations on Lake Turkana due to insufficient staff numbers and funding among local research and management agencies. This reality will make heeding the recommendations above a difficult task. Overexploitation coupled with environmental sensitivity has led to the decline of some species in the past, including the collapse of the *C. citharus* and *D. niloticus* fishery between the 1970's and 1980's (Kolding 1995). Even among the species found to be the least vulnerable in this study there are concerns of overexploitation and subsequent declines (Ojwang, *pers. obs.*). These species' populations will only fare well if they are managed sustainably. The fishery for *O. niloticus* in particular is unrelenting, with fishermen targeting this species by day and night in shallow areas using seine nets. Lake Turkana's catches are relatively minor compared to Lake Victoria's but play an important role in local food security. Furthermore, there is the potential to increase the lake's fishery if done so sustainably, particularly if the fishery could include less valuable but highly productive species like *S. schall*. To ensure that Lake Turkana's fishery does not collapse in this period of multiple stressors, effort should be made to increase the resources available to local organizations monitoring the system.

Conclusions

Local dam and irrigation development and global climate change will alter the Omo River's flow patterns over the coming decade, with a possibility of terminating freshwater inflow to Lake Turkana, dropping lake level and dampening intra-annual fluctuations. The results of this study suggest that *L. niloticus, O. niloticus*, and *S. schall*, which together make up 40% of recent fisheries catch, will be the most resilient to impending ecosystem change. *S. schall* has shown low predation mortality in previous diet studies on the system (Kolding 1993, Hopson 1982) and the fishery for this species could be expanded sustainably if measures are taken to avoid bycatch of other species. Unlike *O. niloticus, T. zillii* is a limited-specialist feeder (*O. niloticus* is a generalist with a non-limiting specialization for microphagy; Sanderson et al. 1996) and will be particularly vulnerable to breeding habitat changes, so these species should not be grouped by the fishery simply because they are both tilapiines. After *L. niloticus* and *O. niloticus, L. horie* is the lake's most important fishery resource and is also one of the least resilient species based on this study. *H. forskallii* is likely to feed primarily on *A. baremoze* and related species. Both *H. forskallii* and *A. baremoze* will be vulnerable to population declines in the altered Lake Turkana, due to their dietary constraints and high breeding vulnerability. In general, fishery management in the region must be improved to account for potential population declines among vulnerable species and to sustainably manage resilient species. Although additional research is needed to fully understand this understudied and climate sensitive ecosystem, this study serves as a robust initial prediction of how Lake Turkana’s fish community will be altered by upstream development, contributes to a still wanting store of baseline data for the ecosystem, and provides a novel use of data on intraspecific diet variation to predict sensitivity to anthropogenic impacts.

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Figures

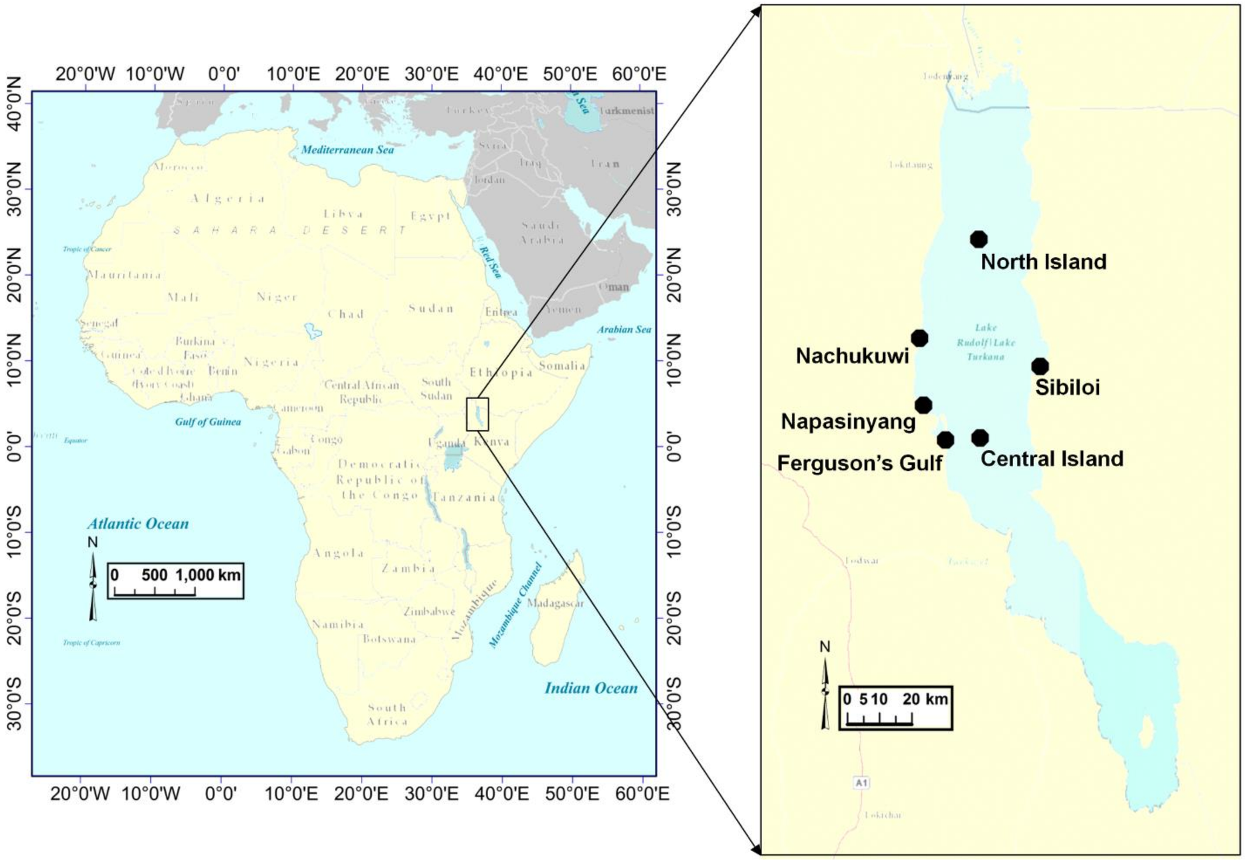

Figure 5.1: Map of Africa with an inset of Lake Turkana showing the study's six sampling sites.

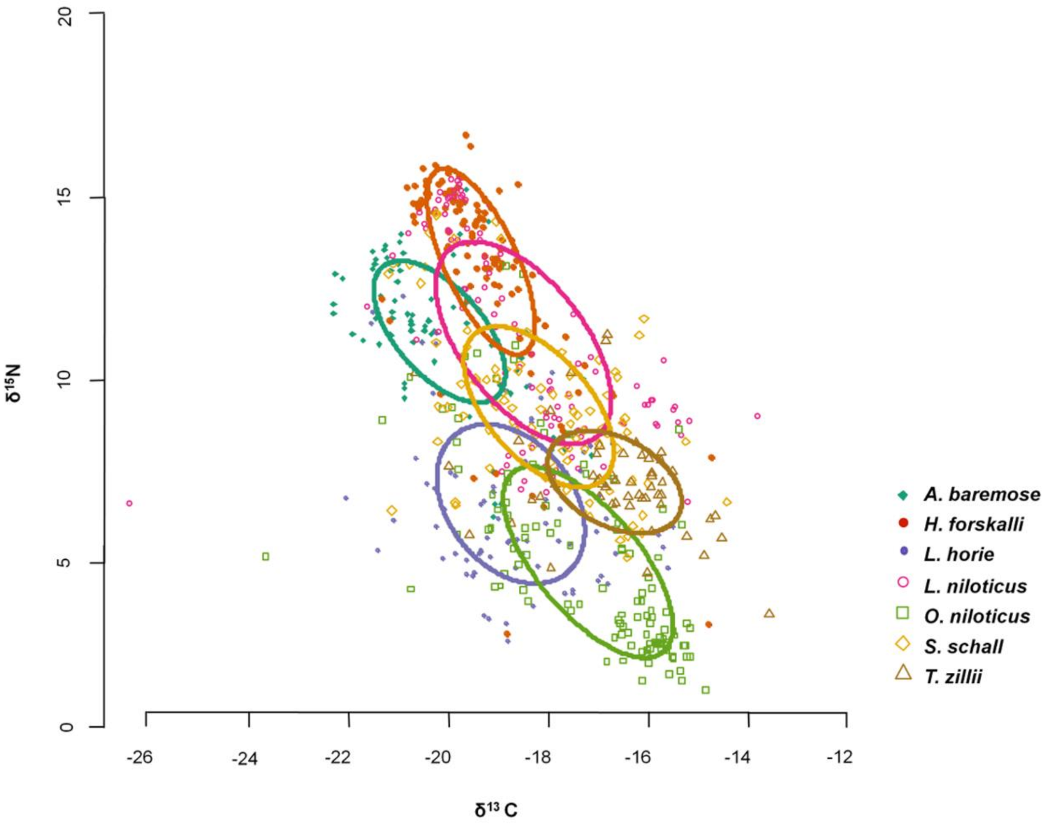

Figure 5.2: Isotopic niches for the seven fish species examined in this study. Symbols represent individual isotope values within species. Isotopic niches were calculated as standard ellipses in R, using the $\delta^{13}C$ and $\delta^{15}N$ signatures for each species.

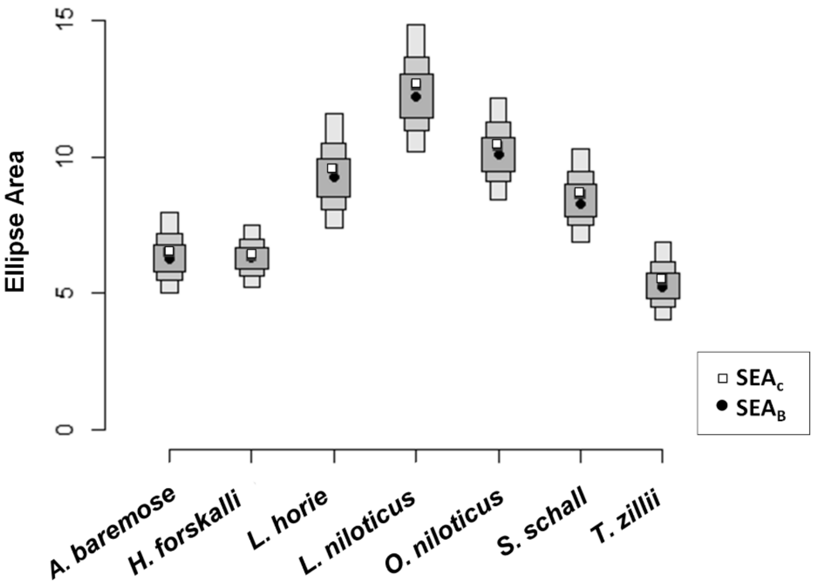

Figure 5.3: Box-plot of the Monte-Carlo stimulation for isotopic niches in R. This simulation accounts for the uncertainty in the isotope data and sizes of the isotopic niches. The black dot in each species' box-plot represents the average isotopic niche size from the Monte-Carlo stimulation, SEA$_B$, while the white box represents the SEA$_c$ isotopic niche value.

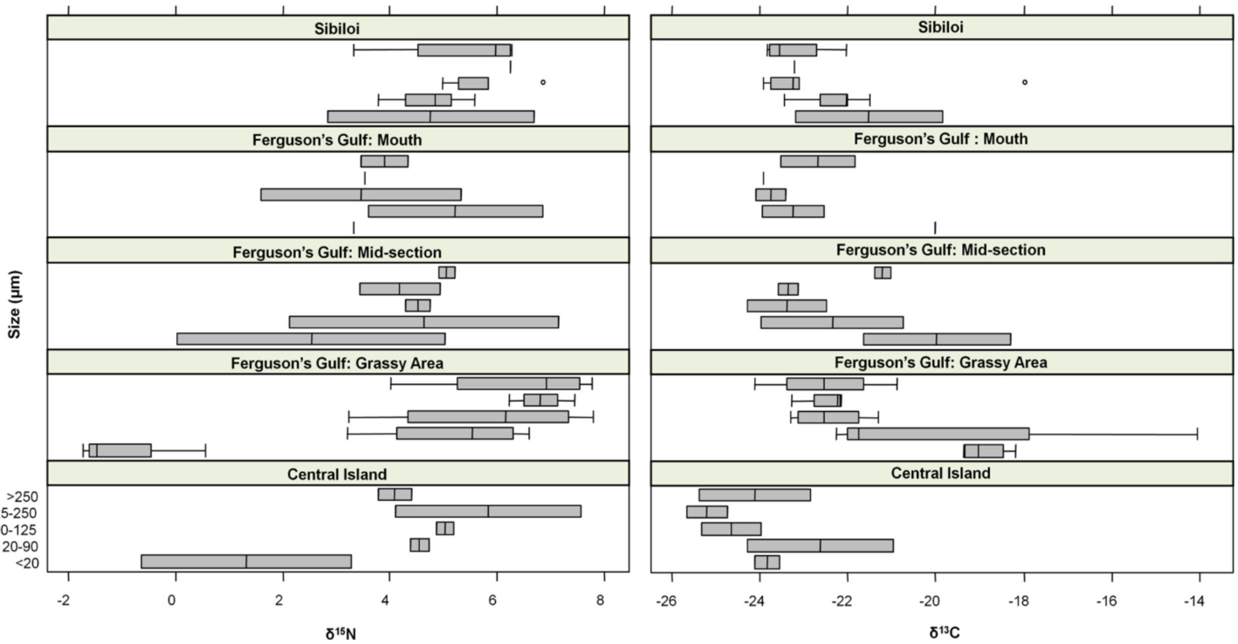

Figure 5.4: Box plot of phytoplankton baseline isotope signatures at the study's six sampling sites. Plankton samples were collected in five size fractions at each sampling site. Significant differences were found between the <20µm size class and all other size classes for δ^{13}C and δ^{15}N. Significant differences were found between the grassy gulf and open lake sites for δ^{13}C.

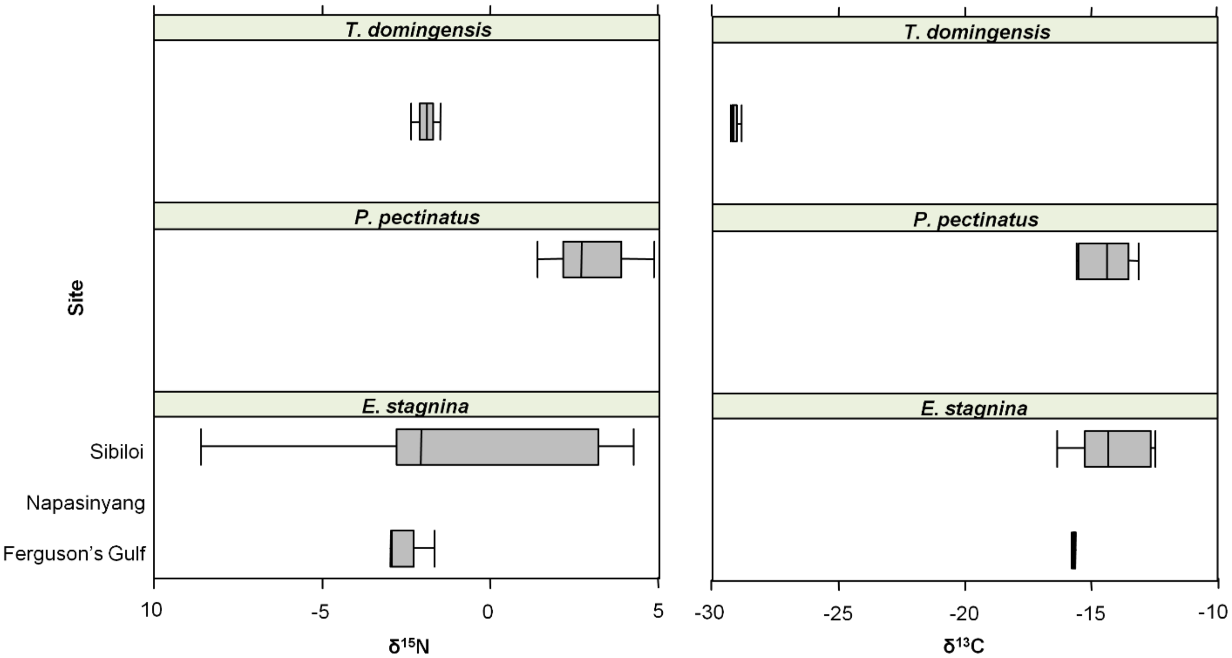

Figure 5.5: Box plot of attached primary producer isotope signatures at three of the study's littoral sites. Hippograss, *Echinochloa stagnina,* was the only species found at multiple sites. There was no significant difference in the signature of *Echinochloa stagnina* between Sibiloi and Ferguson's Gulf.

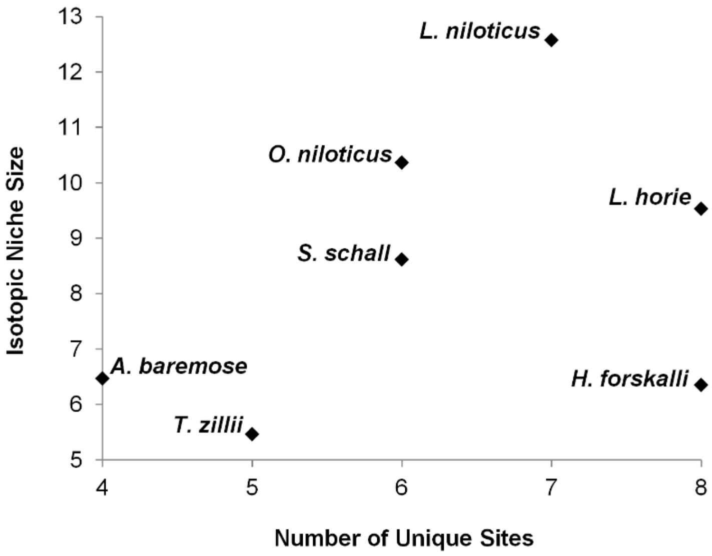

Figure 5.6: The relationship between the number of unique sites and isotopic niche size for each species. The number of unique sites was defined as any unique combinations of site and year at which >5 individuals of a species were sampled. There was no significant relationship beween number of unique sites and isotopic niche size across the species studied (r^2=0.15, p=0.39).

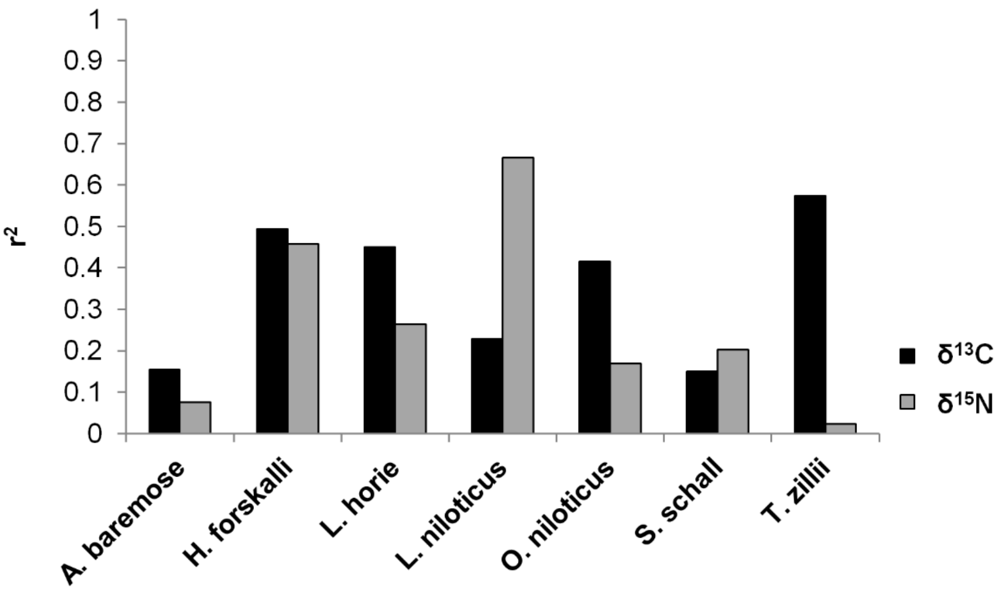

Figure 5.7: Variation in isotopic signature (r^2) described by site, year and their interaction terms. These values were calculated using size-corrected multivariate models, i.e. were run on the residuals of regressions between size and isotope signature for each species, and therefore account for differences in size ranges sampled across sites and years.

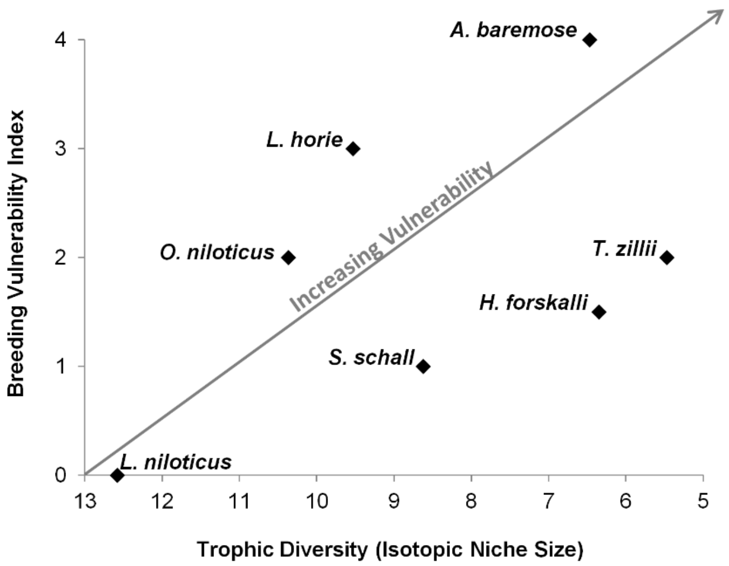

Figure 5.8: Breeding Vulnerability Index versus Trophic Diversity for the seven species studied. The Breeding Vulnerability index was calculated based on flood pulse dependence and breeding habitat requirements. Trophic Diversity (axis in reverse order) is represented by isotopic niche size, calculated using the $\delta^{13}C$ and $\delta^{15}N$ signatures for each species and standard ellipses in R. The grey line represents the direction of increasing vulnerability and is not a trendline.

Tables

Table 5.1: Diet and Fishery Contribution of the Seven Species Studied

Species	**N**	**1960-2011 Average Portion of Catch (%)**	**2011 Portion of Catch (%)**	**Assumed Main Diet Component**
A. baremoze	73	0.5	3	Zooplankton
H. forskallii	113	2.05	2	Fish
L. horie	77	16.48	14	Epibenthic algae/Detritus
L. niloticus	111	16.45	16	Fish/Prawns
O. niloticus	114	27.89	43	Phytoplankton
S. schall	92	2.46	3	Zooplankton/Insects/Benthos
T. zillii	55	N/A	N/A	Macrophytes/Epilithic algae

Table 5.2: Breeding Vulnerability Index Factor Categories and Their Scores

	Categories	**Description**	**Score**
Flood Pulse Dependence			
	Critical	Breeds exclusively during periods of spate.	2
	Moderate	Ripe females ≥50% more abundant during periods of spate.	1
	Low	Consistent breeding year-round or ripe females ≤50% more abundant during periods of spate.	0
Breeding Habitat			
	Most Threatened	Eastern Shore Shallow Areas (steep bathymetry) or Omo River	2
	Threatened	Western Shore Shallow Areas (gradual bathymetry) or All Rivers	1
	Least Threatened	Pelagic	0

Table 5.3: Mean ± SD of Isotopic Signatures, Isotopic Niche and Layman's Metrics for the Seven Species Studied

Species	**N**	**Mean $\delta^{13}C$**	**SD $\delta^{13}C$**	**Mean $\delta^{15}N$**	**SD $\delta^{15}N$**	**SEA_c**	**$Hull_b$**	**CD_b**	**$MNND_b$**	**sd $MNND_b$**
A. baremoze	73	-20.18	1.31	11.34	1.93	6.47	25.56	1.98	0.30	0.23
H. forskallii	113	-19.35	1.07	13.26	2.54	6.35	55.11	2.06	0.29	0.57
L. horie	77	-18.82	1.42	6.66	2.18	9.53	37.20	2.26	0.30	0.21
L. niloticus	111	-18.46	2.86	10.93	2.86	12.58	62.00	2.99	0.33	0.72
O. niloticus	114	-17.21	1.69	5.03	2.61	10.37	56.80	2.72	0.31	0.38
S. schall	92	-18.20	1.49	9.28	2.19	8.62	44.48	2.23	0.34	0.26
T. zillii	55	-16.68	1.33	7.22	1.39	5.47	29.64	1.50	0.44	0.52

Table 5.4: Bayesian Probability for Isotopic Niche Size Comparisons.

	A. baremoze	*H. forskallii*	*L. horie*	*L. niloticus*	*O. niloticus*	*S. schall*	*T. zillii*
A. baremoze	x	0.48	0.99	1	1	0.96	0.17
H. forskallii	0.52	x	1	1	1	0.98	0.15
L. horie	0.01	0	x	0.97	0.73	0.27	0
L. niloticus	0	0	0.03	x	0.08	0	0
O. niloticus	0	0	0.27	0.92	x	0.09	0
S. schall	0.04	0.02	0.73	1	0.91	x	0
T. zillii	0.83	0.85	1	1	1	1	x

Rows- Probability that one isotope niche is smaller than another; Columns- Probability that one isotopic niche is larger than another

Chapter 6: To Manage Fish We Must Manage Water: The Case of African Lakes

A version of this chapter has been submitted as the following:
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Introduction

Humans are profoundly altering hydrological cycles, including the magnitude of water level fluctuations (WLF), on local to global scales through the construction of impoundments, the extraction of water, and climate change (Poff et al. 2007, Döll et al. 2009, Haddelend et al. 2014). The magnitude of WLF is a key characteristic structuring lake ecosystems (e.g. Wantzen et al. 2008ab, Zohary and Ostrovsky 2011). In particular, natural WLF influence the productivity and species diversity of lakes and reservoirs. Seasonal pulses of water often carry nutrients from rivers or surrounding terrestrial ecosystems (Wantzen et al. 2008a). These external nutrient pulses are especially important in relatively shallow, highly fluctuating lakes (Jul-Larsen et al. 2003). In deeper, stratified lakes, WLF may influence internal mixing of nutrients and subsequently the productivity of surface water layers (Zohary and Ostrovsky 2011). Interactions within the aquatic/terrestrial transition zone (ATTZ), the portion of the littoral that fluctuates between wet and dry conditions dependent on seasonal WLF, lead to the accumulation and resuspension of nutrient-rich organic matter and subsequently enhanced productivity (Junk et al. 1989). The breeding movements of freshwater fishes, particularly in systems close to the equator that show little variability in temperature and day length, are often structured around seasonal precipitation patterns with associated WLF and related increases in productivity (Lowe-McConnell 1987, Gownaris et al. 2015).

Water level fluctuations also alter habitat availability, complexity and quality. Depending on the morphology of the system, relatively small changes in water level can lead to large variations in littoral habitat availability, influencing the breeding success of the fauna dependent on newly inundated areas. The region most directly influenced by WLF, the ATTZ, is characterized by high habitat complexity, providing optimal breeding and predatory refuge habitat (Wantzen et al. 2008a). Water level fluctuations may also influence habitat diversity by altering substrate availability (e.g. Gasith and Gafny 1990) and the coverage and diversity of shoreline vegetation (e.g. Hill et al. 1998). In shallow lake systems, for example, changes in WLF have been hypothesized to cause shifts between turbid, phytoplankton dominated and clear, macrophyte dominated states (Janssen et al. 2014).

Until recently, most research examining the importance of WLF in freshwater ecosystems has focused on rivers (e.g. Welcomme 1979, Junk et al. 1989, Welcomme and Halls 2001). Of the studies conducted on lakes, the majority refers to systems in Europe and North America, with far fewer focusing on tropical and subtropical lakes (Leira and Cantonati 2008). Studies in these latter areas are urgent given that upcoming hydropower development will be focused largely on tropical and subtropical regions (Zarfl et al. 2015).

Between 1991-2007, only 5% of the >200 studies published on WLF pertained to the African continent, which is home to some of the most highly fluctuating natural lakes in the world (Butzer 1971, Beadle 1981, Leira and Cantonati 2008). To provide an updated view on these statistics, a simple literature review was conducted using Web of Science. Literature search terms were chosen to mimic Leira and Cantonati (2008) and included "water-levels", "lake-levels", "fluctuation", "variation", "change", and "Africa" in logical combinations. However, the literature search conducted by Leira and Cantonati (2008) was more comprehensive (e.g. Leira and Cantonati 2008 browsed all abstracts), so their findings are not directly comparable to those of the current literature search. Instead, this literature search was used to compare the time period examined by Leira and Cantonati (2008), 1991-2007, to that of 2008-2015. Using these methods, WLF publication rates approximated 38 papers/year (depending on combination of terms) in 1991-2007, on average 11% of which related to African lakes. The rate of publications discussing WLF over the 2008-2015 time period were substantially higher, averaging approximately 92 publications per year. Only 9% of these publications related to Africa, however, suggesting that there is still a lack of research conducted on African Lake WLF.

The few studies that have been conducted on African Lakes show marked links among WLF, biodiversity and fisheries productivity. In Lake Kariba, for example, both inter- and intra-annual WLF show correlations with catch per unit effort, whereas absolute lake level does not (Karenge and Kolding 1995). When normalized by mean depth of the system, the magnitude of WLF is significantly correlated with yield and biodiversity across tropical lakes and reservoirs in Africa and Asia (Kolding and van Zwieten 2012). Furthermore, water levels and their fluctuations have been shown to be as important in predicting yield in African lakes as fishing effort variables are (Jul-Larsen et al. 2003).

Although these studies have furthered the understanding and appreciation of the influence of WLF on African lakes, it is still unclear how WLF influence the ecological structure underpinning fisheries productivity and composition. From a stability standpoint *sensu* Odum (1969), systems with higher magnitude WLF may be less stable and exist at an earlier successional stage than those with less extreme WLF. As a result, theories regarding ecosystem maturity and ecological disturbance may provide a useful framework for considering how ecosystems with differing WLF vary in terms of attributes related to community energetics and structure, nutrient cycling, life history, overall homeostasis, and fisheries (Table 6.1, Figure 6.1). In some cases, these attributes have direct implications for fisheries productivity. In others, they influence how ecosystem production and biomass are distributed across trophic levels, and thus the composition of catches.

Recorded inland fisheries account for approximately one-third of all capture fisheries production in Africa and employ over half of the continent’s fishers (de Graaf and Garibaldi 2014, FAO 2014). Reported catches from inland fisheries are widely regarded as underestimates (e.g. Bartley et al. 2015), so these fisheries may play an even more important role than currently recognized. Fish are also a vital source of protein and nutrients, particularly in the most poverty-stricken regions of Africa (Youn et al. 2014). Demand for fish products will increase concurrent with the continent’s rapidly growing human population (Gerland et al. 2014) and outgrow supply over the next decade (FAO 2014). Therefore, ensuring that African lakes are capable of maintaining a high level of fisheries productivity has widespread implications for the well-being of billions of people living in a continent known for its low adaptive capacity (Boko et al. 2007).

This study relies on a synthesis of Ecopath food web models to test the maturity hypothesis as a framework for comparing African lake ecosystems. Ecopath is the most widely used food web modeling software in aquatic systems, providing temporal ecosystem “snapshots” based on the principles of mass-balance (Christensen and Walters 2004, Colléter et al. 2015). The current synthesis includes 17 published Ecopath models, representing 13 African lakes and reservoirs that cover a broad geographic range (Figure 6.2). Data on sixteen ecological attributes related to the maturity categories outlined in Table 6.1 were compiled directly from Ecopath model publications or calculated using the data available in these publications, similar to other published syntheses (e.g. Pikitch et al. 2014).

This synthesis expands upon earlier Ecopath syntheses (Christensen and Pauly 1993, Christensen 1995) by incorporating a larger number of African lake ecosystems and by placing Odum's ecosystem maturity attributes in the context of WLF. The maturity hypothesis explored here is that the magnitude of WLF across systems will be negatively correlated with ecosystem maturity as measured by the sixteen ecological attributes recorded (Table 6.1, Figure 6.1). In testing this hypothesis, the ultimate goal is to predict the impacts of shifting a system to a state of higher or lower WLF due to flow regulations or climatic change. Understanding of the mechanisms by which African lake fisheries are influenced by WLF will aid in strengthening adaptive management in the face of increasing climatological, and hence also hydrological strains.

Methods

Food Web Models and Ecosystem Attributes

The number of ecosystems studied was constrained by the availability of published Ecopath models and water level data. When two models, representing two distinct time periods, were available for a system, both were used as was done by Christensen and Pauly (1993) and Christensen (1995). In most cases, data missing from publications were obtained directly from model authors, but data gaps persist for some attributes. Data gaps were as follows: 1) three models were missing values for the attributes of transfer efficiency (TE), mean trophic level of catch (MTLC), primary production over respiration (PP/R), and respiration over biomass (R/B) and 2) one model was missing a value for biomass over throughput (B/T) and for path length (PL).

Detailed descriptions of the attributes and how they were calculated can be found in Christensen et al. (2005). All data for a given attribute were converted to common units before analysis. Previous Ecopath syntheses have found that the number of model functional groups has no bearing on the attributes of interest to this study (Christensen and Pauly 1993, Christensen 1995) and preliminary analyses revealed no significant relationships with functional group number, so functional groups were not standardized. For example, SOI may be weakly correlated with the number of model functional groups in some cases (Christensen and Pauly 1993), but this correlation was not found for the current study. Furthermore, the functional group with the highest trophic level for each model consisted of either one species or a small group of closely related species, suggesting that the level of detail of groups (e.g. single species vs. feeding guild) did not influence the NoTL.

To avoid confounding biomass-related attributes, the detritus pool was excluded from calculations (Christensen 1995, Christensen and Pauly 1993). The detritus pool mainly serves as a repository for non-used production in a given Ecopath model and is thus dependent on the accuracy of the ecotrophic efficiency (EE) estimated for the model's functional groups. Ecotrophic efficiency describes the proportion of biomass of a given functional group that is removed by predation or fisheries and is often assumed to be 0.95 following Polovina (1984). The average EE of the models used in this synthesis ranged from 0.31 to 0.95. Several of these models, including those developed for Lake Victoria, Lake Tanganyika, Lake George and Lake Naivasha, relied heavily on the assumed value of 0.95 for their functional groups.

The number of trophic levels (NoTL) was calculated as fractional trophic level based on the published diet matrix for each model. Birds were excluded from the NoTL calculation, as they were only found in two systems (three models) and when present occupied the top trophic level. To quantify detritivory, a system detritivory index (SDI) was developed similar to system omnivory index (SOI), using a weighted average (based on the logarithm of each model group's consumption) of the proportion of detritus in functional groups based on the diet matrix (Christensen et al. 2005).

Water Level Data

Water level data availability varied by system and relied on gauge data for years preceding 1992 and satellite data for ensuing years (Table 6.2). Gauge data were obtained from experts working on the system and, when this was not possible, extracted from published figures using the program DataThief (Tummers 2006). Satellite data were collected from the USDA Global Lakes and Reservoirs Database and were available in approximately 10 day increments starting in 1992 (TOPEX/Poseidon satellite 1992-2003, Jason-1 satellite 2002-2009, OSTM satellite 2008-2015, USDA 2015). The values published online are relative to the satellite's reference datum for each system and had an accuracy of approximately ±10cm (Crétaux and Birkett 2006).

Water level data were not obtainable for Lake George, Uganda. Instead, WLF data for Lake Edward, a system directly connected to Lake George via the Kazinga channel, were used to estimate Lake George WLF. Lake Hayq, Ethiopia was the only system for which no seasonal data could be obtained. The number of years with water level data available for each system ranged from 11 years (Lake Edward) to 112 years (Lakes Victoria and Turkana) (Table 6.2).

The degree to which WLFs impact a given lake is highly dependent on that lake's average depth and physical morphology. As such, Kolding and van Zwieten (2012) proposed the use of relative lake level fluctuations in comparative studies (RLLF). Relative lake level fluctuations are calculated as Average Amplitude/Depth*100, where amplitude represents the difference between the maximum and minimum water level within a given year for seasonal fluctuations ($RLLF_s$) and the absolute difference between two sequential years for annual fluctuations ($RLLF_a$) and where depth represents mean system depth.

Due to the presence of outliers and heteroskedasticity in some of the WLF time series, temporal trends in WLFs were calculated using the Theil-Sen estimator (Theil 1950, Sen 1968). Table 6.2 shows that significant temporal trends in inter-annual WLF existed for six of the thirteen systems, half of which were positive and half negative. Trends in seasonal WLF were significant for ten of the systems and were overwhelmingly positive (Table 6.2). Previous research has found that gauge and satellite data for African lakes are in strong agreement (e.g. L. Tana, r^2=0.76: Ayana 2007, L. Victoria r^2=0.99: Crétaux et al. 2011, L. Kivu, r^2=0.85, Munyaneza et al. 2009), suggesting that data obtained from these sources are comparable.

The time period chosen for the calculation of RLLF was 1990's-2000's, for several reasons: 1) this was the most consistent time period for which lake level data were available across systems, 2) this time period overlapped temporally with many of the Ecopath models synthesized, and 3) high quality satellite monitoring for the systems of study began in 1992. There was a strong, significant positive correlation between the RLLF values calculated for the

1990's-2000's and the RLLF values calculated for the full time series among systems at both annual ($r^2=0.96$, $p<0.0001$) and seasonal ($r^2=0.94$, $p<0.0001$) scales.

Kolding and van Zwieten (2012) summarize a variety of static metrics used to relate chemo-physical characteristics with productivity and species diversity in lakes. To explore the importance of physical characteristics other than RLLF in determining food web structure, data on these characteristics were collected from relevant online databases and publications. Where possible, data collection focused on the International Lake Environment Committee Foundation (ILEC) World Lakes Database for consistency across systems. Physical characteristics collected included climatic (latitude- Lat, altitude- Alt), morphologic (surface area- SA, average depth- D, volume- V, residence time- RT), and hydrologic variables (RLLFs, RLLFa, catchment area- CA) following Kolding and van Zwieten (2012).

Data Analysis and Statistical Approaches

Analysis of the relationships between physical characteristics, including RLLF, and ecosystem attributes was conducted using linear models and principal component analysis (PCA). Sub-hypotheses for specific ecosystem attributes were based on the primary hypothesis that RLLF would be negatively correlated with ecosystem maturity and on expected relationships between these attributes and ecosystem maturity (Table 6.1). To determine whether RLLF are useful in differentiating African lakes and reservoirs, a PCA was run on the matrix of all physical characteristics compiled (PCA_{PC}). The descriptive modes of PCA_{PC} were chosen based on the Kaiser-Guttman criterion (Jackson 1993), which retains modes with eigenvalues greater than mean eigenvalues, and confirmed using the broken stick model, which retains modes that explain a greater variance than the variance explained by random eigenvalues generated for a same-length vector. Linear models were used to determine which PCA_{PC} modes were the best descriptors of ecosystem attributes. Similarly, a PCA was run on the matrix of all ecosystem attributes compiled (PCA_{EA}) to determine whether their descriptive modes coincided with Odum's (1969) ecosystem maturity categories and whether they were related to RLLF.

Ecosystem Biomass and Production

Due to their influence on several other ecosystem attributes of interest and their recent attention in the literature (Link et al. 2015, Kolding et al. 2015), additional analyses were conducted to examine relationships between biomass, production and disturbance. For these analyses, the African lakes and reservoirs of study were broken up into two categories: low RLLF (<2.5) and high RLLF (>2.5). A cut-off of 2.5 was chosen to approximate an even number of systems within each group and because many of the systems with RLLF > 2.5 were small, shallow lakes. These groups were then compared in two ways. First, the slopes of changes in log biomass and log production, respectively, with trophic level were calculated for both groups (following Kolding et al. 2015). Secondly, relationships among cumulative average production (cumP), cumulative average biomass (cumB), and trophic level were examined following Link et al. (2015).

Results

Ecosystem Models

The majority of the published Ecopath models examined here were built using ecosystem data from the 1970's-1990's, with a few models relying on data from the 2000's (Table 6.2). The number of species or functional groups ranged from 7 (pelagic zone of Lake Tanganyika) to 25 (Lake Malawi), with an average of 14. Of the ecosystem attributes Odum (1969) used to scale system maturation, and of attributes related to fisheries, 16 were calculated using the Ecopath data (Table 6.1, Figure 6.1). These 16 ecological attributes were used to conduct the linear regression and principle component analyses discussed below.

Relative Lake Level Fluctuations

$RLLF_a$ values varied from 0.04 (Lake Tanganyika) to 38.70 (Lake Nakuru), with 10 of the 13 systems having $RLLF_a$ values between 0 and 5 (Table 6.2). Similarly, $RLLF_s$ ranged from 0.11 (Lake Kivu) to 40.77 (Lake Nakuru), but 9 of the 12 systems had $RLLF_s$ between 0 and 20 (Table 6.2). Seasonal ($RLLF_s$) and annual ($RLLF_a$) fluctuations were positively correlated with one another ($r^2=0.69$, $p<0.0001$).

Linear Regression Analysis

Sample size for regressions between ecosystem attributes from Ecopath models and $RLLF_a$ ranged from 14-17, with the same regressions having a sample size of 13-16 for $RLLF_s$ due to the lack of seasonal data for Lake Hayq. Most relationships between $RLLF_a$ and ecosystem attributes were linear or exponential (Table 6.3). The strongest relationships existed between $RLLF_a$ and B/T, NoTL, and NoFish (Table 6.3). Similar relationships were seen between $RLLF_s$ and ecosystem attributes, though were in many cases stronger than those seen for $RLLF_a$ (Table 6.3). The strongest relationships for $RLLF_s$ were related to biomass, including B, B/T, R/B, and PP/B (Table 6.3). When considering these ecosystem attributes by category, community energetics and structure are the most consistently related to RLLF, with nutrient cycling showing the weakest links to RLLF (Table 6.3).

Principle Component Analyses

The Kaiser-Guttman criterion identified the first three modes of the PCA_{PC} as descriptive (Figure 6.3), while the broken stick model only identified the first mode of PCA_{PC} as descriptive. The second and third modes, however, approximated the cut-off for the broken stick method and were therefore retained for further analyses. The first three modes described approximately 81% of the variability in the physical characteristic dataset. The first mode was driven by a positive relationship among parameters related to the size of the system (+RT, +V, +D) and their negative relationship with seasonal fluctuations ($RLLF_s$) (Figure 6.4). The second mode was characterized by positive relationships among RT, Alt, and $RLLF_a$, which were negatively correlated with CA. For the third mode, the most important drivers were positive relationships between $RLLF_a$ and $RLLF_s$, which were positively correlated with CA and negatively correlated with Lat.

The Kaiser-Guttman criterion and broken stick model identified four important modes from the PCA_{EA} analysis (Figure 6.3). These four modes describe 77.7% of the variability in the dataset, with the first two modes alone accounting for over 50% of the described variability (Figure 6.3). None of these descriptive modes coincide directly with Odum's maturity categories. The first mode is driven largely by community energetics related to production and biomass (-B, -B/T, -P, -PP), which show a negative relationship with the length and efficiency of the food chain (+NoTL, +TE, Figure 6.4). This was the only descriptive mode significantly correlated with RLLF ($RLLF_a$: $r^2=0.65$, $p<0.001$, $RLLF_s$: $r^2=0.82$, $p<0.0001$). Therefore, of the attributes studied, those related to production, biomass and food web efficiency and length were most directly related to RLLF. For the second mode, several characteristics thought to increase with maturity (-PL, -R/B, -SDI) showed the opposite sign of catch and its mean trophic level (+Catch, +MTLC). Production attributes were drivers of the third mode (-P, -PP, -PP/R) along with fish diversity, organism size, and detritivory (+NoFish, +B/P, +SDI). The last descriptive mode showed similar relationships, with detritivory (-SDI) negatively related to production attributes (+P, -PP), homeostasis (R/B) and the mean trophic level of catch (+MTLC).

Nine of the ecological attributes studied were particularly related to the PCA_{PC} first mode. Two bore marked relationship with the second mode, and five to the third mode (Table 6.2). The strongest of these relationships were positive, between the first mode and the NoTL and NoFish, respectively, and between the third mode and PP (Table 6.3). While RLLF alone was the best physical descriptor of some ecosystem attributes, other ecosystem attributes were better described by a combination of physical characteristics that included RLLF (e.g. PCA_{PC} modes one and three).

Ecosystem Biomass and Production

Biomass (high RLLF: $b=-0.59$, $r^2=0.92$, $p<0.01$, low RLLF: $b=-0.31$, $r^2=0.73$, $p<0.05$) and production (high RLLF: $b=-1.4$, $r^2=0.98$, $p<0.001$, low RLLF: $b=-1.0$, $r^2=0.95$, $p<0.01$) decrease at a faster rate as TL increases in high RLLF systems than in low RLLF systems. Regressions between cumB and cumP and between cumB and trophic level are best described by logistic curves (Figure 6.5), which are situated closer to the origin for low RLLF systems than for high RLLF systems. Inflection points for cumB (y axis) occurred at a similar %cumB for both groups, but the trophic level inflection point (x axis) was lower for high RLLF systems than for low RLLF systems (Figure 6.5).

Discussion

African lake fisheries face profound shifts in productivity and species composition due to water regulation and extraction, the impacts of which will be compounded by climate change. Most regions in Africa have already experienced increases in average, minimum or maximum temperatures due to climate change (Boko et al. 2007), with implications for evaporative water loss from aquatic systems. Based on the Intergovernmental Panel on Climate Change (IPCC) model projections, precipitation in East and Central Africa is expected to increase (Christensen et al. 2007, IPCC 2014). Observations to date do not seem to support this trend (e.g. Lott et al. 2013, Mottram et al. 2014). However, the prediction of widespread increased variability in precipitation across the continent is undisputed (e.g. Sahel: Dai et al. 2004, southern Africa: Tadross et al. 2005).

The water level time series used here demonstrates that changes to African lake WLF regimes are already taking place. The majority of the African lakes analyzed in this study showed significant temporal trends in annual (six systems) and/or seasonal (ten systems) WLF. Increased instability in the annual water levels of several large African lakes (Lakes Victoria, Tanganyika and Turkana) have been noted elsewhere, though we did not find significant trends for some of these systems (c.f. Boko et al. 2007). Importantly, seasonal WLF trends were nearly all positive and therefore consistent with the drier dry seasons and wetter wet seasons expected from climate change.

Africa is also likely to show considerable growth in dam construction over the coming decades (Zarfl et al. 2015) as it is thought to have a large untapped hydroelectricity potential. In fact, several large dam projects (e.g. the Gibe III Dam and Grand Ethiopian Renaissance Dam in

Ethiopia, the Grand Inga Dam in the DR Congo) are currently proposed or underway. The continent's growing population will create further demand for electricity and water consumption. Though hydropower development has the possibility to support socioeconomic improvements in African countries (Ayenew 2015), avoiding unnecessary ecological consequences requires considerable research into the understanding and maintenance of ecologically sufficient WLF regimes. Unfortunately, this kind of research is rarely conducted before dams are established. The construction of dams may reverse the trend of climate change-induced increases in RLLF for some African lakes. For example, the Gilgel Gibe III Dam in Ethiopia is expected to substantially dampen the seasonal flood pulse of Lake Turkana, Kenya (Avery 2012).

Role of Water Level Fluctuations in African Lakes

The analyses conducted here suggest that WLF, expressed as RLLF, are strong drivers of several ecosystem attributes. In fact, in many cases, RLLF was the dominant physical characteristic of these systems, describing more variability in ecosystem attributes than any combination of physical characteristics. Though $RLLF_s$ and $RLLF_a$ are highly correlated with each other, seasonal fluctuations seem to be particularly important to the ecosystem functioning of African lakes. Seasonal fluctuations may also be more sensitive to short-term anthropogenic effects, such as regulation of rivers for hydropower production, than are those that occur at inter-annual scales. Fluctuations occurring at inter-annual scales may, however, be strongly influenced by longer-term processes such as the intensification of El Niño events resulting from climate change (e.g. Cai et al. 2014).

African lakes with high RLLF in this synthesis showed higher rates of primary and overall ecosystem production and supported a greater biomass than those with low RLLF, although mainly at lower trophic levels. It is possible, however, that production rates would begin to decline at more extreme RLLF. In agreement with the dome-shaped relationship hypothesized by others (i.e. Kolding and van Zwieten 2012), the relationship between production and RLLF in this study appears to be nonlinear. These findings have considerable ramifications for maximizing inland fisheries production in Africa. Primary productivity shows a significant positive correlation with fisheries productivity of lakes within Africa (Melack 1976) and elsewhere (Downing et al. 1990). Lakes that support a higher biomass production can also presumably withstand higher rates of biomass removal by fisheries. Given these relationships, any factor decreasing the magnitude of RLLF within African lakes- e.g. dams and their reservoir lakes- is likely to lead to a reduction in fisheries productivity. It should be noted that this study did not find the expected significant relationship between catch and RLLF, as was found by Kolding and van Zwieten (2012) for sixteen African lakes and reservoirs. This unexpected result may be due to the temporal "snapshot" nature of the catch statistics included in Ecopath models, particularly given the notoriously fluctuating nature of many African lake fisheries.

Underlying the more direct fisheries-related attributes are those that determine species diversity and community structure. These attributes have both inherent value and implications for the species composition of African inland fisheries. High RLLF lakes are less efficient at transferring energy to higher trophic levels (TE, NoTL) and support fewer species than do more stable systems (NoFish). Food chain length and fish diversity have been linked to ecosystem productivity (NoTL: Takimoto and Post 2012, NoFish: Pianka 1966, Dodson et al. 2000), complexity (NoTL: Post 2000, NoFish: Amarasinghe and Welcomme 2002), and disturbance (NoTL: Pimm and Lawton 1978, Power et al. 1996, NoFish: Kolding and van Zwieten 2012). The lower transfer efficiency within high RLLF lakes translates not only to fewer trophic levels but also to a steeper drop in biomass with trophic level in these systems as compared to low RLLF lakes (Figure 6.5.5).

Despite decades of research, the mechanisms controlling fish diversity and food web length in ecosystems are still uncertain and debated (e.g. Waide et al. 1999, Takimoto and Post 2012, Warfe et al. 2013). The results of this study are consistent with Vander Zanden and Fetzer (2007), who showed that amongst aquatic ecosystems relatively stable marine systems had, on average, a slightly greater number of trophic levels than did lake systems, and that highly fluctuating stream ecosystems had the shortest food webs of all. The average number of trophic levels among systems in this study (3.52±0.66 SD) compared best with the average for streams (3.46±0.42 SD) rather than with that of lakes (3.95±0.50 SD) (Vander Zanden and Fetzer 2007), possibly due to the high dependence of many of the African lakes on riverine inflow (Kolding and van Zwieten 2006, Kolding and van Zwieten 2012). Furthermore, Vander Zanden and Fetzer's synthesis (2007) focused heavily on temperate freshwater ecosystems, which are more stable in terms of WLF than those in tropical regions.

This synthesis also showed that high RLLF systems tend to have a lower occurrence of omnivory (i.e. narrower dietary niches) than do relatively stable low RLLF systems. While these results differ from what would be expected based on the ecosystem maturity framework, they agree with those of Thompson et al. (2007), who found omnivory to be more prevalent in relatively stable marine ecosystems than in stream ecosystems. All three of the community structure attributes considered are thought to impact ecosystem stability (NoTL: Pimm and Lawton 1978, Post 2002, NoFish: Lévêque 1995, McCann 2000, Gross et al. 2014, SOI: Pimm et al. 1991, Vandermeer 2006, Long et al. 2011), highlighting the existence of complex feedback loops between structure and stability.

This study suggested direct impacts of WLF on fisheries composition, as the mean trophic level of catch (MTLC) was negatively correlated with both $RLLF_a$ and $RLLF_s$. This finding, however, should be considered with caution given the strong relationship between RLLF and NoTL and the uncertainly regarding Ecopath estimated yields. Low trophic level species, including tilapia, cyprinids, and characins, are central components of many African lake fisheries, including those of both highly fluctuating and relatively stable nature. Tilapia often thrive in high RLLF environments as they benefit from a large ATTZ (Kolding 1993a). In many of the lower RLLF lakes examined in this study, existing fisheries focus on small pelagic fishes (e.g. "Kapenta" fishery in Lakes Tanganyika and Kivu, "Dagaa" fishery in Lake Victoria), which can be immensely productive but are also highly sensitive to changes in hydrological regimes (e.g. Sarch and Allison 2001, Karenge and Kolding 1995, Kolding et al. *in press*).

Overall, these findings suggest that altering WLF has major implications for the productivity and composition of African lake fisheries. Environmental considerations including hydrological regimes must be considered in managing the fisheries of African Lakes, particularly where they are known to be important drivers of productivity (e.g. Lake Kariba: Karenge and Kolding 1995, Lake Turkana: Kolding 1995). This point has been argued by experts working on African lake fisheries for over a decade (e.g. Allison and Ellis 2001, Jul-Larsen et al. 2003, Andrew et al. 2007), yet a comprehensive means of incorporating environmental considerations into management plans has yet to be adopted and implemented.

Water Level Fluctuations, Maturity and Stability

Though sometimes treated as straightforward in the literature, the relationships between ecological disturbance, stability and maturity are complex (Kolding 1997) and still poorly understood. The results of this study highlight the complexity of the relationship between one form of disturbance (WLF) and ecosystem maturity. Though the majority of the ecosystem attributes exhibit the relationship expected with RLLF based on the ecosystem maturity hypothesis (Table 6.1, Table 6.3), several show no trend or the opposite trend to what was expected. One such attribute was path length, a measure of how many groups a given inflow or outflow passes through, which is one of the most commonly used indicators of ecosystem maturity but showed no significant relationship with RLLF in this synthesis (Christensen and Pauly 1993). The Shrodinger Ratio (R/B), thought to be a direct measure of stability (Christensen 1995), does show the expected relationship (negative) with $RLLF_s$ but not with $RLLF_a$. Due to these conflicting results, the working hypothesis that RLLF would be negatively correlated with ecosystem maturity is not supported.

The most consistently unexpected relationships were those between RLLF and biomass-related attributes (B, PP/B, B/P). The ecosystem maturity hypothesis predicts that biomass will build up in a system as it matures and primary production begins to exceed respiration needs. Interestingly, all of the systems in this study showed a PP/R ratio of greater than one, with one system exhibiting an extremely high PP/R (>8, L. Kariba). The relationship between PP/R and RLLF (both annual and seasonal) was parabolic in this study, but showed the hypothesized increase over $RLLF_a$ from 0-5 and $RLLF_s$ from 0-20. Trends in this ratio therefore do not seem to explain the unexpected exponential relationship between RLLF and biomass.

One possible explanation for the unexpected relationship between RLLF and biomass is the exclusion of detritus from biomass calculations in this study, as has been done in earlier studies (Christensen and Pauly 1993, Christensen 1995). Detritus is thought to become more abundant and detritivory more prominent as an ecosystem matures (Odum 1969). If a large portion of the biomass present in mature stable systems exists as detritus, this may hinder the ability to capture the true relationship between RLLF and biomass. Interestingly, we found that detritivory (SDI) increased with RLLF, rather than decreased as expected based on ecosystem maturity theory. A greater capacity for biomass production among highly fluctuating lakes as compared to stable lakes is a thought-provoking outcome of this analysis and should be examined further.

Despite the large body of literature that already exists, more research must be conducted on the relationships between regular disturbance, punctuated disturbance, stability, and maturity. Understanding these relationships are particularly important for aquatic ecosystems, due to their differences in community structure as compared to terrestrial ecosystems, which are better studied in terms of maturity theory and form the basis for many of Odum’s ideas. The most striking difference between these systems occurs at the base of the food web, given the low turnover rates but high biomass of terrestrial vegetation and high turnover rates but low biomass of aquatic phytoplankton. It is possible that these differences played into the unexpected relationships between biomass and RLLF.

More specifically, the implications of changes in the frequency of punctuated disturbance versus changes in the magnitude of regular disturbance must be considered further, as humans are likely to alter both in the coming decades. Organisms cannot adapt to punctuated disturbance that increases WLF drastically and temporarily, such as the occurrence of an anomalous flood, but can and do adapt to regular disturbance such as seasonal floods (Wantzen et al. 2008b). The differences between the ecosystem consequences of punctuated disturbance are of interest in comparing the results of this study to those of Link et al. (2015). While Link et al. (2015) found that perturbation led to reduced production and biomass within marine ecosystems, this study showed that lakes with higher magnitude RLLF (a form of regular disturbance) actually have higher rates of production and support a greater biomass than those experiencing lower magnitude RLLF. However, the cumulative biomass of African lakes begins to slow at a lower trophic level in highly fluctuating systems than in relatively stable systems, indicating greater perturbation based on Link et al.'s (2015) conclusions.

Research Comparisons and Needs

While some studies have compared maturity-related ecosystem attributes within a system at different time points (e.g. Heymans et al. 2004, Nuttall et al. 2011, Geers et al. 2014), none of these studies have related changes to WLF in lakes. For example, Nuttall et al. (2011) found a decrease in the ecosystem maturity of Great South Bay, NY throughout the 20th century, due to a combination of factors including nutrient pollution, inlet al.teration, and overfishing. Instead of examining historical changes in ecosystem maturity trajectories, Geers et al. (2014) determined the impact of future fishing management strategies for menhaden on the Gulf of Mexico ecosystem, concluding that increased fishing pressure would result in decreased ecosystem maturity. As in this study, not all of the ecosystem maturity attributes examined by Nuttall et al. (2011) and Geers et al. (2014) fit the expected trend. In contrast with this study, however, biomass tended to increase as a function of perceived ecosystem maturity in both cases.

Of within system comparisons using Ecopath models, few on African lakes have focused on the impacts of hydrological disturbance on community structure. The impact of changes to absolute water level was the primary disturbance examined by Kolding (1993b) for Lake Turkana, Kenya. Kolding (1993b) found that the community structure of Lake Turkana changed substantially from 1973 (relatively high lake level) to 1987 (relatively low lake level). These changes included a shift from a primarily bottom-up system to one controlled by top-down processes (Kolding 1993b). Perhaps of most interest to the impact of WLF are studies comparing eastern boundary current upwelling systems in La Niña and El Niño years (e.g. Northern Humboldt: Tam et al. 2008). Strong periods of upwelling in marine ecosystems are comparable to periods of high riverine inflow in lentic systems, given the influence of both on nutrient and food availability. Although ecosystem maturity was not the focus of the work conducted by Tam et al. (2008), many of their findings regarding differences in ecosystem structure between periods of weak and strong upwelling are in agreement with this study. For example, strong upwelling (La Niña) years showed greater overall production, primary production, biomass and lower transfer efficiency and trophic level of catch than weak upwelling (El Niño) years (Tam et al. 2008).

Even among the relatively well-studied Great Lakes of North America, research on the community-wide impacts of WLF within a system are scarce. Most research focuses on macrophyte community health (Leira and Cantonati 2008), which, while critical, is only one component of ecosystem functioning. Keogh et al. (1999) found that seasonal WLF in these large lakes averages 0.2-0.6m, considerably lower than some of the African lakes studied here (range of 0.3-1.8m). Chow-Fraser et al. (1998) found that changes in water level had community-wide implications for macrophyte, plankton, invertebrate and fish in the Cootes Paradise Marsh of Lake Ontario. White et al. (2008) studied changes in water quality parameters and in macrophyte and invertebrate community health in relation to WLF of sixteen small lakes in the Great Lakes region. Seasonal fluctuations of these small lakes were as high as 1.27 m and have decreased over the past twenty years, in contrast to the temporal trend seen for most of the African lakes used in the current synthesis. Depending on the lake studied, WLF at inter- and intra-annual scales had significant impacts on dissolved organic carbon, pH, and conductivity and on sulfate and calcium concentrations (White et al. 2008). The response of macroinvertebrates to inter-annual WLF was in agreement with the intermediate disturbance hypothesis, with the greatest species richness of macroinvertebrate communities coinciding with years of intermediate WLF (White et al. 2008).

Similarly, the influence of WLF on rivers was widely recognized by the scientific community decades before their influence on lakes was (e.g. Welcomme 1979, Junk et al. 1989, Wantzen et al. 2008b). The body of literature on WLF impacts in riverine ecosystems is therefore much more extensive. Poff and Zimmerman (2010) conducted a meta-analysis of this research that suggests macroinvertebrate diversity and abundance show conflicting responses to altered flow regimes, but that fish diversity and abundance nearly always decline in response to altered riverine flows. This meta-analysis also found that, even among rivers, research on ecosystem-wide processes, such as those compiled in this synthesis, is largely nonexistent (Poff and Zimmerman 2010).

Limitations of Ecopath Model Syntheses

The limitations of the Ecopath modelling suite have been outlined in several other places (Christensen and Walters 2004, Plaganyi and Butterworth 2004, Ainsworth and Walters 2015). These discussions, however, often focus on the suitability of Ecosim, a dynamic model that can be coupled with Ecopath, for informing fisheries management decisions. Instead, a brief description of the Ecopath caveats related specifically to the findings of this synthesis will be included here.

As with any model, the quality of a given Ecopath model is highly dependent on the applicability and accuracy of the input data. Input data vary in quality from low quality “guestimates” to higher quality “same group/species, same system” (Christensen and Walters 2004). Furthermore, model creators may need to combine data collected over different years and, in some cases, decades. To facilitate understanding of the limitations associated with different Ecopath models, a pedigree index was developed that ranges from 0 (poor quality model) to 1 (high quality model) and is based on the quality of input data (Pauly et al. 2000).

Data quality limitations have several implications for the current synthesis. First is that many of the models used in this synthesis were created prior to development of the pedigree index, which was released in 2000. Only five of these models were created after 2000 and only three include published pedigree values, all of which suggest fairly high quality models (Lake Malawi-0.61, Lake Hayq-0.64, Lake Tana-0.86). Nine of the models synthesized (Kolding 1993b, Machena et al. 1993, Moreau et al. 1993a-c, Palomares et al. 1993) were published in the same conference proceeding, suggesting that expectations regarding the level of input data quality may have been similar. In addition, many of the models used in this synthesis relied on data collected from several different time periods. As Plaganyi and Butterworth (2004) point out, the time period over which collected data is relevant will be dependent on how variable the system is. It may therefore be possible that the high RLLF systems used in this study were depicted less accurately than were the relatively stable low RLLF systems.

The last issue of relevance is that of ecotrophic efficiency (EE). This parameter is often adjusted to balance the other basic input parameters in Ecopath models and accounts for the amount of production used for predation or export (fisheries). When data on other basic input parameters is limited, model developers will often assign an EE of 0.95 to functional groups, as this value was used in the original Ecopath model developed by Polovina (1984) based on work conducted by Ricker (1968). The EE of the models used in this synthesis varied substantially, with a few of the models relying heavily on the standard value of 0.95. In addition to its bearing on the other input parameters, the 1-EE determines the proportion of biomass in a given system that winds up in the detritus pool. Detritus and the role of detritivory weigh heavily into the ecosystem maturity concept *sensu* Odum (1969). As discussed, uncertainties regarding EE limit the ability to reach conclusions regarding detritus using Ecopath models.

The shortcomings of Ecopath models make the significant relationships between RLLF and ecosystem attributes in this synthesis even more compelling. These relationships held despite other disturbances present in the ecosystems studied, including eutrophication, overfishing and invasive species introductions (e.g. Cohen et al. 1996, Odada et al. 2003, Ogutu-Ohwayo and Balirwa 2006), and differences among Ecopath models in terms of their complexity and purpose. The ability of these trends to stand out regardless of unrelated system and model disparities suggest that RLLF are unequivocally important to ecosystem structure. Any synthesis across systems will face similar caveats, yet the ability to recognize the observed strong trends using a relatively small sample size suggests that Ecopath is a valuable tool for comparing freshwater ecosystems. The utility of Ecopath models for synthesis studies is greatly aided by the widespread nature of this modelling software, with over 500 peer-reviewed Ecopath publications to date (Colléter et al. 2015).

Conclusions

Regulation of waterways and climate change are modifying WLF regimes globally, the impacts of which are likely to be acutely felt in Africa due to its vulnerability to food shortages. This synthesis is the first to explore the relationships between WLF and processes at the ecosystem scale among African lakes. Increasing the WLF of tropical lakes and reservoirs is likely to increase their primary production and the biomass they support, but to also decrease their fish diversity and the connectivity (SOI), transfer efficiency (TE) and length (NoTL) of their food webs, and thereby diversity. Reducing WLF could have the opposite impact, decreasing primary production and biomass, but increasing fish diversity and food web connectivity, efficiency and length. These ecosystem changes will have implications for the productivity and species composition of inland fisheries in Africa, which are a vital source of protein and nutrients for its growing population. This synthesis and other research conducted over the past decade have provided an enhanced understanding of and appreciation for the influence of WLF on freshwater ecosystems, and particularly their fisheries. However, there is still much to be learned about how these fluctuations affect ecosystem-wide processes in lakes in Africa and elsewhere.

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Figures

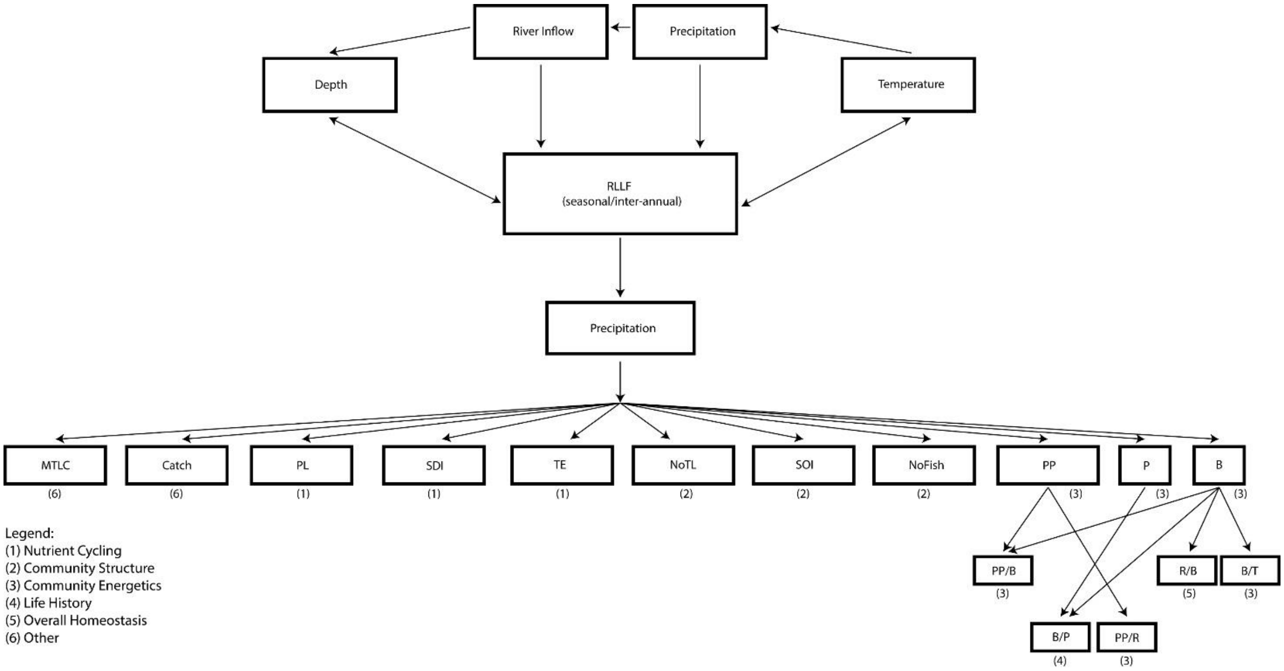


Figure 6.1: Conceptual Diagram showing connections between relative lake level fluctuations (RLLF), stability/maturity, and physical characteristics (see Table 6.1 for acronym descriptions).

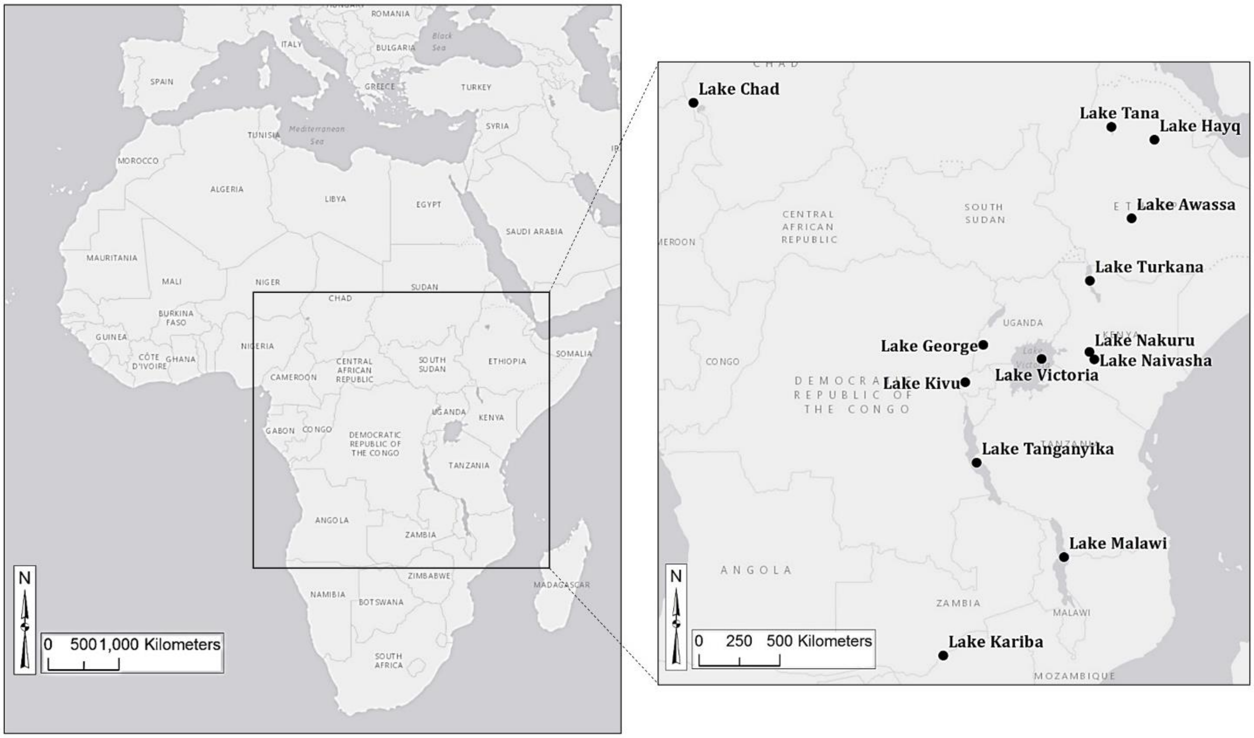


Figure 6.2: Map showing the locations of the thirteen lakes and reservoirs synthesized.

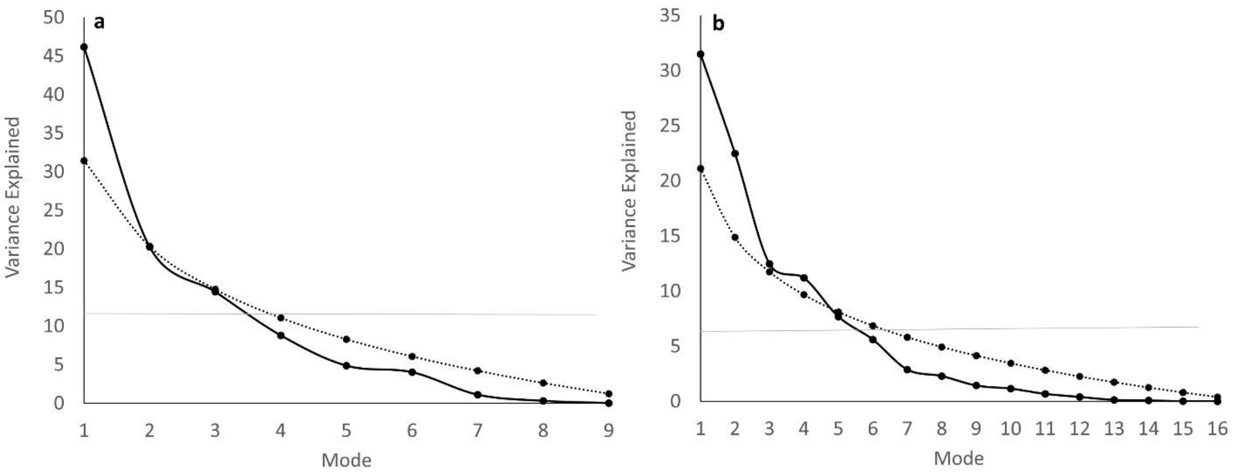


Figure 6.3: Variance explained by the eigenvalues of the physical characteristic (3.a) and ecosystem attribute (3.b) principal components (solid lines) and results of the broken stick model (dashed lines). Horizontal grey line shows the mean variance explained by the eigenvalues. Descriptive modes are those that lie above the horizontal line (Kaiser-Guttman criterion) and for which the variance explained > broken stick model value (solid line lies above dashed line).

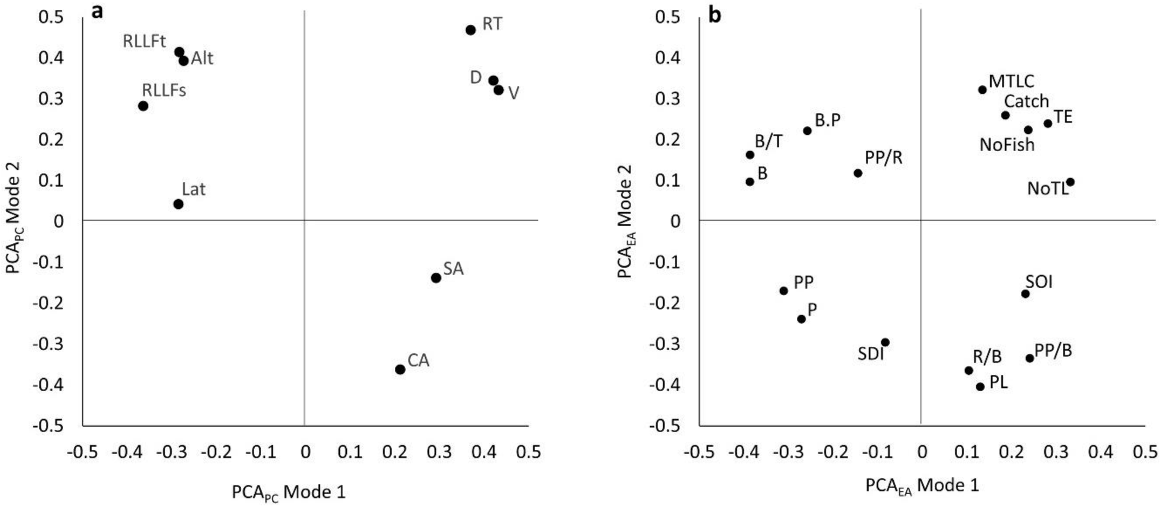


Figure 6.4: Loading values for the first two principal components of the physical characteristic (4.a) and ecosystem attribute (4.b) data matrices (see Table 6.1 for acronym descriptions).

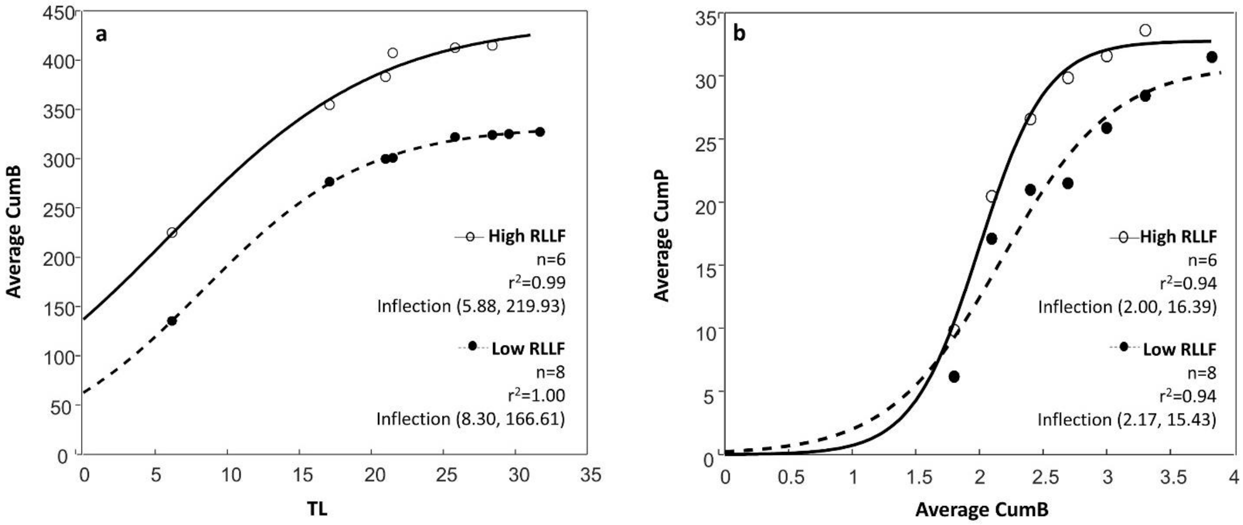
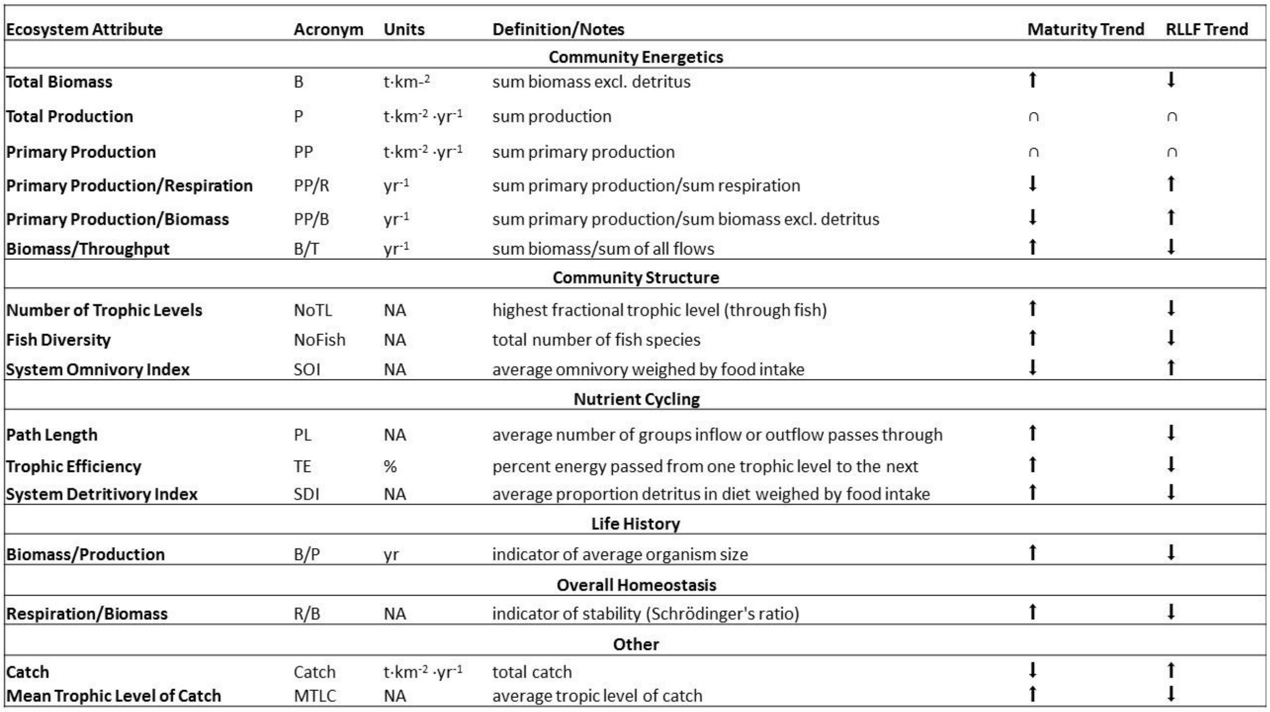


Figure 6.5: Logistic regressions showing the relationship between 5a: average cumulative biomass and trophic level (in bins of 0.3 trophic levels) and 5b: average cumulative production and average cumulative biomass. The low relative lake level fluctuations category represents systems with RLLFa<2.5, while high RLLFa systems have RLLFa>2.5.

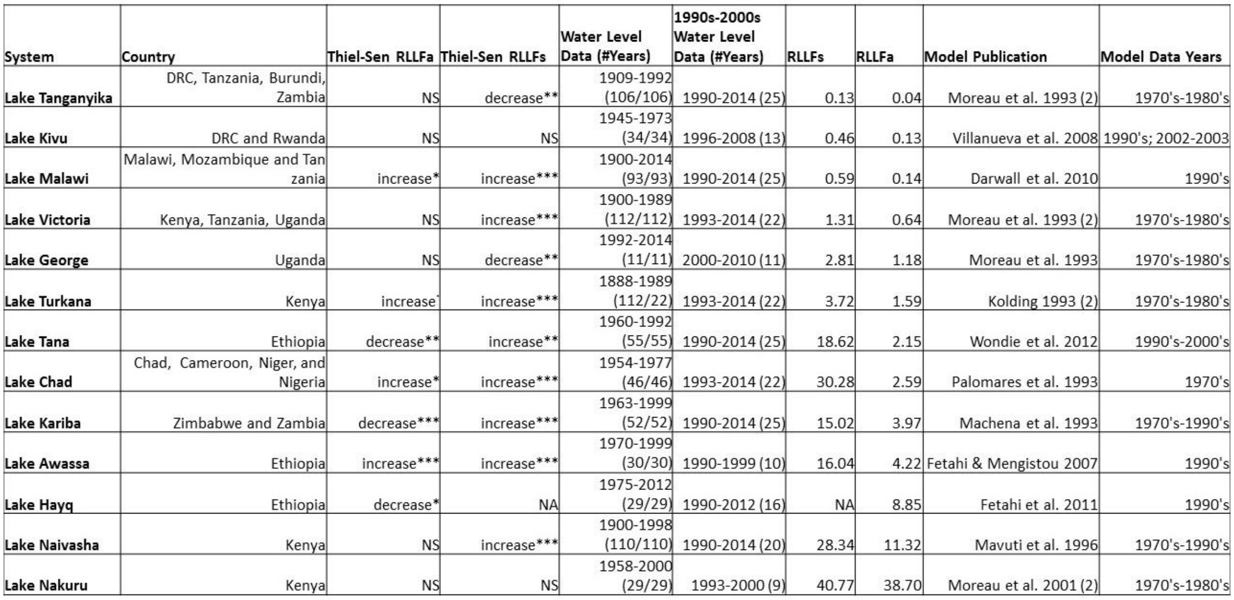
Tables

Table 6.1: Ecosystem Attributes of Study and Their Expected Relationships with Maturity and Relative Lake Level Fluctuations



Ecosystem Attribute	Acronym	Units	Definition/Notes	Maturity Trend	RLLF Trend
Community Energetics					
Total Biomass	B	$t{\cdot}km^{-2}$	sum biomass excl. detritus	↑	↓
Total Production	P	$t{\cdot}km^{-2}{\cdot}yr^{-1}$	sum production	∩	∩
Primary Production	PP	$t{\cdot}km^{-2}{\cdot}yr^{-1}$	sum primary production	∩	∩
Primary Production/Respiration	PP/R	yr^{-1}	sum primary production/sum respiration	↓	↑
Primary Production/Biomass	PP/B	yr^{-1}	sum primary production/sum biomass excl. detritus	↓	↑
Biomass/Throughput	B/T	yr^{-1}	sum biomass/sum of all flows	↑	↓
Community Structure					
Number of Trophic Levels	NoTL	NA	highest fractional trophic level (through fish)	↑	↓
Fish Diversity	NoFish	NA	total number of fish species	↑	↓
System Omnivory Index	SOI	NA	average omnivory weighed by food intake	↓	↑
Nutrient Cycling					
Path Length	PL	NA	average number of groups inflow or outflow passes through	↑	↓
Trophic Efficiency	TE	%	percent energy passed from one trophic level to the next	↑	↓
System Detritivory Index	SDI	NA	average proportion detritus in diet weighed by food intake	↑	↓
Life History					
Biomass/Production	B/P	yr	indicator of average organism size	↑	↓
Overall Homeostasis					
Respiration/Biomass	R/B	NA	indicator of stability (Schrödinger's ratio)	↑	↓
Other					
Catch	Catch	$t{\cdot}km^{-2}{\cdot}yr^{-1}$	total catch	↓	↑
Mean Trophic Level of Catch	MTLC	NA	average tropic level of catch	↑	↓

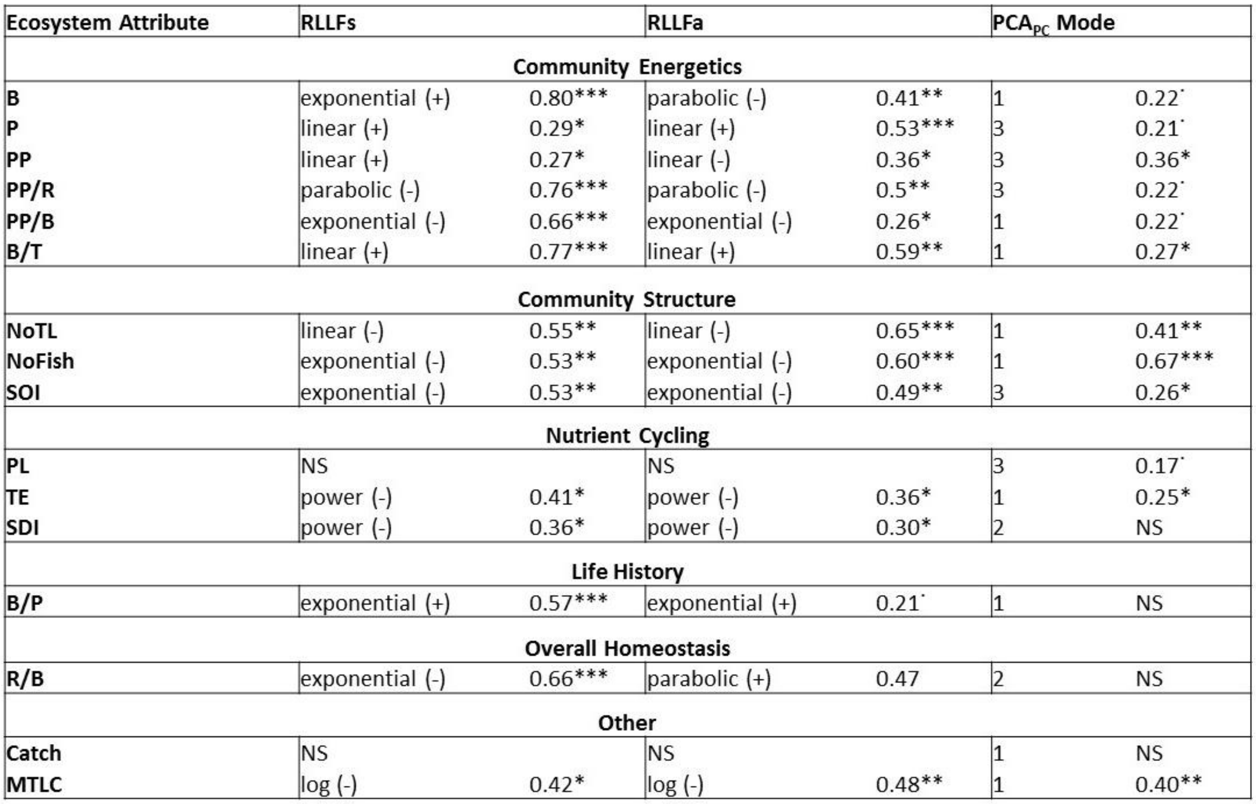
Table 6.2: Lakes and Reservoirs of Study and their Relative Lake Level Fluctuations



System	Country	Thiel-Sen RLLFa	Thiel-Sen RLLFs	Water Level Data (#Years)	1990s-2000s Water Level Data (#Years)	RLLFs	RLLFa	Model Publication	Model Data Years
Lake Tanganyika	DRC, Tanzania, Burundi, Zambia	NS	decrease**	1909-1992 (106/106)	1990-2014 (25)	0.13	0.04	Moreau et al. 1993 (2)	1970's-1980's
Lake Kivu	DRC and Rwanda	NS	NS	1945-1973 (34/34)	1996-2008 (13)	0.46	0.13	Villanueva et al. 2008	1990's; 2002-2003
Lake Malawi	Malawi, Mozambique and Tanzania	increase*	increase***	1900-2014 (93/93)	1990-2014 (25)	0.59	0.14	Darwall et al. 2010	1990's
Lake Victoria	Kenya, Tanzania, Uganda	NS	increase***	1900-1989 (112/112)	1993-2014 (22)	1.31	0.64	Moreau et al. 1993 (2)	1970's-1980's
Lake George	Uganda	NS	decrease**	1992-2014 (11/11)	2000-2010 (11)	2.81	1.18	Moreau et al. 1993	1970's-1980's
Lake Turkana	Kenya	increase˙	increase***	1888-1989 (112/22)	1993-2014 (22)	3.72	1.59	Kolding 1993 (2)	1970's-1980's
Lake Tana	Ethiopia	decrease**	increase**	1960-1992 (55/55)	1990-2014 (25)	18.62	2.15	Wondie et al. 2012	1990's-2000's
Lake Chad	Chad, Cameroon, Niger, and Nigeria	increase*	increase***	1954-1977 (46/46)	1993-2014 (22)	30.28	2.59	Palomares et al. 1993	1970's
Lake Kariba	Zimbabwe and Zambia	decrease***	increase***	1963-1999 (52/52)	1990-2014 (25)	15.02	3.97	Machena et al. 1993	1970's-1990's
Lake Awassa	Ethiopia	increase***	increase***	1970-1999 (30/30)	1990-1999 (10)	16.04	4.22	Fetahi & Mengistou 2007	1990's
Lake Hayq	Ethiopia	decrease*	NA	1975-2012 (29/29)	1990-2012 (16)	NA	8.85	Fetahi et al. 2011	1990's
Lake Naivasha	Kenya	NS	increase***	1900-1998 (110/110)	1990-2014 (20)	28.34	11.32	Mavuti et al. 1996	1970's-1990's
Lake Nakuru	Kenya	NS	NS	1958-2000 (29/29)	1993-2000 (9)	40.77	38.70	Moreau et al. 2001 (2)	1970's-1980's

˙ = $p<0.10$
*= $p<0.05$
**=$p <0.01$
***= $p<0.001$

Table 6.3: Ecosystem Attributes of Study and their Relationship with Relative Lake Level Fluctuations and Physical Characteristic Modes



Ecosystem Attribute	RLLFs		RLLFa		PCA_{PC} Mode	
Community Energetics						
B	exponential (+)	0.80***	parabolic (-)	0.41**	1	0.22$^{\cdot}$
P	linear (+)	0.29*	linear (+)	0.53***	3	0.21$^{\cdot}$
PP	linear (+)	0.27*	linear (-)	0.36*	3	0.36*
PP/R	parabolic (-)	0.76***	parabolic (-)	0.5**	3	0.22$^{\cdot}$
PP/B	exponential (-)	0.66***	exponential (-)	0.26*	1	0.22$^{\cdot}$
B/T	linear (+)	0.77***	linear (+)	0.59**	1	0.27*
Community Structure						
NoTL	linear (-)	0.55**	linear (-)	0.65***	1	0.41**
NoFish	exponential (-)	0.53**	exponential (-)	0.60***	1	0.67***
SOI	exponential (-)	0.53**	exponential (-)	0.49**	3	0.26*
Nutrient Cycling						
PL	NS		NS		3	0.17$^{\cdot}$
TE	power (-)	0.41*	power (-)	0.36*	1	0.25*
SDI	power (-)	0.36*	power (-)	0.30*	2	NS
Life History						
B/P	exponential (+)	0.57***	exponential (+)	0.21$^{\cdot}$	1	NS
Overall Homeostasis						
R/B	exponential (-)	0.66***	parabolic (+)	0.47	2	NS
Other						
Catch	NS		NS		1	NS
MTLC	log (-)	0.42*	log (-)	0.48**	1	0.40**

$^{\cdot}$ = p<0.10
*= p<0.05
**=p <0.01
***= p<0.001

Chapter 7: Conclusions and Recommendations

Introduction

Lake Turkana, Kenya, is a unique, understudied system at the cusp of large-scale changes in ecological function due largely to development along the Omo River, which provides 90% of the lake's freshwater inflow. The recently completed Gibe III dam and others under construction along the Omo River will considerably dampen or eliminate the lake's seasonal flood pulse. Development of large-scale plantations and associated irrigation schemes for sugarcane and cotton will result in substantially lowered lake levels (Chapters 1 and 2). Climate change is already influencing inter and intra-annual variation in the lake's water level (Chapter 6), and this will likely continue in the future.

The objective of this dissertation was to explore Lake Turkana's fish communities and fisheries and to predict how they will be impacted by impending changes to the lake's hydrological cycles. The research outlined in Chapters 2-6 fufills this objective by 1) providing an updated view of the lake's fisheries and their driving forces, 2) by employing stable isotope technology to depict the lake's food web and its resilience to change, and 3) by furthering our understanding of the influence of water level fluctuations across African lakes. As the impacts of upstream development on the lake are likely to be numerous and complex, this dissertation was not able to examine every consideration.

This chapter focuses on providing an overview of the potential changes facing the Lake Turkana ecosystem and highlights areas in which Chapters 2-6 have furthered our understanding of these changes (Figure 7.1). These impacts are discussed in the following sections: 1) Nutrients and Primary Production, 2) Breeding Cues and Habitat, 3) Trophic Structure and Resilience, 4) Salinity and 5) Implications for Fisheries Management. The chapter concludes with recommendations for future research and for managing upstream development to minimize impacts to Lake Turkana.

Synthesis of Impacts to Lake Turkana

Nutrients and Productivity

Primary production in Lake Turkana is nitrogen-limited, with inflow from the Omo River acting as the system's principal nutrient source. A decrease in Omo River inflow will therefore result in a reduction of the lake's primary productivity. These reductions will translate to decreased fish productivity and fisheries catch, given the link between primary productivity and fish productivity in African lakes (Melack 1976) and globally (Downing et al. 1990). Lower nutrient levels will likely affect fishes in pelagic habitats hardest, particularly the small pelagic fishes (*Alestes spp.* and *Brycinus spp.*) that feed low on the food chain and are known to be climate-sensitive (Tweddle and Lewis 1990, Sarch and Allison 2001, Plisnier 1997, Kolding et al. in press).

The consequences of reduced nitrogen inputs will be less severe for the productivity of shallow, sheltered habitats like Ferguson's Gulf, due to the presence there of nitrogen-fixing cyanobacteria (Chapter 2). These habitats, however, will be heavily influenced by changes to the temporal patterns of Omo River inflow. Specifically, a reduction in seasonal flood pulses will lead to a decrease in the extent of the aquatic-terrestrial transition zone (ATTZ), the highly productive region of the lake that is covered by water only during the flood pulse (Chapter 3; Junk et al. 1989, Johnson et al. 1995, Wantzen et al. 2008). Systems with an active ATTZ are more productive than stable ones (Welcomme and Halls 2001, Wantzen et al. 2008), and species that feed within the ATTZ have higher growth rates than those that feed in the main water body, a concept known as the "floodpulse advantage" (Bayley 1991).

Among African lakes, primary productivity is related to the magnitude of water level fluctuations that a given system experiences (Chapter 6). Therefore, in addition to the total volume of Omo River inflow, the timing of nutrient inputs and the degree of interaction between aquatic and terrestrial zones influence Lake Turkana's primary productivity. Consequently, both the total volume and the seasonal patterns of Omo River inflow are significant driving forces of Lake Turkana's fisheries productivity (Chapter 3). This finding is not particularly surprising, as the top two fishery species represent both the littoral (*Oreochromis niloticus*) and pelagic (*Lates niloticus*) components of the lake (Chapter 5) and would therefore be most impacted by changes in seasonal inflow patterns and average annual inflow, respectively. Water levels and their fluctuations are also likely to drive the productivity of the lake's fisheries through their influence on fish breeding success (Chapter 3, Chapter 5).

Breeding Cues and Habitat

Changes in the volume and seasonal patterns of water inflow to Lake Turkana will impact two aspects of fish breeding success: 1) the availability of optimal breeding habitat, and 2) the strength and timing of breeding cues. The fishes of Lake Turkana breed in three major habitats: the lake's pelagic areas, the lake's littoral areas, or inflowing river mouths and their deltas (Chapter 5, Table 7.1; Hopson 1982). All three habitats are threatened by changes to Lake Turkana's hydrological regime.

As water level declines, the lake's non-littoral habitats will begin to disappear. At the maximum decline (22 m) estimated by Avery (2012) due to future irrigation needs along the lower Omo Valley, non-littoral habitat will be reduced by over 60% in volume and nearly 50% in surface area (Chapter 3). Non-littoral habitat will cease to exist in the productive North Sector of the lake (closest to Omo River inflow) at water level declines of greater than 25 m (Chapter 3). Conversely, the availability of littoral habitat will actually increase as lake level declines up to 20 m, after which point it begins to decrease. The quality of this habitat, however, will be degraded by the dampening, or loss in the worst case scenario, of the lake's seasonal flood pulse (Chapter 3). Maintenance of the lake's flood pulse is central to the availability of productive dynamic littoral habitat, the ATTZ, and to the health of aquatic vegetation communities (Chapter 3). Though not the focus of this dissertation, habitat along the Omo River, and particularly that of the Omo Delta, is likely to be greatly altered by these hydrological changes (Chapter 2). For example, the flood pulse concept discussed in reference to Lake Turkana was originally developed for riverine ecosystems, in which the floodplains resulting from seasonal cycles are perhaps even more ecologically crucial than they are in lakes (Junk et al. 1989, Wantzen et al. 2008).

Though riverine breeding habitat is likely to be degraded by upstream development, the largest threat to the breeding success of Lake Turkana's potamodromous fishes will be changes to their breeding cues (Chapter 5). Due to Lake Turkana's proximity to the equator, there is little seasonality in water temperature and day length. Instead, the lake's fishes use the flood pulse, and particularly the related increase in turbidity in the lake (Chapter 2), as a signal to move upriver or inshore to spawn (Chapter 5, Table 7.1; Hopson 1982, Avery 2010). For many fish species in the lake, breeding peaks, defined here based on the occurrence of ripe females, coincide with periods of high inflow. This phenomenon is common in tropical and neotropical freshwater systems (Chapter 5, Table 7.1; Lowe-McConnell 1987). A diminished or absent seasonal flood cycle will cause the lake's fishes to reduce or cease their movement into breeding habitats, therefore leading to declines in their populations. Past experience in regulated watersheds suggests reduced success of spawning runs of potamodromous fishes (Tweddle 1992), even when artificial floods are released (Brooker 1981).

Trophodynamics

Changes in nutrient inflow and the breeding success of Lake Turkana's fishes will ultimately alter the structure of the lake's food web. Both inter- and intra-annual water level fluctuations play significant roles in structuring African lake food webs (Chapter 6). Shifting Lake Turkana to a system with fewer water level fluctuations will likely result in a "more mature" system *sensu* Odum (1969) that has lower rates of primary production and supports a lower biomass. Reducing fluctuations, however, may also increase the complexity, connectivity, and efficiency of the lake's food web (Chapter 6). An increase in the efficiency of the lake's food web would have a substantial impact on the functioning of the ecosystem. The lake's pelagic food web thrives on detritus (Kolding 1993), and increased transfer efficiency will translate to less energy building up in the detritus pool.

Of the other African lakes examined, Lake Turkana's food web structure is most similar to that of Lake Albert, Uganda (Chapter 4). The system's distribution of $\delta^{13}C$ and $\delta^{15}N$ values suggests that an enriched source of carbon is important to the food web as a whole (Chapter 4). This carbon signal likely represents littoral production, as it has been previously documented that many of the lake's pelagic piscivores will move into shallow areas to feed (Kolding 1993). Over half of the lake's fishes exhibit ontogenetic changes in diet (Chapter 4). The most common trend is for fishes to develop a lower trophic level and a more littoral or benthic diet as they grow. Functional redundancy is low to moderate within the lake, with over 60% of species pairs showing no overlap (Chapter 4). A combination of zooplanktivory and mesocarnivory seems to be particularly common in the system, but low overlap among species using this feeding strategy suggests that they effectively partition resources (Chapter 4; Lévêque 1997).

Species' specific responses to changes in the food web will depend on how "flexible" their diets are, as populations of specialist species (small ecological niche) are more vulnerable to perturbation than are populations of generalist species (large ecological niche) (Table 7.1; Levins 1968). For example, when Lake Chad began undergoing extreme reductions in water level in the 1970's, the species that survived were those with flexible diets (Wantzen et al. 2008). The top two fishery species in Lake Turkana, *L. niloticus* and *O. niloticus*, have the broadest dietary niches and are therefore likely to have the most "flexibility" to switch prey items as the system changes (Chapter 5, Table 7.1). *Synodontis schall*, a ubiquitous species in the system that is not yet exploited commercially, has a moderately sized trophic niche. However, its diet overlaps heavily with several other trophic guilds and additional analyses suggest it to be a generalist feeder (Chapter 5, Table 7.1), making it relatively resilient to food web changes. *Labeo horie*, the third most important fishery species in the lake, has a moderately sized trophic niche, but breeding habits that make it vulnerable to hydrological changes (Chapter 5, Table 7.1). *Tilapia zillii*, despite being grouped with *O. niloticus* in the lake's fishery, has a much smaller trophic niche than its tilapia relative and will be more vulnerable to food web changes. *Alestes* *baremoze* and its dependent predator *Hydrocynus forskallii* are currently only lightly fished (<10% of fisheries yield), but may become increasing important to the fishery as it expands (Chapter 3, Table 7.1). These species, however, have small trophic niches and high breeding vulnerability, making it likely that their populations will respond poorly to expected changes to the lake's hydrological regime (Chapter 5, Table 7.1).

Physiochemical Characteristics

Lake Turkana is a "high ion" lake, with a conductivity of 3,500 µS/cm and salinity of 2.5 (Chapter 2; Talling and Talling 1965, Odada 2003). Due to its closed-basin nature, the lake exhibits a natural conductivity increase of approximately 0.45 uS/cm/yr (Hopson 1982). Given that the Omo River is the lake's main freshwater source and that the lake is endorheic, the salinity of the lake has a direct inverse relationship with lake volume (Avery 2010). Therefore, at a lake level decline of 25 m, lake volume would decline by 60% (Chapter 3) and salinity levels would increase by 2.5 times those currently experienced.

Lake Turkana's relatively elevated salinity is already restrictive for the lake's fauna, some of which (e.g. mormyrids due to their sensitive electrosensory systems) are found only in the Omo Delta region where salinity is lowest (Chapter 2; Yuretich and Cerling 1983). The fishes restricted to the Omo Delta are among the poorest studied in the lake, and the ecosystem consequences of their loss from the system is unknown. The only species in Lake Turkana for which salinity tolerance has been extensively studied is *O. niloticus*, and the proposed upper limit of salinity tolerance varies, with most studies showing mortality at salinities greater than 20 (e.g. Watanabe 1985, Nugon 2003, Lemarie et al. 2004, Basiao et al. 2005, Lawson and Anetekhai 2011, Schofield et al. 2011). Much less is known about the salinity tolerance of other fishes in the lake, though the high salinity crater lakes of Central Island give some indication. These crater lakes host populations of only a few of the species found in the rest of the lake (i.e. *O. niloticus, Clarias lazera, S. schall, Haplochromis rudolfianus*), the individuals of which show stunted growth. The species dominating the lake's phytoplankton (Wood and Talling 1988) and invertebrate assemblages (Verschuren 1999) will also change with salinity, further influencing the food web.

Although not the focus of this study, decreasing freshwater inflow will also further reduce the potability of Lake Turkana's waters. Water from Lake Turkana is already highly saline and alkaline and has high fluoride levels, making it unsuitable for human and livestock consumption (Avery 2010). Regardless, it remains one of the most important sources of water for humans and livestock in the region. Hopes regarding the use of the recently discovered aquifer in Turkana County are waning, as initial water tests suggest that this water may also be too salty to drink (Migiro and Arsenault 2015).

Implications for Fisheries Expansion

The yield of Lake Turkana's fisheries has averaged 5,400 tons/year over the last couple of decades but has fluctuated greatly, with peaks of 9,000-10,000 metric tons occurring approximately every five years (Chapter 2, Chapter 3). Fluctuations in yield are significantly related to the lake's absolute water level and the magnitude of its inter- and intra-annual water level fluctuations, but do not appear to be related to the number of people fishing in a given year or to other fishing effort variables (Chapter 3). Although this study did not find a significant link between water level fluctuations and yield across African lakes (Chapter 6), this result is in contrast with past research (Kolding and van Zwieten 2012), and is likely to be due to the temporal snapshot of the data used in the current study. The importance of environmental factors in structuring the lake's fisheries suggest that traditional fisheries management schemes, which assume equilibrium conditions and a link between fisheries yield and effort, are not appropriate for this system (Allison and Ellis 2001, Jul-Larsen and van Zwieten 2002, Jul-Larsen et al. 2003ab, Conway et al. 2005, Andrew et al. 2007). The reduced fisheries yield observed in currently fished habitats that results from declines in lake level and the magnitude of the flood pulse, may result in an increase in illegal fishing within the lake's protected areas (e.g. Sibiloi National Park), further threatening the health of fish stocks.

The majority of the fish catch over the last decade has consisted of *L. niloticus*, *O. niloticus* and other tilapia species, *L. horie*, and *D. niloticus,* which vary in their sensitivity to impending ecosystem change (Chapter 2, Chapter 3, Chapter 5; Table 7.1). Fishing effort has linearly increased in the system in recent decades, but future expansion of the lake's fisheries will likely require exploiting pelagic fish stocks, especially if littoral habitats are degraded and fish catchability in these habitats declines due to reduction of the lake's flood pulse (Chapter 3). Among the most productive African lake fisheries are those focusing on small pelagic fishes (e.g. "Kapenta" fishery in Lakes Tanganyika, Kariba, and Kivu; the "Dagaa" fishery in Lake Victoria; the "Ragoogi" fishery in Lake Albert). Declines in non-littoral habitat (Chapter 3) and the high sensitivity of several of the lake's pelagic species to water level changes (Chapter 5; Table 7.1) will limit this expansion. The greatest potential for fisheries expansion given the impending ecosystem changes will be to include ecologically flexible species with low breeding vulnerabilities, such as the catfish *S. schall* (Chapter 5, Table 7.1), but these species may have lower economic value.

Changes in the availability of productive fishing areas in Lake Turkana is also likely to lead to increased conflict among tribes within Kenya and between tribes in Kenya and Ethiopia. The human population surrounding the lake is growing and population densities are highest in the regions of the lake that will experience some of the greatest changes in habitat availability (Chapter 3). For example, the lake's North Sector will show precipitious declines in non-littoral habitat as water level declines and will be the first of the lake's sectors to dry up completely (Chapter 3). The North Sector region is already marked by high political insecurity due to resource conflict. Changes in the size of the lake and the availability of the resources it provides are likely to heighten these conflicts, with some fearing that Lake Turkana will become an "endless battlefield" (Vidal 2015).

Recommendations for Future Work

The research conducted throughout this dissertation substantially improves our knowledge of Lake Turkana's fishes and fisheries and their response to change. There is still a long way to go to thoroughly understanding the system, however. Little is known regarding how the lake's phytoplankton, zooplankton, and benthic invertebrate communities will respond to changing hydrological cycles, and changes in these communities will have wide-ranging consequences for ecosystem function. For example, juvenile stages of insects, which are highly associated with aquatic vegetation in Lake Turkana, are likely to be key diet components for some of the lake's fishes, including the economically important *O. niloticus* (Chapter 4; Njiru et al. 2004). Furthermore, due to resource constraints and political insecurity in some areas of the lake, sample collection for this dissertation was limited to the Central Sector. This is unfortunate, as the Omo Delta, which is rich in aquatic vegetation and has a higher species diversity than the lake proper, is likely to be the most heavily impacted by hydrological changes. Given that these various components of the ecosystem haven't been studied since the 1980's, they should be a top priority for future Lake Turkana research initiatives.

This dissertation focused primarily on changes to the volume and patterns of water level inflow. Upstream development, however, is likely to have a wide range of consequences for the lake. For example, the Gibe III dam will withhold sediment from the lake, but the clearing of forests for plantation development may ultimately increase sediment loads. The sugarcane and cotton plantations upstream are also likely to require fertilizer inputs, substantial amounts of which will wind up in the Omo River and eventually in Lake Turkana, changing nutrient concentrations and ratios. The region is also seismically active and due for a large earthquake sometime over the next five decades (Carr 2012). If it were to occur, an earthquake of the magnitude predicted could lead to collapse of the dam and extreme volumes of flood water entering the lake, the impacts of which are unknown. These scenarios must be considered before we can fully understand how the Lake Turkana ecosystem will respond to upstream development.

The Lake Turkana region is also experiencing unprecedented development in other sectors, including oil drilling and the construction of the largest wind farm in Africa (Chapter 2). For example, the hiring of locals for oil drilling operations led to a 500% increase in the population of some towns surrounding the lake over 2012-2014 (Anon 2015). These development projects are bringing electricity, roads, and infrastructure to the region and could foster further population growth and attract additional development projects. It is clear that the region will look vastly different by the end of the decade if development proceeds. The changes are also likely to have implications for the lake, which may for example experience growth in fisheries investments. Though development along the Omo River is likely to have the largest impact on the lake of these projects, understanding the ecosystem's future will require that all development sectors are considered. Luckily, improved infrastructure and access to the region are likely to make it more feasible to conduct research that will allow these questions to be answered.

Recommendations for Minimizing Impacts

There has been much criticism and public outcry regarding the consideration of environmental and social impacts of development along the Omo River, or perceived lack thereof (Abbink 2012, Avery 2012, Pearce 2014). The guidelines that should be observed before such large-scale development projects are funded can be illustrated by the Equator Principles, which require a comprehensive overview of all environmental and social impacts and effective methods to mitigate these impacts (IFC 2015). The construction of Gibe III, however, began in 2006, prior to any environmental or social impact studies being conducted (Avery 2012, Carr 2012). The intial impact studies ignored Lake Turkana, which was not considered until an assessment conducted in 2010, four years after dam construction commenced (Carr 2012). The recommendations made in these statements, including those for minimum flows and artifical floods, seem to lack scientific basis (Avery 2012). Furthermore, these environmental and social impact statements failed to mention the irrigation development projects now being realized in the lower Omo Valley (Avery 2012). Although land has already been cleared for these downstream plantations and the construction of irrigation infastructure is underway, no impact statements have yet been released in reference to this development (Pearce 2014). It is important to note that, while this dissertation has focused on Lake Turkana, development along the Omo River is already impacting Ethiopian ecosystems and human populations.

Due to the understudied nature of the lake and the complicated nature of the impacts of upstream development, determining the water inflow patterns necessary to sustain Lake Turkana's ecological function and considering the trade-offs associated with different water management decisions will require considerable research efforts. Species within a given ecosystem are adapted to its natural cycles (Wantzen et al. 2008). Therefore, the best overarching recommendation that can be made regarding this management is that water levels and their fluctuations should be kept within their natural ranges (IFC 2015). The natural range of water levels and their fluctuations for many lakes worldwide can be determined using freely available, high temporal resolution satellite data (Chapter 3). For example, these data can be used to quantify the main components of the seasonal flood pulse that a system experiences, including amplitude, duration, timing, smoothness, continuity, and the rapidity of change (Welcomme and Halls 2001). For Lake Turkana, recent average water levels range between 362-365 masl, with inter-annual changes of -1 to 2 m and intra-annual fluctuations of 1 to 1.5 m (Chapter 3). Given upstream development, and particularly the large-scale irrigation schemes of the lower Omo Valley, it is unlikely that the lake's average water levels will be maintained. Efforts should focus on the release of an artificial flood of ecologically appropriate timing, volume, and duration from the Gibe dams and optimizing the irrigation efficiency of downstream plantations.

As some impacts to Lake Turkana are likely to be unavoidable, efforts must also focus on increasing adaptive capacity and minimizing conflict in the region. Fishermen should be informed of the predicted changes and associated species' declines. For example, increasing fishing pressure on *A. baremore, H. forskallii, T. zillii* and other environmentally sensitive species should be avoided, while fisheries should be developed or expanded for less sensitive species such as *S. schall*. In addition to fishing, alternative livelihoods that could be promoted in the Turkana district include honey production, irrigated agriculture for maize and sorghum, basket-making and handicrafts, processing and selling of hides and skins, and other small-scale business enterprises (Watson and van Binsbergen 2008). In line with resource decline, local enforcement should plan for heightened tensions among the tribes surrounding the lake and especially between tribes in northern Kenya and southern Ethiopia (Vidal 2015).

Agreements between Kenya and Ethiopia regarding water resource management within the Omo River and Lake Turkana basin are necessary, such as those recently signed by Kenya and Tanzania regarding the Mara River Basin (Zablon 2015). Lake Turkana also requires greater international recognition and increased pressure from international organizations to make sure that the lake doesn't become "East Africa's Aral Sea" (IR 2013). Though the World Heritage Committee has been hesitant to list Lake Turkana as a World Heritage Site in Danger, this may occur in the future (UNESCO 2015).

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Figures

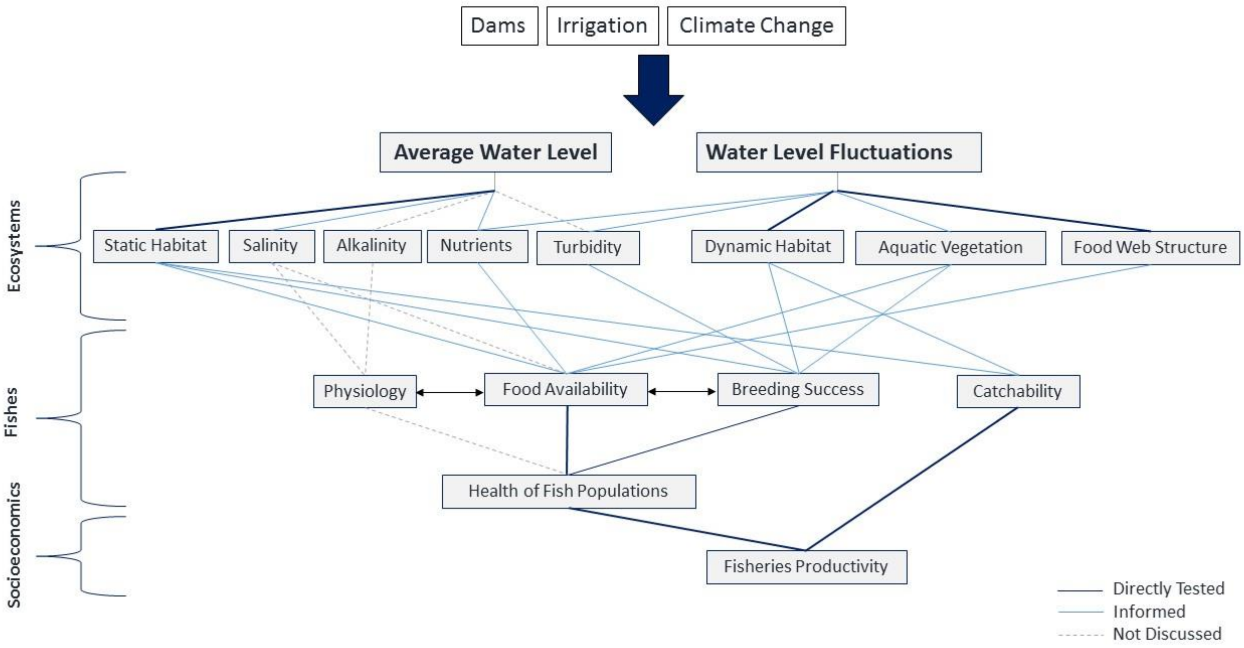
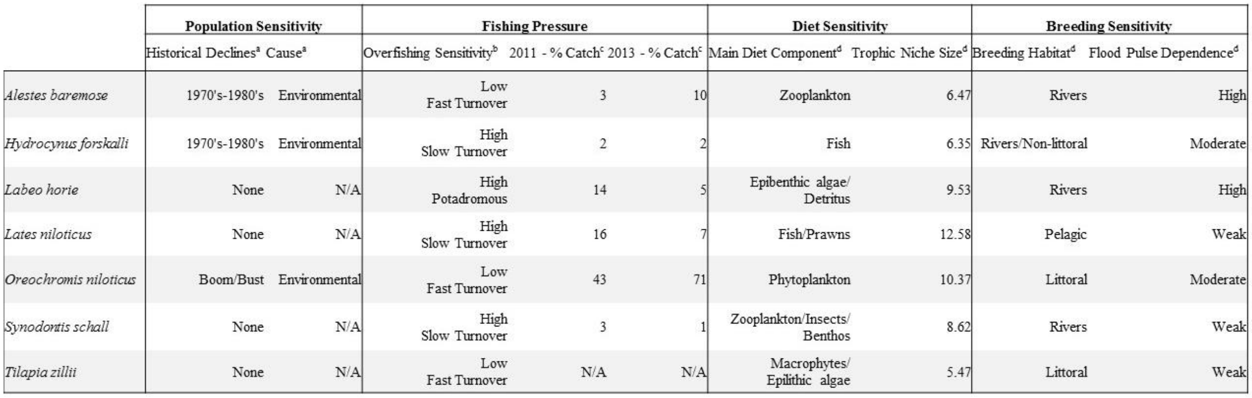


Figure 7.1: Impacts of Omo River development on the average water level and water level fluctuations of Lake Turkana. Water level attributes are central factors structuring African lake ecosystems and changes to these attributes have consequences for ecosystem functioning, the health of fish stocks, and fisheries productivity. Links directly tested throughout this dissertation are shown in dark blue, while those that the dissertation informs but does not directly test are shown in light blue. Links shown as a dashed grey line are not discussed in this dissertation. All light blue and dashed grey links are productive areas of future research.

Table 7.1: Synthesis of Information on the Population Sensitivity, Fishing Pressure, Diet Sensitivity, and Breeding Sensitivity of Focal Fish Species.



	Population Sensitivity		Fishing Pressure			Diet Sensitivity		Breeding Sensitivity	
	Historical Declines[a]	Cause[a]	Overfishing Sensitivity[b]	2011 - % Catch[c]	2013 - % Catch[c]	Main Diet Component[d]	Trophic Niche Size[d]	Breeding Habitat[d]	Flood Pulse Dependence[d]
Alestes baremose	1970's-1980's	Environmental	Low Fast Turnover	3	10	Zooplankton	6.47	Rivers	High
Hydrocynus forskalli	1970's-1980's	Environmental	High Slow Turnover	2	2	Fish	6.35	Rivers/Non-littoral	Moderate
Labeo horie	None	N/A	High Potadromous	14	5	Epibenthic algae/ Detritus	9.53	Rivers	High
Lates niloticus	None	N/A	High Slow Turnover	16	7	Fish/Prawns	12.58	Pelagic	Weak
Oreochromis niloticus	Boom/Bust	Environmental	Low Fast Turnover	43	71	Phytoplankton	10.37	Littoral	Moderate
Synodontis schall	None	N/A	High Slow Turnover	3	1	Zooplankton/Insects/ Benthos	8.62	Rivers	Weak
Tilapia zillii	None	N/A	Low Fast Turnover	N/A	N/A	Macrophytes/ Epilithic algae	5.47	Littoral	Weak

[a] Kolding 1995
[b] van Zwieten et al. 2003
[c] Chapter 3
[d] Chapter 6

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Appendix 1

Brief Description:
Appendix 1 provides information on the environmental parameters (water quality, air temperature, etc.) and fish species samples at various sites during research trips taken to Lake Turkana from 2008-2013. In 2008-2011, length and mass was recorded only for fishes that were sampled (Table A1.8). In 2012-2013, the length and mass of all fishes collected was recorded, allowing for examination of species composition (Table A1.9). All raw stable isotope values will be included in an online stable isotope repository under development, a collaboration between FishBase and Dr. Les Kaufman of Boston University.

Table A1.1: Lake Turkana Sites Sampled, 2011-2013.

Site	Date	Start Time (# mins)	Site Name	Latitude	Longitude
1	11/30/2011	4:05PM (66)	Napasinyang	03°35'26.0"	35°52'40.3"
2	12/1/2011	10:38AM (112)	Open Lake (Central Island)	03°33'07.7"	35°52'20.8"
3	12/2/2011	1:05PM (115)	Sibiloi	03°41'29.4"	36°14'38.0"
4	12/2/2011	1:10PM (148)	Sibiloi	03°41'47.1"	36°14'29.3"
5	12/3/2011	7:05AM (235)	Sibiloi	03°42'45.0"	36°14'49.1"
6	12/3/2011	7:15AM (202)	Sibiloi	03°42'51.1"	36°14'37.1"
7	6/11/2012	11:30AM (60)	Ferguson's Gulf (Grass)	03°30'00.8"	35°55'30.9"
8	6/11/2012	11:57AM (60)	Ferguson's Gulf (Grass)	03°30'01.2"	35°55'31.9"
9	6/11/2012	1:20PM (140)	Ferguson's Gulf (Grass)	03°29'52.5"	35°55'27.1"
10	6/11/2012	1:26PM (140)	Ferguson's Gulf Hippograss	03°29'51.7"	35°55'27.1"
11	6/12/2012	3:34 AM (146)	Ferguson's Gulf Mouth	03°33'03.1"	35°54'25.0"
12	6/12/2012	11:32AM (NA)	Ferguson's Gulf Central	03°31'36.9"	35°54'51.9"
13	6/12/2012	11:37AM (NA)	Ferguson's Gulf Central	03°31'37.5"	35°54'50.6"
14	6/13/2012	1:55PM (158)	Open Lake (Central Island)	03°33'29.0"	35°57'01.6"
15	6/13/2012	NA	Open Lake (Central Island)	03°33'34.6"	35°56'53.4"
16	6/17/2012	11:04AM (127)	Ferguson's Gulf Hippograss	03°29'51.9"	35°55'27.0"
17	6/17/2012	4:40PM (80)	Open Lake (Central Island)	03°33'45.9"	35°55'51.3"
18	6/19/2012	8:12AM (232)	Sibiloi	03°41'25.8"	36°14'32.8"
19	6/19/2012	8:25AM (230)	Sibiloi	03°41'29.5"	36°14'44.8"
20	6/19/2012	8:29AM (236)	Sibiloi	03°41'28.1"	36°14'42.0"
21, 22, 23	8/5/2013	11:08 AM (177)	Sibiloi	03°41'26.2"	36°14'36.9"
24, 25	8/7/2013	5:22 PM (~120)	Ferguson's Gulf (Grass)	03°29'53.0"	35°55'25.9"
26, 27, 28	8/8/2013	2:13 PM (~120)	Open Lake (Central Island)	03°33'27.2"	35°57'11.1"
29, 30, 31	8/9/2013	9:20 AM (~120)	Ferguson's Gulf Mouth	03°32'58.7"	35°54'23.7"
32, 33, 34	8/12/2013	11:00 AM (~120)	Napasinyang	03°35'38.0"	35°51'39.6"
35, 36	8/13/2013	10:10AM (179)	Ferguson's Gulf Hippograss	03°29'05.9"	35°56'1.86"
37	8/13/2013	1:30 PM (~120)	Open Lake (Napasinyang)	03°36'54.4"	35°53'42.1"
38	8/14/2013	12:30 PM (~120)	Open Lake (Central Island)	03°33'20.7"	35°56'47.1"
39	8/20/2013	11:00 PM (125)	Open Lake (Sibiloi)	03°42'47.9"	36°13'23.7"
40	8/21/2013	6:58 PM (~120)	Sibiloi	03°41'31.2"	36°14'31.5"

Table A1.2: Environmental Parameters of Lake Turkana Sites Sampled, 2011-2013.

Site	DO mg/l (%)	Tw ^{0}C	Sal	Cond µS/cm	TDS mg/l	Depth m	Secchi Depth cm	pH	T^A ^{0}C	Wind speed m/s
1	6.75 (86.1)	27.5	1.6	3276	NA	9.0	NA	NA	NA	NA
2	5.29 (66.9)	27.2	1.6	3131	NA	1.1	27	NA	NA	NA
3	6.32 (82.5)	26.9	1.7	3330	NA	2.0	31	NA	NA	NA
4	7.18 (93.3)	28.4	1.7	3260	NA	3.1	42	NA	NA	NA
5	7.05 (96.5)	27.9	1.6	3387	NA	1.6	41	NA	NA	NA
6	7.01 (87.9)	28	1.5	3111	NA	3.4	40	NA	NA	NA
7, 8	9.88 (132.8)	29.2	2.91	5881	3536	0.5	9	9.85	30.3	2.4
9, 10	16.37 (230)	31.9	2.94	6248	3582	1.3	8.6	9.87	NA	NA
11	6.75 (93.6)	29.2	1.92	3971	2392	1.3	116	9.22	NA	NA
12, 13	3.99 (54.7)	27.4	2.97	5776	3594	0.6	NA	NA	29.2	3.2
14, 15	6.82 (93.8)	29.9	1.92	4008	2385	30.0	92.5	9.2	33.4	1.1
16	9.22 (125.9)	25.6	2.95	5518	3555	1.0	9.75	NA	28.9	2
17	6.88 (93.3)	29.3	1.93	3998	2405	10.8	128.5	9.26	29.7	1.1
18, 19, 20	12.08 (158.8)	25.9	1.97	3811	2437	1.0	NA	9.33	NA	NA
21, 22, 23	8.17 (101.2)	26.5	1.6	2926	1989	1.6	136.25	9.61	NA	5.3
24, 25	10.23 (150)	28.1	1.86	3703	2314	0.9	18.5	10.06	NA	1.4
26, 27, 28	7.44 (99.6)	27.2	1.58	3182	1982	31.2	120.5	9.64	NA	0.3
29, 30, 31	7.18 (93.7)	26.2	1.58	3120	1982	1.3	46.5	9.68	NA	NA
32, 33, 34	6.99 (93.1)	27.0	1.63	3258	2041	0.8	26	9.79	NA	1.2
35, 36	4.74 (64.2)	27.2	1.92	3810	2385.5	0.9	17.25	10.16	NA	2.4
37	6.14 (83.5)	38.8	1.57	3254	1976	25.0	137	9.66	NA	NA
38	6.23 (84.8)	27.5	1.58	3200	1989	22.0	NA	9.68	NA	NA
39	4.4 (58.3)	27.2	1.58	3171	1983	14.5	140	9.73	NA	NA
40	4.83 (60.3)	26.8	1.58	1194	1709	5.2	NA	9.69	NA	NA

Table A1.3: Chlorophyll-a and Phycocyanin Concentrations at Sampled Lake Turkana Sites, 2011-2013.

Site	chla 1 (µg/L)	chla 2 (µg/L)	chla 3 (µg/L)	phycocyanin 1 (ppb)	phycocyanin 2 (ppb)	phycocyanin 3 (ppb)
7, 8	1008.40	954.40	1058.00	NA	NA	NA
12, 13	596.80	772.40	610.40	NA	NA	NA
14, 15	21.83	17.14	19.20	NA	NA	NA
16	833.20	779.20	928.00	NA	NA	NA
17	37.17	26.19	33.16	NA	NA	NA
21, 22, 23	39.16	44.38	42.46	2.23	3.67	3.09
24, 25	1319.00	1380.00	1387.00	234.20	238.50	237.50
29, 30, 31	58.96	54.67	57.59	11.56	12.16	14.54
32, 33, 34	222.10	226.20	224.40	40.40	41.68	42.56
35, 36	2000.00	1983.00	1982.00	157.80	158.90	158.20

Table A1.4: Chlorophyll-a and Phycocyanin Concentration Profiles at Sites 26, 27, 28.

	Reading 1		**Reading 2**	
Depth (m)	**chla (µg/L)**	**phycocyanin (ppb)**	**chla (µg/L)**	**phycocyanin (ppb)**
0	33.21	6.10	32.87	6.12
1	39.32	6.17	43.61	6.97
2	37.99	6.31	33.72	5.42
3	32.18	5.10	31.53	4.47
4	31.11	5.86	32.88	3.97
5	39.05	1.72	33.66	3.88
6	29.83	1.45	34.93	3.10
7	32.02	1.77	33.45	1.67

Table A1.5: Chlorophyll-a and Phycocyanin Concentration Profiles at Site 30.

Depth (m)	Chla (μg/L)	Phycocyanin (ppb)
0	28.57	2.43
1	31.27	0.90
2	30.31	1.03
3	28.21	0.77
4	27.77	1.64
5	27.75	1.20

Table A1.6: Chlorophyll-a and Phycocyanin Concentration Profiles at Site 37.

Depth (m)	Chla (µg/L)	Phycocyanin (ppb)
0	35.36	3.46
1	37.95	5.37
2	32.73	4.63
3	34.53	5.02
4	34.18	3.78
5	29.64	2.51
6	32.28	2.77
7	33.67	2.37

Table A1.7: Chlorophyll-a and Phycocyanin Concentration Profiles at Site 38.

Depth (m)	chla (µg/L)	phycocyanin (ppb)
0	NA	NA
1	39.32	6.17
2	37.99	6.31
3	32.18	5.10
4	31.11	5.86
5	39.05	1.72
6	29.83	1.45
7	32.02	1.77

Table A1.8: Length and Mass of Fishes Sampled for Stable Isotopes, 2008-2011.

Site#	Species	TL (cm)	SL (cm)	FL (cm)	Mass (g)
2	*Alestes baremoze*	11.5	8.5	NA	20
2	*Alestes baremoze*	10.5	8	NA	20
2	*Alestes baremoze*	11	8.5	NA	20
2	*Alestes baremoze*	11	8	NA	20
2	*Alestes baremoze*	10.5	8	NA	20
2	*Alestes baremoze*	10.5	8	NA	20
2	*Alestes baremoze*	9.7	7.2	NA	20
2	*Alestes baremoze*	10.5	7.5	NA	20
2	*Alestes baremoze*	10.2	7.2	NA	20
2	*Alestes baremoze*	10.3	7.5	NA	20
2	*Alestes nurse*	7.6	5.5	NA	NA
2	*Bagrus bayad*	37.2	25.6	NA	200
2	*Bagrus bayad*	32.5	29.5	NA	300
2	*Bagrus bayad*	28.5	25.6	NA	189
2	*Chrysichthys auratus*	13.2	11.3	NA	39
2	*Citharinus citharus*	15.2	10.5	NA	40
2	*Hydrocynus forskallii*	28.5	21.5	NA	120
2	*Hydrocynus forskallii*	29	22	NA	120
2	*Hydrocynus forskallii*	27.3	25.2	NA	186
2	*Hydrocynus forskallii*	19.4	18	NA	76
2	*Hydrocynus forskallii*	38.2	26	NA	201
2	*Hydrocynus forskallii*	22.8	21	NA	80
2	*Hydrocynus forskallii*	22.3	20.5	NA	111
2	*Hydrocynus forskallii*	15	13.5	NA	35
2	*Hydrocynus forskallii*	20.5	18.5	NA	84
2	*Hydrocynus forskallii*	32.8	30.5	NA	373
2	*Hydrocynus forskallii*	5.7	4.5	NA	4
2	*Labeo horie*	28.6	21.5	NA	220
2	*Labeo horie*	32.5	25.5	NA	320
2	*Labeo horie*	30.5	22.5	NA	220
2	*Labeo horie*	27	20.5	NA	220
2	*Labeo horie*	30	22.6	NA	240
2	*Labeo horie*	29.8	22.8	NA	240
2	*Labeo horie*	28	21.2	NA	180
2	*Labeo horie*	28.4	21.5	NA	200
2	*Labeo horie*	28.2	21.5	NA	240
2	*Labeo horie*	29	21.5	NA	200
2	*Lates niloticus*	14.8	11.8	NA	41

2	*Lates niloticus*	11.5	9	NA	19
2	*Lates niloticus*	10.6	8	NA	15
2	*Lates niloticus*	10.5	8.5	NA	15
2	*Lates niloticus*	19.2	15.2	NA	93
2	*Lates niloticus*	12	9.3	NA	23
2	*Oreochromis niloticus*	22.5	18	NA	200
2	*Oreochromis niloticus*	16.5	13	NA	100
2	*Oreochromis niloticus*	15.8	12	NA	60
2	*Oreochromis niloticus*	15.8	12	NA	60
2	*Oreochromis niloticus*	22.5	17.5	NA	220
2	*Oreochromis niloticus*	33	26	NA	700
2	*Oreochromis niloticus*	14.6	11.2	NA	40
2	*Oreochromis niloticus*	13.6	10.5	NA	40
2	*Oreochromis niloticus*	14.5	11	NA	40
2	*Oreochromis niloticus*	14.5	11.2	NA	40
2	*Oreochromis niloticus*	16.2	12.3	NA	80
2	*Sarotherodon galilaeus*	15.5	11.5	NA	80
2	*Synodontis schall*	15	11	NA	38
2	*Synodontis schall*	15	10.5	NA	29
2	*Tilapia zillii*	14.5	11.2	NA	80
2	*Tilapia zillii*	11.5	9	NA	40
3, 4	*Alestes baremoze*	22.7	16.8	18.4	68
3, 4	*Alestes baremoze*	27.2	20.3	22.2	114
3, 4	*Alestes baremoze*	24	17.8	19.5	79
3, 4	*Alestes baremoze*	31.6	24.3	26.2	180
3, 4	*Alestes baremoze*	33	24.5	26.3	204
3, 4	*Alestes baremoze*	31.7	24	25.9	194
3, 4	*Alestes baremoze*	17.3	13.2	14.5	33
3, 4	*Alestes baremoze*	17	12.9	14	32
3, 4	*Alestes baremoze*	17.2	12.9	14	29
3, 4	*Alestes baremoze*	18	13.8	15	36
3, 4	*Alestes ferox*	24.5	18.5	20	81
3, 4	*Alestes nurse*	10.1	8	8.8	13
3, 4	*Alestes nurse*	7	5.4	6	4
3, 4	*Alestes nurse*	7.6	5.4	6.3	5
3, 4	*Alestes nurse*	7.3	5.4	6.1	4
3, 4	*Citharinus citharus*	33.4	25.5	28.5	438
3, 4	*Citharinus citharus*	30	22.5	25	295
3, 4	*Citharinus citharus*	33.5	26	28.5	460
3, 4	*Citharinus citharus*	30.3	23	25.5	323
3, 4	*Citharinus citharus*	30.4	22.7	25.4	321

3, 4	*Citharinus citharus*	33.9	25	28.2	475
3, 4	*Citharinus citharus*	28	20.8	23.5	286
3, 4	*Citharinus citharus*	26	19.4	21.7	199
3, 4	*Citharinus citharus*	24	18	20.9	168
3, 4	*Hydrocynus forskallii*	49.9	39	42.5	739
3, 4	*Hydrocynus forskallii*	43	33	35.8	490
3, 4	*Hydrocynus forskallii*	41	32	34	413
3, 4	*Hydrocynus forskallii*	28.5	21.5	23	134
3, 4	*Hydrocynus forskallii*	27.5	20.5	22.6	111
3, 4	*Hydrocynus forskallii*	27.5	20.5	22.5	113
3, 4	*Hydrocynus forskallii*	25.5	19.5	21	84
3, 4	*Hydrocynus forskallii*	23.2	17.5	19	66
3, 4	*Hydrocynus forskallii*	21	15.6	17.3	54
3, 4	*Hydrocynus forskallii*	17	13.2	14	30
3, 4	*Hydrocynus forskallii*	17	12.8	14	27
3, 4	*Labeo horie*	30.4	23.3	26	230
3, 4	*Labeo horie*	31.2	23.4	26.5	231
3, 4	*Labeo horie*	36.2	28	31	372
3, 4	*Labeo horie*	36.5	27.2	31	374
3, 4	*Labeo horie*	32.2	24.2	27.5	259
3, 4	*Lates niloticus*	31.7	25.6	NA	343
3, 4	*Lates niloticus*	30.3	24.5	NA	291
3, 4	*Oreochromis niloticus*	26.5	21.5	NA	383
3, 4	*Synodontis schall*	35	26	29	520
3, 4	*Synodontis schall*	37.5	27.6	30	577
3, 4	*Synodontis schall*	36	24.2	26.5	377
3, 4	*Synodontis schall*	30	21.2	23	246
3, 4	*Synodontis schall*	29.5	19.8	21.5	244
3, 4	*Synodontis schall*	25.5	16.5	19	151
3, 4	*Synodontis schall*	28.5	19.2	21	163
3, 4	*Synodontis schall*	26.5	17.6	19.5	164
3, 4	*Synodontis schall*	23	15.2	17.5	109
3, 4	*Synodontis schall*	22	14.3	15.5	79
3, 4	*Tilapia zillii*	21	16.5	NA	202
3, 4	*Tilapia zillii*	15	11.8	NA	66
3, 4	*Tilapia zillii*	17	14	NA	100
5, 6	*Alestes baremoze*	32.6	25	27	217
5, 6	*Alestes baremoze*	32	24.2	26	182
5, 6	*Alestes baremoze*	30.5	23.2	24.9	171
5, 6	*Alestes baremoze*	32	25.2	26.6	196
5, 6	*Alestes baremoze*	32	24.2	25.9	193

5, 6	*Alestes baremoze*	22.1	16.5	18	59
5, 6	*Alestes baremoze*	26	19.2	21.2	92
5, 6	*Alestes baremoze*	26.5	19.8	21.7	106
5, 6	*Alestes baremoze*	25.3	18.8	20.5	93
5, 6	*Alestes baremoze*	25	18.5	20.6	96
5, 6	*Alestes nurse*	7.6	5.3	6.4	4
5, 6	*Alestes nurse*	7	5	6.2	5
5, 6	*Alestes nurse*	7	5.5	6	4
5, 6	*Alestes nurse*	6.8	5	5.8	4
5, 6	*Alestes nurse*	6.5	5	5.8	2
5, 6	*Alestes nurse*	6.2	4.6	5.5	2
5, 6	*Alestes nurse*	6	4.5	5.3	3
5, 6	*Alestes nurse*	6	4.6	5.4	2
5, 6	*Alestes nurse*	6	4.6	5.4	2
5, 6	*Alestes nurse*	6.3	4.5	5.3	2
5, 6	*Bagrus bayad*	40.4	29.2	30.4	280
5, 6	*Chrysichthys auratus*	27	17.6	19.7	144
5, 6	*Citharinus citharus*	46.5	36.5	40.5	1530
5, 6	*Citharinus citharus*	27.2	20.2	22.5	256
5, 6	*Distichodus nefasch*	66.5	54	59.4	2800
5, 6	*Hydrocynus forskallii*	17.5	13.2	14.3	30
5, 6	*Hydrocynus forskallii*	21.2	16.1	17.5	53
5, 6	*Hydrocynus forskallii*	17.4	13	14.4	34
5, 6	*Hydrocynus forskallii*	17	12.9	13.8	27
5, 6	*Hydrocynus forskallii*	20	15.3	16.5	45
5, 6	*Hydrocynus forskallii*	22.5	17.3	18.5	65
5, 6	*Hydrocynus forskallii*	31.5	24	25.6	147
5, 6	*Hydrocynus forskallii*	29.5	22.1	23.2	114
5, 6	*Hydrocynus forskallii*	30.4	23.4	24.9	150
5, 6	*Hydrocynus forskallii*	42	32.4	35	434
5, 6	*Lates niloticus*	55.6	46	NA	1500
5, 6	*Lates niloticus*	23.5	19	NA	163
5, 6	*Oreochromis niloticus*	20	15	NA	147
5, 6	*Oreochromis niloticus*	19	14.5	NA	118
5, 6	*Oreochromis niloticus*	23	17.3	NA	229
5, 6	*Synodontis schall*	26	18.2	20	179
5, 6	*Synodontis schall*	28	20	21.5	224
5, 6	*Synodontis schall*	22	16	17.5	119
5, 6	*Synodontis schall*	31	21.8	23.5	246
5, 6	*Synodontis schall*	23.8	17	19	136
5, 6	*Synodontis schall*	26	18	20	173

5, 6	*Synodontis schall*	29.8	21.2	23.5	240
5, 6	*Synodontis schall*	26.5	18.8	20.8	168
5, 6	*Synodontis schall*	22	14.5	16	80
5, 6	*Synodontis schall*	21.5	15.5	17	94
5, 6	*Tilapia zillii*	17.5	13.5	NA	98
5, 6	*Tilapia zillii*	10.8	8.4	NA	27
5, 6	*Tilapia zillii*	16.3	12	NA	76
5, 6	*Tilapia zillii*	4.5	3.1	NA	2
5, 6	*Tetraodon lineatus*	20	15.5	NA	183
NA	*Alestes baremoze*	14.5	NA	NA	NA
NA	*Alestes baremoze*	16	NA	NA	NA
NA	*Alestes baremoze*	16.5	NA	NA	NA
NA	*Alestes baremoze*	16.2	NA	NA	NA
NA	*Alestes baremoze*	14.5	NA	NA	NA
NA	*Alestes baremoze*	12.3	NA	NA	NA
NA	*Alestes baremoze*	12	NA	NA	NA
NA	*Alestes baremoze*	12.7	NA	NA	NA
NA	*Alestes baremoze*	13	NA	NA	NA
NA	*Alestes baremoze*	13	NA	NA	NA
NA	*Citharinus citharus*	19.5	NA	NA	NA
NA	*Citharinus citharus*	20.3	NA	NA	NA
NA	*Citharinus citharus*	20.5	NA	NA	NA
NA	*Citharinus citharus*	21	NA	NA	NA
NA	*Citharinus citharus*	19.5	NA	NA	NA
NA	*Citharinus citharus*	19.5	NA	NA	NA
NA	*Citharinus citharus*	21.5	NA	NA	NA
NA	*Citharinus citharus*	20.5	NA	NA	NA
NA	*Citharinus citharus*	20.5	NA	NA	NA
NA	*Hydrocynus forskallii*	22	NA	NA	NA
NA	*Hydrocynus forskallii*	20.5	NA	NA	NA
NA	*Hydrocynus forskallii*	18.5	NA	NA	NA
NA	*Hydrocynus forskallii*	21	NA	NA	NA
NA	*Hydrocynus forskallii*	22	NA	NA	NA
NA	*Hydrocynus forskallii*	20.5	NA	NA	NA
NA	*Hydrocynus forskallii*	21	NA	NA	NA
NA	*Hydrocynus forskallii*	18.5	NA	NA	NA
NA	*Hydrocynus forskallii*	19	NA	NA	NA
NA	*Hydrocynus forskallii*	21	NA	NA	NA
NA	*Labeo horie*	18.5	NA	NA	NA
NA	*Labeo horie*	19.2	NA	NA	NA
NA	*Labeo horie*	19	NA	NA	NA

NA	*Labeo horie*	18	NA	NA	NA
NA	*Labeo horie*	18.7	NA	NA	NA
NA	*Labeo horie*	19.5	NA	NA	NA
NA	*Labeo horie*	19.7	NA	NA	NA
NA	*Labeo horie*	17	NA	NA	NA
NA	*Labeo horie*	17.5	NA	NA	NA
NA	*Labeo horie*	17.8	NA	NA	NA
NA	*Oreochromis niloticus*	11	NA	NA	NA
NA	*Oreochromis niloticus*	11.2	NA	NA	NA
NA	*Oreochromis niloticus*	11.5	NA	NA	NA
NA	*Oreochromis niloticus*	9	NA	NA	NA
NA	*Oreochromis niloticus*	10.5	NA	NA	NA
NA	*Oreochromis niloticus*	12.5	NA	NA	NA
NA	*Oreochromis niloticus*	12	NA	NA	NA
NA	*Oreochromis niloticus*	13.2	NA	NA	NA
NA	*Oreochromis niloticus*	12	NA	NA	NA
NA	*Oreochromis niloticus*	9	NA	NA	NA
NA	*Sarotherodon galileaus*	12.5	NA	NA	NA
NA	*Sarotherodon galileaus*	16.5	NA	NA	NA
NA	*Sarotherodon galileaus*	11	NA	NA	NA
NA	*Sarotherodon galileaus*	12.5	NA	NA	NA
NA	*Sarotherodon galileaus*	13.5	NA	NA	NA
NA	*Sarotherodon galileaus*	13.5	NA	NA	NA
NA	*Sarotherodon galileaus*	14	NA	NA	NA
NA	*Sarotherodon galileaus*	12.5	NA	NA	NA
NA	*Sarotherodon galileaus*	13.5	NA	NA	NA
NA	*Sarotherodon galileaus*	12.5	NA	NA	NA
NA	*Synodontis schall*	10.5	NA	NA	NA
NA	*Synodontis schall*	21.3	NA	NA	NA
NA	*Synodontis schall*	14.5	NA	NA	NA
NA	*Synodontis schall*	16.5	NA	NA	NA
NA	*Synodontis schall*	18.5	NA	NA	NA
NA	*Synodontis schall*	17	NA	NA	NA
NA	*Synodontis schall*	11.2	NA	NA	NA
NA	*Synodontis schall*	11.5	NA	NA	NA
NA	*Synodontis schall*	10.5	NA	NA	NA
NA	*Synodontis schall*	10	NA	NA	NA
NA	*Tilapia zillii*	12	NA	NA	NA
NA	*Tilapia zillii*	13.5	NA	NA	NA
NA	*Tilapia zillii*	12.5	NA	NA	NA
NA	*Tilapia zillii*	12.5	NA	NA	NA

NA	*Tilapia zillii*	12	NA	NA	NA
NA	*Tilapia zillii*	12.5	NA	NA	NA
NA	*Tilapia zillii*	11.5	NA	NA	NA
NA	*Tilapia zillii*	12	NA	NA	NA
NA	*Tilapia zillii*	10.5	NA	NA	NA
NA	*Tilapia zillii*	9.5	NA	NA	NA
NA	*Alestes baremoze*	8	NA	NA	NA
NA	*Alestes baremoze*	8	NA	NA	NA
NA	*Alestes baremoze*	8.5	NA	NA	NA
NA	*Alestes baremoze*	8.5	NA	NA	NA
NA	*Alestes baremoze*	8.5	NA	NA	NA
NA	*Alestes baremoze*	8	NA	NA	NA
NA	*Alestes baremoze*	7.5	NA	NA	NA
NA	*Alestes baremoze*	9	NA	NA	NA
NA	*Alestes baremoze*	9	NA	NA	NA
NA	*Alestes baremoze*	7	NA	NA	NA
NA	*Alestes baremoze*	26	NA	NA	NA
NA	*Alestes baremoze*	29	NA	NA	NA
NA	*Alestes baremoze*	29.5	NA	NA	NA
NA	*Alestes baremoze*	25	NA	NA	NA
NA	*Alestes baremoze*	30	NA	NA	NA
NA	*Alestes baremoze*	28	NA	NA	NA
NA	*Alestes baremoze*	24	NA	NA	NA
NA	*Alestes baremoze*	23	NA	NA	NA
NA	*Alestes baremoze*	23	NA	NA	NA
NA	*Alestes baremoze*	23	NA	NA	NA
NA	*Alestes nurse*	6.5	NA	NA	NA
NA	*Alestes nurse*	5.5	NA	NA	NA
NA	*Alestes nurse*	5.5	NA	NA	NA
NA	*Alestes nurse*	5	NA	NA	NA
NA	*Alestes nurse*	4.5	NA	NA	NA
NA	*Alestes nurse*	6	NA	NA	NA
NA	*Alestes nurse*	5.5	NA	NA	NA
NA	*Alestes nurse*	4	NA	NA	NA
NA	*Alestes nurse*	4.5	NA	NA	NA
NA	*Alestes nurse*	4	NA	NA	NA
NA	*Alestes sp.*	9.5	NA	NA	NA
NA	*Barbus bynii*	36	NA	NA	NA
NA	*Barbus bynii*	35	NA	NA	NA
NA	*Barbus bynii*	47.5	NA	NA	NA
NA	*Barbus bynii*	45	NA	NA	NA

NA	*Barbus bynii*	38	NA	NA	NA
NA	*Barbus bynii*	54	NA	NA	NA
NA	*Citharinus citharus*	42	NA	NA	NA
NA	*Citharinus citharus*	35.5	NA	NA	NA
NA	*Citharinus citharus*	22	NA	NA	NA
NA	*Citharinus citharus*	25	NA	NA	NA
NA	*Citharinus citharus*	25	NA	NA	NA
NA	*Citharinus citharus*	21	NA	NA	NA
NA	*Citharinus citharus*	21	NA	NA	NA
NA	*Citharinus citharus*	16	NA	NA	NA
NA	*Distichodus nefasch*	23	NA	NA	NA
NA	*Distichodus nefasch*	24.8	NA	NA	NA
NA	*Distichodus nefasch*	56	NA	NA	NA
NA	*Distichodus nefasch*	53	NA	NA	NA
NA	*Hydrocynus forskallii*	25.5	NA	NA	NA
NA	*Hydrocynus forskallii*	28	NA	NA	NA
NA	*Hydrocynus forskallii*	26.5	NA	NA	NA
NA	*Hydrocynus forskallii*	25	NA	NA	NA
NA	*Hydrocynus forskallii*	23	NA	NA	NA
NA	*Hydrocynus forskallii*	27.5	NA	NA	NA
NA	*Hydrocynus forskallii*	26	NA	NA	NA
NA	*Hydrocynus forskallii*	25	NA	NA	NA
NA	*Hydrocynus forskallii*	26.5	NA	NA	NA
NA	*Hydrocynus forskallii*	24	NA	NA	NA
NA	*Hydrocynus forskallii*	23.5	NA	NA	NA
NA	*Hydrocynus forskallii*	21	NA	NA	NA
NA	*Hydrocynus forskallii*	10.5	NA	NA	NA
NA	*Hydrocynus forskallii*	10	NA	NA	NA
NA	*Hydrocynus forskallii*	19	NA	NA	NA
NA	*Hydrocynus forskallii*	21.5	NA	NA	NA
NA	*Hydrocynus forskallii*	20	NA	NA	NA
NA	*Labeo horie*	15	NA	NA	NA
NA	*Labeo horie*	15	NA	NA	NA
NA	*Labeo horie*	15.5	NA	NA	NA
NA	*Labeo horie*	16	NA	NA	NA
NA	*Labeo horie*	14	NA	NA	NA
NA	*Labeo horie*	15	NA	NA	NA
NA	*Labeo horie*	10	NA	NA	NA
NA	*Labeo horie*	11	NA	NA	NA
NA	*Labeo horie*	10.5	NA	NA	NA
NA	*Labeo horie*	13.5	NA	NA	NA

NA	*Labeo horie*	19.5	NA	NA	NA
NA	*Labeo horie*	20	NA	NA	NA
NA	*Labeo horie*	21.5	NA	NA	NA
NA	*Lates niloticus*	11	NA	NA	NA
NA	*Lates niloticus*	11	NA	NA	NA
NA	*Lates niloticus*	13.4	NA	NA	NA
NA	*Lates niloticus*	12.5	NA	NA	NA
NA	*Lates niloticus*	24.5	NA	NA	NA
NA	*Lates niloticus*	25.5	NA	NA	NA
NA	*Lates niloticus*	26	NA	NA	NA
NA	*Lates niloticus*	34	NA	NA	NA
NA	*Lates niloticus*	30.1	NA	NA	NA
NA	*Lates niloticus*	28	NA	NA	NA
NA	*Lates niloticus*	25	NA	NA	NA
NA	*Lates niloticus*	12	NA	NA	NA
NA	*Lates niloticus*	15.5	NA	NA	NA
NA	*Lates niloticus*	31	NA	NA	NA
NA	*Lates niloticus*	26.2	NA	NA	NA
NA	*Lates niloticus*	28.5	NA	NA	NA
NA	*Lates niloticus*	52.3	NA	NA	NA
NA	*Lates niloticus*	49	NA	NA	NA
NA	*Lates niloticus*	48.2	NA	NA	NA
NA	*Lates niloticus*	33	NA	NA	NA
NA	*Lates niloticus*	33.5	NA	NA	NA
NA	*Lates niloticus*	32	NA	NA	NA
NA	*Lates niloticus*	31	NA	NA	NA
NA	*Lates niloticus*	29	NA	NA	NA
NA	*Lates niloticus*	30.5	NA	NA	NA
NA	*Lates niloticus*	30	NA	NA	NA
NA	*Lates niloticus*	33	NA	NA	NA
NA	*Lates niloticus*	19.5	NA	NA	NA
NA	*Lates niloticus*	16.5	NA	NA	NA
NA	*Lates niloticus*	17	NA	NA	NA
NA	*Lates niloticus*	12	NA	NA	NA
NA	*Lates niloticus*	11.5	NA	NA	NA
NA	*Lates niloticus*	55.5	NA	NA	NA
NA	*Lates niloticus*	43	NA	NA	NA
NA	*Lates niloticus*	27.5	NA	NA	NA
NA	*Lates niloticus*	36.2	NA	NA	NA
NA	*Lates niloticus*	24	NA	NA	NA
NA	*Oreochromis niloticus*	9	NA	NA	NA

NA	*Oreochromis niloticus*	8	NA	NA	NA
NA	*Synodontis schall*	20	NA	NA	NA
NA	*Synodontis schall*	19	NA	NA	NA
NA	*Synodontis schall*	23	NA	NA	NA
NA	*Synodontis schall*	20	NA	NA	NA
NA	*Synodontis schall*	17	NA	NA	NA
NA	*Synodontis schall*	17.5	NA	NA	NA
NA	*Synodontis schall*	13	NA	NA	NA
NA	*Synodontis schall*	20	NA	NA	NA
NA	*Synodontis schall*	16.5	NA	NA	NA
NA	*Synodontis schall*	23	NA	NA	NA
NA	*Synodontis schall*	15	NA	NA	NA
NA	*Synodontis schall*	23	NA	NA	NA
NA	*Synodontis schall*	23.5	NA	NA	NA
NA	*Synodontis schall*	21	NA	NA	NA
NA	*Synodontis schall*	26.5	NA	NA	NA
NA	*Synodontis schall*	20	NA	NA	NA
NA	*Synodontis schall*	23	NA	NA	NA
NA	*Synodontis schall*	27	NA	NA	NA
NA	*Schilbe uranoscopus*	21.5	NA	NA	NA
NA	*Schilbe uranoscopus*	21.5	NA	NA	NA
NA	*Schilbe uranoscopus*	23	NA	NA	NA
NA	*Schilbe uranoscopus*	20	NA	NA	NA
NA	*Schilbe uranoscopus*	21.2	NA	NA	NA
NA	*Schilbe uranoscopus*	19	NA	NA	NA
NA	*Schilbe uranoscopus*	22	NA	NA	NA
NA	*Schilbe uranoscopus*	21.5	NA	NA	NA
NA	*Schilbe uranoscopus*	19.2	NA	NA	NA
NA	*Schilbe uranoscopus*	19.5	NA	NA	NA
NA	*Schilbe uranoscopus*	17.5	NA	NA	NA
NA	*Schilbe uranoscopus*	18.6	NA	NA	NA
NA	*Schilbe uranoscopus*	23	NA	NA	NA
NA	*Schilbe uranoscopus*	23	NA	NA	NA
NA	*Schilbe uranoscopus*	22.5	NA	NA	NA
NA	*Schilbe uranoscopus*	23	NA	NA	NA
NA	*Schilbe uranoscopus*	25.5	NA	NA	NA
NA	*Schilbe uranoscopus*	21	NA	NA	NA
NA	*Schilbe uranoscopus*	21	NA	NA	NA
NA	*Schilbe uranoscopus*	19	NA	NA	NA
NA	*Tilapia zillii*	18	NA	NA	NA
NA	*Tilapia zillii*	13	NA	NA	NA

NA	*Lates niloticus*	71	NA	NA	NA
NA	*Tilapia zillii*	21.1	NA	NA	NA
NA	*Bagrus bayad*	7.7	NA	NA	NA
NA	*Bagrus bayad*	16.6	NA	NA	NA
NA	*Lates niloticus*	5	NA	NA	NA
NA	*Lates niloticus*	4.6	NA	NA	NA
NA	*Lates niloticus*	8.5	NA	NA	NA
NA	*Lates niloticus*	115	NA	NA	NA
NA	*Lates niloticus*	120	NA	NA	NA
NA	*Lates niloticus*	97	NA	NA	NA
NA	*Lates niloticus*	86	NA	NA	NA
NA	*Lates niloticus*	79	NA	NA	NA
NA	*Lates niloticus*	64	NA	NA	NA
NA	*Lates niloticus*	56	NA	NA	NA
NA	*Lates niloticus*	52.5	NA	NA	NA
NA	*Lates niloticus*	57	NA	NA	NA
NA	*Lates niloticus*	76	NA	NA	NA
NA	*Lates niloticus*	80	NA	NA	NA
NA	*Lates niloticus*	68	NA	NA	NA
NA	*Lates niloticus*	68	NA	NA	NA
NA	*Oreochromis niloticus*	18.6	NA	NA	NA
NA	*Oreochromis niloticus*	19	NA	NA	NA
NA	*Sarotherodon galileaus*	17.1	NA	NA	NA
NA	*Sarotherodon galileaus*	17.9	NA	NA	NA
NA	*Synodontis schall*	24	NA	NA	NA
NA	*Synodontis schall*	28	NA	NA	NA
NA	*Synodontis schall*	28.2	NA	NA	NA
NA	*Synodontis schall*	18.6	NA	NA	NA
NA	*Synodontis schall*	21.6	NA	NA	NA
NA	*Tilapia zillii*	18	NA	NA	NA
NA	*Tilapia zillii*	19.8	NA	NA	NA
NA	*Tilapia zillii*	18	NA	NA	NA
NA	*Tilapia zillii*	22	NA	NA	NA
NA	*Tilapia zillii*	21.8	NA	NA	NA
NA	*Tilapia zillii*	19	NA	NA	NA
NA	*Tilapia zillii*	22.6	NA	NA	NA
NA	*Tilapia zillii*	20.5	NA	NA	NA
NA	*Tilapia zillii*	21.7	NA	NA	NA
NA	*Oreochromis niloticus*	21	NA	NA	NA
NA	*Oreochromis niloticus*	20.5	NA	NA	NA
NA	*Oreochromis niloticus*	22.2	NA	NA	NA

NA	*Oreochromis niloticus*	20	NA	NA	NA
NA	*Oreochromis niloticus*	22.3	NA	NA	NA
NA	*Bagrus bayad*	36	NA	NA	NA
NA	*Bagrus bayad*	31	NA	NA	NA
NA	*Bagrus bayad*	31.5	NA	NA	NA
NA	*Bagrus bayad*	51	NA	NA	NA
NA	*Barbus bynii*	49.5	NA	NA	NA
NA	*Barbus bynii*	25.5	NA	NA	NA
NA	*Barbus bynii*	39	NA	NA	NA
NA	*Barbus bynii*	39	NA	NA	NA
NA	*Labeo horie*	27	NA	NA	NA
NA	*Labeo horie*	29	NA	NA	NA
NA	*Labeo horie*	26	NA	NA	NA
NA	*Labeo horie*	36	NA	NA	NA
NA	*Labeo horie*	34	NA	NA	NA
NA	*Labeo horie*	25.9	NA	NA	NA
NA	*Labeo horie*	38.5	NA	NA	NA
NA	*Lates niloticus*	27.5	NA	NA	NA
NA	*Lates niloticus*	23	NA	NA	NA
NA	*Lates niloticus*	27.7	NA	NA	NA
NA	*Lates niloticus*	24	NA	NA	NA
NA	*Lates niloticus*	21	NA	NA	NA
NA	*Lates niloticus*	26	NA	NA	NA
NA	*Lates niloticus*	23.6	NA	NA	NA
NA	*Synodontis schall*	20	NA	NA	NA
NA	*Schilbe uranoscopus*	16.4	NA	NA	NA
NA	*Schilbe uranoscopus*	14.8	NA	NA	NA
NA	*Schilbe uranoscopus*	15.5	NA	NA	NA
NA	*Schilbe uranoscopus*	15.6	NA	NA	NA
NA	*Tilapia zillii*	17	NA	NA	NA
NA	*Tilapia zillii*		NA	NA	NA
NA	*Tetraodon lineatus*		NA	NA	NA
NA	*Alestes nurse*	7.2	NA	NA	NA
NA	*Bagrus bayad*	24	NA	NA	NA
NA	*Bagrus bayad*	23.5	NA	NA	NA
NA	*Citharinus citharus*	33	NA	NA	NA
NA	*Citharinus citharus*	25	NA	NA	NA
NA	*Citharinus citharus*	38	NA	NA	NA
NA	*Citharinus citharus*	29.5	NA	NA	NA
NA	*Citharinus citharus*	45	NA	NA	NA
NA	*Citharinus citharus*	24	NA	NA	NA

NA	*Citharinus citharus*	21.5	NA	NA	NA
NA	*Citharinus citharus*	24	NA	NA	NA
NA	*Distichodus nefasch*	38	NA	NA	NA
NA	*Distichodus nefasch*	26	NA	NA	NA
NA	*Distichodus nefasch*	29	NA	NA	NA
NA	*Distichodus nefasch*	22	NA	NA	NA
NA	*Distichodus nefasch*	34	NA	NA	NA
NA	*Distichodus nefasch*	34.5	NA	NA	NA
NA	*Distichodus nefasch*	21	NA	NA	NA
NA	*Distichodus nefasch*	25.6	NA	NA	NA
NA	*Hydrocynus forskallii*	31	NA	NA	NA
NA	*Hydrocynus forskallii*	11.7	NA	NA	NA
NA	*Hydrocynus forskallii*	12.5	NA	NA	NA
NA	*Hydrocynus forskallii*	12.5	NA	NA	NA
NA	*Hydrocynus forskallii*	12	NA	NA	NA
NA	*Hydrocynus forskallii*	12.5	NA	NA	NA
NA	*Hydrocynus forskallii*	11	NA	NA	NA
NA	*Hydrocynus forskallii*	11.5	NA	NA	NA
NA	*Hydrocynus forskallii*	12.5	NA	NA	NA
NA	*Labeo horie*	48	NA	NA	NA
NA	*Labeo horie*	46	NA	NA	NA
NA	*Labeo horie*	46	NA	NA	NA
NA	*Lates niloticus*	16	NA	NA	NA
NA	*Lates niloticus*	21	NA	NA	NA
NA	*Lates niloticus*	24	NA	NA	NA
NA	*Lates niloticus*	18	NA	NA	NA
NA	*Lates niloticus*	35.5	NA	NA	NA
NA	*Lates niloticus*	16.5	NA	NA	NA
NA	*Lates niloticus*	17	NA	NA	NA
NA	*Oreochromis niloticus*	37	NA	NA	NA
NA	*Oreochromis niloticus*	30	NA	NA	NA
NA	*Oreochromis niloticus*	22.5	NA	NA	NA
NA	*Oreochromis niloticus*	34	NA	NA	NA
NA	*Oreochromis niloticus*	33	NA	NA	NA
NA	*Oreochromis niloticus*	19.5	NA	NA	NA
NA	*Oreochromis niloticus*	26	NA	NA	NA
NA	*Oreochromis niloticus*	17	NA	NA	NA
NA	*Oreochromis niloticus*	29.5	NA	NA	NA
NA	*Oreochromis niloticus*	30	NA	NA	NA
NA	*Oreochromis niloticus*	25	NA	NA	NA
NA	*Synodontis schall*	16	NA	NA	NA

NA	*Synodontis schall*	12.5	NA	NA	NA
NA	*Synodontis schall*	13	NA	NA	NA
NA	*Synodontis schall*	12.5	NA	NA	NA
NA	*Schilbe uranoscopus*	19.5	NA	NA	NA
NA	*Schilbe uranoscopus*	15.4	NA	NA	NA
NA	*Schilbe uranoscopus*	16.5	NA	NA	NA
NA	*Schilbe uranoscopus*	15	NA	NA	NA
NA	*Schilbe uranoscopus*	17	NA	NA	NA
NA	*Schilbe uranoscopus*	23	NA	NA	NA
NA	*Schilbe uranoscopus*	16	NA	NA	NA
NA	*Schilbe uranoscopus*	20	NA	NA	NA
NA	*Schilbe uranoscopus*	17.5	NA	NA	NA
NA	*Schilbe uranoscopus*	15.5	NA	NA	NA
NA	*Schilbe uranoscopus*	15	NA	NA	NA
NA	*Schilbe uranoscopus*	16	NA	NA	NA
NA	*Barbus bynii*	27	NA	NA	NA
NA	*Barbus bynii*	39	NA	NA	NA
NA	*Barbus bynii*	36	NA	NA	NA
NA	*Barbus bynii*	26	NA	NA	NA
NA	*Barbus bynii*	35.4	NA	NA	NA
NA	*Distichodus nefasch*	33.7	NA	NA	NA
NA	*Distichodus nefasch*	25.9	NA	NA	NA
NA	*Hydrocynus forskallii*	24.5	NA	NA	NA
NA	*Hydrocynus forskallii*	28	NA	NA	NA
NA	*Hydrocynus forskallii*	23	NA	NA	NA
NA	*Hydrocynus forskallii*	27.5	NA	NA	NA
NA	*Hydrocynus forskallii*	17.2	NA	NA	NA
NA	*Labeo horie*	22.8	NA	NA	NA
NA	*Labeo horie*	25.5	NA	NA	NA
NA	*Labeo horie*	30.2	NA	NA	NA
NA	*Labeo horie*	30.3	NA	NA	NA
NA	*Labeo horie*	27.4	NA	NA	NA
NA	*Lates niloticus*	24.6	NA	NA	NA
NA	*Lates niloticus*	17.5	NA	NA	NA
NA	*Lates niloticus*	17.5	NA	NA	NA
NA	*Lates niloticus*	19.5	NA	NA	NA
NA	*Lates niloticus*	18.5	NA	NA	NA
NA	*Synodontis schall*	17.2	NA	NA	NA
NA	*Synodontis schall*	25	NA	NA	NA
NA	*Synodontis schall*	17.5	NA	NA	NA
NA	*Synodontis schall*	16.4	NA	NA	NA

NA	*Synodontis schall*	23	NA	NA	NA
NA	*Schilbe uranoscopus*	9.7	NA	NA	NA
NA	*Schilbe uranoscopus*	15	NA	NA	NA
NA	*Schilbe uranoscopus*	14.4	NA	NA	NA
NA	*Schilbe uranoscopus*	24.7	NA	NA	NA
NA	*Schilbe uranoscopus*	14.9	NA	NA	NA

Table A1.9: Length and Mass of all Fishes Collected, 2012-2013

Site#	Net	Mesh (")	Species	TL (cm)	SL (cm)	FL (cm)	Mass (g)	DNA	Isotope
7	SB	1/2	*Oreochromis niloticus*	7	5.5		5		X
7	SB	1/2	*Oreochromis niloticus*	7	5		5		X
7	SB	1/2	*Oreochromis niloticus*	6.5	5		5		X
7	SB	1/2	*Oreochromis niloticus*	8	6		9		X
8	SB	1	*Oreochromis niloticus*	15	11.5		56		X
8	SB	1/2	*Oreochromis niloticus*	8	6		8		X
9	SB	1/2	*Oreochromis niloticus*	7	5.5		5		X
9	SB	1/2	*Oreochromis niloticus*	7	5.5		5		X
9	SB	1/2	*Oreochromis niloticus*	7	5.5		5		X
9	SB	1	*Oreochromis niloticus*	17	13.5		69		X
9	SB	1	*Oreochromis niloticus*	16	12.5		57		X
10	SB	3	*Oreochromis niloticus*	14	10		53		X
10	SB	1/2	*Oreochromis niloticus*	7	5.5		6		X
11	EU	1	*Hydrocynus forskallii*	27	20	21.5	105		X
11	EU	2	*Hydrocynus forskallii*	29	21.5	23.5	118		X
11	EU	2	*Hydrocynus forskallii*	25	19	20.5	89		X
11	EU	2	*Hydrocynus forskallii*	25.5	19.5	21	99		X
11	EU	2	*Hydrocynus forskallii*	26.5	20	21	118		X
11	EU	2	*Hydrocynus forskallii*	28	21.5	23	117		
11	EU	2	*Hydrocynus forskallii*	27	20.5	22	118		
11	EU	2	*Hydrocynus forskallii*	31	22.5	24.5	151		
11	EU	2	*Hydrocynus forskallii*	35.5	27.5	30	279		
11	EU	2	*Hydrocynus forskallii*	27.5	20.5	22.5	115		
11	EU	2	*Hydrocynus forskallii*	29.5	24.5	22.5	142		
11	EU	2	*Hydrocynus forskallii*	26.5	19.5	21	99		
11	EU	2	*Hydrocynus forskallii*	27	20.5	21.5	101		
11	EU	2	*Hydrocynus forskallii*	26.5	20.5	22	107		
11	EU	2	*Hydrocynus forskallii*	26.5	20.5	22	100		
11	EU	2	*Hydrocynus forskallii*	27	20	22	97		
11	EU	2	*Hydrocynus forskallii*	28	20.5	22	104		
11	EU	2	*Labeo horie*	22	16.5	18	77		X
11	EU	2	*Labeo horie*	23	17.5	20	98		X
11	EU	2	*Labeo horie*	20	15.5	17.5	73		X
11	EU	2	*Labeo horie*	20	15.5	17	72		X
11	EU	2	*Labeo horie*	19	14.5	16	54		X
11	EU	2	*Labeo horie*	23	14	17.5	101		
11	EU	2	*Labeo horie*	21	15.5	17.5	74		
11	EU	2	*Labeo horie*	20	15	17.5	66		

11	EU	2	*Labeo horie*	22	16.5	19	84		
11	EU	2	*Labeo horie*	20	15.5	18	78		
11	EU	2	*Labeo horie*	21	16.5	18.5	80		
11	EU	2	*Tilapia zillii*	13	10		39		X
11	EU	2	*Tilapia zillii*	13.5	10.5		46		X
11	EU	2	*Tilapia zillii*	11.5	9.5		34		X
11	EU	2	*Tilapia zillii*	13	10		40		X
11	EU	2	*Tilapia zillii*	16.5	13		84		X
11	EU	2	*Tilapia zillii*	12	9.5		30		
11	EU	2	*Tilapia zillii*	11.5	9.5		26		
11	EU	2	*Tilapia zillii*	11.5	9.5		27		
11	EU	2	*Tilapia zillii*	10.5	9		25		
11	EU	2	*Tilapia zillii*	13	10		40		
11	EU	2	*Tilapia zillii*	12.5	10.5		40		
11	EU	2	*Tilapia zillii*	10.5	9		32		
11	EU	2	*Tilapia zillii*	12	10		35		
11	EU	2	*Tilapia zillii*	10.5	8.5		32		
11	EU	2	*Tilapia zillii*	11.5	9.5		30		
11	EU	2	*Oreochromis niloticus*	16	12		81		X
11	EU	2	*Oreochromis niloticus*	14	11		48		
11	EU	2	*Oreochromis niloticus*	14	11		45		X
11	EU	2	*Oreochromis niloticus*	12.5	9.5		30		X
11	EU	3	*Hydrocynus forskallii*	30	22.5	24	156		
11	EU	3	*Hydrocynus forskallii*	32	23	26	210		
11	EU	3	*Hydrocynus forskallii*	29.5	22.5	23.5	139		
11	EU	3	*Hydrocynus forskallii*	25	18.5	21.5	102		
11	EU	3	*Hydrocynus forskallii*	28.5	22.5	23	140		
11	EU	3	*Hydrocynus forskallii*	25	19.5	21	97		
11	EU	3	*Hydrocynus forskallii*	33	26.5	28	223		
11	EU	3	*Hydrocynus forskallii*	27	20	22	104		
11	EU	3	*Hydrocynus forskallii*	29	21.5	23	129		
11	EU	3	*Hydrocynus forskallii*	27	20.5	22	104		
11	EU	3	*Hydrocynus forskallii*	28.5	21.5	23	134		
11	EU	3	*Hydrocynus forskallii*	31.5	23.5	26	186		
11	EU	3	*Hydrocynus forskallii*	29	21.5	23.5	127		
11	EU	3	*Hydrocynus forskallii*	30	22.5	24	136		
11	EU	3	*Hydrocynus forskallii*	26.5	20	21	100		
11	EU	3	*Hydrocynus forskallii*	28	21	23	120		
11	EU	3	*Hydrocynus forskallii*	31	22	25	169		
11	EU	3	*Hydrocynus forskallii*	28	20.5	22	121		
11	EU	3	*Hydrocynus forskallii*	28.5	22	23.5	141		

11	EU	3	*Hydrocynus forskallii*	27	20.5	22	107		
11	EU	3	*Hydrocynus forskallii*	29	21.5	23.5	130		
11	EU	3	*Hydrocynus forskallii*	30	22.5	24	138		
11	EU	3	*Hydrocynus forskallii*	26	19	21	94		
11	EU	3	*Hydrocynus forskallii*	29.5	22.5	24	139		
11	EU	3	*Alestes baremoze*	23	18.5	20	100		X
11	EU	3	*Oreochromis niloticus*	14	11		47		X
11	EU	3	*Oreochromis niloticus*	16.5	12		66		X
11	EU	3	*Oreochromis niloticus*	15.5	11.5		37		X
11	EU	3	*Oreochromis niloticus*	14	11		50		
11	EU	3	*Oreochromis niloticus*	13	10		37		
11	EU	5	*Oreochromis niloticus*	25	19.5		253		X
11	EU	5	*Oreochromis niloticus*	21	16.5		171		X
11	EU	3	*Tilapia zillii*	12.5	10		37		
11	EU	3	*Tilapia zillii*	13	10		43		X
11	EU	3	*Tilapia zillii*	13	10		39		X
11	EU	3	*Tilapia zillii*	14	11		44		X
11	EU	3	*Tilapia zillii*	14	11		55		X
11	EU	3	*Tilapia zillii*	11	9		28		
11	EU	3	*Tilapia zillii*	13.5	10.5		39		
11	EU	3	*Tilapia zillii*	13.5	10.5		48		
11	EU	3	*Tilapia zillii*	14	11		47		X
11	EU	3	*Labeo horie*	20	15.5	17	66		
11	EU	3	*Labeo horie*	21	16	18	78		
11	EU	3	*Labeo horie*	21.5	15.5	18	75		
11	EU	3	*Labeo horie*	21	15.5	17.5	73		
11	EU	3	*Labeo horie*	21.5	16.5	18	78		
11	EU	3	*Labeo horie*	23	17.5	19	89		
11	EU	3	*Labeo horie*	20.5	16	18	73		
11	EU	3	*Labeo horie*	21	16.5	18	73		X
11	EU	3	*Labeo horie*	21.5	16	18	75		
11	EU	4	*Lates niloticus*	24	19		148		X
11	EU	4	*Sarotherodon galilaeus*	15	11		69		X
11	EU	4	*Oreochromis niloticus*	23.5	18.5		228		
11	EU	4	*Oreochromis niloticus*	16.5	13		90		
11	EU	4	*Oreochromis niloticus*	16	12.5		67		
11	EU	4	*Oreochromis niloticus*	16	12		77		
11	EU	4	*Oreochromis niloticus*	16	12.5		77		
11	EU	4	*Oreochromis niloticus*	16	12.5		74		
11	EU	4	*Oreochromis niloticus*	22.5	17		182		
11	EU	4	*Oreochromis niloticus*	17.5	13.5		76		

11	EU	4	*Oreochromis niloticus*	16	13		80		
11	EU	4	*Citharinus citharus*	26.5	19.5	22	230		X
11	EU	4	*Oreochromis niloticus*	17.5	13.5		81		
11	EU	4	*Oreochromis niloticus*	16.5	13		75		
11	EU	4	*Oreochromis niloticus*	15.5	12		73		
11	EU	4	*Oreochromis niloticus*	16	13		75		
11	EU	4	*Oreochromis niloticus*	17.5	13.5		79		
11	EU	4	*Tilapia zillii*	16	12.5		82		
11	EU	4	*Tilapia zillii*	11	8.5		30		
11	EU	4	*Tilapia zillii*	15	12		61		
11	EU	4	*Hydrocynus forskallii*	33.5	26.5	28	249		
11	EU	4	*Hydrocynus forskallii*	33	25.5	27	235		
11	EU	4	*Hydrocynus forskallii*	38	30	37	366		X
11	EU	4	*Hydrocynus forskallii*	36	27	29	332		
11	EU	4	*Hydrocynus forskallii*	29	21.5	23.5	133		
11	EU	4	*Hydrocynus forskallii*	24.5	18.5	20.5	86		
12, 13	SB	1/2	*Alestes nurse*	10	8	9	11		X
12, 13	SB	1/2	*Oreochromis niloticus*	7	5.5		5		X
12, 13	SB	1/2	*Oreochromis niloticus*	8	6		7		X
12, 13	SB	1/2	*Oreochromis niloticus*	7	5.5		6		X
12, 13	SB	2	*Oreochromis niloticus*	14	11		4.5		X
12, 13	SB	1/2	*Oreochromis niloticus*	8	6		8		X
15	SB	1	*Lates niloticus*	27	21.5		198		X
15	SB	1	*Alestes sp.*	10.5	8.5		12		
15	SB	1	*Chrysichthys auratus*	10	7.5		9		X
15	SB	2	*Lates niloticus*	25	21		166		X
15	SB	2	*Lates niloticus*	22.5	18		102		X
15	SB	2	*Lates niloticus*	25	20		168		X
15	SB	2	*Lates niloticus*	24	19		145		X
15	SB	2	*Lates niloticus*	26	21		168		X
15	SB	2	*Lates niloticus*	26.5	21		181		X
15	SB	2	*Lates niloticus*	25.5	20.5		166		
15	SB	2	*Lates niloticus*	25	20		173		X
15	SB	2	*Lates niloticus*	31	25		275		X
15	SB	2	*Lates niloticus*	24	19		127		
15	SB	2	*Lates niloticus*	25	20		157		X
15	SB	2	*Lates niloticus*	25	20		136		X
15	SB	2	*Lates niloticus*	19	15.5		75		X
15	SB	2	*Lates niloticus*	20	15.5		78		X
15	SB	2	*Synodontis schall*	20.5	14	15.5	77		X
15	SB	2	*Synodontis schall*	24	16.5	18	129		X

15	SB	3	*Lates niloticus*	25.5	20.5		159		X
14	EU	1	*Hydrocynus forskallii*	34	26.5	28	253		
14	EU	1	*Hydrocynus forskallii*	21	16	17.5	47		X
14	EU	1	*Lates niloticus*	29	23.5		205		
14	EU	2	*Lates niloticus*	25	20		147		
14	EU	2	*Lates niloticus*	31	25		279		
14	EU	2	*Lates niloticus*	24.5	20		157		
14	EU	2	*Lates niloticus*	28	22		208		
14	EU	2	*Lates niloticus*	28	22		200		
14	EU	2	*Lates niloticus*	24.5	20		132		
14	EU	2	*Lates niloticus*	16.5	13.5		47		
14	EU	2	*Synodontis schall*	27	18.5		187		X
14	EU	2	*Synodontis schall*	23	20.5		105		X
14	EU	2	*Barbus bynni*	16.5	12.5		45		X
14	EU	2	*Labeo horie*	18	13.5		49		X
14	EU	3	*Bagrus Bayad*	33.5	23.5	25	142		X
14	EU	3	*Bagrus Bayad*	42	27.5	31	220		X
14	EU	3	*Bagrus Bayad*	38	23.5	26	141		X
14	EU	3	*Bagrus Bayad*	41	24.5	26	167		X
14	EU	3	*Lates niloticus*	25.5	20.5		155		
14	EU	3	*Lates niloticus*	26.5	21		186		
14	EU	3	*Lates niloticus*	25	20		142		
14	EU	4	*Barbus bynni*	26.5	22.5	22.5	179		X
14	EU	4	*Barbus bynni*	27.5	21.5	23.5	201		X
14	EU	4	*Bagrus Bayad*	46	28.5	31	241		X
14	EU	4	*Lates niloticus*	29	23.5		226		X
14	EU	4	*Lates niloticus*	29.5	23		239		
14	EU	4	*Lates niloticus*	27.5	22		219		
14	EU	4	*Lates niloticus*	25.5	20.5		164		
14	EU	4	*Lates niloticus*	21	16		95		
14	EU	5	*Barbus bynni*	32.5	24	26	341		X
14	EU	5	*Barbus bynni*	32.5	26	28.5	356		X
14	EU	5	*Barbus bynni*	33	25	27.5	336		X
14	EU	5	*Barbus bynni*	31.5	22.5	26.5	292		X
14	EU	5	*Synodontis schall*	30.5	21.5	24	223		X
14	EU	5	*Lates niloticus*	26.5	21	no FL	180		
14	EU	5	*Lates niloticus*	26	20.5	no FL	170		
14	EU	5	*Lates niloticus*	30	23.5	no FL	274		
14	EU	5	*Lates niloticus*	27	21.5	no FL	192		
14	EU	5	*Lates niloticus*	26	20.5	no FL	177		
14	EU	5	*Lates niloticus*	16.5	13.5	no FL	45		

16	EU	1	*Oreochromis niloticus*	14	11		52	X	X
16	EU	1	*Oreochromis niloticus*	17	13		70	X	X
16	EU	1	*Oreochromis niloticus*	15	12		55	X	X
16	EU	1	*Oreochromis niloticus*	13	10		43	X	X
16	EU	1	*Oreochromis niloticus*	10	8		21	X	X
16	EU	1	*Oreochromis niloticus*	12	9.5		34	X	X
16	EU	1	*Oreochromis niloticus*	10.5	8.5		19	X	X
16	EU	1	*Oreochromis niloticus*	12	9.5		29	X	X
16	EU	2	*Oreochromis niloticus*	11	8.5		23	X	X
16	EU	2	*Oreochromis niloticus*	10.5	8.5		21	X	X
16	EU	3	*Oreochromis niloticus*	17.5	13.5		86	X	X
16	EU	3	*Oreochromis niloticus*	15	12		58	X	X
16	EU	3	*Oreochromis niloticus*	13.5	11		45	X	X
16	EU	3	*Oreochromis niloticus*	15.5	12		55	X	X
16	EU	3	*Oreochromis niloticus*	12	10		33	X	X
16	EU	3	*Oreochromis niloticus*	13	10		38	X	X
16	EU	4	*Oreochromis niloticus*	16	13		66	X	X
16	EU	4	*Oreochromis niloticus*	16.5	13..5		75	X	X
16	EU	4	*Oreochromis niloticus*	17	14		88	X	X
16	EU	4	*Oreochromis niloticus*	16.5	13		71	X	X
16	EU	4	*Oreochromis niloticus*	15	11.5		63	X	X
16	EU	4	*Oreochromis niloticus*	15.5	12.5		66	X	
16	EU	4	*Oreochromis niloticus*	15.5	12.5		70	X	
16	EU	4	*Oreochromis niloticus*	16	13		74	X	
16	EU	4	*Oreochromis niloticus*	16	13		67	X	
16	EU	4	*Oreochromis niloticus*	16	13.5		71	X	
16	EU	4	*Oreochromis niloticus*	15.5	12		55	X	
16	EU	4	*Oreochromis niloticus*	16.5	13.5		78	X	
16	EU	5	*Oreochromis niloticus*	20	16		110	X	X
16	EU	5	*Oreochromis niloticus*	17	13.5		69	X	X
17	EU	1	*Hydrocynus forskallii*	36	28	30	237	X	X
17	EU	1	*Hydrocynus forskallii*	19.5	15	16	38	X	X
17	EU	1	*Hydrocynus forskallii*	16	12.5	13.5	24	X	X
17	EU	1	*Hydrocynus forskallii*	17	13.5	14.5	27	X	X
17	EU	1	*Synodontis schall*	17	11.5	12.5	39	X	X
17	EU	1	*Synodontis schall*	18	12	13.5	46	X	X
17	EU	2	*Hydrocynus forskallii*	39	30	32.5	305	X	X
17	EU	2	*Hydrocynus forskallii*	26	19.5	21	88	X	X
17	EU	2	*Hydrocynus forskallii*	32	25	265	161	X	X
17	EU	2	*Hydrocynus forskallii*	26.5	19.5	21	89	X	X
17	EU	2	*Hydrocynus forskallii*	20.5	15.5	165	46	X	X

17	EU	2	*Hydrocynus forskallii*	26.5	20	215	93	X	X
17	EU	2	*Hydrocynus forskallii*	33.5	26.5	28	177	X	X
17	EU	2	*Hydrocynus forskallii*	28	21	22.5	107	X	X
17	EU	2	*Hydrocynus forskallii*	21.5	16.5	17.5	54	X	X
17	EU	2	*Hydrocynus forskallii*	28.5	21.5	23	120	X	X
17	EU	2	*Hydrocynus forskallii*	26.5	20.5	21.5	92	X	
17	EU	2	*Hydrocynus forskallii*	27	20	21.5	104	X	
17	EU	2	*Hydrocynus forskallii*	28	21	22.5	113		
17	EU	2	*Hydrocynus forskallii*	28	21	22.5	112		
17	EU	2	*Hydrocynus forskallii*	24	18	19.5	70		
17	EU	2	*Hydrocynus forskallii*	25	19.5	20.5	74		
17	EU	2	*Hydrocynus forskallii*	24.5	18.5	19.5	72		
17	EU	2	*Hydrocynus forskallii*	26.5	20.5	21.5	91		
17	EU	2	*Synodontis schall*	22.5	14	15.5	90	X	X
17	EU	2	*Synodontis schall*	16.5	11.5	12	36	X	X
17	EU	2	*Synodontis schall*	18.5	12.5	13.5	48	X	X
17	EU	2	*Synodontis schall*	18	12.5	13.5	43	X	X
17	EU	3	*Lates niloticus*	25.5	20.5		166		X
17	EU	3	*Labeo horie*	23.5	18.5	20.5	114		X
17	EU	3	*Labeo horie*	23.5	17.5	19.5	101		X
17	EU	3	*Labeo horie*	22.5	18.5	19.5	88		
17	EU	3	*Hydrocynus forskallii*	31	23	24.5	127		
17	EU	3	*Hydrocynus forskallii*	26	19.5	21	93		
17	EU	3	*Hydrocynus forskallii*	29.5	22	23.5	125		
17	EU	3	*Hydrocynus forskallii*	28.5	21.5	23	111		
17	EU	3	*Hydrocynus forskallii*	27	19.5	21.5	98	X	
17	EU	3	*Hydrocynus forskallii*	28.5	21.5	23	116	X	
17	EU	3	*Hydrocynus forskallii*	27.5	20.5	22	98	X	
17	EU	4	*Barbus bynni*	31.5	24.5	26	304		X
17	EU	4	*Barbus bynni*	32	24.5	27.5	305		X
17	EU	4	*Barbus bynni*	30	23.5	26	273		X
17	EU	4	*Barbus bynni*	37	27.5	31	509		X
17	EU	4	*Barbus bynni*	31	23.5	26.5	319		X
17	EU	4	*Barbus bynni*	33.5	26.5	29	396		X
17	EU	4	*Barbus bynni*	28	21.5	23.5	211		X
17	EU	4	*Bagrus Bayad*	42	29.5	33	299		X
17	EU	4	*Bagrus Bayad*	39	24.5	27.5	150		X
17	EU	4	*Synodontis schall*	23.5	16.5	18.5	151	X	X
17	EU	4	*Lates niloticus*	27	20.5		190		X
17	EU	4	*Labeo horie*	29.5	21.5	24.5	209		X
17	EU	4	*Labeo horie*	27.5	20.5	23	187		X

17	EU	4	*Labeo horie*	22	16.5	19	97		X
17	EU	4	*Labeo horie*	27.5	21.5	24	186		
17	EU	4	*Labeo horie*	32.5	24.5	28	299		X
17	EU	4	*Labeo horie*	25	18.5	21	183		
17	EU	4	*Labeo horie*	22.5	16.5	19	109	X	
17	EU	4	*Hydrocynus forskallii*	31.5	24	26	179		
17	EU	5	*Barbus bynni*	33.5	25.5	26.5	369		
17	EU	5	*Barbus bynni*	33	25	28	360		
17	EU	5	*Barbus bynni*	30	28.5	32	319		
17	EU	5	*Barbus bynni*	24.5	25.5	29	386		
17	EU	5	*Barbus bynni*	24	25.5	28.5	373		
17	EU	5	*Barbus bynni*	32.5	24.5	27	326		
18	EU	1	*Lates niloticus*	44	36		846		
18	EU	1	*Tilapia zillii*	19.5	15		132		
18	EU	1	*Hydrocynus forskallii*	36	27.5	29.5	261	X	X
18	EU	1	*Hydrocynus forskallii*	40.5	31.5	33.5	364	X	X
18	EU	1	*Hydrocynus forskallii*	22.5	17	19	62	X	X
18	EU	1	*Hydrocynus forskallii*	18.5	14	15	36	X	X
18	EU	1	*Hydrocynus forskallii*	17.5	13.5	14.5	31	X	X
18	EU	1	*Hydrocynus forskallii*	16.5	12.5	13.5	27	X	
18	EU	1	*Hydrocynus forskallii*	16.5	13	14	25	X	
18	EU	1	*Alestes baremoze*	22.5	16.5	18.5	59		X
18	EU	1	*Alestes baremoze*	19	14	15.5	35		X
18	EU	1	*Alestes baremoze*	20	16	17.5	51		X
18	EU	1	*Alestes baremoze*	17.5	13.5	14.5	32		X
18	EU	1	*Alestes baremoze*	19	14	15.5	32		
18	EU	1	*Alestes baremoze*	16	14	15	32		
18	EU	1	*Alestes baremoze*	18.5	14	15.5	34		
18	EU	1	*Alestes baremoze*	18	13	15	34		
18	EU	1	*Alestes baremoze*	18.5	14	15.5	34		
18	EU	1	*Alestes baremoze*	18	13	14.5	29		
18	EU	1	*Alestes baremoze*	18.5	14	15.5	33		
18	EU	1	*Alestes baremoze*	17	12.5	14	24		
18	EU	1	*Alestes baremoze*	19	14.5	16	36		X
18	EU	1	*Alestes baremoze*	17.5	13.5	14.5	29		
18	EU	1	*Alestes baremoze*	16	11.5	13	22		
18	EU	2	*Labeo horie*	21.5	16.5	19	84		X
18	EU	2	*Labeo horie*	22.5	17.5	19	95		X
18	EU	2	*Alestes baremoze*	24	17.5	19.5	69		X
18	EU	2	*Alestes baremoze*	24	18.5	20.5	71		X
18	EU	2	*Alestes baremoze*	19.5	14.5	16	36		X

18	EU	2	*Alestes baremoze*	22	17	18.5	56		X
18	EU	2	*Hydrocynus forskallii*	26.5	20.5	22	100	X	X
18	EU	2	*Hydrocynus forskallii*	23.5	18.5	20.5	63	X	X
18	EU	2	*Hydrocynus forskallii*	23	17.5	19	65	X	X
18	EU	2	*Hydrocynus forskallii*	19	14.5	15.5	39	X	X
18	EU	3	*Labeo horie*	37	28.5	32.5	407		X
18	EU	3	*Labeo horie*	24	19	21	129		X
18	EU	3	*Labeo horie*	25	19	21.5	127		X
18	EU	3	*Tilapia zillii*	22	17		213		X
18	EU	3	*Sarotherodon galilaeus*	17.5	13.5		113		X
18	EU	3	*Lates niloticus*	22	17.5		123		X
18	EU	3	*Hydrocynus forskallii*	34.5	26.5	28.5	229	X	X
18	EU	3	*Hydrocynus forskallii*	33	22.5	25	134	X	X
18	EU	3	*Hydrocynus forskallii*	31	23.5	26	159	X	X
18	EU	3	*Hydrocynus forskallii*	23.5	17.5	19.5	71	X	
18	EU	3	*Hydrocynus forskallii*	31	23.5	26	155	X	
18	EU	3	*Hydrocynus forskallii*	27	20.5	22	98	X	
18	EU	3	*Hydrocynus forskallii*	32	24	26	156	X	
18	EU	3	*Hydrocynus forskallii*	24.5	19	20.5	79	X	
18	EU	3	*Hydrocynus forskallii*	25.5	19.5	21	83	X	
18	EU	3	*Hydrocynus forskallii*	28.5	21	23.5	114	X	
18	EU	4	*Synodontis schall*	29	22	24.5	308	X	X
18	EU	4	*Synodontis schall*	28	21	24	336	X	X
18	EU	4	*Synodontis schall*	29	20.5	23	300	X	X
18	EU	4	*Synodontis schall*	30	22.5	25.5	298	X	X
18	EU	4	*Synodontis schall*	27	20	22.5	255	X	X
18	EU	4	*Synodontis schall*	24	18	20	179	X	X
18	EU	4	*Synodontis schall*	25	19	21	170	X	X
18	EU	4	*Labeo horie*	42	33	36.5	608		X
18	EU	4	*Labeo horie*	39.5	29.5	34	427		X
18	EU	4	*Labeo horie*	39	29	33	448		X
18	EU	4	*Labeo horie*	40.5	30.5	35	565		X
18	EU	4	*Labeo horie*	30.5	22.5	26	227		X
18	EU	4	*Barbus bynni*	33.5	26	29	379		X
18	EU	4	*Tilapia zillii*	17	13.5		91		X
18	EU	4	*Tilapia zillii*	17	13.5		85		X
18	EU	4	*Tilapia zillii*	18.5	15.5		128		X
18	EU	4	*Oreochromis niloticus*	15.5	12.5		72	X	X
18	EU	4	*Labeo horie*	28	20.5	23.5	175		
18	EU	4	*Hydrocynus forskallii*	38.5	30	33	337	X	X
18	EU	4	*Hydrocynus forskallii*	30.5	23	25.5	168	X	

18	EU	4	*Hydrocynus forskallii*	36	28.5	30	266	X	X
18	EU	4	*Hydrocynus forskallii*	37	27.5	31.5	254	X	
18	EU	4	*Hydrocynus forskallii*	33.5	26	28	221	X	
18	EU	4	*Hydrocynus forskallii*	33	25.5	28.5	214	X	
18	EU	4	*Hydrocynus forskallii*	31.5	24	26	171	X	
18	EU	5	*Tilapia zillii*	21	16.5		210		
18	EU	5	*Tilapia zillii*	20.5	16.5		176		
18	EU	5	*Tilapia zillii*	20	15.5		166		
18	EU	5	*Tilapia zillii*	19	15		132		
18	EU	5	*Tilapia zillii*	25	19.5		350		X
18	EU	5	*Tilapia zillii*	22.5	18		103		
18	EU	5	*Tilapia zillii*	18.5	14.5		122		
18	EU	5	*Tilapia zillii*	23.5	18		258		X
18	EU	5	*Tilapia zillii*	19	14.5		145		
18	EU	5	*Tilapia zillii*	20.5	15.5		166		
18	EU	5	*Tilapia zillii*	19.5	15		165		
18	EU	5	*Tilapia zillii*	19	15		141		
18	EU	5	*Tilapia zillii*	22	17.5		201		
18	EU	5	*Sarotherodon galilaeus*	20.5	17		180		X
18	EU	5	*Sarotherodon galilaeus*	20	15.5		189		X
18	EU	5	*Sarotherodon galilaeus*	16.5	13		102		X
18	EU	5	*Sarotherodon galilaeus*	18	14		127		X
18	EU	5	*Sarotherodon galilaeus*	21.5	17		194		X
18	EU	5	*Labeo horie*	44	34	39.5	744		X
18	EU	5	*Labeo horie*	44	33.5	36	732		X
18	EU	5	*Labeo horie*	42	32	36	554		X
18	EU	5	*Labeo horie*	39	29	33	502		
18	EU	5	*Labeo horie*	38.5	30	33.5	455		
18	EU	5	*Labeo horie*	37	29	32	435		
18	EU	5	*Labeo horie*	37.5	29	33	449		
18	EU	5	*Labeo horie*	40	31	35	536		
18	EU	5	*Labeo horie*	39	29.5	33	439		
18	EU	5	*Labeo horie*	40.5	32	35	557		
18	EU	5	*Labeo horie*	41	32	36	573		
18	EU	5	*Labeo horie*	37	29	32	450		
18	EU	5	*Labeo horie*	40	31.5	35	537		
18	EU	5	*Labeo horie*	40	30	34	272		
18	EU	5	*Barbus bynni*	36	27.5	31	453	X	
18	EU	5	*Synodontis schall*	33.5	23.5	25.5	346	X	
18	EU	5	*Hydrocynus forskallii*	42.5	32.5	36	439	X	
18	EU	6	*Synodontis schall*	36	25.5	28.5	421	X	X

18	EU	6	*Synodontis schall*	28.5	21.5	25	293	X	X
18	EU	6	*Synodontis schall*	27.5	21.5	22.5	227	X	X
18	EU	6	*Tilapia zillii*	24	19.5		267		
18	EU	6	*Tilapia zillii*	25.5	20		316		
18	EU	6	*Tilapia zillii*	23.5	18		240		X
18	EU	6	*Tilapia zillii*	22	18		204		
18	EU	6	*Tilapia zillii*	27	21.5		436		
18	EU	6	*Tilapia zillii*	26.5	22		309		
18	EU	6	*Oreochromis niloticus*	25	19.5		218	X	X
18	EU	6	*Oreochromis niloticus*	23.5	18.5		201	X	X
18	EU	6	*Sarotherodon galilaeus*	23	18.5		201		
18	EU	6	*Sarotherodon galilaeus*	22	17.5		195		
18	EU	6	*Labeo horie*	43.5	33	37.5	675		
18	EU	6	*Labeo horie*	44.5	34.5	39	781		
18	EU	6	*Labeo horie*	46	36	40.5	834		
18	EU	6	*Labeo horie*	42.5	33	36.5	642		
18	EU	7	*Labeo horie*	53	42	48	1630		
18	EU	7	*Alestes baremoze*	16.5	12.5	13.5	21		X
19	SB	3	*Hydrocynus forskallii*	29	22.5	24.5	142	X	
19	SB	3	*Hydrocynus forskallii*	28.5	21.5	24	129	X	
19	SB	3	*Hydrocynus forskallii*	30.5	22.5	24.5	125	X	
19	SB	3	*Hydrocynus forskallii*	33	25.5	27.5	170	X	
19	SB	4	*Tilapia zillii*	29	23		585		
19	SB	4	*Oreochromis niloticus*	30	23.5		489	X	X
19	SB	4	*Oreochromis niloticus*	25	19.5		291	X	X
19	SB	4	*Oreochromis niloticus*	24.5	19.5		286	X	X
19	SB	4	*Synodontis schall*	32	24	27	345	X	
19	SB	4	*Labeo horie*	39.5	30	34	574		
19	SB	5	*Hydrocynus forskallii*	40	32	35	375	X	
20	SB	4	*Labeo horie*	27.5	21.5	24	150		
20	SB	4	*Labeo horie*	24.5	19	21.5	132		
20	SB	4	*Hydrocynus forskallii*	34	26	29.5	227	X	
20	SB	4	*Hydrocynus forskallii*	30	23.5	26	138	X	
20	SB	4	*Hydrocynus forskallii*	42.5	32	35	424	X	
20	SB	5	*Oreochromis niloticus*	26	20		303	X	X
20	SB	5	*Oreochromis niloticus*	24	19		254	X	X
20	SB	5	*Oreochromis niloticus*	25	19.5		291	X	X
20	SB	6	*Hydrocynus forskallii*	55	43.5	47	1160	X	X
21	SB	6	*Oreochromis niloticus*	35.5	28.5		857	X	X
21	SB	1	*Hydrocynus forskallii*	14.5	11	11.5	17	X	X
21	SB	1	*Alestes baremoze*	18.5	13	15	34	X	X

21	SB	1	*Alestes baremoze*	16.5	11.5	14	25	X	X
21	SB	1	*Hydrocynus forskallii*	15	11	12.5	21	X	X
21	SB	2	*Hydrocynus forskallii*	28	21.5	23.5	103	X	X
21	SB	4	*Tilapia zillii*	26	21		341	X	X
21	SB	4	*Oreochromis niloticus*	26	20.5		331	X	
22	SB 2	4	*Tilapia zillii*	23.5	18.5		312	X	X
22	SB 2	1	*Alestes baremoze*	18.5	13.5	15.5	33	X	X
22	SB 2	1	*Alestes baremoze*	18.5	14	15.5	36	X	X
22	SB 2	1	*Alestes baremoze*	19.5	14.5	16	41	X	X
22	SB 2	1	*Alestes baremoze*	19.5	15	16.5	45	X	X
22	SB 2	1	*Alestes baremoze*	18.5	14.5	15.5	36	X	X
22	SB 2	1	*Alestes baremoze*	17.5	13.5	14.5	29	X	X
22	SB 2	2	*Hydrocynus forskallii*	30	23	25.5	149	X	X
22	SB 2	2	*Hydrocynus forskallii*	29.5	23	25	114	X	X
22	SB 2	2	*Hydrocynus forskallii*	30.5	23.5	25.5	154	X	X
22	SB 2	2	*Hydrocynus forskallii*	28.5	21.5	24.5	121	X	X
22	SB 2	2	*Hydrocynus forskallii*	30	23.5	26	147	X	X
22	SB 2	2	*Hydrocynus forskallii*	32	24.5	27.5	150	X	X
22	SB 2	2	*Alestes baremoze*	20.5	15.5	17	48	X	X
22	SB 2	6	*Oreochromis niloticus*	37	29		863	X	X
23	EU	1	*Alestes baremoze*	23	17.5	19.5	77	X	X
23	EU	1	*Alestes baremoze*	18.5	13.5	14.5	33	X	X
23	EU	1	*Alestes baremoze*	20.5	15.5	17	46	X	X
23	EU	1	*Alestes baremoze*	22	16.5	18	56	X	X
23	EU	1	*Alestes baremoze*	21	16	17.5	51	X	X
23	EU	1	*Alestes baremoze*	16.5	12.5	13.5	23	X	X
23	EU	1	*Alestes baremoze*	21	15.5	17	49		
23	EU	1	*Alestes baremoze*	18.5	13.5	15	34		
23	EU	1	*Alestes baremoze*	19	14.5	16	36		
23	EU	1	*Alestes baremoze*	20	15	16.5	45		
23	EU	1	*Alestes baremoze*	18	13.5	15	33		
23	EU	1	*Alestes baremoze*	21	15.5	17.5	51		
23	EU	1	*Alestes baremoze*	20	15	15.5	40		
23	EU	1	*Alestes baremoze*	20	15	16	41		
23	EU	1	*Alestes baremoze*	18	13.5	15	31		
23	EU	1	*Alestes baremoze*	19.5	15	16.5	42		
23	EU	1	*Alestes baremoze*	21	15.5	17.5	46		
23	EU	1	*Alestes baremoze*	20.5	15.5	17	46		
23	EU	1	*Alestes baremoze*	17.5	13	14.5	30		
23	EU	1	*Alestes baremoze*	17.5	13	14.5	26		
23	EU	1	*Alestes baremoze*	17.5	13.5	15	30		

23	EU	1	*Alestes baremoze*	14.5	11	12	17		
23	EU	1	*Alestes baremoze*	17.5	13.5	14.5	30		
23	EU	1	*Hydrocynus forskallii*	18	14	15.5	31		
23	EU	1	*Alestes baremoze*	18	14	15	32		
23	EU	1	*Alestes baremoze*	17	13	14.5	28		
23	EU	1	*Alestes baremoze*	20.5	15	16.5	29		
23	EU	1	*Alestes baremoze*	17.5	13	14.5	27		
23	EU	1	*Alestes baremoze*	16	12.5	13	22		
23	EU	1.5	*Tilapia zillii*	21	17		207	X	X
23	EU	1.5	*Tilapia zillii*	21.5	16.5		187	X	X
23	EU	1.5	*Tilapia zillii*	13	10.5		44	X	X
23	EU	1.5	*Tilapia zillii*	20.5	16.5		168	X	X
23	EU	1.5	*Alestes baremoze*	25	19.5	21	88	X	X
23	EU	1.5	*Hydrocynus forskallii*	28.5	21	23	118	X	X
23	EU	1.5	*Hydrocynus forskallii*	22.5	17	18.5	62	X	X
23	EU	1.5	*Hydrocynus forskallii*	29.5	23	25	133	X	X
23	EU	1.5	*Alestes baremoze*	22.5	17	18	56	X	X
23	EU	1.5	*Alestes baremoze*	27	20.5	22.5	99	X	X
23	EU	1.5	*Alestes baremoze*	25	19.5	22	93	X	X
23	EU	1.5	*Alestes baremoze*	23	17.5	19	59	X	X
23	EU	1.5	*Alestes baremoze*	23.5	18	19.5	79	X	X
23	EU	1.5	*Alestes baremoze*	23	17.5	19.5	63		
23	EU	1.5	*Alestes baremoze*	23	17.5	19	70		
23	EU	1.5	*Alestes baremoze*	22	17.5	19	61		
23	EU	1.5	*Alestes baremoze*	22	16.5	18.5	53		
23	EU	1.5	*Alestes baremoze*	19	14.5	15.5	35		
23	EU	1.5	*Alestes baremoze*	18.5	14.5	16	38		
23	EU	1.5	*Alestes baremoze*	22	16.5	19	52		
23	EU	1.5	*Alestes baremoze*	23	17	19	60		
23	EU	1.5	*Alestes baremoze*	21.5	16	17.5	51		
23	EU	1.5	*Alestes baremoze*	19.5	14.5	16	35		
23	EU	1.5	*Alestes baremoze*	20.5	16	17.5	51		
23	EU	1.5	*Alestes baremoze*	19	14	15.5	38		
23	EU	1.5	*Alestes baremoze*	20	14	16.5	45		
23	EU	1.5	*Alestes baremoze*	20	15.5	17	45		
23	EU	1.5	*Alestes baremoze*	21.5	16	18	52		
23	EU	1.5	*Hydrocynus forskallii*	27	20.5	22	93	X	X
23	EU	1.75	*Tilapia zillii*	18	14		111	X	
23	EU	1.75	*Tilapia zillii*	15	12		53	X	X
23	EU	1.75	*Hydrocynus forskallii*	33	24.5	27	162	X	X
23	EU	1.75	*Alestes baremoze*	27	20	22	107	X	X

23	EU	1.75	*Alestes baremoze*	26.5	20.5	22.5	105	X	
23	EU	1.75	*Alestes baremoze*	36	20	32	104	X	
23	EU	3.25	*Labeo horie*	38	30	35	457	X	X
23	EU	3.25	*Labeo horie*	37	28.5	33	427	X	X
23	EU	4	*Oreochromis niloticus*	19.5	15.5		132	X	X
23	EU	4	*Tilapia zillii*	20	16		163	X	X
23	EU	4	*Tilapia zillii*	20	16		228		
23	EU	4	*Tilapia zillii*	26.5	21.5		372	X	X
23	EU	4	*Tilapia zillii*	24	19		259	X	X
23	EU	4	*Sarotherodon galilaeus*	19	15		139	X	X
23	EU	4	*Tilapia zillii*	19.5	15.5		141		X
23	EU	4	*Oreochromis niloticus*	23	18.5		221	X	X
23	EU	4	*Sarotherodon galilaeus*	23.5	18.5		219	X	X
23	EU	4	*Tilapia zillii*	25.5	20		300		X
23	EU	4	*Oreochromis niloticus*	26	20.5		333		X
23	EU	6	*Tilapia zillii*	20.5	16.5		174		X
23	EU	6	*Tilapia zillii*	25	20		286		X
23	EU	6	*Tilapia zillii*	24	19		262		X
24, 25	SB/EU	NA	*Alestes nurse*	9	8	7	5		X
24, 25	SB/EU	NA	*Alestes nurse*	8	7.5	6	3		X
24, 25	SB/EU	NA	*Alestes nurse*	8	7	6.5	3.1		X
24, 25	SB/EU	NA	*Alestes nurse*	8	7	6	4.6		X
24, 25	SB/EU	NA	*Alestes nurse*	9	8	6.5	7.1		X
24, 25	SB/EU	NA	*Alestes nurse*	8.5	7.5	6.5	6.8		X
24, 25	SB/EU	NA	*Alestes nurse*	7	6.5	5.5	3.7		X
24, 25	SB/EU	NA	*Alestes nurse*	8	6.5	5.5	4.7		X
24, 25	SB/EU	NA	*Alestes nurse*	8	6.5	5.5	4.7		X
24, 25	SB/EU	NA	*Alestes nurse*	8.5	7.5	6.5	5.8		X
24, 25	SB/EU	NA	*Alestes nurse*	8	7	6	5.4		X
24, 25	SB/EU	NA	*Alestes nurse*	8	7	6	4.5		X
24, 25	SB/EU	NA	*Alestes nurse*	7.5	6.5	5.5	4.2		X
24, 25	SB/EU	NA	*Alestes nurse*	6	5.5	4.5	2		X
24, 25	SB/EU	NA	*Alestes dentex*	13	11.5	10	21.7		X
24, 25	SB/EU	NA	*Lates niloticus*	19.5		16	88.6	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	29.5	25	23	89.7	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	26.5	22	20.5	95.7	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	27	22.5	20.5	105.8	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	25	20.5	18.5	49.1	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	32	26.5	24.5	112.1	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	30.5	25.5	23.5	94.9	X	X
24, 25	SB/EU	NA	*Hydrocynus forskallii*	29.5	24.5	22.5	113.9	X	X

24, 25	SB/EU	NA	*Alestes nurse*	7.5	6.5	5.5	4		X
24, 25	SB/EU	NA	*Oreochromis niloticus*	11.2		8.5	24.9	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	7.5		6	8.4	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	7.5		6.5	6.2	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	7.5		6	7.5	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	8		6	8.1	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	7.5		6	7.3	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	19		15	139.1	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	31.5		17	148.7	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	17		13.5	74.5	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	19		15	111.4	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	14.5		11.5	54.9	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	16.5		13	77.3		X
24, 25	SB/EU	NA	*Oreochromis niloticus*	13		10.5	44.1	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	13		10	32.6	X	X
24, 25	SB/EU	NA	*Oreochromis niloticus*	15		12	60	X	X
26	EU	1	*Lates niloticus*	33.5	18.5		108.9	X	X
26	EU	1	*Lates niloticus*	38.5	23		198.1	X	X
26	EU	1	*Lates niloticus*	12	10		16.5	X	X
26	EU	1	*Chrysichthys auratus*	13	9.5	10.5	17.7		X
26	EU	1.5	*Lates niloticus*	14.5	11.5		28.1	X	X
26	EU	1.5	*Lates niloticus*	12	10		15.2	X	X
26	EU	1.5	*Synodontis schall*	24	15.5	17	104.3	X	X
26	EU	1.5	*Synodontis schall*	26.5	18.5	20.5	172.5	X	X
26	EU	1.5	*Synodontis schall*	26.5	17.5	20	143.9	X	X
26	EU	1.5	*Synodontis schall*	25	17	19	122	X	X
26	EU	1.5	*Synodontis schall*	25	17	19	116.6	X	X
26	EU	2	*Lates niloticus*	14.5	11.5		25.4	X	X
26	EU	2	*Hydrocynus forskallii*	24	17.5	19.5	65.4	X	X
26	EU	3	*Alestes baremoze*	36	27.5	30	263.4	X	X
26	EU	3	*Alestes baremoze*	37	28.5	31	287.4	X	X
26	EU	3	*Alestes baremoze*	36	28	30.5	259.2	X	X
26	EU	3	*Alestes baremoze*	33.5	25.5	29.5	236.3	X	X
26	EU	3	*Alestes baremoze*	36	26	28	226.9	X	X
26	EU	3	*Synodontis schall*	25.5	16	17.5	107.6	X	X
26	EU	3	*Synodontis schall*	24.5	17.5	19.5	129.3	X	X
26	EU	3	*Synodontis schall*	24.5	15.5	17	99.9	X	X
27	CZ	3	*Synodontis schall*	23.5	16.5	17	113.7	X	X
27	CZ	3	*Synodontis schall*	24	17	19	111.1	X	X
27	CZ	3	*Synodontis schall*	23.5	16	18	111.5		X
27	CZ	3	*Synodontis schall*	27.5	19	21	200.7	X	

27	CZ	3	*Synodontis schall*	25	17	19	122	X	
27	CZ	3	*Synodontis schall*	25.5	17	19.5	144.3	X	
27	CZ	3	*Synodontis schall*	24	10.5	18.5	128.7	X	
27	CZ	3	*Synodontis schall*	23.5	15.5	17.5	101.9	X	
27	CZ	3	*Synodontis schall*	23.5	15	17	102.8	X	
27	CZ	3	*Synodontis schall*	24	16	18	109.9	X	
27	CZ	3	*Synodontis schall*	24.5	16	18	98.9	X	
27	CZ	3	*Synodontis schall*	23.5	15	17	104.9	X	
27	CZ	3	*Synodontis schall*	22.5	15	16.5	85.5	X	
28	SB	2	*Alestes baremoze*	30.5	23.5	36	183.5	X	X
28	SB	2	*Alestes baremoze*	36	27.5	30	259.3	X	X
29	SB	4	*Hydrocynus forskallii*	52	40.5	44.5	906	X	X
29	SB	2	*Hydrocynus forskallii*	32	24.5	27	172	X	
29	SB	2	*Hydrocynus forskallii*	33.5	25	27	170	X	X
29	SB	2	*Hydrocynus forskallii*	27.5	21	23	112	X	X
29	SB	2	*Hydrocynus forskallii*	34	25.5	27.5	191	X	X
29	SB	2	*Hydrocynus forskallii*	28	21	23	120	X	X
29	SB	2	*Hydrocynus forskallii*	28.5	21.5	23	126	X	X
29	SB	2	*Hydrocynus forskallii*	28.5	21.5	23.5	132	X	
29	SB	2	*Hydrocynus forskallii*	30	23	25	138	X	X
29	SB	2	*Hydrocynus forskallii*	29	22	24	135	X	X
29	SB	2	*Hydrocynus forskallii*	30.5	23.5	25.5	153	X	X
29	SB	2	*Hydrocynus forskallii*	31	23.5	25.5	157	X	X
29	SB	2	*Hydrocynus forskallii*	33	24.5	26.5	168	X	
29	SB	2	*Hydrocynus forskallii*	27.5	21	23	118	X	X
29	SB	2	*Oreochromis niloticus*	14.5	11.5		52	X	X
29	SB	2	*Oreochromis niloticus*	14	11		42	X	X
29	SB	2	*Oreochromis niloticus*	14.5	11.5		48	X	X
29	SB	1	*Alestes baremoze*	23.5	18	20	75	X	X
29	SB	1	*Alestes baremoze*	21.5	16	17.5	55	X	X
29	SB	1	*Alestes baremoze*	23.5	17.5	19.5	74	X	
29	SB	1	*Alestes baremoze*	25.5	19.5	21.5	92	X	
29	SB	1	*Hydrocynus forskallii*	27	21	23	107	X	X
29	SB	1	*Alestes baremoze*	21.5	16	18	55	X	X
29	SB	1	*Alestes baremoze*	23	17.5	19	70	X	
29	SB	1	*Alestes baremoze*	24	18	20.5	84	X	X
29	SB	1	*Alestes baremoze*	22	16	19	58	X	X
29	SB	1	*Alestes baremoze*	24.5	18.5	20	79	X	X
29	SB	1	*Alestes baremoze*	24	18	20	75	X	X
29	SB	1	*Alestes baremoze*	21	16	17.5	49	X	X
29	SB	1	*Alestes baremoze*	22	17	18.5	60	X	

29	SB	1	*Alestes baremoze*	25	19.5	21	91	X	
29	SB	1	*Alestes baremoze*	33	19	23	72	X	
29	SB	1	*Alestes baremoze*	23	17	19	66	X	
29	SB	1	*Alestes baremoze*	21.5	16.5	18	57	X	
29	SB	1	*Alestes baremoze*	21	16	17.5	54	X	
29	SB	1	*Alestes baremoze*	23	17.5	19	67	X	
29	SB	1	*Alestes baremoze*	24	18	20	79	X	
29	SB	1	*Alestes baremoze*	26.5	20.5	22.5	101	X	
29	SB	1	*Alestes baremoze*	20.5	17	19	50.5	X	
29	SB	1	*Alestes baremoze*	23.5	18.5	19.5	74	X	
29	SB	1	*Alestes baremoze*	20	16	17	50	X	
29	SB	1	*Alestes baremoze*	23.5	17.5	19.5	71	X	
29	SB	1	*Alestes baremoze*	21	16.5	18	55	X	
29	SB	1	*Alestes baremoze*	22.5	16.5	18.5	64	X	
29	SB	1	*Alestes baremoze*	22	16.5	18.5	55	X	
29	SB	1	*Alestes baremoze*	21.5	16.5	18	60	X	
29	SB	1	*Alestes baremoze*	22.5	16.5	19	60	X	
29	SB	1	*Alestes baremoze*	23.5	18	19.5	71	X	
29	SB	1	*Alestes baremoze*	22	16.5	18	60	X	
29	SB	1	*Alestes baremoze*	19	14.5	16	41	X	
29	SB	1	*Alestes baremoze*	21.5	16.5	18.5	61	X	
29	SB	1	*Alestes baremoze*	22	16.5	18	61		
29	SB	1	*Alestes baremoze*	21	16	17.5	54		
29	SB	1	*Alestes baremoze*	20.5	15.5	17	46		
29	SB	1	*Alestes baremoze*	21.5	17	19	61		
29	SB	1	*Alestes baremoze*	20	15.5	17	48		
29	SB	1	*Alestes baremoze*	21	15.5	17	50		
29	SB	1	*Alestes baremoze*	21	16	18	57		
29	SB	1	*Alestes baremoze*	21	16.5	18	50		
29	SB	1	*Labeo horie*	28.5	21.5	24	163		X
29	SB	1	*Tilapia zillii*	14	11		46	X	X
29	SB	1	*Tilapia zillii*	15	12		64	X	X
29	SB	1	*Sarotherodon galilaeus*	19.5	10.5	13.5	45	X	X
29	SB	1	*Sarotherodon galilaeus*	19.5	10.5	13.5	41	X	X
29	SB	1	*Oreochromis niloticus*	15.5	12.5		66	X	X
29	SB	1	*Oreochromis niloticus*	14	11		46	X	X
29	SB	1	*Oreochromis niloticus*	18.5	14.5		98	X	X
29	SB	1	*Hydrocynus forskallii*	27	20	21.5	93	X	X
29	SB	1	*Hydrocynus forskallii*	29	22	23.5	127	X	X
29	SB	1	*Hydrocynus forskallii*	26	19.5	22.5	93	X	X
29	SB	1	*Hydrocynus forskallii*	25.5	19.5	21.5	96	X	X

29	SB	1	*Hydrocynus forskallii*	29	21.5	22.5	111	X	
29	SB	1	*Hydrocynus forskallii*	27.5	21	23	120	X	
29	SB	1	*Hydrocynus forskallii*	29	22	24	129	X	
29	SB	1	*Hydrocynus forskallii*	16.5	13	14	29	X	X
29	SB	1	*Hydrocynus forskallii*	28	21	23.5	123	X	
29	SB	1	*Hydrocynus forskallii*	26	21.5	22	104	X	
29	SB	1	*Hydrocynus forskallii*	26	19.5	21	102	X	
29	SB	2	*Alestes baremoze*	24.5	18.5	20	79		
29	SB	2	*Hydrocynus forskallii*	26.5	20	22.5	109		
29	SB	2	*Sarotherodon galilaeus*	15.5	13		68		X
29	SB	2	*Sarotherodon galilaeus*	13	10		47		X
29	SB	2	*Sarotherodon galilaeus*	14	11		53		X
29	SB	2	*Sarotherodon galilaeus*	14.5	11.5		63		
29	SB	2	*Oreochromis niloticus*	19	15		118	X	X
29	SB	2	*Oreochromis niloticus*	18	14.5		106	X	X
29	SB	2	*Oreochromis niloticus*	19	15		104	X	X
29	SB	2	*Oreochromis niloticus*	15.5	12		56	X	X
29	SB	4	*Oreochromis niloticus*	17.5	13.5		85	X	X
29	SB	4	*Hydrocynus forskallii*	28	20.5	23	107		
30	CZ	4	*Sarotherodon galilaeus*	14	10		50		X
30	CZ	4	*Oreochromis niloticus*	24.5	19.5		227	X	X
30	CZ	4	*Oreochromis niloticus*	23	18.5		204	X	X
30	CZ	4	*Oreochromis niloticus*	25	20		251	X	X
30	CZ	4	*Oreochromis niloticus*	17.5	14		103	X	X
30	CZ	1.5	*Hydrocynus forskallii*	27	20.5	23	104		
30	CZ	1.5	*Hydrocynus forskallii*	31	23.5	26	121		
30	CZ	1.5	*Hydrocynus forskallii*	26	19.5	21.5	93		
30	CZ	1.5	*Hydrocynus forskallii*	26	20	22	80		
30	CZ	1.5	*Hydrocynus forskallii*	26	20	22	81		
30	CZ	1.5	*Hydrocynus forskallii*	28	21.5	23	118		
30	CZ	1.5	*Hydrocynus forskallii*	24	18	20	77		
30	CZ	1.5	*Hydrocynus forskallii*	26	20	22	102		
30	CZ	1.5	*Hydrocynus forskallii*	27	19	22	82		
30	CZ	1.5	*Hydrocynus forskallii*	29.5	21.5	23.5	96		
30	CZ	1.5	*Hydrocynus forskallii*	28.5	21.5	23.5	103		
30	CZ	1.5	*Hydrocynus forskallii*	26	19.5	22	91		
30	CZ	1.5	*Hydrocynus forskallii*	31	23.5	26	169		
30	CZ	1.5	*Hydrocynus forskallii*	27	20.5	23	105		
30	CZ	1.5	*Hydrocynus forskallii*	27.5	20.5	22.5	108		
30	CZ	1.5	*Hydrocynus forskallii*	29	22	25	132		
30	CZ	1.5	*Hydrocynus forskallii*	29.5	22.5	25	137		

30	CZ	1.5	*Hydrocynus forskallii*	27.5	21	23	127		
30	CZ	1.5	*Hydrocynus forskallii*	28	21	23	125		
30	CZ	1.5	*Hydrocynus forskallii*	29.5	22	25	131		
30	CZ	1.5	*Hydrocynus forskallii*	27.5	20.5	22.5	114		
30	CZ	1.5	*Hydrocynus forskallii*	28	21	23	112		
30	CZ	1.5	*Hydrocynus forskallii*	28.5	22.5	24.5	123		
30	CZ	1.5	*Hydrocynus forskallii*	27.5	21.5	23.5	116		
31	EU	1.5	*Hydrocynus forskallii*	26.5	20	21.5	96		
31	EU	1.5	*Hydrocynus forskallii*	28	21	23	115		
31	EU	1.5	*Hydrocynus forskallii*	26.5	20.5	22	75		X
31	EU	1.5	*Hydrocynus forskallii*	27	21	23	111		
31	EU	1.5	*Hydrocynus forskallii*	26.5	20.5	22	118		
31	EU	1.5	*Hydrocynus forskallii*	24	18.5	20	67		
31	EU	1.5	*Hydrocynus forskallii*	23	17.5	19	70		
31	EU	1.5	*Hydrocynus forskallii*	24.5	19	20.5	80		
31	EU	1.5	*Hydrocynus forskallii*	20.5	16	18	55		
31	EU	1.5	*Hydrocynus forskallii*	25.5	19	21	76		
31	EU	1.5	*Hydrocynus forskallii*	27	20	22	105		
31	EU	1.5	*Hydrocynus forskallii*	23	16.5	18.5	55		
31	EU	1.5	*Hydrocynus forskallii*	25.5	19.5	21	81		
31	EU	1.5	*Hydrocynus forskallii*	26	19.5	21	86		
31	EU	1.5	*Hydrocynus forskallii*	27.5	21	23	115		
31	EU	1.5	*Hydrocynus forskallii*	28.5	22	24	128		
31	EU	1.5	*Alestes baremoze*	23.5	17.5	20	71		
31	EU	1.5	*Alestes baremoze*	22	17.5	19	75		
31	EU	1.5	*Alestes baremoze*	27	20.5	22.5	111		
31	EU	1.5	*Alestes baremoze*	21.5	16.5	19	65		
31	EU	1.5	*Alestes baremoze*	22.5	17	18.5	65		
31	EU	1.5	*Alestes baremoze*	21	16.5	18	69		
31	EU	1.5	*Alestes baremoze*	22.5	17	19	65		
31	EU	1.5	*Alestes baremoze*	22.5	17	19.5	69		
31	EU	1.5	*Alestes baremoze*	26.5	20	22	113		
31	EU	1.5	*Alestes baremoze*	22.5	16.5	19	62		
31	EU	1.5	*Alestes baremoze*	24	18	20	76		
31	EU	1.5	*Alestes baremoze*	22	16.5	18	62		
31	EU	1.5	*Alestes baremoze*	25.5	19	21	92		
31	EU	1.5	*Alestes baremoze*	24	18.5	20.5	85		
31	EU	1.5	*Alestes baremoze*	21.5	16.5	18.5	67		
31	EU	1.5	*Sarotherodon galilaeus*	17	13.5		80		X
31	EU	1.5	*Sarotherodon galilaeus*	14	11		50		
31	EU	1.5	*Oreochromis niloticus*	13	10		40	X	

31	EU	1.5	*Oreochromis niloticus*	13.5	10.5		46	X	
31	EU	1.5	*Oreochromis niloticus*	15	12		58	X	
31	EU	1.5	*Oreochromis niloticus*	14	11		47	X	
31	EU	1.5	*Oreochromis niloticus*	13.5	10		47	X	X
31	EU	1.5	*Oreochromis niloticus*	17	14		42		
31	EU	1.5	*Oreochromis niloticus*	16.5	13		65		
31	EU	1.5	*Oreochromis niloticus*	15	11.5		61		
31	EU	1.5	*Oreochromis niloticus*	15	12		55		
31	EU	4	*Citharinus citharus*	28	20.5	23	225		X
31	EU	4	*Alestes baremoze*	23	18	20	67		
31	EU	4	*Alestes baremoze*	23	17.5	19	63		
31	EU	4	*Hydrocynus forskallii*	29	22	24.5	112		
31	EU	4	*Hydrocynus forskallii*	26.5	21.5	23.5	105		
31	EU	4	*Hydrocynus forskallii*	26	20.5	22.5	102		
31	EU	4	*Oreochromis niloticus*	17	13		76		
31	EU	3	*Labeo horie*	35.5	27	30.5	408		X
31	EU	3	*Labeo horie*	36.5	28.5	31.5	436		X
31	EU	3	*Labeo horie*	26.5	25.5	23.5	251		X
31	EU	3	*Labeo horie*	24.5	26	29.5	371		
31	EU	3	*Oreochromis niloticus*	24		19	195		
31	EU	3	*Oreochromis niloticus*	20		16	135		
31	EU	3	*Oreochromis niloticus*	20.5		17	175		
31	EU	3	*Oreochromis niloticus*	20		16	155		
31	EU	3	*Oreochromis niloticus*	20.5		16	154		
31	EU	3	*Oreochromis niloticus*	19		15.5	131		
31	EU	3	*Oreochromis niloticus*	20		15.5	131		
31	EU	3	*Oreochromis niloticus*	19.5		15.5	131		
31	EU	3	*Oreochromis niloticus*	19		15	123		
31	EU	3	*Oreochromis niloticus*	20.5		15.5	123		
31	EU	3	*Oreochromis niloticus*	21		16.5	146		
31	EU	3	*Oreochromis niloticus*	19		14.5	127		
31	EU	3	*Oreochromis niloticus*	20.5		15.5	132		
31	EU	3	*Oreochromis niloticus*	17.5		14.5	95		
31	EU	3	*Oreochromis niloticus*	18.5		14.5	118		
31	EU	3	*Oreochromis niloticus*	18		14.5	118		
31	EU	3	*Oreochromis niloticus*	15.5		12.5	58		
31	EU	3	*Oreochromis niloticus*	18		14	105		
31	EU	3	*Sarotherodon galilaeus*	19		14.5	129		
31	EU	3	*Sarotherodon galilaeus*	18.5		15.5	134		
31	EU	2	*Tilapia zillii*	16.5		13	83		X
31	EU	2	*Tilapia zillii*	16		12.5	76		X

31	EU	2	*Labeo horie*	29.5	25.5	22	223		X
31	EU	2	*Labeo horie*	28.5	25	22.5	195		X
31	EU	2	*Sarotherodon galilaeus*	16.5		13	94		
31	EU	2	*Sarotherodon galilaeus*	16		13	86		
31	EU	2	*Sarotherodon galilaeus*	16		12	79		
31	EU	2	*Sarotherodon galilaeus*	16		12	80		
31	EU	2	*Sarotherodon galilaeus*	13		12	70		
31	EU	2	*Sarotherodon galilaeus*	13		10	48		
31	EU	2	*Sarotherodon galilaeus*	13		10	48		
31	EU	2	*Sarotherodon galilaeus*	13.5		10.5	54		
31	EU	2	*Sarotherodon galilaeus*	15		12	71		
31	EU	2	*Sarotherodon galilaeus*	15		11.5	72		
31	EU	2	*Sarotherodon galilaeus*	13		10.5	54		
31	EU	2	*Sarotherodon galilaeus*	14		10.5	59		
31	EU	2	*Oreochromis niloticus*	16		13	85		
31	EU	2	*Oreochromis niloticus*	17		14	93		
31	EU	2	*Oreochromis niloticus*	17		14	90		
31	EU	2	*Oreochromis niloticus*	17		14	94		
31	EU	2	*Oreochromis niloticus*	16		13	71		
31	EU	2	*Oreochromis niloticus*	20.5		16	127		
31	EU	2	*Sarotherodon galilaeus*	16		13	88		
31	EU	2	*Sarotherodon galilaeus*	14		11	59		
31	EU	2	*Sarotherodon galilaeus*	13.5		10.5	57		
31	EU	2	*Oreochromis niloticus*	16		13.5	76		
31	EU	2	*Oreochromis niloticus*	17		14	84		
31	EU	2	*Oreochromis niloticus*	17		14	86		
31	EU	2	*Oreochromis niloticus*	16.5		12.5	85		
31	EU	2	*Oreochromis niloticus*	16		13	74		
31	EU	2	*Oreochromis niloticus*	15		12	60		
31	EU	2	*Hydrocynus forskallii*	32	27	25	188		
32	CZ	?	*Oreochromis niloticus*	15.5		12.5	69		X
32	CZ	?	*Oreochromis niloticus*	13.5		11	42	X	X
32	CZ	?	*Oreochromis niloticus*	16		13	76	X	X
32	CZ	?	*Oreochromis niloticus*	16		12.5	68	X	X
32	CZ	?	*Oreochromis niloticus*	14		11	50	X	X
32	CZ	?	*Oreochromis niloticus*	15		12	66	X	
32	CZ	?	*Oreochromis niloticus*	22		17	169	X	X
32	CZ	?	*Sarotherodon galilaeus*	17		13	93		VS
32	CZ	?	*Sarotherodon galilaeus*	17		14	104	X	X
32	CZ	?	*Tilapia zillii*	15		12	63		VS
32	CZ	?	*Tilapia zillii*	16.5		13	82	X	X

32	CZ	?	*Hydrocynus forskallii*	36	30	27	250	X	X
32	CZ	?	*Hydrocynus forskallii*	26.5	23	20.5	105	X	X
32	CZ	?	*Hydrocynus forskallii*	25.5	21	19.5	87		VS
32	CZ	?	*Hydrocynus forskallii*	33.5	28.5	26	210	X	X
32	CZ	?	*Hydrocynus forskallii*	25.5	21.5	19	101	X	X
32	CZ	?	*Hydrocynus forskallii*	16	13.5	12.5	29	X	X
32	CZ	?	*Hydrocynus forskallii*	21	17.5	15.5	57	X	X
32	CZ	?	*Hydrocynus forskallii*	18.5	15.5	14.5	41	X	X
33	SB	2	*Oreochromis niloticus*	16		12.5	77	X	X
33	SB	2	*Oreochromis niloticus*	14.5		11.5	51	X	X
33	SB	2	*Oreochromis niloticus*	15.5		12.5	65	X	X
33	SB	2	*Oreochromis niloticus*	14		11	46	X	X
33	SB	2	*Oreochromis niloticus*	15		11.5	56	X	X
33	SB	2	*Oreochromis niloticus*	13		10	44	X	
33	SB	2	*Oreochromis niloticus*	14		10	45	X	X
33	SB	2	*Oreochromis niloticus*	13		10	45	X	X
33	SB	2	*Oreochromis niloticus*	13		10	45	X	X
33	SB	2	*Oreochromis niloticus*	13.5		10.5	42	X	
33	SB	2	*Oreochromis niloticus*	13.5		10.5	44	X	
33	SB	2	*Oreochromis niloticus*	13.5		10.5	44	X	
33	SB	2	*Oreochromis niloticus*	13		10	40	X	
33	SB	2	*Oreochromis niloticus*	14.5		11	55	X	
33	SB	2	*Oreochromis niloticus*	13.5		10.5	48	X	
33	SB	2	*Oreochromis niloticus*	14		11	44	X	
33	SB	2	*Oreochromis niloticus*	12.5		10	38	X	
33	SB	2	*Oreochromis niloticus*	14		11	41	X	
33	SB	2	*Labeo horie*	28		21	185		X
33	SB	2	*Labeo horie*	30		23	230		X
33	SB	2	*Hydrocynus forskallii*	36.5		28	238	X	X
33	SB	4	*Oreochromis niloticus*	25		20	284	X	X
33	SB	4	*Oreochromis niloticus*	24		19	251	X	X
34	EU	1	*Oreochromis niloticus*	15		13	59	X	
34	EU	1	*Oreochromis niloticus*	19.5	14.5		114	X	X
34	EU	2	*Hydrocynus forskallii*	27.5	21.5	23	109	X	
34	EU	2	*Hydrocynus forskallii*	32	23.5	26	129	X	
34	EU	2	*Hydrocynus forskallii*	30.5	22.5	25	93	X	
34	EU	3	*Brycinus ferox*	25.5	19	21	98	X	X
34	EU	3	*Hydrocynus forskallii*	32	24.5	27	147	X	
34	EU	3	*Hydrocynus forskallii*	27	20.5	27.5	96	X	
34	EU	3	*Hydrocynus forskallii*	29	21.5	24	104	X	
34	EU	3	*Hydrocynus forskallii*	31	23	25.5	134	X	

34	EU	3	*Hydrocynus forskallii*	29	21.5	22.5	100	X	
34	EU	3	*Hydrocynus forskallii*	27	19.5	21.5	53	X	
34	EU	3	*Hydrocynus forskallii*	29.5	22.5	24.5	101	X	
34	EU	3	*Oreochromis niloticus*	15	12		54	X	
34	EU	3	*Oreochromis niloticus*	14.5	11		54	X	
34	EU	3	*Oreochromis niloticus*	14	10.5		41	X	
34	EU	4	*Labeo horie*	45	31	35	357		X
34	EU	4	*Labeo horie*	33.5	26	29.5	324		X
34	EU	4	*Oreochromis niloticus*	17	13		79	X	X
34	EU	4	*Oreochromis niloticus*	17	14		90	X	
34	EU	4	*Oreochromis niloticus*	15.5	12.5		66	X	
34	EU	4	*Oreochromis niloticus*	15.5	12		65	X	
34	EU	4	*Oreochromis niloticus*	15.5	13		68	X	
34	EU	4	*Oreochromis niloticus*	16	13		69	X	
34	EU	4	*Oreochromis niloticus*	16	12.5		73	X	
34	EU	4	*Oreochromis niloticus*	16.5	13		70	X	
34	EU	4	*Oreochromis niloticus*	14.5	11.5		57	X	
34	EU	4	*Oreochromis niloticus*	16	12.5		70	X	
34	EU	4	*Oreochromis niloticus*	15	12		53	X	
34	EU	4	*Oreochromis niloticus*	16	12.5		71	X	
34	EU	4	*Oreochromis niloticus*	15.5	12.5		66	X	
34	EU	4	*Sarotherodon galilaeus*	14	11		56	X	
35	EU	N/A	*Lates niloticus*	17		14	51	X	X
35	EU	N/A	*Lates niloticus*	20		16	109	X	X
35	EU	N/A	*Lates niloticus*	14.5		11.5	33	X	X
35	EU	N/A	*Lates niloticus*	15		12	39	X	X
35	EU	N/A	*Lates niloticus*	11		8.5	14	X	X
35	EU	N/A	*Lates niloticus*	20.5		16.5	110	X	X
35	EU	N/A	*Lates niloticus*	16		13	47	X	X
35	EU	N/A	*Hydrocynus forskallii*	26.5	22	20	88	X	X
35	EU	N/A	*Hydrocynus forskallii*	30	26	22.5	98	X	X
35	EU	N/A	*Hydrocynus forskallii*	28	23	20.5	90	X	X
35	EU	N/A	*Hydrocynus forskallii*	29	24	20.5	95	X	X
35	EU	N/A	*Hydrocynus forskallii*	28.5	25	22.5	93	X	X
35	EU	N/A	*Hydrocynus forskallii*	17.5	15.5	13.5	48		X
35	EU	N/A	*Hydrocynus forskallii*	16.5	14.5	12.5	39		X
35	EU	N/A	*Hydrocynus forskallii*	17.5	15	13.5	39		
36	CZ	N/A	*Hydrocynus forskallii*	29.5	25	23	135	X	X
36	CZ	N/A	*Hydrocynus forskallii*	28.5	23.5	21.5	118	X	X
36	CZ	N/A	*Oreochromis niloticus*	17.5		14	99	X	X
36	CZ	N/A	*Oreochromis niloticus*	15		12	65	X	X

36	CZ	N/A	*Oreochromis niloticus*	15		12	60	X	
36	CZ	N/A	*Oreochromis niloticus*	15		12	68	X	X
36	CZ	N/A	*Oreochromis niloticus*	14.5		11.5	59	X	X
36	CZ	N/A	*Oreochromis niloticus*	13.5		11	45	X	X
36	CZ	N/A	*Oreochromis niloticus*	14		11	47	X	X
36	CZ	N/A	*Oreochromis niloticus*	17		14	85	X	X
36	CZ	N/A	*Oreochromis niloticus*	15		12	67	X	X
36	CZ	N/A	*Oreochromis niloticus*	14		11	56	X	X
36	CZ	N/A	*Oreochromis niloticus*	14.5		11.5	54	X	
36	CZ	N/A	*Oreochromis niloticus*	14.5		11.5	57	X	
36	CZ	N/A	*Oreochromis niloticus*	16		12.5	73	X	
36	CZ	N/A	*Oreochromis niloticus*	16		13.5	77	X	
36	CZ	N/A	*Oreochromis niloticus*	14.5		11.5	57	X	
36	CZ	N/A	*Oreochromis niloticus*	14.5		11.5	50	X	
36	CZ	N/A	*Oreochromis niloticus*	15		11.5	56	X	
36	CZ	N/A	*Oreochromis niloticus*	13		10	42	X	
36	CZ	N/A	*Oreochromis niloticus*	12		9.5	36	X	
36	CZ	N/A	*Oreochromis niloticus*	12		10	30	X	
36	CZ	N/A	*Oreochromis niloticus*	13.5		10.5	45	X	
36	CZ	N/A	*Oreochromis niloticus*	14		11	55	X	
36	CZ	N/A	*Oreochromis niloticus*	12.5		10	39	X	
36	CZ	N/A	*Oreochromis niloticus*	12		9.5	32	X	
36	CZ	N/A	*Alestes nurse*	7.5	6.5	5.5	4.4		X
36	CZ	N/A	*Alestes nurse*	8	7	6	5.5		X
36	CZ	N/A	*Alestes nurse*	8	6	7	5.9		X
36	CZ	N/A	*Alestes nurse*				5.5		X
36	CZ	N/A	*Alestes nurse*	7	5	6	3.8		X
36	CZ	N/A	*Alestes nurse*	7.5	5.5	6.5	4.4		X
36	CZ	N/A	*Alestes nurse*	7.5	5.5	6.5	5.1		X
36	CZ	N/A	*Alestes nurse*	8	6	7	5.7		X
36	CZ	N/A	*Alestes dentex*	11	8.5	9.5	16.4		X
36	CZ	N/A	*Alestes dentex*	10.5	8	9	13.2		X
36	CZ	N/A	*Alestes dentex*	13.5	10.5	12.5	31.7		X
36	CZ	N/A	*Alestes baremoze*	17.5	14	15.5	38.1		X
36	CZ	N/A	*Alestes baremoze*	16	12.5	14	26		X
36	CZ	N/A	*Alestes dentex*	12.5	9.5	11	21.7		X
36	CZ	N/A	*Oreochromis niloticus*	16	12.5		67.1	X	
36	CZ	N/A	*Oreochromis niloticus*	18	13.5		92.8	X	X
36	CZ	N/A	*Oreochromis niloticus*	17	13.5		87	X	X
36	CZ	N/A	*Oreochromis niloticus*	10.5	8		22.9	X	X
36	CZ	N/A	*Oreochromis niloticus*	12	8		19.6	X	X

36	CZ	N/A	*Oreochromis niloticus*	10	8		20.4	X	X
36	CZ	N/A	*Oreochromis niloticus*	15.5	11.5		62.4	X	X
36	CZ	N/A	*Oreochromis niloticus*	9.5	7.5		17	X	X
37	Multi	N/A	*Chrysichthys auratus*	12	8.5	10	14.2		X
37	Multi	N/A	*Chrysichthys auratus*	11.5	8	9	10.8		X
37	Multi	N/A	*Distichodus nefasch*	35	27.5	31	390.3		X
37	Multi	N/A	*Distichodus nefasch*	37	29.5	32	427.8		X
37	Multi	N/A	*Barbus bynni*	33	25.5	29	374.1		X
37	Multi	N/A	*Barbus bynni*	31.5	24	27	269.1		X
37	Multi	N/A	*Barbus bynni*	18.5	13.5	15.5	55.2		X
37	Multi	N/A	*Barbus bynni*	13.5	10	11.5	20.3		X
37	Multi	N/A	*Barbus bynni*	19.5	14.5	16.5	72		X
37	Multi	N/A	*Schilbe uranoscopus*	17.5	14.5	16.5	31.7		X
37	Multi	N/A	*Schilbe uranoscopus*	19	15	17	29.9		X
37	Multi	N/A	*Schilbe uranoscopus*	18	14.5	16.5	27.6		X
37	Multi	N/A	*Schilbe uranoscopus*	19	15	16.5	29.4		X
37	Multi	N/A	*Lates niloticus*	32	25		258	X	X
37	Multi	N/A	*Lates niloticus*	31	25		232.4	X	X
37	Multi	N/A	*Lates niloticus*	26.5	21		150.1	X	X
37	Multi	N/A	*Lates niloticus*	27	21.5		150.9	X	X
37	Multi	N/A	*Lates niloticus*	25.5	20.5		150.3	X	X
37	Multi	N/A	*Lates niloticus*	28.5	23		200.2	X	X
37	Multi	N/A	*Lates niloticus*	28	22.5		186.4	X	X
37	Multi	N/A	*Lates niloticus*	25	20.5		152	X	X
37	Multi	N/A	*Lates niloticus*	23	18.5		113	X	X
37	Multi	N/A	*Lates niloticus*	11	8.5		15.8	X	X
37	Multi	N/A	*Lates niloticus*	13		10.5	17.3	X	X
37	Multi	N/A	*Lates niloticus*	11.5		9	16.1	X	X
37	Multi	N/A	*Lates niloticus*	12		9.5	15.4	X	
37	Multi	N/A	*Synodontis schall*	27.5	20.5	18.5	171.8	X	X
37	Multi	N/A	*Synodontis schall*	30	22	20	206.9	X	X
37	Multi	N/A	*Synodontis schall*	27	20.5	19	176.1	X	X
37	Multi	N/A	*Synodontis schall*	29.5	21	19	179.6	X	X
37	Multi	N/A	*Synodontis schall*	23	17.5	13.5	109.8	X	X
37	Multi	N/A	*Synodontis schall*	29	21	19.5	199.9	X	X
37	Multi	N/A	*Synodontis schall*	28	22.5	20.5	228.1	X	X
37	Multi	N/A	*Synodontis schall*	26.5	20	18	169.5	X	X
37	Multi	N/A	*Synodontis schall*	26.5	20.5	18.5	194	X	X
37	Multi	N/A	*Synodontis schall*	27.5	20.5	18.5	160.6	X	X
37	Multi	N/A	*Synodontis schall*	23	17.5	16	109.1		X
37	Multi	N/A	*Synodontis schall*	24	18	16.5	123.3	X	X

38	Multi	1	*Lates niloticus*	14	11		27	X	X
38	Multi	1	*Lates niloticus*	14.5	11.5		29	X	X
38	Multi	1	*Lates niloticus*	16.5	13.5		42	X	X
38	Multi	1	*Lates niloticus*	15.5	12.5		35	X	X
38	Multi	1	*Lates niloticus*	11.5	9.5		13	X	X
38	Multi	1	*Lates niloticus*	11	8.5		10	X	X
38	Multi	1	*Lates niloticus*	12	9.5		16	X	X
38	Multi	1	*Lates niloticus*	10	8		8	X	X
38	Multi	1	*Lates niloticus*	12	9.5		16	X	X
38	Multi	1	*Lates niloticus*	15.5	12.5		32	X	X
38	Multi	1	*Synodontis schall*	29	19.5	22	198	X	X
38	Multi	1.5	*Lates niloticus*	30.5	24.5		242	X	X
38	Multi	1.5	*Lates niloticus*	25.5	20		145	X	X
38	Multi	1.5	*Lates niloticus*	25	20		131	X	X
38	Multi	1.5	*Lates niloticus*	14	11		25	X	X
38	Multi	1.5	*Lates niloticus*	15.5	12.5		32	X	X
38	Multi	1.5	*Lates niloticus*	14	11		33	X	X
38	Multi	1.5	*Lates niloticus*	13.5	10.5		22	X	X
38	Multi	1.5	*Lates niloticus*	12.5	10.5		19	X	X
38	Multi	1.5	*Synodontis schall*	27	16.5	18	43		X
38	Multi	1.5	*Synodontis schall*	29	19	22	184	X	X
38	Multi	1.5	*Synodontis schall*	28.5	19.5	21.5	195	X	X
38	Multi	1.5	*Synodontis schall*	29	20	22.5	234	X	X
38	Multi	1.5	*Synodontis schall*	26	17	19	120	X	X
38	Multi	1.5	*Synodontis schall*	21	13	15	68	X	X
38	Multi	2	*Lates niloticus*	31	25.5		257	X	X
38	Multi	2	*Lates niloticus*	26	21		138	X	X
38	Multi	2	*Lates niloticus*	25	20		152	X	X
38	Multi	2	*Lates niloticus*	22	17.5		185	X	X
38	Multi	2	*Synodontis schall*	26.5	17.5	20	152	X	X
38	Multi	2	*Synodontis schall*	25	17.5	19.5	141	X	X
38	Multi	2	*Synodontis schall*	23.5	16.5	17.5	111	X	X
38	Multi	2	*Synodontis schall*	22.5	15.5	17.5	107	X	X
38	Multi	2	*Synodontis schall*	23	14.5	16.5	87		
38	Multi	2	*Synodontis schall*	23	14.5	16	88	X	X
38	Multi	2	*Synodontis schall*	26	18	20	163	X	X
38	Multi	2	*Synodontis schall*	21	14	15.5	84	X	X
38	Multi	2.5	*Lates niloticus*	29	23.5		175	X	X
38	Multi	2.5	*Lates niloticus*	24	19.5		108	X	X
38	Multi	2.5	*Lates niloticus*	29	23.5		182	X	X
38	Multi	2.5	*Lates longispinus*	26	20.5		138	X	X

38	Multi	2.5	*Lates niloticus*	29.5	23.5		192	X	X
38	Multi	2.5	*Distichodus nefasch*	36	28.5	31.5	422	X	X
38	Multi	2.5	*Distichodus nefasch*	22.5	17.5	19.5	96		X
38	Multi	2.5	*Synodontis schall*	30.5	20.5	23.5	252	X	X
38	Multi	2.5	*Synodontis schall*	28	20	22.5	179	X	X
38	Multi	2.5	*Synodontis schall*	25	15.5	17	108	X	X
38	Multi	2.5	*Synodontis schall*	27	19	21	166	X	X
38	Multi	2.5	*Synodontis schall*	30	20	22	214	X	X
38	Multi	2.5	*Synodontis schall*	26	18	21	158	X	X
38	Multi	2.5	*Synodontis schall*	26.5	18.5	21	154	X	X
38	Multi	2.5	*Synodontis schall*	24	14.5	16	83	X	X
38	Multi	2.5	*Synodontis schall*	24.5	16.5	18.5	109	X	X
38	Multi	2.5	*Synodontis schall*	23	14.5	16.5	91		X
38	Multi	2.5	*Synodontis schall*	20.5	13.5	15	73		X
38	Multi	2.5	*Synodontis schall*	26	17	19	154		X
38	Multi	2.5	*Synodontis schall*	26	19.5	22	142		X
38	Multi	2.5	*Synodontis schall*	25	13.5	17.5	96		X
38	Multi	2.5	*Synodontis schall*	25	16	19	121		X
38	Multi	2.5	*Synodontis schall*	26	17	19	148		X
38	Multi	2.5	*Synodontis schall*	27	18	20	174		X
38	Multi	2.5	*Synodontis schall*	25.5	17	19	126		X
38	Multi	2.5	*Synodontis schall*	24	17	19	109		X
38	Multi	2.5	*Barbus bynni*	42	27	29	170		X
38	Multi	3	*Lates niloticus*	32.5	25.5		243	X	X
38	Multi	3	*Lates niloticus*	29	23		198	X	X
38	Multi	3	*Distichodus nefasch*	38	29.5	33	488		X
38	Multi	3	*Distichodus nefasch*	34	28	31	391		X
38	Multi	3	*Synodontis schall*	29.5	20	22	214		X
38	Multi	3	*Synodontis schall*	30	22	24	192		X
38	Multi	3	*Synodontis schall*	27	18.5	21	220		X
38	Multi	3	*Synodontis schall*	28.5	19.5	22	228		X
38	Multi	3	*Synodontis schall*	26	17.5	19.5	169		X
38	Multi	3	*Synodontis schall*	28	20	22	211		X
38	Multi	3	*Synodontis schall*	26.5	18	20	170		X
38	Multi	3	*Synodontis schall*	28	20.5	22	191		X
38	Multi	3	*Synodontis schall*	29	18.5	21.5	192		X
38	Multi	3	*Synodontis schall*	26.5	18	20	144		X
38	Multi	3	*Synodontis schall*	28.5	19	21.5	148		X
38	Multi	3	*Synodontis schall*	27	16	18	118		X
38	Multi	3	*Synodontis schall*	29	20	22.5	220		X
38	Multi	3	*Synodontis schall*	26	17.5	19.5	166		X

38	Multi	3	*Synodontis schall*	28	18.5	20.5	184		X
38	Multi	3.5	*Lates longispinus*	32	26		267	X	X
38	Multi	3.5	*Distichodus nefasch*	41	32	36.5	674		X
38	Multi	3.5	*Distichodus nefasch*	38.5	30.5	34	525		X
38	Multi	3.5	*Distichodus nefasch*	44	34	38.5	790		X
38	Multi	3.5	*Distichodus nefasch*	36.5	28.5	32	429		X
38	Multi	3.5	*Distichodus nefasch*	44	34.5	38.5	732		X
38	Multi	3.5	*Distichodus nefasch*	36	29	32	431		X
38	Multi	3.5	*Distichodus nefasch*	32	25	28.5	304		X
38	Multi	3.5	*Distichodus nefasch*	32.5	26	29	327		X
38	Multi	3.5	*Synodontis schall*	30.5	21	23.5	245		X
38	Multi	3.5	*Synodontis schall*	29	20	22.5	228		
38	Multi	3.5	*Synodontis schall*	31	22	24	278		X
38	Multi	3.5	*Synodontis schall*	31	22.5	24	290		X
38	Multi	3.5	*Synodontis schall*	28	19	21	184		
38	Multi	4	*Lates longispinus*	26	20.5		167	X	X
38	Multi	4	*Lates niloticus*	29	23		201	X	X
38	Multi	4	*Lates niloticus*	29	23.5		202	X	
38	Multi	4	*Lates niloticus*	27	22		160	X	X
38	Multi	4	*Lates niloticus*	24.5	19.5		146	X	
38	Multi	4	*Distichodus nefasch*	47	38.5	42	1085		X
38	Multi	4	*Distichodus nefasch*	45	35	40	986		X
38	Multi	4	*Distichodus nefasch*	40.5	33	36.5	683		X
38	Multi	4	*Lates niloticus*	27	22		166		X
38	Multi	4	*Lates niloticus*	14.5	11.5		31		X
38	Multi	4	*Synodontis schall*	30.5	20	22.5	244		X
38	Multi	4	*Synodontis schall*	30.5	20	22.5	203		X
39	Multi	N/A	*Hydrocynus forskallii*	68.5	53.5	58.5	2980	X	X
39	Multi	N/A	*Alestes baremoze*	42.5	32.5	36.5	479	X	X
39	Multi	N/A	*Alestes baremoze*	40	30.5	33.5	363	X	X
39	Multi	N/A	*Alestes baremoze*	39.5	30.5	33	388	X	X
39	Multi	N/A	*Alestes baremoze*	38	29.5	32.5	352	X	X
39	Multi	N/A	*Alestes baremoze*	38.5	30.5	32.5	336	X	X
39	Multi	N/A	*Alestes baremoze*	42	32.5	35	423	X	X
39	Multi	N/A	*Alestes baremoze*	38	29.5	32.5	353	X	X
39	Multi	N/A	*Citharinus citharus*	25	18.5	21	153		X
39	Multi	N/A	*Chrysichthys auratus*	24.5	18	19.5	131		X
39	Multi	N/A	*Chrysichthys auratus*	22	15	17	70		X
39	Multi	N/A	*Chrysichthys auratus*	10.5	8	9.5	9		X
39	Multi	N/A	*Barbus bynni*	42	27	29	180		X
39	Multi	N/A	*Synodontis schall*	36.5	25.5	28	400	X	X

39	Multi	N/A	*Lates niloticus*	35	28.5		343	X	X
39	Multi	N/A	*Alestes baremoze*	36.5	28.5	30	285	X	X
39	Multi	N/A	*Hydrocynus forskallii*	36	28	30	235	X	X
39	Multi	N/A	*Alestes baremoze*	37	29	31	323	X	X
39	Multi	N/A	*Alestes baremoze*	33.5	26.5	29	239	X	X
39	Multi	N/A	*Alestes baremoze*	36.5	29	32	263	X	X
39	Multi	N/A	*Alestes baremoze*	34	26.5	28.5	237	X	X
39	Multi	N/A	*Citharinus citharus*	28.5	21.5	24.5	264		X
39	Multi	N/A	*Hydrocynus forskallii*	29.5	22	24	113	X	X
39	Multi	N/A	*Alestes baremoze*	30	22.5	25	152	X	X
39	Multi	N/A	*Alestes baremoze*	32.5	25.5	28	196	X	X
39	Multi	N/A	*Alestes baremoze*	35.5	27.5	30.5	264	X	X
39	Multi	N/A	*Brycinus ferox*	10	7	8.5	8.4		X
39	Multi	N/A	*Brycinus ferox*	9.5	7	8	7.4		X
39	Multi	N/A	*Brycinus ferox*	7	5	6	5		X
39	Multi	N/A	*Brycinus ferox*	7	5	6	3		X
40	Multi	7	*Distichodus nefasch*	62	50.5	56.5	2860		X
40	Multi	7	*Lates niloticus*	65	54		3325	X	X
40	Multi	6	*Distichodus nefasch*	60	48.5	54	2226		X
40	Multi	6	*Synodontis schall*	28.5	20.5	22.5	236		
40	Multi	6	*Distichodus nefasch*	55.5	46	51	2186		X
40	Multi	6	*Distichodus nefasch*	54	44	48.5	1721		X
40	Multi	6	*Distichodus nefasch*	53.5	43.5	48.5	1704		X
40	Multi	6	*Distichodus nefasch*	67.5	57	63	4660		X
40	Multi	6	*Distichodus nefasch*	59.5	49	54.5	2616		
40	Multi	6	*Distichodus nefasch*	59.5	47	53	2305		
40	Multi	6	*Lates niloticus*	63.5	53		2760	X	X
40	Multi	5.5	*Distichodus nefasch*	49.5	40	44.5	1250		X
40	Multi	5.5	*Distichodus nefasch*	53.5	43.5	47	1391		X
40	Multi	5.5	*Distichodus nefasch*	51	41.5	46.5	1427		
40	Multi	5.5	*Distichodus nefasch*	46	37.5	41.5	1089		X
40	Multi	5.5	*Distichodus nefasch*	56	45	50	1806		
40	Multi	5.5	*Distichodus nefasch*	56	45	49	1730		
40	Multi	5.5	*Oreochromis niloticus*	33.5	26.5		715	X	X
40	Multi	5.5	*Oreochromis niloticus*	33	26		755	X	X
40	Multi	5.5	*Distichodus nefasch*	56	45	50	1841		
40	Multi	5	*Labeo horie*	53.5	43.5	49	1679		X
40	Multi	5	*Distichodus nefasch*	61	48	54	2575		X
40	Multi	5	*Distichodus nefasch*	60.5	48.5	52	2750		
40	Multi	5	*Distichodus nefasch*	57	44	51	1936		
40	Multi	5	*Distichodus nefasch*	54	43	48	1503		

40	Multi	4.5	*Distichodus nefasch*	68	57	63	4173		X
40	Multi	4.5	*Distichodus nefasch*	60	49.5	54.5	2591		
40	Multi	4.5	*Distichodus nefasch*	49	39	45	1062		
40	Multi	4.5	*Citharinus citharus*	28.5	21	25	261		X
40	Multi	4.5	*Oreochromis niloticus*	27	22		359	X	X
40	Multi	4.5	*Oreochromis niloticus*	27	21		350	X	X
40	Multi	4.5	*Tilapia zillii*	27	21.5		427		X
40	Multi	4.5	*Tilapia zillii*	27.5	22		370		X
40	Multi	4.5	*Citharinus citharus*	28.5	21.5	24	261		X
40	Multi	4.5	*Labeo horie*	55	42.5	47.5	1565		X
40	Multi	4.5	*Labeo horie*	54.5	44	50	1460		X
40	Multi	4.5	*Distichodus nefasch*	50	41	45	1220		
40	Multi	4.5	*Distichodus nefasch*	45.5	38	41.5	963		X
40	Multi	4.5	*Distichodus nefasch*	48	39	43	967		
40	Multi	4.5	*Distichodus nefasch*	46.5	39	42.5	1308		
40	Multi	4.5	*Synodontis schall*	27	19.5	22	227		X
40	Multi	4.5	*Synodontis schall*	23	16	18	113		X
40	Multi	4.5	*Synodontis schall*	27.5	20.5	22	252		X
40	Multi	4.5	*Synodontis schall*	26.5	20	22	254		X
40	Multi	4.5	*Synodontis schall*	24	18.5	20.5	206	X	X
40	Multi	4	*Citharinus citharus*	26	19.5	22	200		
40	Multi	4	*Citharinus citharus*	28.5	21	24	219		X
40	Multi	4	*Citharinus citharus*	25.5	19	21.5	174		X
40	Multi	4	*Citharinus citharus*	26	19.5	22	189		X
40	Multi	4	*Labeo horie*	50.5	41	47	1172		X
40	Multi	4	*Labeo horie*	49	37.5	42	985		X
40	Multi	4	*Hydrocynus forskallii*	53.5	42	45	1038	X	
40	Multi	4	*Citharinus citharus*	26	19	22	180		X
40	Multi	4	*Lates niloticus*	45	36		1027	X	X
40	Multi	4	*Tilapia zillii*	25	20		336		X
40	Multi	4	*Citharinus citharus*	26.5	19.5	22.5	217		X
40	Multi	4	*Synodontis schall*	31	23	25	330	X	X
40	Multi	4	*Synodontis schall*	28.5	21.5	24	295	X	
40	Multi	4	*Synodontis schall*	30.5	23.5	26	386	X	X
40	Multi	4	*Synodontis schall*	28	21	21.5	230	X	X
40	Multi	4	*Synodontis schall*	35	25.5	28	246	X	
40	Multi	4	*Synodontis schall*	31	23	25	326	X	X
40	Multi	4	*Synodontis schall*	23.5	16.5	18.5	118	X	X
40	Multi	4	*Synodontis schall*	28.5	21	22	253	X	X
40	Multi	4	*Distichodus nefasch*	45	36.5	41	910		X
40	Multi	4	*Distichodus nefasch*	49	40.5	45	1174		X

40	Multi	4	*Distichodus nefasch*	39	31	35	525		
40	Multi	4	*Distichodus nefasch*	34	28	30	445		
40	Multi	3.5	*Citharinus citharus*	23	16.5	19	125		X
40	Multi	3.5	*Citharinus citharus*	29	21	24	251		X
40	Multi	3.5	*Citharinus citharus*	26.5	20.5	22.5	222		X
40	Multi	3.5	*Citharinus citharus*	23.5	17.5	20	146		X
40	Multi	3.5	*Labeo horie*	49.5	37	42	914		X
40	Multi	3.5	*Labeo horie*	43	33	37	616		X
40	Multi	3.5	*Tilapia zillii*	22	17		213		X
40	Multi	3.5	*Synodontis schall*	23	23.5	26.5	305	X	X
40	Multi	3.5	*Synodontis schall*	27	20	22	221	X	
40	Multi	3.5	*Synodontis schall*	25.5	18.5	20.5	179	X	X
40	Multi	3.5	*Synodontis schall*	30.5	22	24.5	278	X	X
40	Multi	3.5	*Synodontis schall*	33	23.5	26	252	X	X
40	Multi	3.5	*Synodontis schall*	24	17.5	19	143	X	X
40	Multi	3.5	*Synodontis schall*	25.5	19	21	207	X	
40	Multi	3.5	*Synodontis schall*	27.5	21.5	24	257		X
40	Multi	3.5	*Synodontis schall*	27.5	21	23	248		X
40	Multi	3.5	*Synodontis schall*	26.5	19.5	21	205		X
40	Multi	3.5	*Synodontis schall*	24.5	18	19.5	171		
40	Multi	3.5	*Synodontis schall*	28	20.5	22	235		
40	Multi	3.5	*Synodontis schall*	25	18	20	205		
40	Multi	3.5	*Synodontis schall*	25.5	19	20.5	202		
40	Multi	3.5	*Synodontis schall*	27	19.5	22	188		
40	Multi	3.5	*Synodontis schall*	25	18	20	221		
40	Multi	3.5	*Synodontis schall*	28	21	23	252		
40	Multi	3.5	*Synodontis schall*	24	17.5	19.5	177		
40	Multi	3.5	*Synodontis schall*	26	19.5	21.5	203		
40	Multi	3.5	*Synodontis schall*	22	16.5	18	115		
40	Multi	3.5	*Synodontis schall*	28	21.5	24	244		
40	Multi	3.5	*Synodontis schall*	28.5	20.5	22.5	276		
40	Multi	3.5	*Synodontis schall*	28.5	20.5	23	236		
40	Multi	3.5	*Alestes baremoze*	21.5	16.5	18	57		X
40	Multi	3.5	*Alestes baremoze*	13	10	11	17		X
40	Multi	3.5	*Alestes baremoze*	13.5	9.5	11	11		X
40	Multi	3.5	*Alestes baremoze*	13.5	10.5	11.5	13		X
40	Multi	3.5	*Alestes baremoze*	17.5	12.5	14.5	30	X	X
40	Multi	3.5	*Alestes baremoze*	20	15	16.5	44	X	X
40	Multi	3.5	*Alestes baremoze*	14	10.5	11.5	14	X	X
40	Multi	3.5	*Alestes baremoze*	17	12.5	14	27	X	X
40	Multi	3.5	*Alestes nurse*	9.5	7.5	8.5	23		X

40	Multi	3.5	*Alestes baremoze*	19	14	15.5	39	X	X
40	Multi	3.5	*Alestes baremoze*	19	15.5	17	52	X	X
40	Multi	3.5	*Alestes baremoze*	17	13	14.5	25	X	X
40	Multi	3.5	*Alestes baremoze*	18	14	15.5	39	X	X
40	Multi	3.5	*Alestes baremoze*	19.5	15	16.5	49	X	X
40	Multi	3.5	*Alestes baremoze*	13	10	11.5	14	X	X
40	Multi	3.5	*Alestes baremoze*	14.5	11	12	13		
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	7	5.5		4.8		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	7	5.5		5.2		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	7	5.5		4.4		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	5.5	4.5		2		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	5	4		1.5		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	4.5	3.5		1.2		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	4	3.5		0.9		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	4	3		0.8		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	4	3		0.9		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	4	3		0.9		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	3.5	2.5		0.8		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	3	2.5		0.6		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	3.5	2.5		0.6		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	3	2.5		0.5		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	2.5	2		0.4		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	2.5	2		0.4		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	2.5	2		0.2		X
Seine	KMFRI Seine	N/A	*Haplochromis spp.*	2.5	1.5		0.3		X
Seine	KMFRI Seine	N/A	*Lates niloticus*	8	6.5		5.2	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	6	4.5		2.9	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	5.5	4		2	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	5.5	4		1.5	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	4.5	3.5		0.9	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	4	3		0.9		X
Seine	KMFRI Seine	N/A	*Lates niloticus*	3.5	2.5		0.4		X

Seine	KMFRI Seine	N/A	*Lates niloticus*	3.5	2.5		0.5	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	3	2.5		0.6	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	3	2		0.5	X	
Seine	KMFRI Seine	N/A	*Lates niloticus*	3	2.5		0.4	X	X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	6.5	5		5.6		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	4.5	3.5		1.5		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	6	5		4.4		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	6.5	5		5.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	7	5.5		7.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5.5	4.5		2.9		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	6	4.5		4		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	7	5.5		6.2		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	6	4.5		3.5		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5.5	4.5		2.7		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5	4		2.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5.5	4.5		3.5		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5	4		2.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5	4		2.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	4	3.5		2		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5	4		2.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5	4		2.6		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	4.5	3.5		1.8		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5.5	4		2.3		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	5	4		2.1		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	4.5	3.5		1.5		X
Seine	KMFRI Seine	N/A	*Tilapia zillii*	4.5	3.5		1.3		
Seine	KMFRI Seine	N/A	*Tilapia zillii*	4.5	3.5		1.8		
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	7.5	6		8	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	7	5.5		5.3	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	7	5.5		6.9	X	X

Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	5.5	4.5		3.1	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	5	4		1.9	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	5.5	4.5		2.7	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	5.5	4		2.8	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	5.5	4.5		2.3	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	4.5	3.5		1.8		X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	4.5	3.5		1.3	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	4.5	3.5		1.7	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	13.5	11		52.2	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	31.5	25.5		330.5	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	31	25.5		298	X	X
Seine	KMFRI Seine	N/A	*Lates niloticus*	25	20		165	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	10.5	8.5		21.8	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	10.5	7.5		15.8	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	8.5	6.5		10	X	X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	8	6		9.5		X
Seine	KMFRI Seine	N/A	*Oreochromis niloticus*	7.5	6		8		X

Appendix 2

Brief Description:
Appendix 2 provides fisheries data compiled for Lake Turkana, Kenya, which was used to develop the models discussed in Chapter 3. The water level data used in Chapter 3 is freely available online at the United Stated Department of Agriculture Global Reservoirs and Lakes database (G-REALM) so is not included here. All fisheries data for 1993-2014 (yield, value and effort data) were compiled with the help of the Kenya Marine and Fisheries Research Institute and the Ministry of Livestock and Fisheries Development of Kenya. Fisheries composition data for years prior to 1993 were compiled by Dr. Jeppe Kolding.

Table A2.1: Catch, Value and Fishing Effort for the Lake Turkana Fishery, 1993-2014.

Year	Catch (MT)	Value (Ksh '000)	Fishermen (No.)	Rafts (No.)	Boats (No.)	Nets (No.)	Hooks (No.)
1993	871	10,842	1,931	85	124	1,640	23,649
1994	1,125	12,491	1,903	NA	123	5,819	19,279
1995	2,232	23,420	990	44	81	2,742	7,070
1996	4,799	36,286	1,972	19	89	7,773	13,500
1997	3,837	33,741	3,646	46	95	3,188	17,868
1998	10,610	68,865	3,360	100	336	6,740	12,106
1999	5,239	76,001	4,612	114	427	5,159	12,556
2000	2,108	48,122	3,872	226	374	5,614	13,098
2001	3,737	49,587	5,974	292	693	10,785	15,250
2002	4,004	68,756	7,014	596	651	7,174	9,722
2003	3,964	69,013	7,014	596	636	7,250	10,110
2004	9,067	148,935	6,582	592	553	6,880	10,300
2005	2,493	86,471	6,630	652	545	7,000	10,220
2006	4,559	103,711	7,609	581	578	8,855	13,040
2007	5,122	245,366	8,855	496	474	NA	11,740
2008	8,070	229,171	NA	NA	NA	NA	NA
2009	9,445	268,218	NA	NA	NA	NA	NA
2010	6,430	182,598	NA	NA	NA	NA	NA
2011	7,250	317,209	NA	NA	NA	NA	NA
2012	3,001	287,493	NA	NA	NA	NA	NA
2013	4,338	NA	NA	NA	NA	NA	NA
2014	4,165	NA	NA	NA	NA	NA	NA

Table A2.2: Percent Species Composition of the Lake Turkana Fishery, Select Years 1963-2013.

Species	**63**	**69**	**70**	**72**	**73**	**74**	**75**	**76**	**82**	**85**	**86**	**87**	**88**	**04**	**06**	**11**	**13**
Lates niloticus	23	2	0	14	14	14	0	0	8	32	38	31	30	21	10	16	7
Tilapias	3	2	0	5	7	13	56	80	69	16	11	25	17	29	56	43	71
Labeo horie	0	0	0	21	26	29	13	0	13	23	36	31	27	42	15	14	5
Bagrus bayad	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1
Barbus bynni	0	0	0	3	10	12	7	0	2	3	2	2	5	1	1	2	0
Citharinus citharus	70	90	80	24	13	3	1	0	1	3	1	1	3	0	2	3	1
Distichodus nefasch	4	5	0	17	9	3	2	0	4	5	2	1	5	0	4	8	2
Clarias gariepinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Synodontis schall	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	3	1
Schilbe uranoscopus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrocynus forskallii	0	0	0	8	10	9	0	0	1	2	2	1	1	0	1	2	1
Alestes barmoze	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	3	10
Others	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	3	0
Unspecified	0	0	20	0	0	0	0	20	0	0	0	0	0	0	0	0	0

Table A2.3: Seasonal Catch Data (metric tons) from the Lake Turkana Fishery.

	2004	**2006**	**2011**	**2013**	**2014**
January	734	308	406	NA	NA
February	684	385	380	99	375
March	670	422	447	93	284
April	757	399	226	74	1633
May	859	420	306	99	NA
June	942	534	256	NA	495
July	643	430	196	NA	497
August	1008	400	259	NA	NA
September	1037	303	360	244	NA
October	493	338	275	NA	NA
November	683	306	264	219	NA
December	557	314	371	224	NA

Appendix 3

Brief Description: Appendix 3 contains two tables that provide information on depth, one for a transect run across Ferguson's Gulf, Lake Turkana and one for a transect run across Lake Turkana, from Ferguson's Gulf to Sibiloi National Park.

Table A3.1: Bathymetry Transect for Ferguson's Gulf.

Latitude (N)	Longitude (E)	Depth (m)
03° 29' 52.96"	35° 55' 29.97"	0.3
03° 29' 56.00"	35° 55' 24.83"	0.5
03° 29' 57.80"	35° 55' 22.80"	0.7
03° 29' 59.90"	35° 55' 22.00"	0.9
03° 30' 02.56"	35° 55' 21.10"	1.8
03° 30' 05.62"	35° 55' 20.20"	1.1
03° 30' 08.02"	35° 55' 19.63"	1.2
03° 30' 10.46"	35° 55' 19.02"	1.5
03° 30' 13.10"	35° 55' 18.38"	1.6
03° 30' 16.70"	35° 55' 17.54"	1.8
03° 30' 20.63"	35° 55' 16.80"	1.2
03° 30' 24.40"	35° 55' 16.02"	1.3
03° 30' 29.01"	35° 55' 15.04"	1.2
03° 30' 32.75"	35° 55' 14.12"	1.8
03° 30' 36.45"	35° 55' 13.15"	1.8
03° 30' 40.18"	35° 55' 12.36"	1.6
03° 30' 44.14"	35° 55' 11.49"	1.5
03° 30' 47.98"	35° 55' 10.66"	2.0
03° 30' 51.55"	35° 55' 09.93"	1.4
03° 30' 55.20"	35° 55' 09.18"	1.9
03° 30' 59.02"	35° 55' 08.41"	1.7
03° 31' 02.77"	35° 55' 07.66"	1.8
03° 31' 06.43"	35° 55' 06.93"	2.2
03° 31' 10.16"	35° 55' 05.99"	1.8
03° 31' 14.22"	35° 55' 04.92"	1.8
03° 31' 17.86"	35° 55' 04.17"	1.8
03° 31' 21.43"	35° 55' 03.69"	1.4
03° 31' 25.37"	35° 55' 03.16"	1.6
03° 31' 29.40"	35° 55' 02.66"	1.2
03° 31' 32.85"	35° 55' 01.99"	1.8
03° 31' 37.35"	35° 55' 01.57"	1.7
03° 31' 39.85"	35° 55' 01.11"	1.6
03° 31' 43.65"	35° 55' 00.49"	1.3
03° 31' 47.47"	35° 54' 59.93"	1.2
03° 31' 51.30"	35° 54' 59.25"	1.2
03° 31' 55.42"	35° 54' 58.53"	1.2
03° 31' 59.32"	35° 54' 57.83"	1.3
03° 32' 03.16"	35° 54' 57.20"	1.2

03° 32' 06.97"	35° 54' 56.81"	1.4
03° 32' 10.97"	35° 54' 56.33"	1.3
03° 32' 14.82"	35° 54' 55.85"	1.5
03° 32' 18.96"	35° 54' 55.48"	1.4
03° 32' 22.63"	35° 54' 55.07"	3.4
03° 32' 26.33"	35° 54' 54.37"	1.5
03° 32' 30.18"	35° 54' 53.59"	1.3
03° 32' 33.85"	35° 54' 52.75"	2.0
03° 32' 37.87"	35° 54' 51.77"	1.3
03° 32' 41.12"	35° 54' 51.05"	2.0
03° 32' 44.69"	35° 54' 49.98"	1.6
03° 32' 48.35"	35° 54' 48.61"	1.8
03° 32' 51.55"	35° 54' 47.01"	1.6
03° 32' 54.66"	35° 54' 44.23"	1.4
03° 32' 57.87"	35° 54' 42.14"	0.8
03° 33' 01.24"	35° 54' 27.48"	0.9
03° 33' 03.44"	35° 54' 25.77"	1.2
03° 33' 07.36"	35° 54' 23.45"	2.0
03° 33' 11.26"	35° 54' 21.61"	2.2
03° 33' 14.94"	35° 54' 20.37"	2.0
03° 33' 19.11"	35° 54' 19.57"	2.6
03° 33' 21.48"	35° 54' 19.24"	3.4
03° 33' 24.57"	35° 54' 18.79"	3.2
03° 33' 27.43"	35° 54' 18.51"	3.6
03° 33' 31.34"	35° 54' 18.79"	4.9
03° 33' 35.12"	35° 54' 19.46"	6.1
03° 33' 38.85"	35° 54' 20.57"	6.8
03° 33' 42.77"	35° 54' 21.46"	7.8
03° 33' 46.65"	35° 54' 21.79"	7.5
03° 33' 50.44"	35° 54' 21.43"	7.6
03° 33' 54.02"	35° 54' 21.61"	8.9
03° 33' 57.86"	35° 54' 21.90"	8.8
03° 34' 00.94"	35° 54' 22.35"	9.7
03° 34' 02.58"	35° 54' 22.76"	10.5

Table A3.2: Bathymetry Transect from Ferguson's Gulf to Sibiloi National Park.

Latitude (N)	**Longitude (E)**	**Depth (m)**
03° 40' 45.55"	36° 13' 04.52"	20.20
03° 33' 41.53"	35° 57' 41.73"	45.00
03° 38' 39.30"	36° 12' 24.66"	60.10
03° 36' 53.34"	36° 11' 09.87"	61.80
03° 35' 42.12"	36° 09' 21.80"	63.40
03° 34' 30.84"	36° 07' 33.76"	57.70
03° 33' 14.59"	36° 05' 48.21"	61.70
03° 32' 09.64"	36° 03' 56.59"	74.60
03° 32' 25.87"	36° 01' 49.67"	45.00
03° 33' 06.02"	35° 59' 46.32"	28.90

Appendix 4

Brief Description: This appendix provides water level data and data on other physical characteristics of the African lakes studied in Chapter 6. The water level data for these systems is only included for years preceding 1993, as satellite altimetry data from 1993-present is freely available online at the United Stated Department of Agriculture Global Reservoirs and Lakes database (G-REALM). Water level data for years prior to 1993 was compiled with the assistance of Dr. Jeppe Kolding.

Table A4.1: Physical Characteristics of Thirteen African Lakes and Reservoirs.

Lake	**RLLF$_a$**	**RLLF$_s$**	**RT (yrs)**	**SA (km^2)**	**V (km^3)**	**Catchment (km^2)**	**Depth (m)**	**Altitude (m)**
Awassa	4.22	16.04	1.25	129	1.30	1,300.00	11.00	1,708.00
Chad	2.59	30.28	1.00	1,540	6.30	106,336.20	4.11	280.00
George	1.18	2.81	0.25	250	0.80	9,705.00	2.40	914.00
Hayq	8.85	NA	83.53	22	0.87	65.00	37.37	2,030.00
Kariba	3.97	15.02	3.00	5,400	160.00	663,000.00	31.00	485.00
Kivu	0.13	0.46	88.00	2,220	333.00	4,940.00	240.00	1,460.00
Malawi	0.14	0.59	114.00	29,500	8,400.00	6,593.00	202.00	500.00
Naivasha	11.32	28.34	2.00	140	5.00	3,200.00	6.00	1,890.00
Nakuru	38.70	40.77	83.53	40	0.09	1,760.00	2.30	1,759.00
Tana	2.15	18.62	8.90	3,600	28.00	10,000.00	9.00	1,788.00
Tanganyika	0.04	0.13	440.00	32,000	17,800.00	263,000.00	572.00	773.00
Turkana	1.59	3.72	12.50	6,750	203.60	130,860.00	30.20	360.40
Victoria	0.64	1.31	23.00	68,800	2,750.00	184,000.00	40.00	1,134.00

Table A4.2: Lake Awassa Water Level, 1970-1999.

Year	**Lake Level (m)**
1970	1.08
1971	1.67
1972	1.16
1973	0.81
1974	0.68
1975	0.68
1976	1.10
1977	1.78
1978	2.10
1979	1.62
1980	1.20
1981	0.98
1982	1.55
1983	1.55
1984	1.09
1985	1.26
1986	1.57
1987	1.73
1988	1.99
1989	2.10
1990	1.66
1991	1.27
1992	1.72
1993	2.09
1994	2.07
1995	1.85
1996	2.76
1997	2.88
1998	3.48
1999	2.38

Table A4.3: Lake Chad Water Level, 1954-1977.

Year	Lake Level (masl)
1954	361.25
1955	407.08
1956	447.83
1957	472.58
1958	443.67
1959	422.50
1960	419.00
1961	434.58
1962	489.75
1963	513.50
1964	499.25
1965	494.58
1966	442.67
1967	401.92
1968	389.08
1969	348.00
1970	315.75
1971	301.50
1972	244.00
1973	136.42
1974	170.36
1975	224.08
1976	265.25
1977	247.25

Table A4.4: Lake Hayq Water Level, 1975-2012.

Year	Lake Level (m)
1975	1.09
1976	1.36
1977	1.02
1978	0.79
1979	0.62
1980	0.48
1981	0.52
1982	0.53
1983	0.59
1986	0.26
1987	0.15
1988	0.36
1989	0.12
1990	0.18
1991	0.48
1998	0.93
1999	1.12
2000	1.51
2001	2.17
2002	2.55
2003	2.38
2004	2.17
2006	1.26
2007	1.26
2008	0.93
2009	0.69
2010	0.98
2011	1.62
2012	1.33

Table A4.5: Lake Kariba Water Level, 1963-1992.

Year	**Lake Level (masl)**
1963	484.89
1964	482.30
1965	484.50
1966	483.80
1967	483.40
1968	484.00
1969	484.80
1970	483.60
1971	483.80
1972	484.00
1973	482.90
1974	485.83
1975	485.22
1976	485.84
1977	486.30
1978	486.72
1979	486.20
1980	485.86
1981	486.36
1982	484.12
1983	481.45
1984	478.89
1985	478.42
1986	478.77
1987	478.72
1988	479.45
1989	482.29
1990	481.55
1991	480.36
1992	477.73

Table A4.6: Lake Kivu Water Level, 1945-1973.

Year	Lake Level (m)
1945	0.25
1946	0.38
1947	0.57
1948	0.50
1949	0.33
1950	0.35
1951	0.41
1952	0.61
1953	0.27
1954	0.22
1955	0.27
1956	0.37
1957	0.60
1958	0.57
1959	0.48
1960	0.67
1961	0.66
1962	1.02
1963	1.26
1964	1.04
1965	0.82
1966	0.77
1967	0.73
1968	1.08
1969	0.82
1970	0.81
1971	0.83
1972	0.80
1973	0.70

Table A4.7: Lake Malawi Water Level, 1900-1992.

Year	Lake Level (masl)
1900	470.99
1901	470.55
1902	470.36
1903	470.49
1904	470.49
1905	470.74
1906	470.49
1907	470.36
1908	470.18
1909	470.36
1910	470.05
1911	469.99
1912	469.93
1913	469.86
1914	469.74
1915	469.74
1916	469.74
1917	470.24
1918	470.61
1919	470.43
1920	470.43
1921	469.93
1922	470.34
1923	470.23
1924	470.32
1925	470.41
1926	470.58
1927	470.80
1928	470.93
1929	470.98
1930	471.26
1931	471.53
1932	471.95
1933	472.25
1934	472.30
1935	472.85
1936	473.37
1937	473.88

1938	473.88
1939	473.68
1940	473.84
1941	473.66
1942	473.42
1943	473.22
1944	472.60
1945	472.87
1946	473.26
1947	473.33
1948	473.73
1949	473.22
1950	472.82
1951	473.00
1952	473.04
1953	473.11
1954	472.60
1955	472.32
1956	472.74
1957	473.44
1958	473.66
1959	472.91
1960	472.82
1961	472.74
1962	473.09
1963	473.75
1964	474.19
1965	473.97
1966	473.59
1967	473.44
1968	473.48
1969	473.53
1970	473.40
1971	473.51
1972	473.40
1973	473.26
1974	473.53
1975	473.97
1976	473.88
1977	474.12
1978	474.14

1979	474.54
1980	475.15
1981	474.98
1982	474.63
1983	474.47
1984	474.01
1985	473.73
1986	474.16
1987	473.77
1988	473.29
1989	473.66
1990	473.90
1991	473.66
1992	473.20

Table A4.8: Lake Naivasha Water Level, 1900-1992.

Year	Lake Level (masl)
1900	1891.55
1901	1891.02
1902	1891.77
1903	1892.59
1904	1893.40
1905	1894.25
1906	1894.51
1907	1894.17
1908	1893.83
1909	1893.50
1910	1893.15
1911	1892.83
1912	1892.48
1913	1892.15
1914	1891.82
1915	1891.47
1916	1891.43
1917	1893.67
1918	1894.67
1919	1894.11
1920	1893.53
1921	1892.97
1922	1892.40
1923	1893.08
1924	1892.84
1925	1892.22
1926	1891.89
1927	1891.85
1928	1890.62
1929	1890.03
1930	1891.24
1931	1891.61
1932	1890.88
1933	1890.19
1934	1889.26
1935	1888.44
1936	1888.53
1937	1889.27

1938	1889.05
1939	1887.84
1940	1887.00
1941	1886.72
1942	1886.86
1943	1886.02
1944	1885.10
1945	1884.78
1946	1884.64
1947	1886.23
1948	1885.84
1949	1885.18
1950	1884.75
1951	1885.64
1952	1885.82
1953	1884.86
1954	1885.04
1955	1885.04
1956	1885.75
1957	1886.36
1958	1886.98
1959	1886.83
1960	1886.01
1961	1885.61
1962	1888.17
1963	1888.88
1964	1889.66
1965	1889.75
1966	1888.96
1967	1888.77
1968	1889.48
1969	1889.30
1970	1888.93
1971	1888.85
1972	1888.66
1973	1887.94
1974	1887.51
1975	1887.43
1976	1887.06
1977	1887.54
1978	1889.03

1979	1889.61
1980	1889.10
1981	1889.14
1982	1889.07
1983	1889.09
1984	1888.36
1985	1887.71
1986	1887.36
1987	1886.77
1988	1886.61
1989	1886.94
1990	1888.00
1991	1887.60
1992	1887.04

Table A4.9: Lake Nakuru Water Level, 1956-2000.

Year	Max Depth (m)
1956	0.24
1957	0.93
1958	1.13
1959	1.01
1960	0.52
1961	0.19
1962	1.74
1963	1.98
1964	2.97
1965	3.14
1966	2.49
1967	2.19
1968	2.61
1969	3.33
1970	2.13
1971	2.77
1972	2.66
1973	2.01
1974	1.54
1975	1.53
1990	1.99
1991	1.43
1994	0.16
1995	0.11
1996	0.38
1997	0.53
1998	3.86
1999	3.51
2000	2.00

Table A4.10: Lake Tana Water Level, 1960-1992.

Year	Lake Level (m)
1960	1.62
1961	1.52
1962	1.39
1963	1.45
1964	1.31
1965	1.28
1966	1.57
1967	1.66
1968	1.62
1969	1.52
1970	1.39
1971	1.45
1972	1.31
1973	1.28
1974	1.57
1975	1.66
1976	1.65
1977	1.61
1978	1.57
1979	1.46
1980	1.44
1981	1.43
1982	1.37
1983	1.24
1984	1.30
1985	1.55
1986	1.61
1987	1.53
1988	1.61
1989	1.61
1990	1.41
1991	1.56
1992	1.53

Table A4.11: Lake Tanganyika Water Level, 1909-1992.

Year	Lake Level (masl)
1909	774.67
1910	774.27
1911	773.88
1912	773.84
1913	773.51
1914	773.82
1915	773.80
1916	773.86
1917	774.22
1918	774.24
1919	774.14
1920	773.98
1921	773.98
1922	773.78
1923	773.45
1924	773.57
1925	773.45
1926	773.37
1927	773.92
1928	773.65
1929	773.45
1930	773.41
1931	774.08
1932	774.37
1933	774.45
1934	774.31
1935	774.18
1936	774.53
1937	774.78
1938	775.10
1939	774.98
1940	774.94
1941	774.67
1942	774.59
1943	774.65
1944	774.27
1945	773.96
1946	773.71

1947	773.67
1948	773.82
1949	773.55
1950	773.35
1951	773.24
1952	773.65
1953	774.12
1954	773.86
1955	773.61
1956	773.65
1957	773.92
1958	773.98
1959	773.80
1960	773.88
1961	773.90
1962	774.35
1963	775.55
1964	776.20
1965	776.43
1966	776.08
1967	775.76
1968	775.92
1969	776.16
1970	775.80
1971	775.53
1972	775.24
1973	774.96
1974	774.73
1975	774.55
1976	774.27
1977	774.35
1978	774.55
1979	775.02
1980	775.18
1981	775.02
1982	774.73
1983	774.73
1984	774.55
1985	774.29
1986	774.20
1987	774.31

1988	774.55
1989	774.55
1990	775.10
1991	774.96
1992	774.94

Table A4.12: Lake Turkana Water Level, 1888-1989.

Year	Lake Level (masl)
1888	374.50
1889	374.50
1890	374.80
1891	375.40
1892	376.10
1893	377.00
1894	378.30
1895	379.40
1896	380.20
1897	380.00
1898	379.30
1899	377.60
1900	376.00
1901	374.50
1902	373.00
1903	371.80
1904	370.70
1905	369.70
1906	368.80
1907	368.20
1908	367.55
1909	367.20
1910	366.80
1911	366.50
1912	366.30
1913	366.00
1914	366.00
1915	366.30
1916	367.00
1917	368.50
1918	370.00
1919	369.60
1920	366.70
1921	366.00
1922	366.20
1923	366.70
1924	367.10
1925	367.60

1926	367.90
1927	368.00
1928	367.70
1929	367.20
1930	366.30
1931	364.80
1932	363.90
1933	363.30
1934	363.40
1935	364.50
1936	364.30
1937	363.90
1938	362.10
1939	361.70
1940	361.50
1941	361.50
1942	360.80
1943	360.60
1944	360.20
1945	360.00
1946	360.00
1947	361.80
1948	362.00
1949	361.40
1950	361.20
1951	361.06
1952	360.97
1953	360.33
1954	360.19
1955	360.09
1956	360.37
1957	361.49
1958	361.06
1959	361.01
1960	361.01
1961	361.70
1962	363.50
1963	365.27
1964	365.19
1965	364.54
1966	364.29

1967	364.64
1968	364.29
1969	365.31
1970	365.72
1971	365.48
1972	365.23
1973	364.72
1974	364.27
1975	364.05
1976	364.61
1977	365.73
1978	367.19
1979	367.36
1980	366.37
1981	364.38
1982	363.82
1983	364.49
1984	364.05
1985	362.49
1986	362.08
1987	361.41
1988	360.62
1989	361.06

Table A4.13: Lake Victoria Water Level, 1900-1988.

Year	Lake Level (masl)
1900	1133.78
1901	1133.96
1902	1133.60
1903	1134.40
1904	1134.40
1905	1134.27
1906	1134.64
1907	1134.36
1908	1134.07
1909	1134.04
1910	1133.82
1911	1133.64
1912	1133.69
1913	1133.80
1914	1133.78
1915	1134.00
1916	1134.42
1917	1134.82
1918	1134.44
1919	1133.82
1920	1133.69
1921	1133.42
1922	1133.38
1923	1133.67
1924	1133.78
1925	1133.58
1926	1134.31
1927	1133.93
1928	1133.96
1929	1133.76
1930	1134.02
1931	1134.31
1932	1134.40
1933	1134.18
1934	1133.98
1935	1133.96
1936	1134.20
1937	1134.56

1938	1134.40
1939	1134.20
1940	1134.22
1941	1134.13
1942	1134.47
1943	1134.00
1944	1133.96
1945	1133.62
1946	1133.60
1947	1134.31
1948	1134.07
1949	1133.78
1950	1133.73
1951	1133.82
1952	1134.42
1953	1134.04
1954	1134.04
1955	1134.09
1956	1134.09
1957	1134.07
1958	1133.91
1959	1133.98
1960	1133.91
1961	1134.64
1962	1135.71
1963	1135.96
1964	1135.82
1965	1135.56
1966	1135.33
1967	1135.38
1968	1135.60
1969	1135.40
1970	1135.29
1971	1135.24
1972	1135.11
1973	1135.00
1974	1135.07
1975	1135.07
1976	1135.29
1977	1135.73
1978	1135.47

1979	1135.07
1980	1134.89
1981	1135.02
1982	1135.07
1983	1134.71
1984	1134.71
1985	1134.82
1986	1134.84
1987	1135.07
1988	1135.20