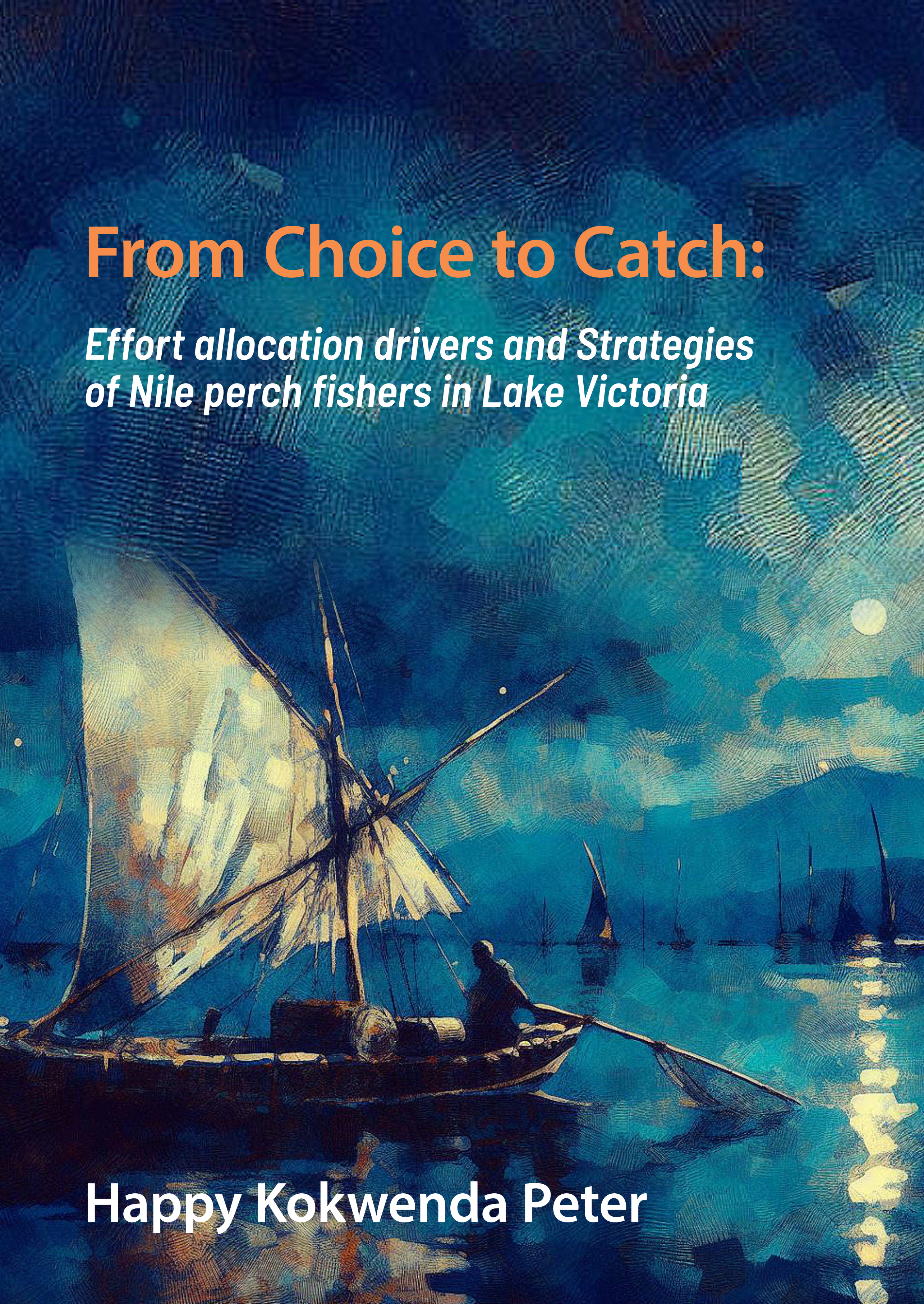

From Choice to Catch:

Effort allocation drivers and Strategies of Nile perch fishers in Lake Victoria

Happy Kokwenda Peter

Propositions

✓ 1. Bet hedging is the solution for Nile perch fishers in Lake Victoria to cope with catch variability.
(This thesis)

✓ 2. Nile perch fishers who catch multiple sizes are ahead of common management ideas regarding selective fishing.
(This thesis)

✓ 3. Traditional medicine has benefited from Covid19.

✓ 4. Legumes and fish should never be used as animal feed.

✓ 5. The PhD marathon is tougher when you're running in heels.

✓ 6. AI is a threat to human society

Propositions belonging to the thesis, entitled

From Choice to Catch: Effort allocation drivers and Strategies of Nile perch fishers in Lake Victoria

Happy Kokwenda Peter
Wageningen, 20 December 2023

From Choice to Catch:

Effort allocation drivers and Strategies of Nile perch fishers in Lake Victoria

Happy Kokwenda Peter

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This research was conducted under the auspices of the Graduate School, Wageningen Institute of Animal Sciences (WIAS).

From Choice to Catch:

Effort allocation drivers and Strategies of Nile perch Fishers in Lake Victoria

Happy Kokwenda Peter

Thesis

submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
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Prof. Dr A.P.J. Mol,
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To my dearest mother, Elmelda Kenshonga

For your unwavering support, endless encouragement, and boundless love,

To my beloved children, Chloe-ella and Ty Ebro

For inspiring me every day and being my motivation,

This Thesis is dedicated to you, my precious loved ones...

Table of Content


HAPO SAWA
HABARI NDO HIY
AKA WATU PORI!!
Marshall
Flint, Mich
June 22, 20

Chapter 1

General Introduction

Background

Lake Victoria is one of the African Great Lakes, the world's largest tropical lake (Saundry and Boukerrou 2012), and the world's second-largest freshwater lake by surface (Awange and Ong'ang'a 2006; Wikipedia). It supports one of the world's largest inland fisheries in terms of catch volume (0.8-1 million tons), numbers of fishers (220,000), and landing sites (>1500) along the 3500km coastline and the numerous islands of the lake (LVFO, 2017; Kolding et al., 2014).

The Lake's history and current statistics indicate significant environmental and biological changes, including its diversity of fish species (Mungai et al., 2019). The deterioration of the environment presumably causes these changes, the introduction of foreign species, overfishing, and the ban on fish exports (Njiru et al., 2008). Before the 1980s, the lake ecology was home to hundreds of endemic haplochromine fishes (Hecky et al., 2010; Kaufman 1992). Commercial fishing was limited to traditional table fish species: tilapiines, *Bagrus, Clarias, Labeo, Protopterus, Mormyrus,* and *Barbus* (Kudhongania et al., 1992). The fish community changed after the 1980s, becoming simpler as only economically significant species dominated its biomass: Nile perch (*Lates niloticus* L.), Nile tilapia (*Oreochromis niloticus* L.), and Dagaa (*Rastrineobola argentea*) (Kolding 2008; Kudhongania et al., 1992; Natugonza et al., 2022).

Among these three species, Nile perch is commercially the most important stock in the lake, intensively targeted and receiving the strongest management attention (Geheb et al., 2008; Mkumbo and Marshall 2015; Njiru et al., 2014). In the 1950s, Nile perch was introduced to Lake Victoria to boost the fishing industry (Goudswaard et al., 2008). Nile perch gradually spread all over the Lake, and from the mid-1980s to the 1990s, the population increased dramatically. The abundance of Nile perch led to a considerable reduction in the abundance of other fish species that were important in the fisheries by then (Downing et al., 2013; Goudswaard et al., 2008), thereby causing fishers to switch their targets from their usual fish species to dominant species: Nile perch, Nile tilapia, *Rastrineobola* and *Caridina* (Kolding et al., 2008; Medard 2015).

After the Nile perch upsurge in the 1980s (Kolding et al., 2008), its harvest reached a maximum of around 300,000 tons in 1990 and since then has been fluctuating around 240,000 tons. With this strong growth in Nile perch catches, the number of people dependent on Nile perch, i.e., fishers and traders (Njiru et al., 2014; Ogutu-Ohwayo et al., 1997) rose concomitantly. Fishers increased from less than 20,000 before 1980 to 60,000 between 1985 and 2000 and 100,000 and 150,000 between 2010 and 2020 (MLF, 2008; LVFO, 2017; LVFO, 2020; Natugonza et al., 2022).

There are claims of a decline in Nile perch (Sobo et al., 2017), yet the reasons remain unclear. Some studies suggest links to environmental shifts, including lake eutrophication (Silsbe 2004; Silsbe et al., 2006), Nile perch's preference for haplochromine prey (Kaufman and Schwartz 2002) and increased fishing efforts (Balirwa 2003; Mkumbo 2002; Njiru et al., 2007; Njiru et al., 2005). The claims of a decline in Nile perch catches conflict with the available data. In 1990, Nile perch caught surged by over 300,000 tons, followed by a decrease. However, for over two decades, catches have stabilized around 240,000 tons (Kolding et al., 2014; Kolding et al., 2008). This challenges the view that a single year of high catches triggered a downward trend. A consistent catch level for more than two decades challenges the idea of a decline.

The fishery of Nile perch is carried by artisanal fishers using gillnets and longlines as main gears. Fishers operate fishing using wooden vessels of varying sizes from 5 to 11 meters, propelled by paddles (60%), small outboard engines (32%) and sail (8%) (LVFO, 2017; LVFO, 2017). Fishing in Lake Victoria takes place from many landing sites along the shore. Most fishing operations are day trips, with limited use of ice, further limiting the potential action radius of a fishing trip. Nile perch fisheries are regulated through a minimum mesh (6 inches, 152 mm stretched mesh) and a recommended hook size (<10). Nonetheless, the enforcement of these regulations has been relatively weak (Medard Ntara 2015). A strategy of engaging local communities in fisheries management through the so-called “Beach Management Units” (BMU) is used to enhance regulatory compliance.

Overfishing is seen as the most significant threat to the fishing industry. According to some authors, a collapse of Nile perch stocks is about to occur if the increase in exploitation pressure is not controlled (Matsuishi et al., 2006; Njiru et al., 2005). However, this assumption is based on the idea that Lake Victoria's ecosystem is in a steady state. This assumption is questionable as the Lake is subject to eutrophication (Hecky et al., 1994; Odada and Olago 2006; Silsbe et al., 2006). Eutrophication increases primary production and, as the food chain to Nile perch is short (Ligtvoet and Witte 1991), may lead to a higher carrying capacity for the Nile perch stocks. In that case, eutrophication may compensate for the increased exploitation pressure on the Nile perch. However, the significant risk is that compensation for increased fishing pressure by increased productivity could fail when eutrophication becomes too intense (Silsbe et al., 2006). In this case, Nile perch stocks could collapse due to overfishing and nutrient loading due to eutrophication. The broader research program in this PhD aims to investigate both scenarios' likelihood.

This study aims to untangle how fishing pressure, characterized by effort allocation, and nutrient loading due to eutrophication interact to shape the size distribution of Nile perch in the lake (Fig. 1.1). Both fishing effort and nutrient loading have different effects, affecting shallow areas near homeports and deeper open waters differently. Assessing how these two factors balance out in these distinct areas is crucial.

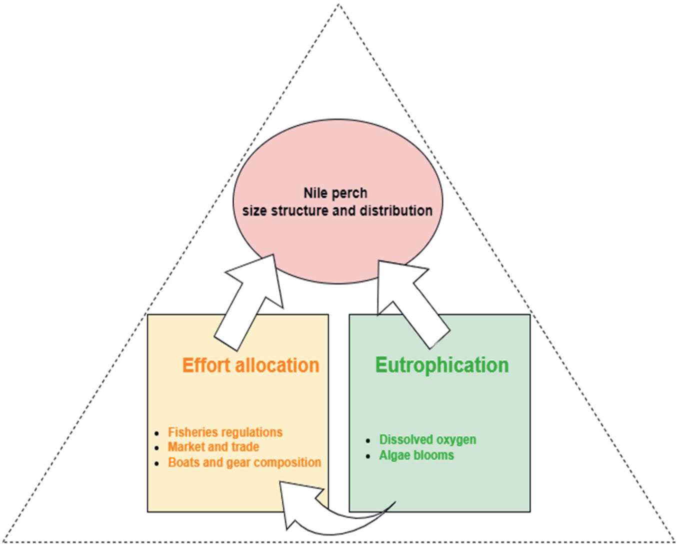

Figure 1.1: *Diagram illustrating the interaction between effort allocation and eutrophication as drivers of Nile perch size structure and distribution.*

With regard to fishing effort allocation, factors like fishing logistics, fish presence and density and the environment play a role in the choice of fishers where and when to fish. In addition, as more large individuals of Nile perch are found in deeper waters and more smaller individuals near shallow homeport areas, it's expected that fishers will catch Nile perch of different sizes depending on where they fish or, even more, will search the fishing ground where they expect to find the size range they want for their customers. It is also likely that the gear choice, e.g., gillnets or longlines and the mesh, resp. hook size is based on a rational decision based on the expected and desired catch. To analyse this, it's important to investigate where gillnet and longline fishers focus their efforts.

Additionally, the impacts of eutrophication, including oxygen depletion, might differ between shallow areas and open water regions. To understand this, our study will examine the dissolved oxygen levels and Chlorophyll-a across the study area. This will provide insights into how fishing pressure and nutrient loading interact and impact the Nile perch size distribution.

Effort allocation

Numerous factors influence the daily spatial effort allocation: previous fishing success, market demands, costs of fishing, type of gear and so on. Spatial effort allocation is not random but expected based on fishers' knowledge of the distribution of the targeted species, the density of fishers, and the fishing costs (Gillis 2003; Gillis et al., 1993). If Nile perch distribution is stable and habitat-specific in Lake Victoria, previous catch information is a primary driver of effort allocation (Hinz et al., 2003). Fishers will select fishing grounds and gear based on the fish distribution as they assume it using past information on previous fishing ground selections. Effort allocation changes according to various factors that drive fisher's decisions on where, what, and when to fish. All the decisions are left to the skippers of the vessels, who are often the custodians of the entire fishing operations (Fulton et al., 2011; Gezelius 2007; Sampson 1991; Vignaux and Sciences 1996). Besides information on the distribution of the Nile perch based on previous catches and information from other fishers, the size of the vessel, type of gear, and availability of engines play a role in the choices made during fishing (Bergmann et al., 2004; van Putten et al., 2011). In Lake Victoria, vessels are either motorised (outboard engines), sail, or oar-driven (MLF, 2015; LVFO, 2017; LVFO, 2020), limiting the fishing operation's extent and duration of the stay on the lake. Both may be extended depending on the availability of collector boats. Furthermore, the type of gear used (gillnets or longlines) and weather (water currents, winds, rainfall) determine where and when to fish.

Models suggest that fishers tend to fish closer to their homeports (Tsitsika and Maravelias 2008), but reducing competition is advantageous with the increased number of fishers over the lake. It is anticipated that fishers will target fishing grounds offshore if the probability of catches increases and the profitability of the fishing operations is not affected. Targeting fishing grounds far from homeports may be the reason for recent changes in the Nile perch fishery in Lake Victoria, like the increased size of fishing vessels and the use of motorised vessels (LVFO, 2017; Njiru et al., 2008). Furthermore, there is a shift from gillnet to longline fishing and the use of collector boats, which increase the time fishers can spend on the lake fishing.

Fishing modifies the size structure of the exploited communities. Fishers selectively target a specific size range of fish through their gear choices. For example, during this study in Lake Victoria, the dominant mesh size was 5 inches (128mm), and hook sizes were >10 (Lake Victoria fisheries frame survey 2008). Yet, Mkumbo et al., (2007) reported a dominant mesh size of 3" and less. In the 1990s, most fishers used gillnets with a mesh size of 8 inches (Schindler et al., 1998), and over the years, there has been a clear shift to smaller mesh sizes. Heavy pressure on specific size ranges will change the size structure of the Nile perch stocks. Pressure is mainly exerted on the large exportable sizes (slot size), yet large sizes are important to maintain the chances of high recruitment levels. Nile perch is a periodic strategist, which, according to Winemiller and Rose (1992), is highly productive with longer life spans. Maintaining a critical density of adult stocks of the large old specimen is considered good management practice with these species (Hixon et al., 2014; King et al., 2003). Fishing patterns and fishing efforts have changed and will change further with increased fishing pressure, eventually impacting the Nile perch size structure and distribution.

Eutrophication

Eutrophication results from increased nutrient loading (Carpenter 2005; Winemiller and Rose 1992). In Lake Victoria, increased nutrient loading is greatly attributed to agricultural activities, deforestation, swamp clearing (Scheren 2000; Tamatamah et al., 2005), and urban pollution (Shayo et al., 2011). In Lake Victoria specifically, eutrophication should be a significant concern for fisheries and environmentalists because of the lake’s shallowness (Kateregga and Sterner 2007; Scheffer 1998) and low water volume. These two factors lead to a long water retention time of around 20 years (Kayombo and Jorgensen 2003); the lake cannot provide temporary buffers against water quality deterioration like in the deep African Lakes (Hecky 1993; Odada and Olago 2006). Nutrient enrichment in Lake Victoria started as early as the 1920s and continuously increased to eutrophic levels during the 1960s to early 1970s due to rapid human population growth (Hecky 1993). Eutrophication in Lake Victoria increases algal biomass, altering the lake's physical, chemical, and biological environment (Hecky 1993; Hecky et al., 1994; Ochumba and Kibaara 1989; Seehausen et al., 1997a; Wanink et al., 2001). In particular, the lake's water quality in terms of transparency and dissolved oxygen is strongly affected (Silsbe et al., 2006).

Nutrient input changes seasonally and inter-annually with changes in rainfall and wind stress (Kolding et al., 2008). Seasonal changes will impact dissolved oxygen concentration in areas close to the shore. The most striking phenomenon resulting from increased eutrophication is a permanent depletion of oxygen (hypoxia) in deeper waters (Hecky et al., 1994) and the formation of large anoxic layers during the lake's stratification. Stratification occurs during the rainy season due to reduced water mixing. Hypoxic conditions with dissolved oxygen levels below 2mgL^{-1} have been a long-term phenomenon in Lake Victoria but were restricted to deeper waters of more than 60m depth and often for short periods during the rainy seasons. However, Wanink et al., (2001) found continuous hypoxic and anoxic conditions at depths below 50m. Seasonal changes in nutrient inputs may affect near-shore areas, but wind stress will be a major determinant of the monthly and annual shifts of the anoxic layer within the entire Lake (Silsbe 2004).

The immediate effect of hypoxia is a reduction in available habitat for hypoxia-intolerant species, resulting in a shift in species distribution (Schofield and Chapman 2000). Wanink et al., (2001) showed a clear correlation between catch rates and dissolved oxygen in the Nile perch fishery, with nearly zero catches at < 0.2mgL^{-1} dissolved oxygen and an increase in catches from 1mgL^{-1} dissolved oxygen and onwards. As a result, eutrophication may also affect the distribution and size structure of Nile perch, which is considered a hypoxia intolerant species (Chapman 1995; Wanink et al., 2001).

Aim and Research Questions

This study intends to assess changes in fishing pressure, fishing patterns, and the effects of eutrophication on the distribution and size structure of Nile perch populations in the southern part of Lake Victoria—Tanzania. The goal is to understand to which extent the size structure of the Nile perch stocks is determined by the fishery or by ecological (eutrophication) factors of the lake.

Two important questions must be answered to understand the impact of effort allocation (fishing) and eutrophication on Nile perch size structure and distribution:

1. Which physical and short-term ecological factors drive the fishing effort allocation and fishing patterns in the southern part of Lake Victoria—Tanzania?
2. What impact have effort allocation, fishing, and lowered oxygen levels on the Nile perch size structure and distribution?

Study area

This study was conducted in the southern part of Lake Victoria, in the territorial waters of Tanzania (Fig. 1.2). The southern part of Lake Victoria is where around 49% of all fishers on the Lake are found (MLF, 2015; LVFO, 2017). Four landing sites were selected based on their position along the shallower Speke Gulf and the deeper open Lake (Fig. 1.2). The chosen sites represented other landing sites in southern Lake Victoria. Kayenze and Muluseni landing sites were located along the Speke Gulf (gulf region). At the same time, Muhula and Kome-Mchangani faced the open Lake (open lake region) (Fig. 1.2). The gulf region ranges to 40m depth but is mostly <25m deep; the open lake region is characterised by steep descending slopes down to 57m depth.

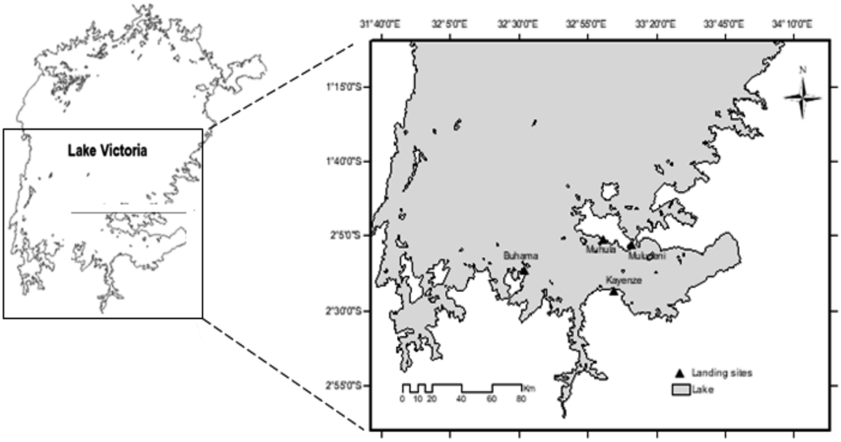

***Figure 1.2**: A map of the study area, the southern part of Lake Victoria, in the territorial waters of Tanzania.*

Outline of the thesis

This thesis is composed of a general introduction (**Chapter 1**), four research chapters (**Chapters 2, 3, 4, 5**) Fig. 1.3, and a final general discussion (**Chapter 6**).

Chapter 2 focuses on historical changes in fishing efforts regarding the Nile perch fisheries. This chapter will examine the type of fishing gear, the number of fishing gear, where the fishing has been conducted, and fishing patterns for the gillnet and longline fisheries, with a specific focus on mesh and hook size dynamics. By knowing how the fishing effort has been undertaken over time and space, I can discuss how fishing contributed to the decline of the Nile perch. The long-term changes in fishing effort will show where in the Lake more or less fishing effort has been exerted.

After knowing how the fishing effort has been distributed and changed over time, it is significant to understand how the targeted species (Nile perch) is distributed in its environment. In **Chapter 3**, I will examine the distribution of Nile perch and assess the relationship between Nile perch distribution and the physico-chemical factors in the lake. The expectation is to find the juvenile Nile perch more in shallow inshore waters and the adult Nile perch more in deep offshore waters. The assumption is that the size structure, physico-chemical factors, and food availability influence the distribution patterns of Nile perch.

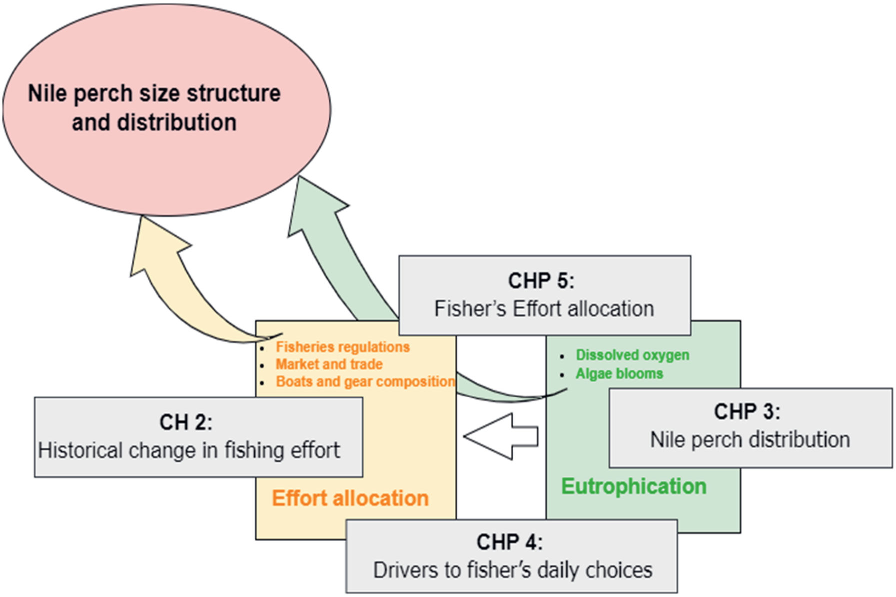

***Figure 1.3**: Conceptual diagram of the connection between chapters and how they relate to the factors influencing Nile perch's size, structure, and distribution.*

In **Chapter 4**, I studied the fishing effort allocation, analysing the factors driving fishers' daily fishing choices. Strategies that individual Nile perch fishers employ to remain in the fishing activities with high variability in daily catches will be investigated. Variability in daily catches puts fishers at risk of losing their capital. I propose that Nile perch fishers may reduce variability in the catches, hence risk, by using a bet-hedging strategy. Lastly, operational, environmental, and resource productivity factors driving the spatial distribution of fishers targeting the Nile perch will be examined in **Chapter 5**. Operational, environmental, and resource productivity limits an available space. This chapter focuses on a better understanding how fisher's effort is allocated spatially and temporally. Spatial and temporal allocations of fishing efforts result from constraints in fishing operations, expected fish densities and size distribution of fish, and short-term environmental factors.

Finally, in the general discussion (**chapter 6**), the main findings of the various studies described in this thesis are discussed in a broader context. A critical reflection of the research done is presented. I will summarise the findings of various studies and elaborate on some of the assumptions made. Furthermore, future perspectives, conclusions, and recommendations are given.


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Chapter 2

Two decades of change in fishing patterns: mesh and hook size dynamics in the gillnet and longline fisheries in the southern part of Lake Victoria (Tanzania)

Happy K. Peter, Johan A. J. Verreth and Paul A.M van Zwieten

Abstract

The ecological sustainability of fisheries is a global concern that demands a thorough understanding of the various factors influencing fishing practices. Understanding developments in fishing efforts regarding the number of fishers and gears and gear configuration is important as it provides deeper insights into the dynamics and trends of fishing activities. This paper focuses on the Nile perch fishery at Lake Victoria's Tanzanian side. We used historical data from past frame surveys (2000-2020) collected from recognised landing sites around the lake and assessed the changes in fishing patterns and pressure along the study area. Data reveals changes in fishing dynamics. Fishers and fishing vessels rose from 2000 to 2020, shifting from gillnets to longline gear. Predominant mesh sizes (5-6 inches) and hook sizes (8-10) remained constant. When there is no congestion in the Nile perch market and no regulations to limit nominal fishing effort (number of fishers, vessels, and gear), the fishing effort may continue to increase until the biological limitations of the Nile perch populations may be reached. Focusing on total effort – e.g., through licensing - instead of size related regulations may be more appropriate.

Introduction

The ecological sustainability of fisheries is a global concern that demands a thorough understanding of the various factors influencing fishing practices. Over the past three decades, discussions in the field have focused on identifying the challenges facing fisheries and seeking multidisciplinary solutions (Clay and McGoodwin, 1995; Fulton et al., 2011; Hilborn, 2007; Mkumbo, 2002; Mora et al., 2009; Peter and van Zwieten 2018; Rijnsdorp et al., 2007). While catches from fisheries have traditionally served as indicators of the status of a fishery, and of the target species abundance and overall ecosystem health ((Branch et al., 2011; Carruthers et al., 2012), understanding of the temporal and spatial dynamics of fishing effort is much less developed but is crucial for effective fisheries management (Selgrath et al., 2017; Stewart et al., 2011).

Understanding developments in fishing efforts in terms of the number of fishers and gears and gear configuration is important as it provides deeper insights into the dynamics and trends of fishing activities (Orofino et al., 2023). While fishery catches offer information about catch levels, they do not provide a comprehensive picture of exploitation patterns, i.e., where and how fishing effort is distributed across the fishery and what selection patterns are involved. Exploitation patterns are driven by fishers adopting various strategies responding to changing social and economic conditions, management regulations, enforcement and resource availability (Mpomwenda et al., 2022). Having reliable information on fishing efforts and gear used in specific locations and times is essential for determining the overall health and direction of the fishery (FAO 2020). Examining nominal effort and fishing patterns makes it possible to identify the factors driving changes in the fishery, such as shifts in gear preferences, alterations in fishing effort allocation, and adaptations in fishing strategies.

Lake Victoria, the second-largest freshwater body globally, faces significant challenges concerning its fishery (Kolding et al., 2008; Natugonza et al., 2022; Njiru et al., 2014; Nyamweya et al., 2023; Ogutu-Ohwayo et al., 1997). To ensure sustainable fishery management, assessing catch levels and understanding the development of fishing efforts in the region is important (Natugonza et al., 2020). According to frame survey data and reports in Lake Victoria (LVFO, 2017), the number of fishers has significantly increased across the entire lake. In Tanzania alone, the number increased from approximately 55,000 in 2000 to 100,000 fishers in 2020, e.g., an 82% increase (LVFO, 2020). Population increases in the area surrounding the lake basin (Juma et al., 2014) may have contributed to the rise in fishers. However, Lake Victoria has no regulations to limit nominal fishing effort (Cowx et al., 2003) as there are no regulations regarding the numbers of fishers, vessels or fishing gear. The existing regulations only focus on gear selectivity and catchability by limiting gillnet mesh sizes, hook sizes, allowable sizes in the catch and several fishing methods. Hence, enforcement is directed at controlling illegal gears, called "q-management" (Kolding and van Zwieten, 2011).

The Nile perch from southern Lake Victoria is targeted by small-scale gillnet and longline fishers. Nile perch is one of Lake Victoria's three main commercially targeted species, contributing an average of 240,000 tons per year or up to 30% of the total landings (Kolding et al., 2014; Mkumbo and Marshall, 2015). Furthermore 2021, the total catch was 221,640 tons (Nyamweya et al., 2022). Adult Nile perch (≥54 cm male; ≥76 cm female) are distributed over all habitats, while juveniles are more common in shallower coastal waters (Peter and van Zwieten, 2018). The main gears targeting Nile perch are gillnets and longlines operated from 5–11 m wooden vessels. These vessels are propelled by paddles (60%), small outboard engines (32%) and by sail (8%) (MLF, 2015; LVFO, 2017). Fishing in Lake Victoria takes place from many landing sites along the shore. Most fishing operations are day trips, with limited use of ice, further limiting the possible action radius of a fishing trip. Nile perch fishers on Lake Victoria appear to distribute themselves according to the underlying productivity distribution of the resource within the constraints of their available resource space within a radius of around 7 km from the shore (Peter and van Zwieten, 2018; Peter and van Zwieten, 2022).

Nile perch fisheries are regulated through a minimum mesh (5 inches = 127 mm stretched mesh) for gillnets and a recommended hook size (<10; smaller numbers are larger hook sizes) for longlines, both related to a minimum landing size. Additionally, the legal size range of catchable fish is regulated: between 50 and 84 cm. The primary market for Nile perch is the fish factories that are only allowed to buy Nile perch of ≥50 cm total length, but a large regional market for dried and smoked juvenile Nile perch also exists (Medard Ntara, 2015).

While enforcement of these regulations has been weak in the past (Medard Ntara, 2015), in 2017, a strong effort to enforce management regulations took place in Uganda and Tanzania. Uganda abolished co-management arrangements and established the Fisheries Protection Unit (FPU) under the Uganda Peoples Defence Forces (UPDF) to eliminate illegal fishing gear and activities. The military presence on the lake has been maintained to date. Tanzania established a multi-sector task force (MTF) called "Operation Sangara" to combat illegal fishing between 2017 and 2019. This operation was a response to reports of rampant illegal fishing, particularly on juvenile Nile perch, and the unauthorised sale of fish products, such as swim bladders (Brierley, 2018), which made it difficult to maintain the sustainability of the Nile perch fishery. While these enforcement efforts had a notable impact on reducing the number of illegal gears, they had a limited effect on the overall fishing effort. Additionally, the objectives of increasing the biomass of commercial species and big Nile perch (50 cm) and the total catch of Nile perch were not achieved (Nyamweya et al., 2023).

The Nile perch fishery faces significant challenges due to declining catch rates and increasing fishing pressure (Nyamweya et al., 2023). Economic incentives, operational constraints and enforcement of management regulations drive the size selection by Nile perch fishers. Hence, achieving sustainable fisheries in the southern part of Lake Victoria requires a comprehensive understanding of these factors influencing fishing practices. In the south part of Lake Victoria, fishing locations are situated along diverse habitats, ranging from shallow gulf regions to deep open waters. They further vary in proximity to main markets, roads, and cities, potentially leading to different gear use developments. Studying fishing efforts over time and space provides valuable insights into shifts in gear preferences, adaptations in fishing strategies, and changes in fishing locations due to economic incentives, operational constraints, markets, and enforcement. By analysing the resultant interplay of these factors in the choices of mesh and hook sizes used in the lake's Nile perch fishery of the southern Tanzanian part, we aim to provide valuable insights for sustainable fishery management in the Lake Victoria region.

Methodology

Scope of the study

This study will focus on the Nile perch fishery on Lake Victoria's Tanzanian side. Data from past frame surveys (e.g., 2000 to 2020) will be used to assess the changes in fishing patterns and fishing pressure along the study area. Frame survey data were collected from every landing site recognised by the Tanzania Fisheries Research Institute (TAFIRI) and the Fisheries Department (Fig. 2.1).

Frame survey

From 2000 to 2020, frame surveys were done biannually in the southern part of Lake Victoria. The surveys were administered by staff from the Fisheries Division, TAFIRI, Local Government Authorities, and Beach Management Unit (BMU) members. The surveys collected information on absolute effort (number of fishers, boats and gears) and fishing patterns (the gear composition and number of panels used in gillnets). Information about the number of landing sites, number of fishers and types of fishing vessels by gear type, and the mode of propulsion of fishing boats were also collected.

Biannually between 2000 and 2020, total numbers of gillnets and longline hooks were available, allowing a time series of change of total gear numbers. However, for some years, information on numbers by mesh size or hook sizes was either unavailable by the landing site or was completely missing. In 2018, a survey was not done.

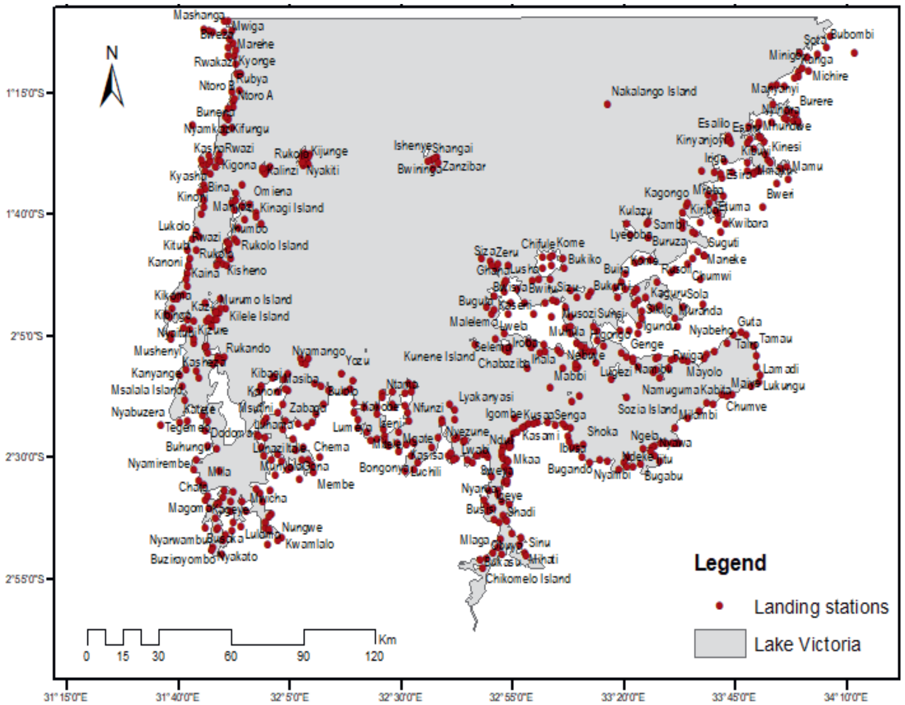

Figure 2.1: *A map showing the landing site used on Frame surveys as recognised by the Tanzania Fisheries Research Institute (TAFIRI) and the Fisheries Department.*

Data Treatment and Analysis

In the southern part of Lake Victoria, the lake has diverse broad habitat types, including gulf regions, open waters, shallow and deep sections, and locations varying in proximity to markets and means of transport. We expected to observe differences in the developments in fisheries activities based on the constraints the various areas represent and, therefore, divided the landing sites on the Tanzanian side of Lake Victoria over two main habitats (shallow gulfs and deep open lake areas) and six distinct zones. The six zones are the gulf regions Mwanza Gulf, Speke Gulf and Emin Pasha Gulf, and the open lake zones North-West open lake, North-East open lake, and Open Lake South (Fig. 2.2).

Gears targeting Nile perch were also grouped. Gillnets had mesh sizes ranging from very small (1 inch) to large (10 inches). To reduce the number of variables, we grouped gillnet mesh sizes into seven categories (Table 2.1), further categorised as small, medium and large mesh sizes. Reported longline hook sizes varied between size 4 (large hooks) to size 13 and larger (small hooks). We grouped them into five categories (Table 2.1), further categorised as small, medium and large hook sizes.

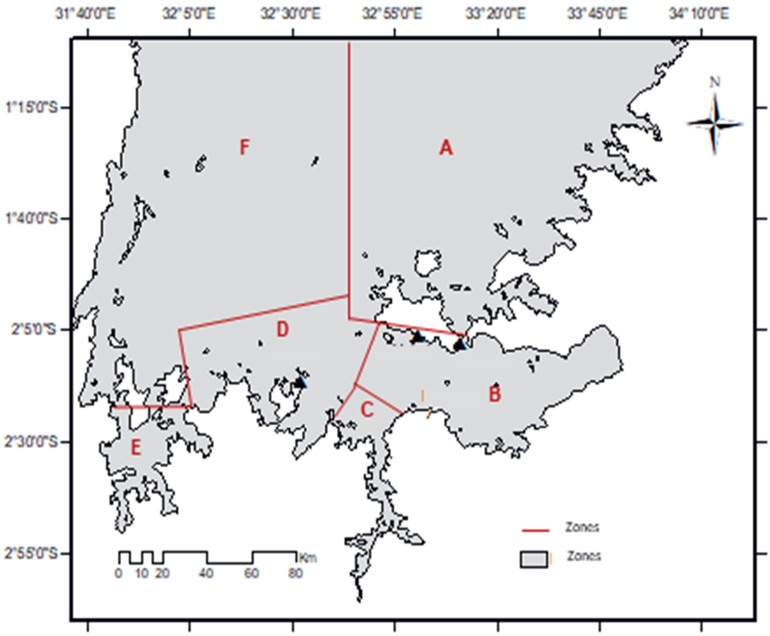

***Figure 2.2**: Map of the Southern Lake Victoria showing the division of the lake into zones: a) North-East open lake, b) Speke Gulf, c) Mwanza Gulf, d) Open Lake South, e) Emin pasha Gulf, and f) North-west open lake.*

Table 2.1: Mesh and hook sizes for gillnet and longline gears, respectively, with corresponding size categories.

Gears			
Gillnet		Longline	
Mesh size	Size class	Hook size	Size class
<5	Small	>13	Small
5-5.5	Medium	≥10-13	Small
6	Medium	8 - <10	Medium
6.5	Medium	5 - <8	Large
7	Large	≤4	Large
7.5-8	Large	-	-
>8	Large	-	-

To analyse long-term changes in mean mesh and hook size used in the fishery by fishing zone, we employed the following analysis of co-variance,

$$\boldsymbol{M_{ij} = \mu + Zone_i + b.Year_{ij} + c.\left(Zone_i * Year_{ij}\right) + \varepsilon_{ij}}$$

$$\boldsymbol{\varepsilon_{ij}} \sim N(0, \sigma^2)$$

M is the vector of mesh sizes or hook sizes by zone and year, and ε is the residual error with normal distribution and homoscedasticity. In the analysis, the year was centred around the mean year.

Results

Overall, we observed an increase in the number of fishers from 2000 to 2020 and a gradual rise in the number of vessels from 2000 to 2006, whereafter it reached a plateau. However, the preference for fishing gear shifted notably during this period. From 2000 to 2004, gillnets were widely favoured, but their popularity sharply declined from 2006 onwards. Subsequently, there was a significant increase in the popularity of longlines starting in 2008 and onward (Fig. 2.3). These findings highlight the dynamic nature of fishing practices in the region and call for a comprehensive examination of the underlying factors driving these pronounced changes.

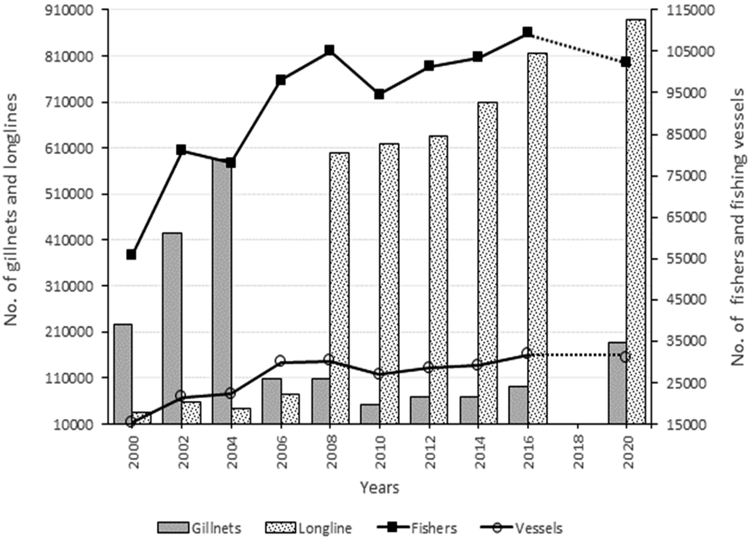

***Figure 2.3**: Trend of fishing efforts; the number of fishing gears (longline and gillnets), number of fishing vessels, and fishers over 20 years from 2000 to 2020 at Lake Victoria, Tanzanian part.*

Gillnets

Between 2000 and 2020, the number of gillnets with larger mesh sizes (>5 inches) fluctuated between 550,000 and 1,100,000 (Fig. 2.4). At the start of the period, their usage was at its lowest, reaching its highest point towards the end of the study period. On the other hand, small mesh sizes (<5 inches) fluctuated, with numbers ranging between 80,000 and 220,000. Generally, the relative importance of larger mesh sizes decreased between 2004 and 2016. However, in 2020, a steep decrease in mesh sizes < 5 inches was observed co-occurring with a steep increase in mesh sizes >5 inches.

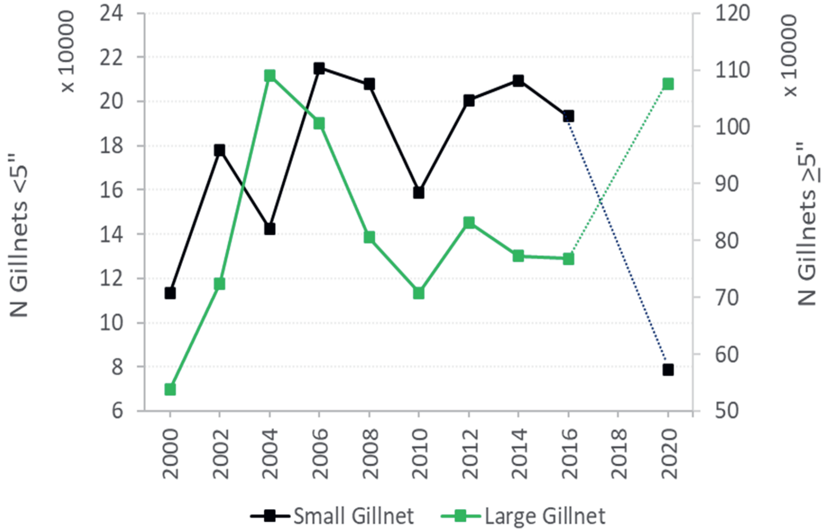

Figure 2.4: *Total number of gillnets categorised as smaller than 5 inches and larger than 5 inches recorded from 2000 to 2020 frame survey in the southern part of Lake Victoria.*

We further investigated the specific changes in general trends of numbers of small and large mesh sizes in each zone. Mesh sizes ranging from 5 to 5.5 inches were consistently preferred across all zones and increased from 2000 to 2008 (Fig. 2.5). However, from 2010 onwards, there was a decline, reaching its lowest point in 2014. Although other gear sizes were less preferred than mesh sizes of 5 to 5.5 inches, they followed a similar pattern. Interestingly, in 2014, the popularity of mesh sizes of 5 to 5.5 inches decreased, and the use of mesh size 6 inches began to rise. From 2016 to 2020, a mesh size of 6 inches became the favoured choice among fishers (Fig. 2.5).

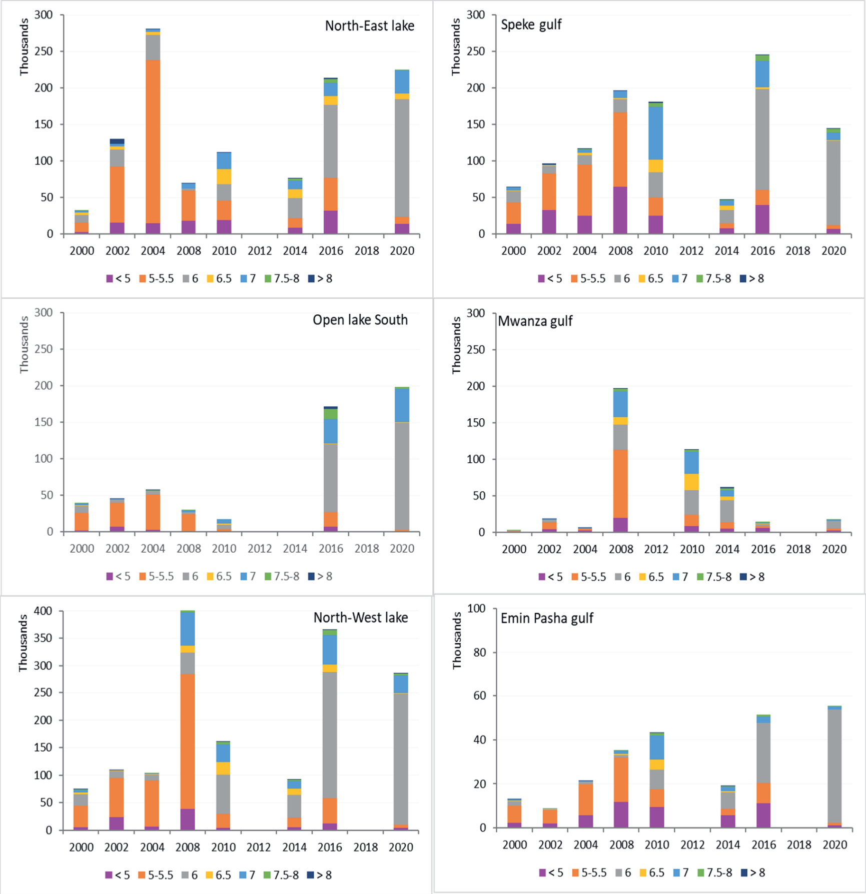

Figure 2.5: Total number of gillnets by mesh size per survey year (2000-2020) in different zones of the southern part of Lake Victoria

A linear regression analysis using the average mesh sizes per frame-survey year within each fishing zone indicated a consistent and steady increase of the average mesh size used with no clear difference between zones except the Mwanza Gulf (Figure 2.6). However, this change occurred gradually, with a factor of 0.02 to 0.07 inches per year. The Speke Gulf and Open Lake South zones experienced the highest change, while the Mwanza Gulf exhibited the lowest change in average mesh size, fluctuating around 5.5 inches. Whether the increase resulted from decreased numbers of small mesh gillnets or an increase in the number of large mesh gillnets or both will be analysed next.

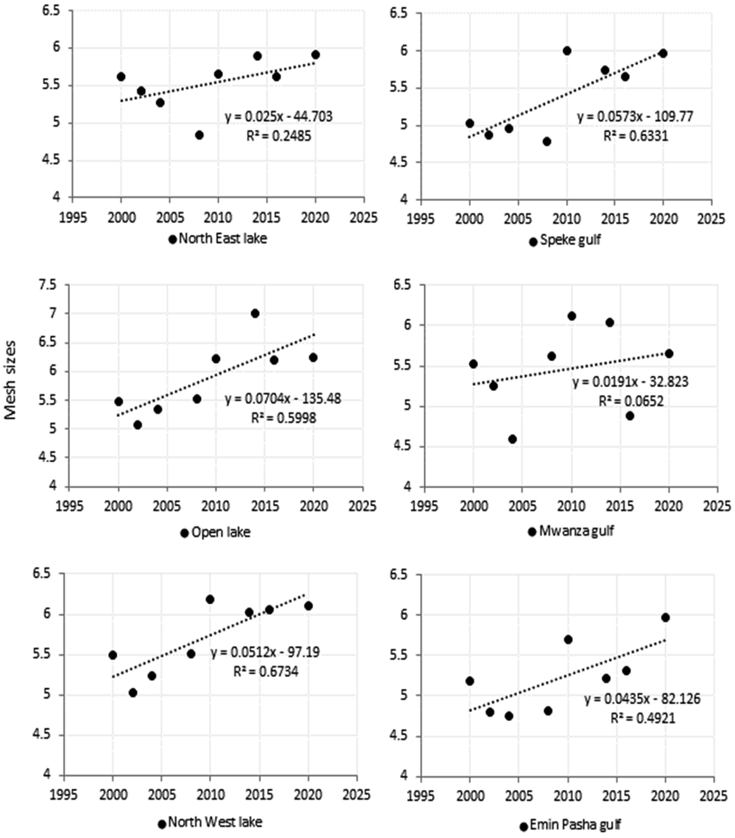

Figure 2.6*: A trend in mesh size uses from 2000 to 2020 in different zones of the southern part of Lake Victoria*

The medium class mesh size (5 to 6.5 inches) was the most widely used gillnet throughout the study. Yet, its usage fluctuated in all zones. This mesh size range was highly popular during the initial period from 2000 to 2005. Between 2005 and 2015, its proportional use decreased, but it regained popularity between 2015 to 2020. As mesh sizes ranging from 5 to 6.5 inches consistently remained the most preferred among the different mesh size classes throughout the entire study period, it is clear that they were of continued importance in the fishing practices in all zones (Fig. 2.7). The proportion of small mesh sizes was generally lower (<20%) in the open lake zones compared to the gulf areas (20-30%). It decreased from around 2010 onwards (North-East open lake) or decreased consistently over the two decades (Open lake South and North-West open lake). In the gulf zones, the proportion of small mesh sizes was initially higher than in the open lake areas and either remained stable over the whole period (Mwanza Gulf) or decreased quite sharply from 2015 onwards (Emin Pasha Gulf, or over the whole time series (Speke Gulf). In all decreasing cases, they reached the lowest proportion in 2020.

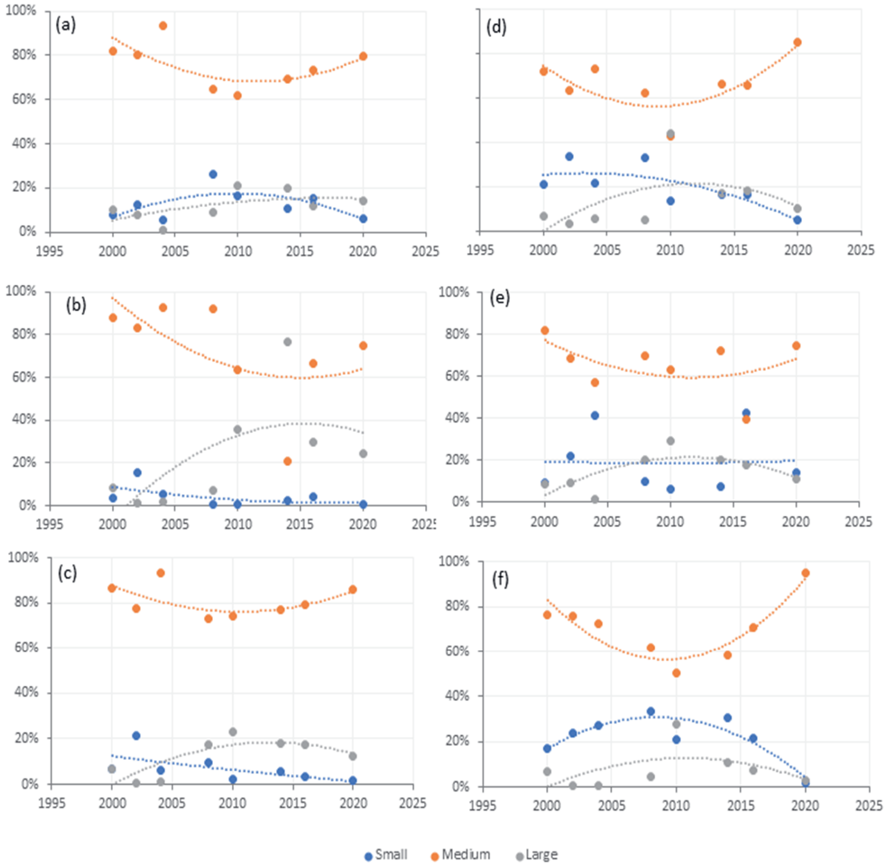

Figure 2.7*: Percentage use of mesh size classes: small class (>5), medium class (5-6.5), and large class (≥7) from 2000 to 2020 in different zones of the southern part of Lake Victoria: Open lake zone – ((a) North-East open lake, (b) Open lake South and (c) North-West open lake) and Gulf regions ((d) Speke Gulf,(e) Mwanza Gulf, and (f) Emin Pasha Gulf).*

The proportion of large mesh sizes in virtually all zones was less than 20% of the total gillnets. From 2010 onwards, we observed a stabilisation or slight decrease in all zones. Only in the Open Lake South did large mesh sizes increase to around 30-40% of the total gillnets.

Overall, it can be concluded that the steady increase in average mesh size in all zones is caused mainly by a decrease in small mesh sizes and only in the Open Lake South, both by a decrease in numbers of small and a concomitant increase in numbers of large mesh sizes.

Longline

The total number of hooks generally increased in all lake zones from around 2006-2008 onwards, with some differences between zones: in Open lake South, hooks became prevalent only in 2016. Total numbers increased or remained approximately stable in all parts of the lake until 2020, except in the Mwanza Gulf, where the number of hooks decreased. Between 2008 and 2020, a consistent preference for hook sizes 8 to <10 and 10-13 was observed in all zones (Fig. 2.8). Conversely, the larger hook size 4 was the least favoured over the study period.

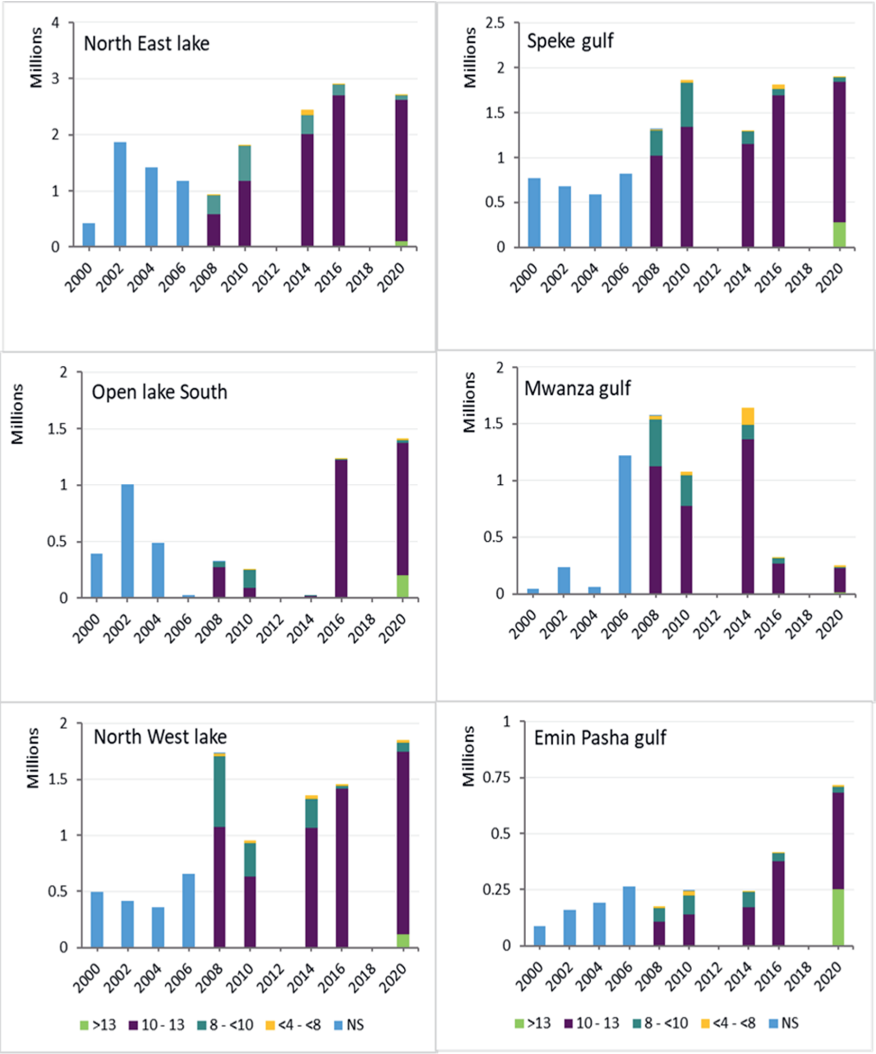

Figure 2.8: *Total number of hooks by size per year (2008-2020) in different zones of the southern part of Lake Victoria.NS=No hook size information, 11->13 = hook sizes eleven and upward; (small hook sizes), 8-10 = median hook sizes eight, nine and ten; <4-7 = hook sizes seven and downward (large hook sizes)*

However, notable changes have emerged in recent times. Hook sizes 11 to 13 and even smaller sizes >13 became more popular, while hook sizes 8-10 have decreased by 3-10 in all zones by 2020, and hook sizes <4-7 almost disappeared from the fishery.

Generally, in all zones, the average hook size has decreased since 2008, when information on hook sizes started to be collected in the frame surveys (Fig. 2.9). The smallest change towards smaller hook sizes occurred in Mwanza Gulf (15% per year) compared to the Emin Pasha Gulf, where the average hook sizes decreased with 26% per year. In all zones, 60% of all hooks used were the smaller hook sizes (Fig. 2.10).

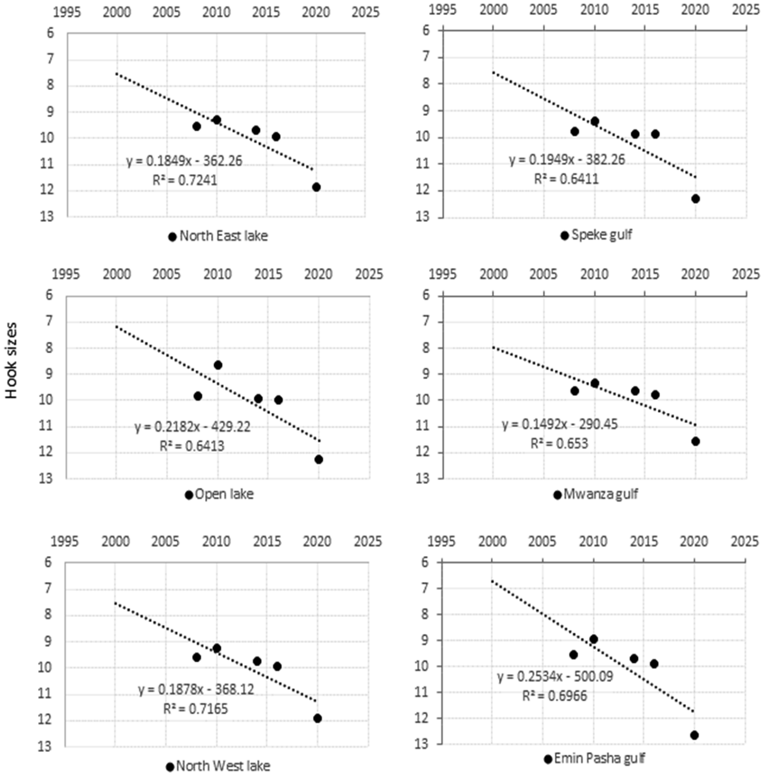

***Figure 2.9**: A trend in average hook size from 2006 to 2020 in different zones of the southern part of Lake Victoria*

The decrease in average hook size is caused by a proportional decrease in large and, in particular, medium (legal-sized) hook sizes and a parallel increase in small hook sizes. The decline was consistent in all zones where small hook sizes (> 10) now constitute close to 100% of the number of hooks used in the fishery (Fig. 2.8)

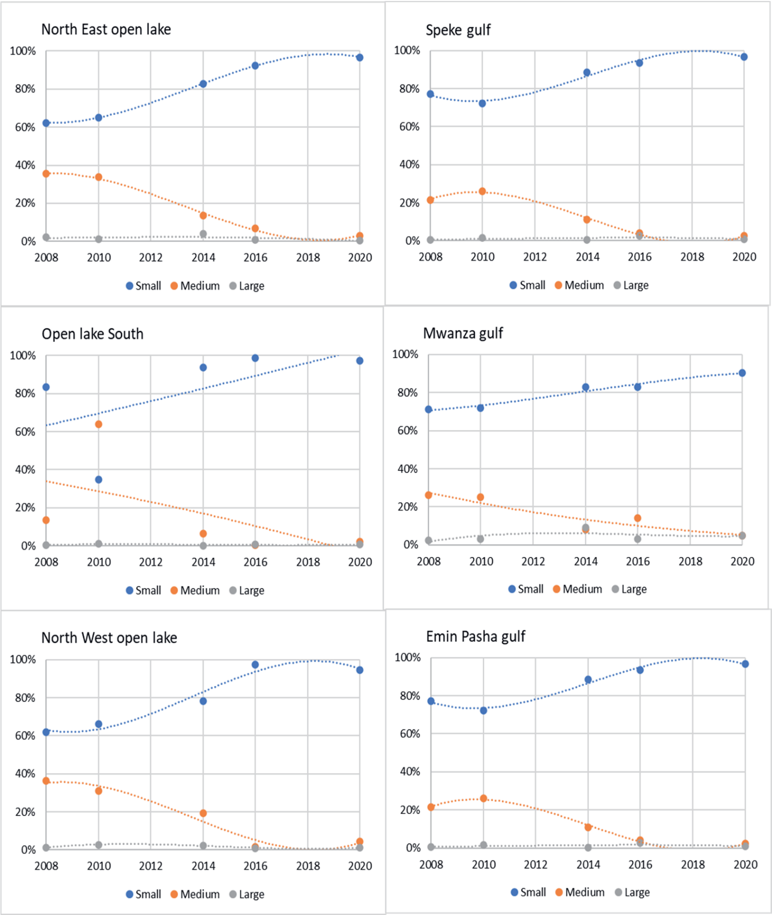

__Figure 2.10__: Percentage use of hook size classes small (≥10, blue), medium (8 - <10, orange) and large (<8 - <4, grey) from 2008 to 2020 in different zones of the southern part of Lake Victoria:

ANCOVA survey year and zone

The ANCOVA analysis (Table 2.2) of long-term changes in mean mesh and hook sizes related to survey year and zone was significant for both mesh size ($p<0.001$, $r^2=0.11$) and hook sizes ($p<0.001$, $r^2=0.41$). For gillnet mesh sizes, most variation was explained by the trend (year). Nevertheless, only 8% of the variation in mesh sizes was explained by the trend, indicating gradual changes. The increasing trend in mesh sizes for different zones varied between 0.03 to 0.06 inches per year (so, over 20 years, an increase of 0.6 – 1.2 inches) over the average mesh sizes ranging from 5.3 to 5.8 inches for the different zones. Though slopes and intercepts were significantly different for all zones ($p<0.001$ for all parameter estimates, differences were slight. The overall mean mesh size for the 20 years examined was 5.6 inches, just below the legal mesh size of 6 inches.

Table 2.2: Results of the analysis of co-variance of long-term changes in mean mesh and hook size used in Nile perch fishery. All slopes and intercepts are significant at p<0.001). The difference in means was tested through multiple comparison tests with a Bonferroni correction. A positive slope for mesh sizes and hook sizes means larger and smaller hook sizes.

Gillnet (mesh size)					
Model		DF	Sums of Squares	p	r^2
		11	642408	<.0001	0.11
	Zone	5	177266	<.0001	0.03
	Year	1	442847	<.0001	**0.08**
	Zone*Year	5	22295	<.0001	0.00
Error		5055923	5228220		
Total		5055934	5870629		
Zone		Slope	Mean mesh size (centred intercept)		
	North East open lake	0.03	5.6		
	Open lake South	0.06	5.8		
	North West open lake	0.05	5.7		
	Speke gulf	0.06	5.4		
	Mwanza gulf	0.03	5.8		
	Emin Pasha gulf	0.05	5.3		
	Overall mean mesh size			**5.6**	
Longlines (hook size)					
Model		DF	Sums of Squares	p	r^2
		11	30616830	<.0001	0.41
	Zone	5	3320217	<.0001	0.05
	Year	1	25764407	<.0001	**0.35**
	Zone*Year	5	1532205	<.0001	0.02
Error		36131720	42794270		
Total		36131731	73411100		
Zone		Slope	Mean hook size (centred intercept)		
	North East open lake	0.22	10.1		
	Open lake South	0.27	10.2		
	North West open lake	0.19	10.3		
	Speke gulf	0.21	10.4		
	Mwanza gulf	0.08	9.9		
	Emin Pasha gulf	0.32	10.3		
	Overall mean hook size			**10.3**	

Changes in hook sizes were more pronounced: the trend explained 35% of the variation in hook sizes. Slopes for the different zones were significantly different from each other, ranging from 0.19 (North West open lake) to 0.32 (Emin Pasha Gulf) per year (so an increase (i.e., hook sizes becoming smaller) of 2.3 – 4.8 In hook size number over the 12 years examined). Only the Mwanza Gulf showed a less steep slope of a factor of 0.08 per year (1.0 in hook size number over 12 years). The overall mean hook number over the years examined was 10.3, slightly higher than the recommended size. Mean hook numbers were significantly different for the six zones but ranged from 9.9 to 10.4, differing again slightly around the recommended size.

No clear patterns of change in hook or mesh sizes by zone or by groups of zones (open lake areas, gulfs) could be concluded from this analysis. However, differences in the timing of increases in mesh or hook sizes were observed, as well as of overall increases or decreases in nets and hooks, that may be related to specific economic or regulatory factors in the different areas of the lake. The Mwanza Gulf showed the lowest change and had the largest mesh and hook sizes (low average hook number) compared to all other regions.

Discussion

While the total nominal effort in numbers of fishers, boats and engines increased in all zones, we observed a noticeable shift from the use of gillnets towards longlines in the course of the 20 years of observation (LVFO (2020), Fig. 2.3). Over the years and zones, the dominant, preferred, mesh sizes remained rather constant, around 5-6 inches, and hook sizes around sizes 8-10 though the latter decreased in number by a factor 3-10 in recent years (Fig. 2.5 & 2.8). After 2018, the preferred gillnet mesh size increased to 6 inches (Fig. 2.5), while the number of small hooks >10 increased, and medium and large hooks became even less prevalent. There were no notable differences in the fishery's evolution over time and space in the different open water and gulf zones of Lake Victoria, with other ecological, fishery, social, and environmental characteristics. The same changes in preference of gillnet meshes and hook numbers were found all over the lake, albeit sometimes with different timing and speed of change.

Various factors can influence the fishery's temporal and spatial evolution. While fisheries management regulations are important, social and economic drivers also play significant roles in the target sizes of Nile perch. In the case of Lake Victoria, fisheries regulations focus on gillnet mesh size and, to a lesser extent, on hook sizes, but not on the nominal fishing effort - numbers of fishers, boats and engines (Cowx et al., 2003). The socioeconomic drivers are related to the fact that the Nile Perch fishery in Lake Victoria has boosted the local economy, based on both international trade of fresh fillets of large Nile perch and, more recently, fish-maw and regional market of dried and smoked Nile perch, attracting more people – fishers, traders and associated business - to the area. The Lake Victoria region also has one of the highest population densities (250 people.km2) and growth rates (Kenya 2.0%, Tanzania 3.0%, Uganda 3.3% per year) in Africa (PRB 2022). The fishery's development results from the balance between these diverse drivers, which we will discuss next.

Regulation 66(3) establishes a minimum mesh size requirement of 6 inches. However, despite this regulation, there has been a noticeable increase in the popularity of mesh sizes smaller than 5 inches. In comparison, larger mesh sizes exceeding 5 inches have experienced a sudden surge in use after 2016. Notably, a mesh size of 6 inches has become widely adopted in all parts of Tanzanian waters (LVFO, 2020, Peter and van Zwieten 2018, Fig. 2.5 & 2.7). A rapid decrease in the use of small nets alongside an increase in the adoption of larger nets was observed in the 2020 survey. However, it is important to exercise caution before directly attributing this outcome primarily to "Operation Sangara" undertaken in 2017/2018 - 2019/2020 (Kandoya 2018). Though a decrease in the numbers of fishers (-6.5%), boats (-6.7%), monofilament nets (-24.4%, mainly targeting Tilapia) and beach/boat seines (-14%) was reported for Tanzania before and after the operation (Nyamweya et al., 2023) it is less clear what impact the enforcement effort had on illegal mesh sizes used in the Nile perch fishery. Other factors might have contributed to the shift to large mesh sizes. For instance, the fish-maw market's prevalence for larger Nile perch could have favoured the preference for larger mesh sizes, though the market is little understood (Sadovy de Mitcheson et al., 2019).

Nevertheless, the predicted fleet size selectivity with the current make-up of mesh sizes in the gillnet fishery used in Tanzania comparing 2010 with 2020 showed a decrease in overall size retention for smaller sizes, also evident in the empirical catch of gillnets (Gómez-Cardona et al., 2022). The peak retention of the selectivity curve of all mesh sizes combined shifted from 52 to 55 cm SL and maximum (at 10% retention) around 115 cm SL. Given the biomass size distribution of Nile perch, the expected peak size from the range of gillnets used in the fishery in the catch shifted between 2010 and 2020 from 45 to 53 cm SL (Gómez-Cardona et al., 2022)

The Fisheries (Amendment) Regulations of 2009, already referred to, recognise longline hooks as fishing gear but do not provide information about permissible hook sizes. However, regulation 54(2) permits the use of hook sizes 8, 9, 10, and 11 exclusively, but without the use of a fishing vessel or fishing raft. Due to the lack of comprehensive regulations governing longline hook sizes and weak enforcement of Nile perch catch size limits, as well as a high regional demand for dried and smoked Nile perch, many fishers have flocked to this method, resulting in a continued significant increase in the utilisation of smaller hooks with sizes greater than 11. According to Mkumbo and Marshall (2015), our study also confirmed that fishers in Lake Victoria have increasingly abandoned large-meshed gillnets in favour of small hooks on longlines. Longline hooks have specific advantages over gillnets as they can be used to fish in rocky areas where it is challenging to set them up.

Longline hooks, particularly sizes 8-10, are the most commonly used in all zones (Fig. 2.8), and the trend shows an increased use of smaller hook sizes over time. Retrieving selectivity curves for Longlines is a challenge. Using longline Nile perch catch data from Lake Victoria, Gómez-Cardona et al., (2022) found no evidence that changes in hook size correspond with changes in average size retained, except for the bigger hooks sizes (i.e., those with smaller numbers 8 and less) and that there is a considerable size class overlap with hooks from 11 – 14. Hook numbers 11 to 13 catch Nile perch within sizes of 20-100cm, with a selection peak at around 75cm, while the selection peak of hook size 14 Is slightly lower at app. 60 cm (Chitamwebwa et al., 2009; Gómez-Cardona et al., 2022). According to Gómez-Cardona et al., (2022), the size distribution in the catch given the biomass size distribution of Nile perch they used and the range of hook sizes in the fishery, ranged from 20-95 cm SL (at 10% retention) with a peak at 55 cm with no change in hook size configurations in the fishery between 2010 and 2020. However, to complicate matters, hooks' effectiveness is also influenced by the type of bait used, as it enhances their selectivity. For instance, using *Clarias* bait, Nile perch sizes caught ranged from 20-100 cm, peaking at 60 cm, while haplochromine bait caught the same size range, peaking at 40 cm (Peter and van Zwieten 2018). This versatility in catching both small Nile perch for the regional market and larger ones (for the international market) with the same range of small hooks represents a bet-hedging strategy that was found to be employed by Lake Victoria Nile perch fishers (Peter and van Zwieten 2022).

When the overall fishing fleet selectivity is considered, including both gillnets and longlines with the fishing patterns of 2010 and 2020, no change in the peak at 60 cm of the selectivity curve is seen, and no change in selectivity in the downward part of the selection curve towards larger sizes. However, there is a decreased selectivity for smaller sizes, which leads to predicted maximum retention, given the biomass-size distribution, shifting from 45 to 52 cm. This change is mainly due to the changes in gillnet selectivity (Gómez-Cardona et al., 2022). However, with the increased use of smaller hooks (>13), not taken into account by Gómez-Cardona et al., (2022), a shift towards smaller sizes can be expected. In other words, the overall selection pattern of the gillnet and longline fleets combined may not have changed much over the period examined despite or perhaps due to the divergent shifts in mesh sizes and hook sizes observed. This means that nearly half of the Nile perch catch will be <50cm: these are illegal sizes caught mostly by legal or recommended mesh and hook sizes!

Although fisheries regulations cover the whole Tanzanian fisheries, disparities in enforcement attention may exist among different regions (Cepić and Nunan, 2017; Medard Ntara, 2015; Nunan et al., 2018). For example, in the Mwanza Gulf, the observed lower rate of increase in the use of small hook sizes and dominant use of larger mesh sizes compared to other regions may be attributed to Mwanza's proximity to fisheries management offices, resulting in more frequent supervisor visits and potentially influencing fishers' choices in mesh and hook sizes. But we will see next that another explanation may also be relevant: the presence of Nile perch filleting factories.

Thus, enforcement efforts appear limited in steering fishing patterns and sizes of Nile perch retained. Fishers' specific choices in gears and effort allocation may lead to different métiers (Salas and Gaertner, 2004; Salas et al., 2019) targeting other markets. The market's allure and reliability attract fishers, prompting fishers who have access to capital to invest in larger boats and engines. The Mwanza region, encompassing zone B (Speke Gulf) and C (Mwanza Gulf) in Fig. 2.2, hosts an impressive 75% (9 out of 12) of Tanzania's Nile perch processing factories, establishing itself as a major international trading hub for fishers to bring their catches. The frame survey report of 2020 highlighted Mwanza's importance, revealing a high number of engine users (6,164 or 52% of engines in the Tanzanian portion of the lake) and large fishing vessels above 11 meters in length (252 or 33% in Mwanza; and 295 or 39% in Kagera).

Nile perch processing factories process Nile perch according to fisheries regulations, where the allowable slot size is 50-85 cm (Njiru et al., 2014), which strategically leads fishers to adapt and efficiently meet demand. Investments in larger vessels and the use of engines enable them to reach grounds with less competition and stocks of larger-sized Nile perch. Besides this group of fishers who have access to capital, there is a large group of fishers that do not have access to the necessary capital and rely on smaller-scale operations closer to the shore targeting stock with a larger Nile perch size range (Peter and van Zwieten 2018) and employing a bet-hedging strategy with gillnets or longlines (Peter and van Zwieten 2022).

The Nile perch processing industry serves as the gateway to the international market for Nile perch. Abiding by fishing laws and industry standards, large fish (ranging from 50-85 cm) meet the criteria for the international market, while smaller fish below 50 cm, considered illegal sizes, are destined for domestic markets. Gillnet mesh sizes between 4 and 8 inches specifically target Nile perch within the size range of 40-70 cm (Msuku et al., 2011). Fishers often combine mesh sizes or longlines to ensure a broader range of catch sizes. However, this approach becomes challenging due to legal restrictions prohibiting gillnet mesh sizes below 6 inches and a legal minimum size of 50 cm, leading to the eternal clash between fishers and managers over the goals of the fishery (Kolding and van Zwieten 2009; Misund et al., 2002; Nunan 2020).

Many people around the lake depend on the lake for their livelihoods. Therefore, effective management measures are vital to ensure fishery sustainability and a healthy sector. In Lake Victoria, current gear regulations have as objectives to protect immature and also called “undersized” fish, with the ultimate goal to increase the biomass of commercial species and, particularly, of big Nile perch (>50 cm) as well as the total catch of Nile perch (Nyamweya et al., 2023). For this purpose, gear regulations focus on restricting the use of small mesh sizes of gillnets. Through enforcing fishing regulations and market demands, fishers have been able to adapt to appropriate mesh sizes. However, the question remains whether this shift in fisher's response also contributed to reaching the set management goals. While small gillnet mesh sizes were largely abandoned, a change from gillnet to longlines, including an increase in the smallest hook sizes and size ranges in the catch, remained the same. Nyamweya et al., (2023) did not observe an increase in biomass of the larger Nile perch nor an increase in total Nile perch catch, as was aimed for by the enforcement efforts. So, although stricter enforcement of the fisheries regulations may effectively change the fishers' behaviour, overall largely unchanged size selection and the lack of a substantial impact on Nile perch stocks indicates room for closer scrutiny of the regulations themselves and a possible balancing of the regional and international demands for different sizes of Nile perch.

Advancements in handling, storage, and technology ensure the preservation of fish quality, enabling access to distant markets. It's fascinating to note that even in far-off markets within the country (Dar es Salaam city ~ 1,130km), fish can reach and still arrive fresh. There seems to be no congestion in the market for Nile perch: dried, smoked or fresh – apparently, all captured Nile perch can be sold (Josupeit, 2006). In such a situation, the nominal fishing effort (number of fishers, vessels, and gear) may continue to increase until the biological limitations of the Nile perch populations may be reached. A focus on total effort – e.g., through licencing - instead of size-related regulations may be more appropriate.

Chapter 3

Acoustic assessment of Nile perch distribution in South-Eastern Lake Victoria: Identifying key factors and drivers.

Happy K. Peter, Paul A.M van Zwieten, Robert J. Kayanda, Leo A. J. Nagelkerke and Johan A. J. Verreth.

Abstract

Nile perch is commercially the most important species in Lake Victoria, contributing to the economy of riparian countries. It is distributed over the entire lake, and distribution is often related to spatial differences in environmental conditions or, more specifically, to hypoxia. Besides dissolved oxygen, other factors such as food availability, fish habitat, and competition with other fish species may also influence the spatial distribution of Nile perch. In this study, we analysed the distribution dynamics of Nile perch using hydroacoustic methods to obtain detailed information regarding the dynamics of Nile perch distribution in relation to the biotic and abiotic factors at the south-eastern part of Lake Victoria. Nile perch densities correlated strongly and positively with their possible food items. Dissolved oxygen did not affect Nile perch densities as oxygen levels were above $3mgL^{-1}$, a critical level for Nile perch. The study highlights the role of food availability in determining Nile perch densities and emphasises the need for continued research on the factors influencing Nile perch populations in Lake Victoria. Acoustic studies on small areas are important to designing proper management of the Nile perch fishery since different parts of the lake may differ significantly and thus deserve special attention.

Introduction

Nile perch is commercially the most important species in Lake Victoria, contributing to the economy of the riparian countries (Abila et al., 2014; Kulindwa, 2004). Nile perch is distributed over the entire depth range of Lake Victoria, with juveniles more concentrated inshore and large and mature individuals (≥50cm) more in offshore areas (Katunzi et al., 2006; Mkumbo and Ezekiel, 1999; Peter and van Zwieten, 2018).

Although not yet fully understood, this size distribution of Nile perch is often related to spatial differences in environmental conditions and, more specifically, to hypoxia. The assumption is that large, adult Nile perch is more sensitive to low oxygen levels (hypoxia) than small Nile perch (Chapman, 1995; Njiru et al., 2012; Wanink et al., 2001).

In hypoxic waters, Nile perch are stressed, leading to decreased activity and growth rates. Additionally, hypoxia can alter the distribution of prey species, making it harder for Nile perch to find food. As a result, the availability of suitable habitats for Nile perch may shrink in areas with persistent hypoxia, negatively impacting their distribution and abundance. Low oxygen levels might be more prevalent in eutrophic inshore areas; the assumption is that adult Nile perch might escape these conditions by moving to areas with more oxygen, such as offshore areas.

Hypoxia conditions can be induced by seasonal thermal stratification under the influence of temperature and wind. During the dry/mixed season between June and October, the southern part of Lake Victoria experiences strong winds, which reduce surface water temperatures (Crul, 1993; Goudswaard et al., 2004; Taabu-Munyaho et al., 2014). The lake is calm and stratified during the wet/stratified season from November to March. In the southern Mwanza gulf (Tanzania), water temperature is higher from January to May (Cornelissen et al., 2015) and in the northern Murchison Bay (Uganda) from February to March (Ssebiyongaa et al., 2013). Hypoxia conditions may emerge from prolonged periods of stratification resulting from temperature rises (Hecky et al., 1994; Kolding et al., 2008), and this may influence the densities and size distribution of Nile perch (Taabu-Munyaho et al., 2013).

The occurrence of hypoxia results from the dynamic interaction between different factors and is, therefore, difficult to predict in time and place. For example, earlier studies found increased hypoxia in deeper (>40m) waters (Hecky et al., 1994; Kaufman, 1992) and/or in the Mwanza gulf during the stratified (wet) season (Wanink et al., 2001). Also, Sitoki et al., (2010) found dissolved oxygen (DO) levels of ~3mgL-1 in deeper waters in 2000. However, during the stratified period in 2005, they found DO levels of $\sim 6mgL^{-1}$, whereby the hypoxia in the deeper waters was reduced. A more recent study by Cornelissen et al. (2015), found that hypoxia conditions in the Mwanza gulf were less severe, with dissolved oxygen levels all over the water column above 3mgL^{-1}.

Besides dissolved oxygen, other factors such as food availability, fish habitat (e.g., water depth), and competition with other fish species may also influence the spatial distribution of Nile perch. Differences in food availability for the different size classes of Nile perch could affect their spatial distribution. Nile perch is an opportunistic hunter (Cornelissen et al., 2015); its diet ranges from *Caridina nilotica* (uduvi), *Rastrineobola argentea* (dagaa), haplochromines (furu) to even juveniles of their species. Kayanda (2012) observed a correlation between Nile perch density of both juvenile and (<50cm) and adult (≥50cm) animals with its prey, which was more pronounced in inshore waters during the wet/stratified season — a season when abiotic conditions would instead predict size segregation. Yet, Cornelissen et al. (2015) found Nile perch is more affected by abiotic than biotic (food availability) factors.

Hence, from the above, it is clear that Nile perch distribution is affected by local differences in the different drivers. A more thorough understanding of how environmental and biotic factors influence Nile perch distribution on a local scale is essential for resource management. Fishers operate at local scales, making choices in spatial effort allocation, leading to a specific distribution of fishing pressure on small and large Nile perch (Peter and van Zwieten 2018; Peter and van Zwieten 2022). The lake is not uniform (Taabu-Munyaho et al., 2014), and the Nile perch is not uniformly distributed. Studies on Nile perch distribution in Lake Victoria range from lake-wide surveys (Kayanda, 2012; Taabu-Munyaho et al., 2014) to surveys of small selected areas (Cornelissen et al., (2015). So far, the study of Cornelissen et al. (2015) is the only one reporting on the distribution of Nile perch on the small scale of the Mwanza Gulf. These authors used a multifilament gillnet in their study, which has the disadvantage of size selectivity and has limitations in assessing the sampling area (Witte and van Densen 1995), limiting an understanding of Nile perch distribution dynamics. A hydroacoustic technique could avoid the pitfalls of the methodology used by Cornelissen et al. (2015).

Therefore, in the present study, we will analyse the distribution dynamics of Nile perch using hydroacoustic methods, which can provide detailed information to understand the dynamics of Nile perch distribution in relation to the biotic and abiotic factors at a local scale. Oxygen levels and food availability influence the size, structure, and distribution of Nile perch, with areas having both high oxygen levels and high food densities having the largest and most numerous fish. Knowing the distribution and abundance of Nile perch can help understand the spatial distribution of fishing efforts and assist in improving regulating catches and livelihoods. Additionally, understanding the distribution of Nile perch can inform effective management practices and ensure sustainable use of the resources.

Materials and Methods

Study area

The study was conducted in the southeastern part of Lake Victoria (Figure 3.1) on three transects around 30-40km from each other and named from east to west Speke gulf, Open Mwanza Gulf, and Open water. The transects (Fig. 3.1) were selected based on nutrient loading (Ballatore et al., 2014) and depth gradients (Hamilton et al., 2016). Speke gulf transect was the shallowest, with depths ranging up to 40m; however, most parts were <25m deep. The Open Mwanza gulf transect had a depth range down to 50m, and the Open lake transect down to 57m. Each transect was approximately 20km long from inshore to offshore (Table 2.1).

Table 3.1: Transect coordinates

Transect	Latitude Start	Longline Start	Latitude End	Longline End
Speke gulf	2°25.70'S	33°11.98'E	2°14.72'S	33°14.51'E
Open Mwanza gulf	2°13.74'S	32°52.48'E	2°26.34'S	32°51.04'E
Open lake	2°10.82'S	32°36.49'E	2°22.97'S	32°35.01'E

Five surveys were conducted (May 2010, December 2010, February 2011, May 2011 and July 2011) based on the rain pattern in the region. Data for the dry season were obtained from the May 2010, May 2011 and July 2011 surveys and data for the wet season from the December 2010 and February 2011 surveys. During the dry season, the lake experiences strong winds, mixing the lake's waters. This study will refer to the dry season as the mixed season. During the wet season, the lake is calm, leading to the lake's stratification. Therefore, we will refer to the wet season as the stratified season.

Data collection

Data were collected on the RV Lake Victoria Explorer, a research vessel from the Tanzania Fisheries Research Institute (TAFIRI). Physico-chemical data were obtained using a hydrolab DS5 multiprobe (OTT Messtechnik GmbH & Co, Kempten, Germany): temperature (°C), chlorophyll-a (µg/l), and dissolved oxygen (mgL^{-1}) were measured at 1m intervals from surface to the bottom at each probe station. Measurements were taken from inshore to offshore at an interval of approximately 3km apart, resulting in 7 probe stations per transect (Fig. 3.1). At least two bottom trawl hauls were taken for each survey: one between Speke gulf and Open Mwanza gulf transects, and the other between Open lake and Open Mwanza gulf transects, at a towing speed of 3 knots or ~1.5m/s. With a head rope of 24m, a fishing rope of 29m (see Appendix 1), and a trawl duration of 30 minutes, an area of ~ 32 km2 was swept (LVFO, 2005; Sparre and Venema 1989). This calculation includes a correction factor to account for the fact that the net is curved in deployment, and therefore, the headline length is larger than the width swept. We employed a correction factor of 0.33 times the headline length as the substratum usually is mud (Ligtvoet et al., 1995).

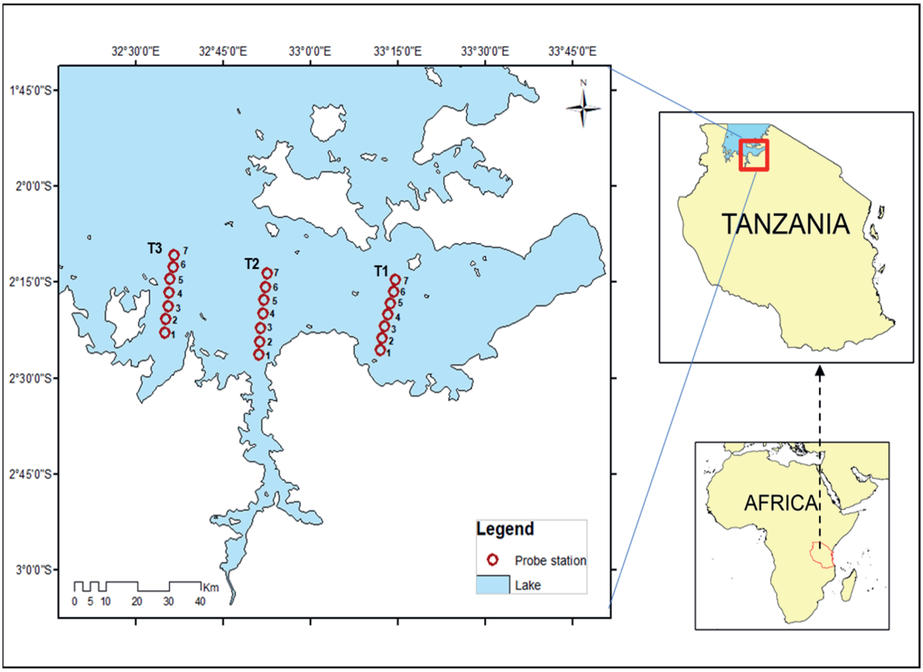

***Figure 3.1**: South-eastern part of Lake Victoria showing transects w (T1=Speke gulf, T2=Open Mwanza gulf and T3 = Open lake transects) and probe stations (Probe station 1 to 7 per each transect) where we collected data.*

The fish data collected from the bottom trawls were the total biomass of captured Nile perch and other fish species and the total length of individual Nile perch. Acoustic data were collected using a hull-mounted Simrad EK60 scientific echosounder (Kongsberg Maritime AS, Horten, Norway) operating with dual frequencies (70 and 120 kHz) at a ping rate of 0.5/s, pulse duration of 0.256m/s and transmitted power 200 W connected at 7° beam angle. Transducers were mounted and directed vertically downward at about 2m from the surface, as the boat draft was 2.2m. We calibrated the transducers at the beginning and end of each survey.

Data preparation and treatment

Physico-chemical data

Physico-chemical data were uploaded from the Hydrolab machine (Hydrolab DS 5) and averaged over 1m intervals before further analysis. The horizontal position was divided based on the seven probe stations (Fig. 3.1), whereby we grouped stations 1 and 2 as Inshore, 3, 4 and 5 as mid-shore, and 6 and 7 as offshore.

Acoustic data

Raw data were processed through Echoview 5.00 (Myriax Inc., Hobart, Australia). We adopted the protocol from Everson et al. (2013), Kayanda et al. (2012), and Parker-Stetter et al. (2009) to process the raw into final data. Loading the raw files to the echoview program was followed by visually examining and correcting the sounder detected bottom: a back step of 0.5m from the detected bottom was applied to avoid the inclusion of lakebed echoes. We excluded the upper 4m depth (2.2m deep RV Explorer draft plus 2m below the vessel hull) from the surface to compensate for vessel drift, transducer near field effect and inclusion of near-surface bubbles. A grid of 2 minutes (~0.5km) Elementary Distance Sampling Unit (EDSU) by 1m depth layer was established before each probe station.

Acoustic data were extracted in two separate categories: Nile perch with a total length larger than 10cm and everything else below a total length of 10cm. We used a single target detection method (Kayanda 2012; Ona 1996; Taabu-Munyaho et al., 2013) to extract only Nile perch larger than 10cm from the acoustic data set. A threshold TS of -60dB was used to exclude Nile perch smaller than 10 cm, haplochromines, *Clarias* and other species with smaller swim bladders, as Kayanda et al. (2012) proposed. Catch data collected parallel to the hydroacoustic survey indicated that *Bagrus docmak,* whose swim bladder is big and could potentially interfere with assigning targets to Nile perch, was less than 1% of the total catch.

The number of Nile perch larger than 10cm was determined from single target export files and then divided by their corresponding beam volume to obtain mean densities (number of fishes per m3, for each 1m interval). We estimated mean lengths from Target Strength (TS) to the length relationship (equation 1) (Kayanda et al., 2012), and we subsequently calculated mean weights from the length-weight relationship (equation 2; (Kayanda et al., 2012). Then, we multiplied mean weight by mean density to estimate density expressed in kilogram per m3 of Nile perch larger than 10cm in each 1m depth interval.

$$TS_{120} = 30.13 * \log (TL) - 84.14 \quad (1)$$

$$Weight = 0.0042*TL^{3.26} \quad (2)$$

Everything below 10cm is comprised of dagaa (*Rastrineobola argentea*), haplochromines, Nile perch (<10cm TL) and shrimp (*Caridina nilotica*). This group's total density will be referred to as "Others" in this study. "Others" density was estimated by echo integration. The backscattered values (Sv) obtained from the echo integration were converted to total Area Backscattered ABC.

$$\mathrm{ABC}_{(\mathrm{Total})} = 10^{\mathrm{Sv}/10} \quad (3)$$

The ABC values attributable to Nile perch >10 cm TL were estimated using Equation (3) (Everson et al., 2013; Taabu-Munyaho et al., 2014):

$$\mathrm{Sv}_{(\mathrm{Nile\ perch})} = \mathrm{TS} + 10 \log NT - 10 \log BV - 2.3 \quad (4)$$

Sv(Nile perch) = Nile perch backscatter, TS = mean target strength, NT = number of targets, BV = beam volume and 2.3 is a constant to correct the TS values to the equivalent ‘on axis’. Subtracting this from the total ABC, we obtained the ABC due to “Others". The value was converted to Sv and finally to weight density using the TS per kilogram (TSkg) of -25.17 dB according to Equation (4) (Everson et al., 2013; Taabu-Munyaho et al., 2014):

$$\mathrm{Density}_{(\mathrm{Others})} = 1000^{((Sv - TS\ kg)/10)} \quad (5)$$

These weight densities represent the weight of "Others" in each grid of EDSU 2 minutes (~0.5 Km) by 1m deep, calculated according to equation 5 above.

To summarise, the database on which we did our analyses was constructed with consecutive steps. First, we collected acoustic and environmental data at three transects during a stratified and mixed season. Second, on each transect 20km long, we had seven (7) probe stations distributed at an equal distance (e.g., at an interval of about 3.3km), whereby we collected environmental data from the surface at each probe station to the bottom. Third, acoustic data were from an Elementary Distance Sampling Unit (EDSU) of 2 minutes long (~0.5km) by 1m deep before each probe station; thus, from each probe station, we had multiple EDSU from the surface to the bottom. Finally, each layer of 1m thick related to environmental data at that depth to properly compare acoustic data with environmental data. An assumption is that the environmental variables at a particular depth layer are the same over the whole 0.5km section of the transect in which we calculated the fish densities.

Data exploration

Data exploration was carried out according to the methods described by Zuur et al. (2010). We plotted different responses and explanatory variables for detecting outliers, examined collinearity between explanatory variables, and determined the statistical distribution of the data. After checking for normality, data were log-transformed when deviating from normality. Physico-chemical parameters, Nile perch densities, and "Others" densities were analysed by a one-way ANOVA, followed by a Bonferroni post-hoc test to show differences between seasons and transects. To test the differences in Nile perch size between transect and season from acoustic deduced and bottom trawl data, we used Ggstatsplot in R (Patil 2021). We explored data using SAS/STAT software version 9.2 of the SAS system for Windows.

We used principal component analysis (PCA) to assess the influence of explanatory variables on Nile perch densities and size response variables. "Others" densities, dissolved oxygen, temperature, depth and chlorophyll-a were used as explanatory variables. We made two biplots, one for the mixed season and the other for the stratified season. In visualising the influence of explanatory variables on Nile perch size and densities, we used the factorextra package described by Kassambara and Mundt (2019). The prcomp() function from R Core Team (2017) was used to compute the principal component.

After the physico-chemical parameters and acoustic data were matched, we excluded 4m from the surface on the acoustic data due to vessel depth and surface effects. We reduced cross-correlations among explanatory variables by removing redundant and non-significant variables to obtain a more parsimonious model, according to Zuur et al. (2010). Redundant variables were reduced by examining collinearity between explanatory variables. Where collinearity was found, one variable was chosen to be on the model by considering theoretical justification, the importance of interpretation, statistical significance (with an emphasis on the importance of the variable rather than solely relying on statistical significance), effect size (taking into account the context of the research question and practical relevance of the effect), and model performance (such as comparing R-squared or adjusted R-squared values of different models).

Data analysis

We used a generalised additive model (GAM) to assess the relationship between response variables (Nile perch number density) and explanatory variables (“Others” density, depth, temperature, dissolved oxygen, chlorophyll-a, Nile perch maximum length, Nile perch minimum length, and “Others” density). GAM, a non-parametric technique, was used in our analysis because it handles polynomial data (Hastie and Tibshirani 2017). GAM performs better than other predictive models (Drexler and Ainsworth 2013; Moisen and Frescino 2002; Walsh and Kleiber 2001) as it can capture the non-linear signature of many environmental variables. After checking for collinearity, a refined model was obtained by adjusting the model by removing the non-significant variables, then rerun several times until the best-simplified model was obtained by considering the AIC/BIC criteria. The goal was to select the model with the smallest AIC value, representing the best trade-off between model complexity and goodness of fit. So, the model with the smallest AIC value was the best.

A simplified Generalised Additive model obtained (equation 6) included all the remaining explanatory variables.

$$y = \alpha + f1(x1) + f2(x2) + \text{.........} + fp(xp) + \varepsilon \qquad (6)$$

Where y is the response variable to be predicted (square root of Nile perch number densities), α is the intercept term, f1, f2, ..., fp are the smooth functions of the explanatory variables x1, x2, ..., xp (“Others” density, depth, temperature, dissolved oxygen, chlorophyll-a, and “Others” density) and ε is the random error term.

For all model analyses, we used R 4.1.0 for Windows (R Foundation for Statistical Computing, Vienna, Austria). We used the magrittr package for easily readable manipulation and transformation of data and the mgcv and amgcviz packages for fitting the Generalized Additive Models (GAMs). The tidyverse package was used for data manipulation, visualization, and modelling, and we utilized the MuMIn package to explore all possible models ('dredge'). Additionally, we used the performanceAnalytics package for chart correlation, Goodman-Kruskal for associations between categorical variables, vegan for multivariate analysis, and ggplot2 and ggrepel for creating and arranging plots.

Results

Physico-chemical characteristics

Generally, variations in physico-chemical variables across seasons and locations are minor (Fig. 3.2). Dissolved oxygen varied only slightly between the transects (Speke gulf (μ =5.9mgL^{-1}, N=449), Open Mwanza gulf (μ= 5.8mgL^{-1}, N=1869), Open lake (μ=6.0mgL^{-1}, N=930)) (Fig. 3.2a) and between seasons (Open Mwanza gulf: dry season μ=6.1mgL^{-1}, N= 1153; wet season μ =5.4mgL^{-1}, N=716; Open lake: dry season μ=6.0mgL^{-1}, N= 605; wet season μ=5.7mgL^{-1}, N=325) (Fig. 3.2a). The same can be said for the temperature. The mean temperature in the three transects was 25.1°C, and between seasons, the temperature varied from 24.8°C to 25.1°C (Fig. 3.2c). Additionally, we observed a gradient of chlorophyll concentration from the shallowest to the deepest transect, with the highest concentrations in the shallowest transect Speke Gulf (μ =5μgL^{-1}, N=449) to the lowest concentration in the deepest transect Open lake (μ =3μgL^{-1}, N=930) (Fig. 3.2b).

Spatial and temporal distribution of Nile perch and “Others” densities

The study found that Nile perch and “Others” densities were higher during the stratified season compared to the mixed season (Table 3.2). Specifically, during the stratified season, the densities of Nile perch were significantly higher in the shallow transects of Speke Gulf (3 t/0.5km2) and Open Mwanza Gulf (1.5 t/0.5km2) compared to the deepest transect, Open Lake (0.7 t/0.5km2). Similarly, the densities of "Others" were also higher during the stratified season and were observed mostly at shallow transects of Speke Gulf (1.5 t/0.5km2) and Open Mwanza Gulf (1.2 t/0.5km2) compared to the deeper transect (0.3 t/0.5km2) (Table 3.2).

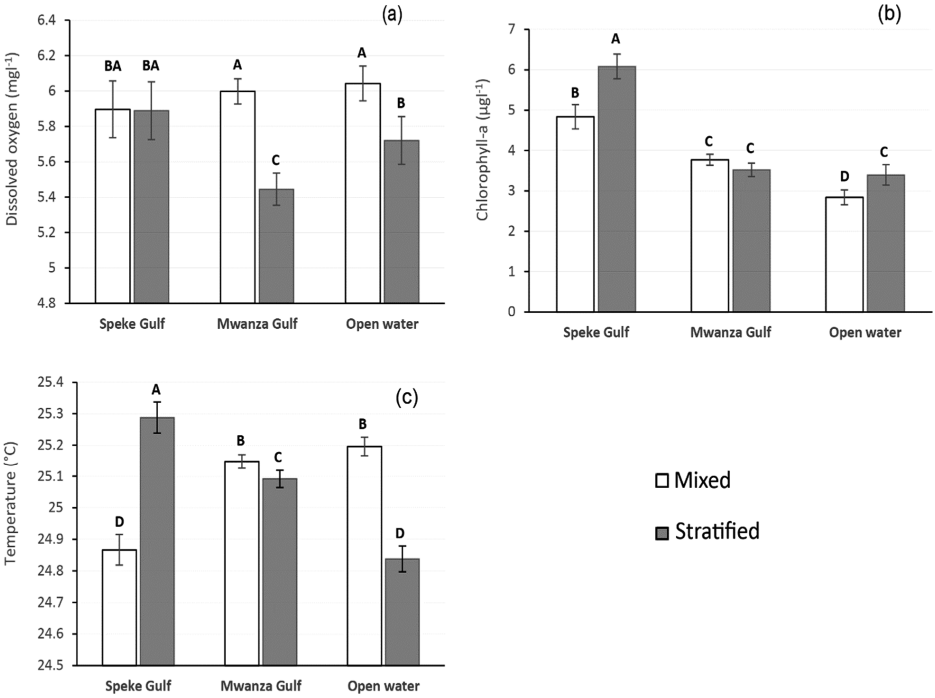

***Figure 3.2**: LS-means of Dissolved oxygen (b), Chlorophyll-a (b) and Temperatures (c) at Speke Gulf, Mwanza Gulf, and Open water transects in dry and wet seasons. LS-means with the same letter are not significantly different (Open Mwanza gulf N=1869 (N wet=1153 dry=716); Speke gulf N= 449 (N wet =220 dry=229); Open lake N=960 (N wet=325, dry=605)) and error bars represent 95% confidence limits.*

From the acoustically deduced length-frequency data, we observe variations in the Nile perch size between the transects during the mixed and stratified seasons (Fig. 3.3). However, the difference in size between transects is only 5cm, and generally, both the Open lake and the Speke gulf have larger Nile perch. A one-way ANOVA was used to compare the F-trimmed mean length between transects during the stratified season and found a significant difference (F (2, 133.7) = 4.5, p = 0.013). Mean lengths during the stratified season at Open lake, Open Mwanza Gulf, and Speke Gulf transects were 23cm, 21cm, and 22cm, respectively (Fig. 3.3a). Furthermore, during the mixed season, we found a significant difference as well between transects (F (2, 120.5) = 32.7, p < 0.0001), where Mean lengths at Open lake, Open Mwanza Gulf, and Speke Gulf transects were 24cm, 19cm and 22cm, respectively (Fig. 3.3b).

Table 3.2: Average densities of Nile perch and "Others" at Speke Gulf, Open Mwanza Gulf, and Open lake transects during the mixed and stratified season.

Transects	**Nile perch density** (t/0.5km^2)			
	Mixed season		Stratified season	
	Mean	Std error	Mean	Std error
Speke Gulf	1.6	0.2	3.0	0.3
Open Mwanza Gulf	0.5	0.1	1.5	0.1
Open lake	0.8	0.1	0.7	0.1
	"Others" density (t/0.5km^2)			
	Mixed season		Stratified season	
	Mean	Std	Mean	Std
Speke Gulf	0.7	0.1	1.5	0.2
Open Mwanza Gulf	0.7	0.1	1.2	0.1
Open lake	0.4	0.04	0.3	0.04

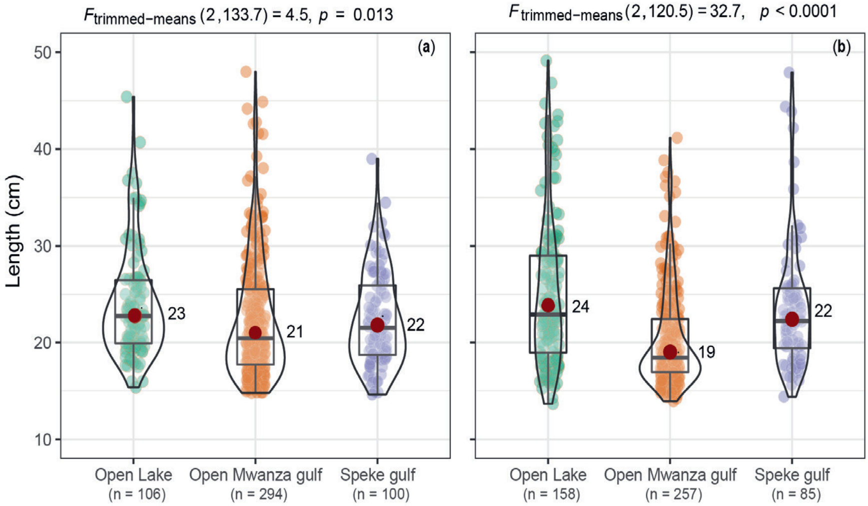

Figure 3.3*: Comparison of Nile perch length between Open lake, Open Mwanza Gulf, and Speke Gulf transects during the stratified season (a) and mixed season (b) from the acoustic deduced length-frequency data. The numbers inside the figure represent the trimmed means (i.e., extreme values from both ends of the distribution are trimmed to avoid skewing). F trimmed means- indicates whether means sizes of Nile perch in the two transects differ.*

The Bottom trawl samples have an average larger Nile perch than observed through acoustic surveys. However, they supported the conclusion drawn from the acoustically derived data, small variation in the size of the Nile perch between seasons (Fig. 3.4b) and no difference between transects.

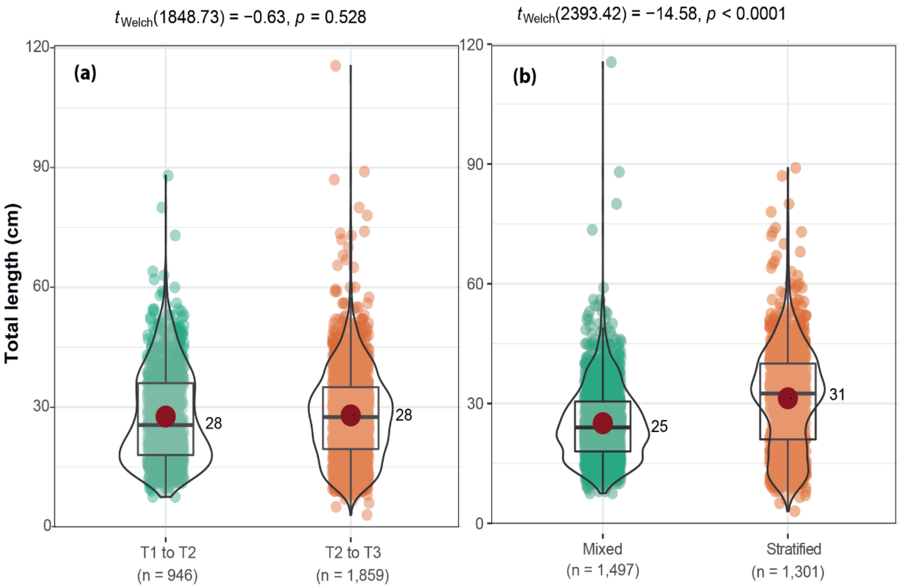

***Figure 3.4**: Comparison of Nile perch length between the transects, i.e., T1 to T2 (area between Speke Gulf and Open Mwanza Gulf) and T2 to T3 (area between Open Mwanza Gulf and the Open lake transects during the stratified (a) and mixed season (b) from bottom trawl length-frequency data. The numbers inside the figure represent the trimmed means (i.e., extreme values from both ends of the distribution are trimmed to avoid skewing). F trimmed means- indicates whether means sizes of Nile perch in the two transects differ. The t-Welch test is a modified standard independent samples t-test used when the variances of the two groups being compared are unequal.*

During the stratified season, the first axis on the principal component analysis (PCA) explains 39.1% of the variance. The second axis defines 25%, meaning the two capture together 64.1% of the information in the data axes (Fig. 3.5a). During the mixed season, the first axis explains 32.5% of the variance, and the second axis explains 24%, which means the two axes capture 56.5% of the information in the data (Fig. 3.5b).

The PCA shows the distribution of Nile perch densities in the three transects is highly overlapping, indicated by the overlapping ellipses. Considering the direction of the variables (NP_length, NP_weight and other_density) during both seasons, they increase in the same order, meaning “Others” densities are highly correlated to Nile perch length and Nile perch densities (Fig. 3.5a & 3.5b). Furthermore, both seasons' physico-chemical parameters (Chlorophyll-a, dissolved oxygen and temperature) show no relationship with Nile perch length and densities (Fig. 3.5a & 3.5b). Physico-chemical variables (dissolved oxygen, chlorophyll-a) in both seasons negatively correlate with depth (Fig. 3.5a & 3.5b).

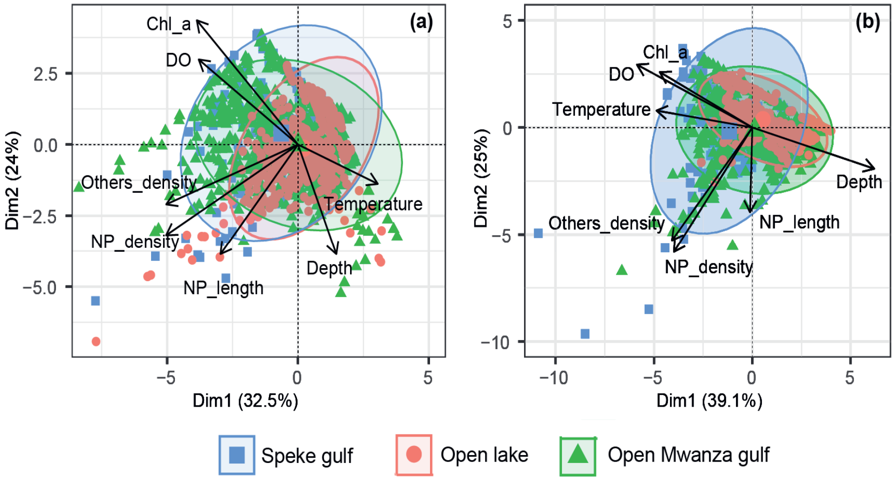

***Figure 3.5**: Biplot of Nile perch densities (NP_density) and Nile perch size (NP_length) in relation to explanatory factors ("Others" densities, depth, temperature, chlorophyll-a and dissolved oxygen) at Speke gulf, Open Mwanza gulf and Open lake transects during the mixed season(a) and stratified season (b).*

Factors Affecting Nile perch Population Densities and Nile perch sizes

The output from the Generalized Additive Model (GAM) shows that the Nile perch densities depend on both environmental and food conditions at different scales. Nile perch densities (number) correlate highly and positively with “Others” densities, e.g., with their possible food items (Table 3.3). This positive correlation is consistent in both seasons and all three transects (Fig. 3.6). As the partial Akaike Information Criterion (dAIC) shows, “others” densities contribute overwhelmingly and by far most of all explanatory variables to the variation in Nile perch densities (Table 3.3).

In contrast to our hypothesis, dissolved oxygen (DO) played a minor role in explaining the variation in Nile perch densities (Table 3.3): only in the Mwanza Gulf during the stratified season and in the Open lake transect during the mixed season, DO contributed significantly to the model, but, compared to “Others” densities, at a modest level (Table 3.3). Similar results are shown for temperature: either it did not contribute significantly to the model, or its contribution was of minor importance when it happened (Table 3.3) and complex to interpret (Fig. 3.6). On the other hand, chlorophyll-a, in most cases, did not contribute significantly to the model. The relationship is linear where it happens to be significant, which is at Mwanza Gulf in all seasons (Table 3.3) (Fig. 3.6). Furthermore, depth correlates with Nile perch densities in all transects and seasons (Table 3.3). Except for the Speke Gulf transect, Nile perch densities decrease with depth until 10-15m (Fig. 3.6), whereafter, the numbers stabilise at a low level with increasing depth.

Table 3.3: General additive models (GAM) of non-parametric regressions between Nile perch number densities and explanatory (environmental and biological) variables on Speke gulf, Open Mwanza gulf and Open lake transects during the mixed and stratified seasons. The green row represents the linear part of the model. Lmax is the Nile perch maximum length, Lmin is the Nile perch minimum length, edf is the explained degree of freedom, ns stands for a non-significant variable dropped on the final model, and dAIC is a partial Akaike Information Criterion.

Nile perch	**Mixed season**					**Stratified season**				
Number Density	**F-value**	**edf**	***pvalue***	**dAIC**	**Std**	**F-value**	**edf**	***p-value***	**dAIC**	**Std**
Speke gulf	N= 156	R-sq.(adj) = 0.92				R-sq.(adj) = 0.92				
Chlorophyll-a	—	—	ns	—		—	—	ns	—	
Temperature	1.5	1.6	<0.001	8.8		—	—	ns	—	
Dissolved oxygen	—	—	ns	—		—	—	ns	—	
"Others" density	83.5	2.6	< 0.001	65.6		53.9	4.4	< 0.001	217.8	
Depth	4.6	3.5	< 0.001	17.5		3.6	5.8	< 0.001	15.7	
Lmax	1	2.1	0.005	5.6		1.7	2.2	<0.001	8.9	
Lmin	1.5	1.9	<0.001	5.2		1.7	2.2	<0.001	5	
Open Mwanza gulf	N=890	R-sq.(adj) = 0.91				R-sq.(adj) = 0.91				
Chlorophyll-a	*t-value 6.9*	*Estimate 0.02*	< 0.001	44.1	0.002	*t-value 3.7*	*Estimate 0.015*	< 0.001	10.9	0.004
Temperature	—	—	ns	—		2.3	5	<0.001	10.1	
Dissolved oxygen	—	—	ns	—		5.8	5.3	< 0.001	43.3	
"Others" density	203.5	5.5	< 0.001	971.1		167.5	3.5	< 0.001	769.6	
Depth	26.3	7.7	< 0.001	147.8		15.1	7.1	< 0.001	94.4	
Lmax	23.5	7.7	< 0.001	170		6.2	4.9	< 0.001	45.7	
Lmin	7.9	3.1	< 0.001	70.8		21.9	5.5	< 0.001	194.2	
Open lake	N=393	R-sq.(adj) = 0.87				R-sq.(adj) = 0.87				
Chlorophyll-a	—	—	ns	—		—	—	ns	—	
Temperature	6.5	5.4	< 0.001	48.6		—	—	ns	—	
Dissolved oxygen	1.5	3	<0.001	7.6		1.7	4.4	0.003	10.1	
"Others" density	47.3	3.1	< 0.001	302		22.7	5	< 0.001	146.8	
Depth	27.6	7	< 0.001	145		26.2	6.5	< 0.001	158.4	
Lmax	5	5.6	< 0.001	34.8		8.6	6	< 0.001	78.8	
Lmin	10.9	3.3	< 0.001	90.0		16.2	3	< 0.001	124.8	

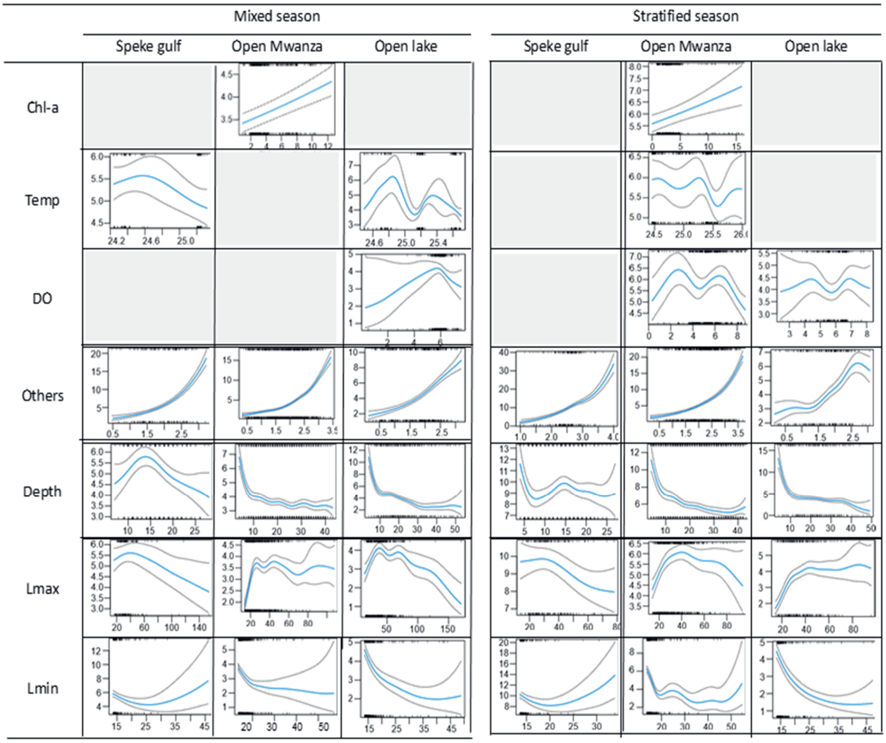

Figure 3.6: The GAM-derived effects of the physico-chemical and biological variables on Nile perch number density (response variable) at Speke Gulf, Open Mwanza Gulf and Open lake transect during the mixed and stratified season. Graphs indicate relationships between explanatory variables (x-axis) and partial predictions of the response variable (y-axis). Blue lines show the model fit; the 95% confidence intervals are black dotted. A grey colour represents a variable not included in the final model.

Discussion

The present study showed that food availability strongly influenced Nile perch densities and size distribution. Lake Victoria is monomictic, with an annual overturn in the cool (mixed season) between May and August (Talling 1966). This seasonal overturn of the lake impacts food availability, temperature, and the amount of dissolved oxygen, which may affect the Nile perch distribution. Our acoustically deduced data showed that Nile perch densities were higher in the shallow transects, e.g., Speke Gulf and Open Mwanza Gulf (Table 3.2). Equally, the presumed prey organisms of Nile perch (smaller fishes of a size below 10cm ("Others")) were also more concentrated in the shallow transects (Table 3.2). In Speke Gulf and Open Mwanza

Gulf, densities are higher during the stratified season than during the mixed season (Table 3.2).

Nile perch densities are significantly more affected by biotic factors (food) than abiotic ones (Fig. 3.5). These findings differ from Cornelissen et al. (2015) and Bernardes (2010) but tie in with Kayanda (2012). According to Cornelissen et al. (2015), Nile perch was significantly affected more by abiotic than biotic factors, as in Bernardes's (2010) study, where more Nile perch were found along with increasing oxygen levels. Cornelissen et al. (2015) study was conducted in a smaller area near our study location, where we would expect a similar outcome as ours. However, since Lake Victoria is not uniform, it’s like many lakes in one lake (Taabu-Munyaho et al., 2014); thus, other parts of the lake may have different characteristics, impacting the Nile perch differently. If food availability for Nile perch is sufficient such that there is no measurable gradient in food availability in the study area, the observers won’t detect an effect of food on the distribution, as it is not limited by food. This could have been the case during the Cornelissen et al. (2015) study.

Chlorophyll-a measures the concentration of phytoplankton in the water and is often used to indicate nutrient levels. Speke Gulf and Open Mwanza Gulf transects receive nutrient loading from river discharge (Kabenge et al., 2016; Ngupula et al., 2012). Our results showed a gradient of chlorophyll-a concentration from the Speke Gulf to the Open Mwanza Gulf transect (Fig. 3.2). A strong positive linear correlation between chl-a and Nile perch densities was found in the Open Mwanza Gulf (Fig. 3.6). The fact that we did not find such a relation in the Speke gulf, but yes in the Open Mwanza gulf might be explained by the presence of a concentration gradient and thus a different impact on the Nile perch densities in the latter transect, while chlorophyll-a was possibly uniform in the Speke gulf.

Furthermore, this study hypothesised that areas with high oxygen levels and food availability would have the largest and most numerous fish. During the stratified season, nutrient loading from river runoff increases food availability. Still, excessive nutrient loading may decrease oxygen levels (Mugidde 2001), leading to large Nile perch avoiding these areas (Njiru et al., 2012). However, during this study, the lake conditions showed oxygen levels above 3mgL^{-1} (Fig. 3.2b), a critical level for Nile perch (Akiyama et al., 1977; Hecky et al., 1994; Kishe 2004). The condition was good both in shallow and deep transects and during both seasons). This favourable environmental condition (Fig. 3.2) and the presence of food (Table 3.2) supported higher densities of Nile perch in the shallow transects (Speke Gulf and Open Mwanza Gulf) than in the Open lake transect (Table 3.2), which was especially visible during the stratified season (Fig. 3.3 and 3.4)

Interestingly, despite the importance of dissolved oxygen in supporting fish populations (Richards et al., 2009), we found no significant correlation between Nile perch densities and dissolved oxygen, especially at the shallow transects. Where it was significant, the effect was insufficient to impact Nile perch densities (Table 3.3) considerably. Our results suggest that food availability may be more critical in determining Nile perch densities than oxygen levels. Our results support the hypothesis that locations with high food densities have the largest and most numerous Nile perch populations. During the stratified seasons, Nile perch densities were higher in the shallow Speke Gulf and Open Mwanza Gulf (Table 3.2). This finding aligns with a previous lake-wide survey conducted by Taabu-Munyaho et al. (2013), which found higher Nile perch densities in inshore waters during this season. Adequate food supply will encourage small and large Nile perch movements to inshore areas.

Further research is needed to determine the factors that influence chlorophyll-a concentrations in the lake and how these factors interact with Nile perch populations. The study highlights the critical role of food availability in determining Nile perch populations. These findings have important implications for the management of Lake Victoria fisheries. There is a need for maintaining healthy prey populations, implementing measures to limit overfishing of key prey species, protecting key habitats where prey species are known to thrive, and improving water quality by reducing nutrient loading.

Our study emphasizes the need for continued research on the factors influencing Nile perch populations in Lake Victoria. Acoustic studies on small areas are important to designing proper management of the Nile perch fishery since different parts of the lake may differ significantly and thus deserve special attention.

Acknowledgement

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Chapter 4

Operational, environmental, and resource productivity factors driving spatial distribution of gillnet and longline fishers targeting Nile-perch (*Lates niloticus*), Lake Victoria.

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Abstract

Operational and environmental factors limited available resource space of gillnet and longline fishers targeting Nile perch in the Speke Gulf and open lake of southern Lake Victoria and drove their encounter rates with patches of fish, resulting in gear specific distributional patterns. Catch-rate patterns were similar by region and gear: large (>50cm) Nile perch densities increased over distance from the homeport and deeper in the water column, while small Nile perch (<50cm) densities decreased. Effects of season, (setting) depth and region were present but small and obscured by high variations in daily catch rates and individual fisher strategies. Both fisheries distributed themselves over the size-productivity spectrum of Nile perch. Still, they reacted differently to patterns in the size distribution of Nile perch: gillnetters focused more on numbers of productive juveniles between 30-60cm at an average 5km distance (59min travel time) from homeport and longliners on larger sized 40-80cm Nile perch deeper in the water column at 7km (108min). Sampled fishers likely were representative of most of the Nile perch fisheries. If so, fishing pressure is mainly exerted on nearshore lake areas. More lightly fished offshore areas may be a refuge for adult Nile perch. According to ideal free distribution predictions, total catch rates by gear were generally equalized over the resource space, increasing slightly with distance from homeport. Nile perch fishers on Lake Victoria appear to distribute themselves according to the underlying productivity distribution of the resource within the constraints of their available resource space.

Introduction

The distribution of fishers over a resource is determined by operational and observational constraints of individual operations as well as environmental factors and resource productivity features. In small-scale fisheries, characterized by limited investment in assets such as vessels, gears and other technology, the resource space over which fishers can allocate their effort is bounded. The type of propulsion used, gear setting demands, and onboard preservation limit their action radius. Fishers prefer fishing close to their homeports (Salas and Gaertner 2004) as operational costs (time, money) are minimized. Seasonal weather patterns, associated stratification, and other environmental patterns affect encounter rates with patches of fish and thus co-determine the effort allocation options of fishers.

Nevertheless, it can be expected that over the long run, and averaged over their resource space, fishers will distribute themselves over the available resources within that space such that catch rates reflect the underlying dynamics in the resource distribution. This distribution is a prediction of the Ideal Free Distribution (IFD) theory that describes how predators distribute themselves over a prey resource, where the number of predators at a given location is proportional to the rate at which prey are produced at that location, while all individual predators obtain the same prey intake rate (Kacelnik et al., 1992). IFD theory has been used to predict that effort will be distributed spatially over a fished resource so that catch per unit of effort is equalized over all locations (Gillis et al., 1993; Gillis and van der Lee, 2012). The concentration of fishing effort in a resource space creates crowding, local competition and, potentially, interference competition and induces redistribution of effort over larger spaces within the operational constraints of small-scale fishers (Gillis. 2003; Gillis et al., 1993; Poos and Rijnsdorp, 2007) resulting in such equalising of catch-rates.

The IFD argument can be extended to the selection of sizes of the available resources in relation to their productivity when unconstrained by strong preferences of sizes and species or externally imposed size regulations. Individual fishers' attempts to optimize their CPUE imply that fishing effort will be distributed in proportion to the productivity of the resource (Plank et al., 2017), leading to the emergence of balanced harvesting (Garcia et al., 2012, Garcia et al., 2016). Such distribution over the size spectrum of the resource has been observed in small-scale freshwater fisheries in Africa (Kolding et al., 2015; Kolding et al., 2016; Kolding and Zwieten, 2011). A shift to target smaller resource sizes with increased effort within species populations and in a multispecies fishery is a well-known and common phenomenon in small-scale fisheries (van Zwieten et al., 2003; Welcomme, 1999). This shift is also an outcome of harvesting over a size spectrum leading to balanced harvesting, described by Plank et. al (2017), as smaller sized fish are generally more productive. This result implies that under unconstrained conditions, the spatial allocation of effort will reflect the distribution of the productivity of a resource, meaning that, within their resource space, fishers can be expected to fish at locations where renewal rates are highest. It follows that in the long run and averaged over their available resource space, signals from fishing outcomes will lead fishers to distribute themselves according to the underlying productivity distribution of the resource.

We focus on Nile perch from southern Lake Victoria, targeted by small-scale gillnet and longline fishers. Nile perch is one of Lake Victoria's commercially targeted species, contributing, on average, 240,000 tons per year or up to 30% of the total landings (Mkumbo and Marshall, 2015). After an introduction, the species initially dominated in shallower waters, but over time, the abundance of larger fish in deeper waters appeared to be increasing, and Nile perch is now found at all depths (Goudswaard et al., 2008; van Zwieten et al., 2016). Adult Nile perch (≥54cm male; ≥76cm female, Hughes (1992), Mkumbo (2007)) are distributed over all habitats, while juveniles are more dominant in shallower coastal waters (Katunzi et al., 2006). Nile perch densities change seasonally with stratification patterns: during the stratified season (November to March), densities increase in upper water layers, while during the windy mixing season (June to October), higher densities are encountered in deeper water (Taabu-Munyaho et al., 2013).

The main gears targeting Nile perch are gillnets and longlines operated from 5-11m wooden vessels. These vessels are propelled by paddles (60%), small outboard engines (32%) and sail (8%) (MLF, 2015; LVFO, 2017). Fishing in Lake Victoria takes place from many landing sites along the shore. Most fishing operations are day trips, with limited use of ice, further limiting the potential action radius of a fishing trip. Nile perch fisheries are regulated through a minimum mesh (6 inches, 152 mm stretched mesh) and a recommended hook size (<10) next to a minimum landing size. However, enforcement of these regulations is weak (Medard Ntara 2015). While the primary market for Nile perch is the fish factories that can only buy Nile perch of ≥ 50cm total length, a large regional market for smoked juvenile Nile perch exists (Medard Ntara, 2015).

The probabilities of catching large Nile perch are expected to be higher further from the shore (Schofield and Chapman 1999). As the numbers of fishers have increased (Mkumbo and Marshall, 2015), they increasingly compete over the same nearshore resources, suggesting that, as a result of this competition and according to IFD predictions, the distribution of effort will be extended to deeper waters further from the shore. This distribution also will depend on the productivity and spatial patterns of the different size classes of Nile perch. As the productivity of Nile perch decreases with size, spatial separation of size classes should lead to spatially differentiated production patterns (Natugonza et al., 2016).

Given the size-selectivity characteristics of their gears, fishers using longlines or gillnets are expected to target different size classes of the Nile perch stock that are in part spatially separated (Chitamwebwa et al., 2009; Msuku et al., 2011). A further differentiation in spatial allocation may be setting depths of different gears. While Nile perch are found all over the water column, the highest densities are found in the upper 20m of water in nearshore shallow regions, while in coastal and deep waters, distribution is more even or bimodal with a deep water peak at 30-40m depth (Cornelissen et al., 2015; Taabu-Munyaho et al., 2013). Reported distributional patterns over the water column are derived from aggregated lake-wide acoustic observations, a scale much larger than the individual scales of operation of Nile perch fishers. Such generalized patterns will be obscured for an individual fisher when variability in encounter rates of patches of fish is high due to locality, seasonal environmental effects and species-specific distributional characteristics (van Densen, 2001).

The focus of this paper is to better understand how fisher effort is allocated spatially and temporally, resulting from fishing operational factors as well as fish presence, fish density and environmental factors. Operational factors limit the resource space of fishers and drive the encounter rates with fish densities, leading to a specific distribution of the fishery over a resource, which is expected to follow IFD predictions on effort distribution over its size-productivity spectrum. We will examine (1) the distributional patterns of longline and gillnet fishers targeting Nile perch in Lake Victoria in two contrasting regions (gulf and open lake region); (2) the operational and environmental factors driving encounter rates and observed patch densities of different size classes of Nile perch; (3) compare the relative biomass estimates of Nile perch with what is known about the patterns in spatial distribution of different size classes of Nile perch; and (4) discuss the resulting variability in spatial distribution and catch rate patterns of the two fisheries in the light of the IFD predictions on distribution over the size-productivity spectrum of a resource. Effort allocation studies (Hilborn and Ledbetter 1985) in small-scale and artisanal fisheries in the tropical marine realm are scarce (Pet-Soede et al., 2001; van Oostenbrugge et al., 2001) and, to our knowledge, are non-existent for tropical freshwater systems.

Materials and methods

Study Area

Lake Victoria is the world's largest freshwater fishery, with nearly 1 million tons of fish harvested annually (Kolding et al., 2013). This study was conducted in the southern part of the lake in the territorial waters of Tanzania, where around 49% of the fishers are found (MLF, 2015, LVFO, 2017). Four landing sites in two regions were selected based on their locations along the shallower Speke Gulf and the deeper open lake area and on our knowledge of the fishery gained in discussion with the Tanzanian Fisheries Research Institute staff and scientists who have worked there. The sites were likely to be representative of other landing sites in southern

Lake Victoria: Kayenze and Muluseni were located along the Speke Gulf (gulf region), and Muhula and Kome-Mchangani were facing the open lake (open lake region) (Fig. 4.1; Table 4.1). The gulf region ranges to 40m deep but is mostly <25m deep; the open lake region is characterized by steep descending slopes down to 57m deep. Fishers operate from both gulf shores, so fishing areas were more likely to overlap than open lake fisheries. While the number of fishers per km shoreline may be the same, fishing pressure per unit area was expected to be higher in the Gulf region. Of the villages chosen, Kayenze is more developed regarding landing facilities and is accessible by an all-weather road. However, fishers in all four villages had daily access to traders and weighing scales, and all had fisheries officers responsible for enumeration and levy collection. All four villages had substantial longline and gillnet fisheries.

Table 4.1: Daily mean standardised catches of Nile perch in kilogram and number and coefficient of variation (CV) by individual fisher. G1-G8=gillnet fisher, L1-L7=longline fisher, E=engine; P= paddle/sail.

Village, coordinates	Gear, Fisher	Propulsion (Nobs)	Fishing days (N)	No fishing days (N)	Mean (kg)	CV (kg)	Mean (N)	CV (N)
Kayenze (Gulf)	G1	E	271	14	17	59	16	66
02°23.335' S	G2	E	204	13	22	48	22	49
	G3	E	275	7	28	87	23	76
33°4.730' E	L1	P	177	9	38	68	13	83
	L2	P	239	5	37	78	10	76
Muluseni (Gulf)	G4	E	188	4	30	57	34	59
02°8.265' S	G5	E (189), P (23)	212	51	26	69	22	71
33°11.054' S	G6	E (79), P (108)	189	6	41	62	27	62
Muhula (Open lake)	L3	P	239	11	40	93	17	115
02°4.993'S	L4	P	272	1	37	81	12	111
32°57.44 E	G7	E (105), P	226	0	27	42	21	45
Buhama (Open lake)	G8	E (102), P (20)	121	46	25	75	15	71
	L5	P	107	30	37	49	18	54
2°16.652' E	L6	P	151	0	34	68	17	77
33°32.172' S	L7	P	212	56	35	55	13	68
Total	**15**		**3077**	**254**				

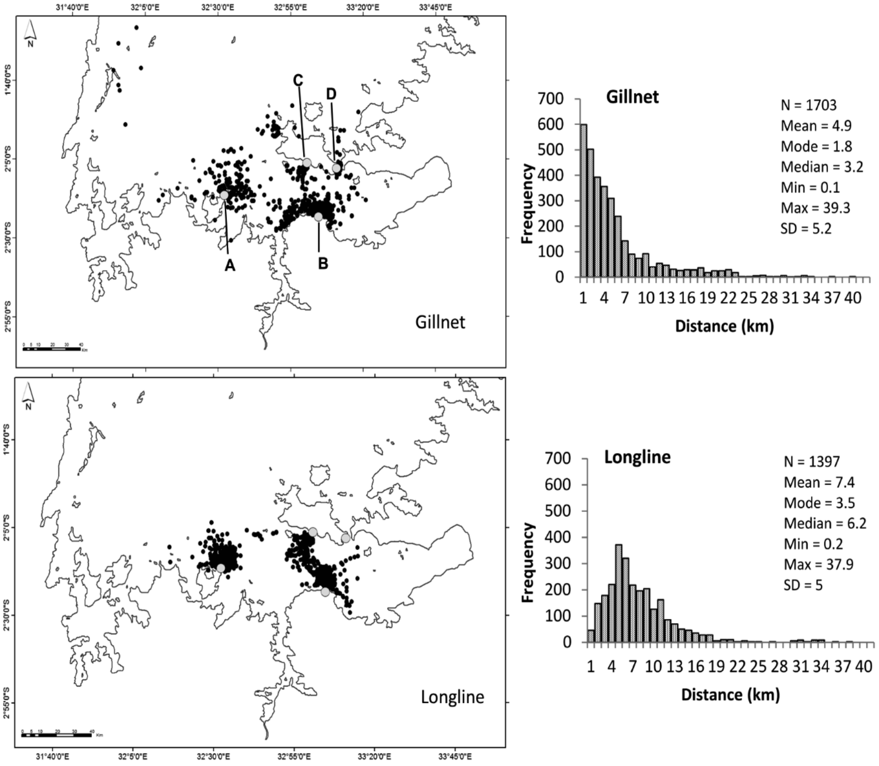

Figure 4.1. *Map of the southern part of Lake Victoria with landing stations (A-Kome-Mchangani, B- Kayenze, C- Muhula and D- Muluseni) included in this study and frequency of daily effort allocation by distance covered by gillnet fishers (above) and longline fishers (below).*

In the southern part of Lake Victoria, three seasons are distinguished, during which the lake experiences winds of different strength. During the long rains from February-May, there is less or no wind, resulting in the stratification of the lake and the build-up of deep water hypoxia and anoxia that affects the available habitat for hypoxia-intolerant species like Nile perch (Schofield and Chapman 2000). During the dry period from June to August, the lake experiences strong winds that mix up the lake water (Mugidde et al., 2005, Njiru et al., 2011). The short rains from October to January transition from the dry (mixed) to the wet (stratified) season. The pronounced impact of the seasonal wind regime on the mixing of the lake waters is likely to influence the size and density distributions of Nile perch.

Logbooks

Ten gillnet fishers and nine longline fishers targeting Nile perch and operating from four fishing locations were trained to record their daily operations and resulting catches using their fishing gear in logbooks and using a handheld GPS device (Table 4.1). The training was done in a series of interactive sessions where fishers tested an initial logbook in the field and, after discussion with them, adjusted it to a final version (Ticheler et al., 1998) (Appendix 1). Fishers were selected based on experience in Nile perch fishing, type of gear used, landing site, and willingness to participate in the research project. The selected fishers were representative of the majority of the fishers on the lake in that they (1) targeted Nile perch as over a half number of fishers (116,000 = 52%) on Lake Victoria do (LVFO, 2017); (2) used either gillnets or longlines, where almost 100% of longlines and 85% of the gillnets used in the lake are reported to target Nile perch. In 2010, 84% of the hooks used in longlining were small hooks with sizes >10 (that is, numbers 11, 12 and 13), while 90% of the meshes used were within the range of 4-8 inches (101–203 mm stretched mesh) (Fig. 4.2). Lastly (3), the selected fishers used so-called "Sesse boats", planked vessels that are either propelled by paddle and sail (67% of the in total 77000 vessels used on the lake) or with outboard engines of 9.9hp or 15hp (34%) (MLF, 2015; LVFO, 2017).

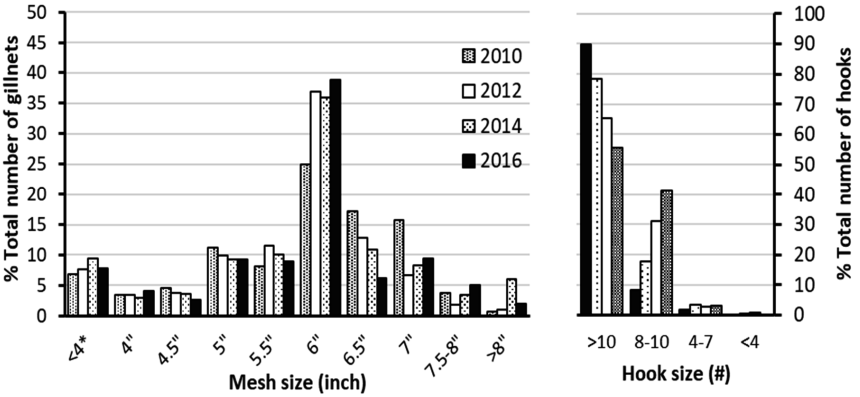

***Figure 4.2**: Proportion of total number of gillnets meshes, and longline hooks by size in Lake Victoria based on frame surveys held between 2010 and 2016 (LVFO, 2017)*

Furthermore, to examine the representativeness of the selected fishers, we interviewed 49 gillnet fishers and 58 longline fishers from Buhama (Kome-Mchangani), Kayenze, Muhula and Muluseni on gear use, effort allocation (travel time, fishing time, seasonality, fishing grounds), catch, average cost of fishing and reasoning behind location choices in time and space. In addition, in each village, two focus group discussions were held, one for longline and one for gillnet fishers, attended by a minimum of 7 fishers each, to verify insights obtained through the individual interviews and the training of fishermen using logbooks.

The logbooks distributed to the fishers focused on catch characteristics and operational factors. The total catch per trip in number of fish and weight (kg) was recorded in two size categories of Nile perch, <50cm (small Nile perch) and >50cm (large Nile perch), together with the catch in number and weight for other species. Each category was noted whether the catches were sold or consumed. Concerning operational factors, fishers recorded their mode of propulsion; travel time from the homeport to the fishing location and back; soak-time (start and end time); fishing location by name and GPS coordinate; setting depth of the gear; depth of location; gillnet fishers recorded the number and size of gillnets (length by depth) used by mesh-size; longline fishers recorded the hook-size, number of hooks and type of bait. Lastly, reasons for not going out fishing on a day were reported. Fishers recorded data daily, and logbooks were collected monthly for data entry and quality checking. A post-hoc check on the data quality was conducted by examining the frequency distributions of the catch records expected to be close to log-normal. As it cannot be expected that fishers can deliberately record approximately log-normal distributed data when noting catches on a day-to-day basis, substantial deviations from log-normality are strong evidence for inventing data (Ticheler et al., 1998). We gave fishers monthly feedback on their performance and a fee if they had performed well. All fishers used their gear. Each set of gillnets used was recorded by their mesh size. Sizes of gear were recorded by measuring the length and depth of gillnet panels of different mesh sizes, and a surface area per each panel (m2) was calculated. For longlines, the sizes and number of hooks used were recorded each day in the logbook.

Data were collected for ten months from October 2010 to July 2011, capturing the main periods in lake stratification. Months were categorized based on the rain pattern, with October 2010 to January 2011 as the short rain season, February to April 2011 as the long rain season and May to July 2011 as the dry season.

Data treatment and statistical analysis

Data exploration

Data exploration was carried out according to Zuur et al. (2010), in particular by plotting the different response and explanatory variables to detect outliers and examine collinearity between explanatory variables, determine the statistical distribution of the data as well as checking for zero catches 166 – 171).

Representativeness of logbook fishers

Representativeness of the selected logbook fishers was analysed by comparing their daily reports of travel time, as a proxy for distance travelled and spatial effort allocation, with those of 107 gillnet and longline fishers who reported the travel time of their last two fishing operations on interviews. The two groups' travel time was then examined in a MANOVA with propulsion type and gear type as explanatory factors and outcomes compared.

Finding an unbiased catch rate and standardization

Standardization of observed daily total catch rates per trip was done by adjusting for sizes of gillnet and numbers of hooks, hook size, bait type, and soak time of both gear types. Total observed catch rates were the sum of the weights and numbers of the size categories small and large Nile perch: there were no zero daily total catches of Nile perch. For longlines, a multiple regression analysis of the observed catch rates was carried out with bait and hook size, the number of hooks and soak time – the time the hooks were in the water – as explanatory variables:

$$log_{10}(CPUE_{ijk}^{obs}) = a + \beta_1 log_{10}(N_i) + \beta_2 log_{10}(S_i) + b_j + h_k + (b * h)_{jk} + \epsilon_{ijk} \qquad (1)$$

ε_{ijk}~ iid(N($0, \sigma^2$),

where, $CPUE_{ijk}^{obs}$ = observed CPUE in number of fish or weight (kg) on the i-th fishing trip, which is classified by the bait type j and the hook-size k used on that trip, and where Ni, number of hooks and S_i, soak-time, are the continuous predictor variables for that trip. The model coefficients to be estimated are the intercept a, the slopes β_z, for the continuous variables and the effects of the levels of the categorical variables bait type (b_i) and hook-size (h_k) and their interaction. The errors are assumed to be independent and normally distributed with average 0 and variance σ^2. Two categories of hook sizes were defined: small (13) and large (11 and 12). The bait had four categories (haplochromines, dagaa, *Clarias* and *Synodontis*). Model (1) had “small hooks (13)” and “*Synodontis*” as baselines.

We examined whether specific mesh sizes were consistently used at different lake depths, setting depths or by region for gillnets. Although mesh size would be an important predictor of fish size caught, it was impossible to associate mesh sizes with size categories of fish, as these were not reported with the mesh sizes in which they were caught. Therefore, we used the total surface area of the daily nets - the sum of the surface area of each mesh size used on a trip - to standardise catch rates. Then, for gillnets, a multiple regression analysis of the observed catch rates was carried out with soak time and the surface area of the gillnet as explanatory variables.

$$log_{10}(CPUE_{i}^{obs}) = a + \beta_1 log_{10}(N_i) + \beta_2 log_{10}(S_i) + \epsilon_i \qquad (2)$$

ε_i~ iid(N($0, \sigma^2$)

Where N_i, the size of the net, and S_i, soak-time, are the continuous predictor variables a fisher uses on the i-th fishing trip. Other symbols as previous. A standardised daily catch rate $CPUE^{st}$ was subsequently calculated with appropriate corrections for bait type and hook size in case of longlines (Tsehaye 2007) as:

$$CPUE_i^{st} = \left(CPUE_i^{obs} \left(\frac{\overline{N}}{N_i}\right)^{\beta_2} \left(\frac{\overline{S}}{S_i}\right)^{\beta_1} \right) * 10^{-\left(b_j + h_k + (bh)_{jk}\right)_i} \qquad (3)$$

where, $CPUE_i^{st}$ = standardised catch rate on the i-th trip in weight (kg) or number of fish per standard trip duration and gear size, $CPUE_i^{obs}$= observed catch rate in weight or number of fish on the i-th trip, $\overline{N}$= median net size or average number of hooks and $\overline{S}$= average soak-time over all fishers and days fished by gear type, and where the term $(b_j + h_k + (bh)_{jk})_i$ adjust for the effects of bait-type (b_j) hook size (h_k) and the interaction between bait-type and hook size. Other symbols are as previously.

While there were no trips with no catch of Nile perch, the two size categories reported in the logbooks were not always caught together on each trip. Therefore, zero daily catches had to be accounted for when analysing catch rates by size category. When catch rates must be log-transformed to obtain approximate normality in model residuals, a low number is often added to remove the zeroes (Deroba and Bence 2009). However, we retained them because zero daily catches contain information on Nile perch's encountered presence. We used a hurdle model to examine factors determining relative densities, such as encounter rate (P_c) times patch density ($CPUE_{st}$). The encounter rate (P_c) was defined as the probability of catch per trip of small or large Nile perch and was determined by analysing the presence/absence of a catch through a binary logistic model; patch density (CPUEst) was defined as the weight (kg) or number of the positive catch per trip and was examined by analysing the positive catch-rates. A multiplication of the two yielded the catch-rates
($CPUE_{ad} = P_c \times CPUE_{st}$) (kg/trip).

Encounter rates: factors determining the probability of catch

In the next section, we present the general full model that includes effects for all categorical and continuous variables and their interactions. As described, we adopted a model selection process that evaluated alternative models with only a subset of the effects. The occurrence of a positive catch of Nile perch is modelled as coming from a binomial distribution with probability of a positive catch of Nile perch Pc. We analysed the observed positive occurrences using a generalized linear mixed modelling approach with a logit-link function:

$$log\left(\frac{P_c}{1-P_c}\right)_{ijk} = \mu + \sum_{l=1}^{z} \gamma\left(B_{ijkl}\right) + \sum_{m=1}^{n} \beta_m X_{imjk} + two - way\ interactions + \varepsilon_i \qquad (4)$$

$\varepsilon_i \sim iid(N(0, \sigma_a{}^2)$

where *i* represents fisher or the combination of fisher and fish size category, *j* is trip, *k* is size category, μ is an intercept, B_{ijkl} is the value of the l-th categorical variable for category *i*, trip *j* and size *k*, $\gamma(B_{ijk}l)$ is the coefficient for that categorical variable, β_m is the coefficient of the m-th continuous variable, X_{mjk} is the value of the m-th continuous variable for trip *j* and size *k*. The number of categorical and continuous variables included in the model are z and n, respectively. Continuous X variables for gillnets and longlines are the distance from the homeport to the fishing location (km) and setting depth (m). Categorical variables are region (gulf, open lake), season (dry, long, short) and Nile perch size categories (<50cm, ≥50cm). To take account of longline characteristics, the continuous variables $\log_{10}$(hook number), $\log_{10}$(soak-time) and the categorical variables bait (*Clarias*, haplochromines, dagaa, *Synodontis*) and hook-size (large, small) were added to the longline model. For the gillnet model, these were $\log_{10}$(net size) and $\log_{10}$(soak-time). Only two-way interactions between all the variables were examined. The error ε_i is assumed to be independent and normally distributed with average zero and variance $\sigma_a{}^2$. Fisher or the interaction between fisher×size was modelled as a random effect (random intercept), as clustering of sampled data can be expected due to differences in fishers skills and operational characteristics not accounted for by the fixed effect model. As fishers appeared to make different choices in using meshes or hook sizes, this led to examining the interaction between fisher×size as a random effect. The final model choice was based on several criteria: the most likely model was obtained by backward selection of variables in a full random intercept model with all fixed effects (variables and their two-way interactions) by minimizing the Akaike Information Criterion (AIC). The size of the decrease in AIC was also used to compare a random intercept model with no fixed effects to an intercept-only model. The significance of the final mixed model was compared to a random intercept model with no fixed effects through a Likelihood Ratio Test (deviance test). Model fit was further examined through the dispersion parameter (χ^2/df). To overcome overdispersion, different random intercepts, including bait and size of hooks, were always tested with fisher or fisher×size included. For the final model, we used the interaction between fisher×size of Nile perch as a random intercept, leading to a dispersion parameter close to 1. The contribution of the random effect to the total variability in *Pc* was tested by examining the Intraclass Correlation Coefficient (ICC) calculated as $ICC= \theta/(\theta+3.29)$ where θ = estimate of the covariance parameter (random intercept) (O'Connell et al., 2008). The significance of the estimate of the covariance parameter was tested using a Wald Z test.

Odds ratios – i.e., the ratio between the odds p1/(1-p1) of encountering Nile perch at one set of factors against the odds p2/(1-p2) of encountering Nile perch at a contrasting set, were calculated to make broad comparisons over factors season, region, size and bait. The continuous variables distance and setting depth were fixed at respectively 5 km, 4 m depth and 20 km, 15 m depth for gillnets and for median net size. For longlines, distance and setting depth were fixed at 7 km, 4 m depth and 20 km,15 m depth, respectively, the average number of hooks and *Synodontis* as bait.

Patch densities: factors determining positive standardised catch rates

The standardised positive catch rates of Nile perch (CPUEst) are log-normally distributed and are modelled after log transformation as coming from Gaussian distribution. We analysed the observed positive catch rates using a generalized linear mixed modelling approach with an identity link function:

$$log_{10}(CPUE_{ijk}^{st}) \; = \; \mu + \sum_{l=1}^{z} \gamma\left(B_{ijkl}\right) + \sum_{m=1}^{n} \beta_m X_{mijk} + two - way\ interactions + \varepsilon_i \quad (5)$$

ε_i ~iid(N($0, \sigma_a{}^2$)

where, $CPUE_{ijk}^{st}$, is the standardised positive catch rate of fisher *i*, by size category *k* on the *j*-th fishing day in weight (kg) or number of fish. Other effects are defined in equation 4 above, excluding the effects of bait type, soak-time, number of hooks, hook size and net size, as these are accounted for in the standardisation step (model 3). Fisher was included as a random effect. The AIC criterion examined the choice of the random effect by comparing an intercept-only model with a fixed effect model with no random effects included. A range of models was examined through backward selection of the full model based on the AIC criterion, and significance was tested on the restricted log-likelihood ratio. The contribution of the random effect to the total variability in the probability of catching Nile perch was tested by examining the Intraclass Correlation Coefficient (ICC) calculated as ICC= $\theta/(\theta + \theta_{res})$ where θ = estimate of the covariance parameter (intercept) and θ_{res} the residual variability. The significance of the covariance intercept parameter estimate was tested using a Wald Z test. As individual fishers can be expected to return to sites with successful catches, auto-correlation can violate the assumption of independence. However, it is less likely that daily catches between fishers are correlated, reducing the impact of auto-correlation when modelling overall data. We checked for such a correlation between fishers in daily catches over successive days, which was not the case.

Relative densities and individual average size of Nile perch in the catch

Relative densities were calculated by multiplying the probability of catch and the positive standardised catch rates as ($CPUE_{ad}$ = Pc × $CPUE_{st}$) in weight and number of fish. We provide some sense of the length of fish in the catch by calculating the length of a fish from this average weight. By necessity, our equation for length given weight (in gram) is the inverse function $L=(W/0.0042)^{(1/3.26)}$ based on a regression of log-length on log-weight with parameters taken from the W-L relation for Nile perch (Kayanda, 2012). This equation is reasonable given the typically tight relationship between weight and length. To determine the average size of Nile perch targeted by fishers using the two gears, we divided the

$CPUE_{ad}$(weight)/$CPUE_{ad}$(number). We examined the results graphically over the relevant explanatory variables.

All statistical models were carried out using SAS/STAT software version 9.2 of the SAS system for Windows using the GLM and GLIMMIX procedures.

Results

Descriptive results

Out of the 19 trained fishers who participated in this study, four (two gillnets and two longlines) gave incomplete data and were dropped from the analysis. The remaining 15 fishers consistently wrote day-to-day operations and catch data, including GPS positions. The consolidated database had a total of 3100 fishing trips (1703 gillnet;1397 longline) and 253 days of no fishing (141 gillnet;112 longline) (Table 4.1). Both gears predominantly caught Nile perch: 748 non-Nile perch catches were found (720 gillnets; 28 longlines), representing 11% and 0.16% of the total catch weight. Bycatch consisted in terms of weight of 0.01% *Alestes*, 7.3% Tilapia, 0.8% *Mormyrus*, 1.0% *Bagrus*, 0.7% *Protopterus*, 0.3% *Clarias spp* and 0.1% *Synodontis spp* in gillnets, and 0.15% *Bagrus*, <0.01% Tilapia and <0.01% Haplochromines in longlines. These data were not further considered. No-fishing days occurred because of operational (gear was stolen, boat burst, gear repair and no bait), environmental (heavy rain, strong winds), personal (illness, resting and holidays, village meetings, elections and travel) and economic (no fish) reasons.

The average (sd) total gillnet size used was 15000 (12000) m^2 (median 12000 m2) with panels of mesh sizes ranging from 4″ to 8″. Longlines were equipped with 800 (130) hooks, with hook sizes 11, 12 and 13. Individual fishers often changed nets and lines between trips, resulting in different total net sizes and hook numbers as well as mesh sizes and hook sizes per trip. In the gulf area, mesh sizes from 4-7″ were used in about equal proportion (~18%) of the time, while 8” mesh sizes were used in around 8% of the trips; in the open lake area, 61% of mesh sizes used were 5″ and 6″, while mesh-sizes 4″, 5″, 7.5″ and 8″ were used in about equal proportion (app. 10%) of the trips (Fig. 4.3, top).

Small hook sizes (13) were dominant in both regions, but more so in the open lake region, while the largest hook size (11) was only used in the gulf region. All mesh and hook sizes were used at all distances from the homeport. Larger meshes and hook sizes tended to be used further offshore, and small mesh sizes in both regions and small hook sizes in the gulf region were used more often nearshore up to approximately 5 km (Fig. 4.3, bottom). On average, smaller hook sizes were used in the open lake area compared to the gulf, with no trend in hook size over distance from the homeport. In subsequent catch-rate analyses, hook sizes were categorised as small (13) and large (11 and 12), as these groups differed significantly in total catch weight ($F_{1,1312}$ = 44.67, $P<0.001$, r^2 = 0.03). Soak-time for gillnets ranged from 4-15 hr with an average (sd) of 10 (2) hr and longline 2-13 hr with an average of 6 (1) hr.

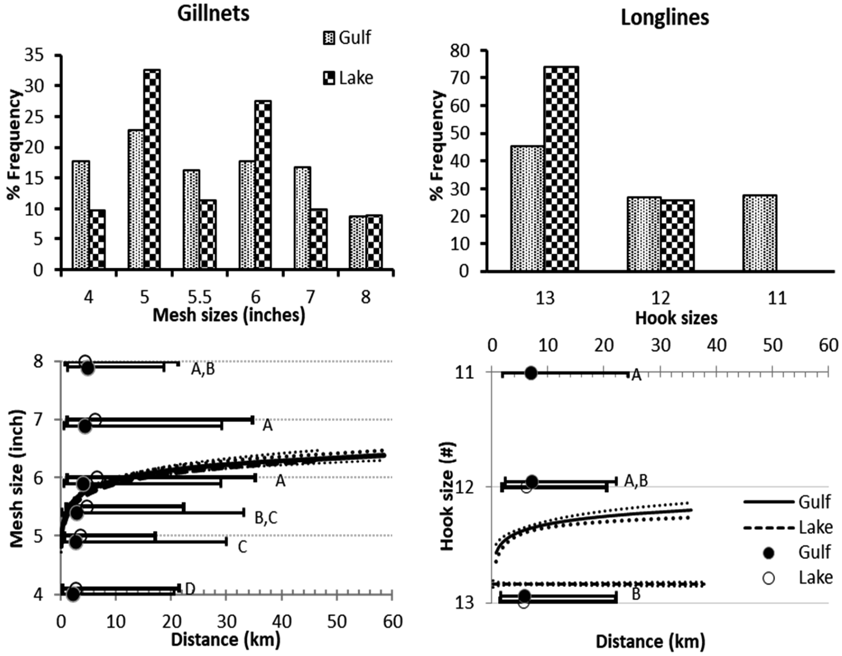

***Figure 4.3**: Top: % Frequency distribution of mesh and hook sizes used by gillnet and longline fishers in the Gulf and Lake region ($N_{meshsize\ Gulf}$ =5404, $N_{meshsize\ lake}$ =928, $N_{hooksize\ Gulf}$ =2075, $N_{hooksize\ Lake}$=754). Bottom: Mesh and hook size in relation to distance from the homeport, indicating the geometric mean distance (± 2 standard deviations) (circles and error bars) and the average mesh size over distance (lines) by lake region. Letters indicate significantly different groups of mean distances of mesh size or hook size use based on a Bonferroni corrected multiple comparisons test.*

Standardisation of observed catch rates

Haplochromines, Dagaa, *Synodontis*, and *Clarias,* were the main bait types used in longline fishing. The operational factors bait type, hook size and their interaction all had a significant effect on the observed catch rates both for weight ($F_{1312,7}$ = 28.8, p<0.001, r^2 = 0.13) and number (F1$_{312,7}$ = 40.0, $P<0.001$, r^2 = 0.17). Bait types *Clarias* and *Synodontis* had a higher CPUE in terms of weight both for small and large hook-sizes compared to Haplochromines and Dagaa, while Haplochromines and, to a lesser extent, *Clarias* on average, caught larger numbers of Nile perch. Average Nile perch sizes caught for all bait types except *Synodontis* ranged between 0.7kg (dagaa, large hook size) to 2.3kg (*Clarias*, large hook size), with an average of

1.5 kg over these bait types. *Synodontis* bait resulted in an average individual fish size of 3 kg and 8.8 kg for small and large hook sizes, respectively (Fig. 4.4).

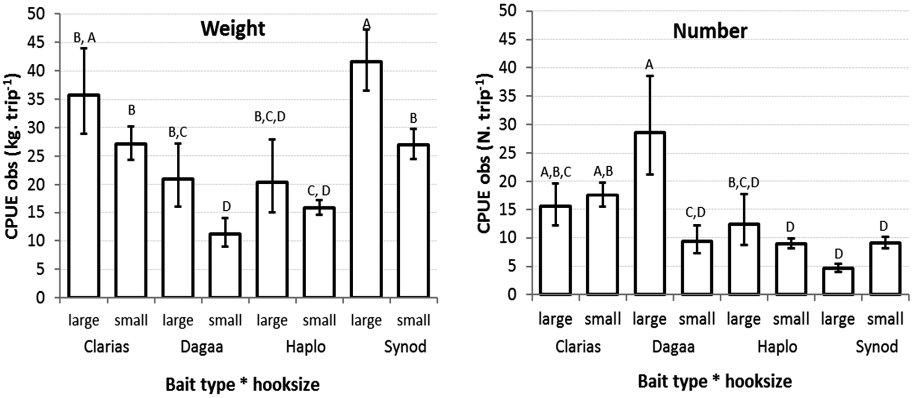

Figure 4.4: *Mean CPUE$_{observed}$ in weight (left) and number (right) of Nile perch by bait types Clarias spp., Rastrineobola argentea (Dagaa), Haplochromines (Haplo) and Synodontis afrofislhery (Synod) and hooksize (large= 11, 12) and small (13). Letters indicate significantly different groups of mean CPUE$_{observed}$ based on a Bonferroni corrected multiple comparisons test.*

The operational factors of net size, number of hooks and soak-time all significantly affected the size of the catch per trip expressed in the weight of fish. Net size and hook number did not significantly affect observed catch per trip in number; only soak time was significant (Table 4.2). Both weight and number of Nile perch catch per trip for gillnets were standardised to the median size of a net of 12000m^2 and a soak-time of 10 hr; for longlines catch per trip in weight was standardised to 800 hooks and a soak-time of 6 hr according to model (3) with parameter estimates as in Table 4.2.

Table 4.2: Parameter estimates for hook size, bait, net size, hook number and soak time used to standardise observed catch rates (kg.trip^{-1} and N.trip^{-1}). Hook size was standardised to "small hooks (13)"; bait was standardised to "*Synodontis*". A trip is a 6-hour duration with 800 hooks for longlines and 10 hours with 12000m^2 of net for gillnets. *** p<0.001, ** p<0.01, * p<0.05, ns= non-significant. Df=Degree of Freedom, F=F-statistic, r^2= coefficient of determination, Hs=Hooksize.

Gear type	Nile perch	Netsize /hook number (β_1)	Soak time (β_2)	Bait	Hook size	Bait* Hs	N	Df model	F	r^2
Gillnet	Weight	0.095***	-0.622***	-	-	-	1792	2	100.4	0.10
	Number	ns	-0.364***	-	-	-	1792	2	19.6	0.01
Longline	Weight	0.467***	0.347**	***	***	***	1313	9	25.7	0.15
	Number	0.657***	ns	***	*	***	1313	9	34.6	0.19

Average daily standardised catch rates of Nile perch ranged between 17-32 kg.day^{-1} and 15-25 fish for gillnets, and 34-40 kg.day^{-1} (10-18 fish.day-1) for longlines. Variation in standardised daily catch rates in gillnets and longlines was high on average, both in weight (CV=68% and 72%, respectively) and number (CV=67% and 83%) (Table 4.1). Gillnet fishers caught less large (>50 cm) Nile perch (median=10 trip^{-1}) compared to longlines (23 trip-^{1}) and around the same number of small Nile perch (10 trip^{-1}). The weight of small Nile perch caught was higher for gillnets (10 kg.trip-^{1}) than for longlines (7 kg.trip-1). In contrast, the weight of large Nile perch caught by longlines (23 kg.trip^{-1}) was larger than those caught by gillnets (10 kg.trip^{-1}) (Table 4.3), suggesting that long-liners focus more on larger sizes of Nile perch than gillnetters.

Table 4.3: Average (Mean), Median, standard deviations (SD) and coefficient of variation (CV) of standardised positive catch rates CPUE for small (<50 cm) and large (>50cm) Nile perch with gillnet and longlines gears in weight.trip^{-1} and number.trip^{-1}. The median trip duration and effort for longlines is 6 hours with 800 hooks; for gillnet, it is 10 hours with 12000m^{2} of net. Total number of observations Gillnets, N=3636; Longlines N=2636.

CPUE$_{stand}$	Gear	Size	Prob	Mean	CV	Median
N.trip^{-1}	Gillnet	<50	0.89	10	83	12
		≥50	0.91	13	115	6
	Longline	<50	0.64	6	141	3
		≥50	0.95	7	114	5
kg.trip^{-1}	Gillnet	<50	0.89	11	94	10
		≥50	0.91	13	112	10
	Longline	<50	0.64	9	142	6
		≥50	0.95	28	88	21

Resource space

The resource space of gillnet and longline fishers overlapped, but on average, gillnet fishers fished closer to the shore than longline fishers, while both appeared to fish over the same range. The distance travelled daily from a homeport to a fishing location for gillnets ranged between 0.1-39.3 km and was on average (sd) 5 (5.6) km; longlines travelled within a range of 0.2-37.9 km with an average (sd) of 7 (5) km (Fig. 4.1). These calculations included gillnet fishers who temporarily took residence in other areas in the lake and thus appeared to extend their resource space to other areas. However, within those new locations, distances travelled to fishing grounds from the new port fell within the same ranges as their original locations. Fishing operations of fishers who normally operated from the sites around the Speke Gulf but who temporarily moved to open lake sites were, in subsequent analyses, considered as open lake operations. Gillnet fishers with engines travelled 6 km (5%-95% range 1.7-21.4 km, N=864) compared to gillnet fishers with paddles 2 km (5%-95% range 0.23-10.5 km, N=945). One of the longline fishers with an engine dropped from further analyses travelled on average 5 km (2.3-10.9 km, N=17), suggesting a large overlap in resource space between propulsion types in this fishery.

The travelling time to cover these distances, recorded daily by the fishers participating in the logbook survey, appeared to be highly comparable to those of a group of 107 longline and gillnet fishers interviewed on their fishing activities, suggesting that the participating fishers are representative of a large proportion of southern Lake Victoria fishers. The geometric average logbook recorded travelling time for gillnet fishers was 59 minutes (5%-95% range: 24-121 min). Average travelling time between gillnet fishers ranged between 36–83 min, indicating different fishing strategies, though within fisher variation was high ($F_{7,1637}$=66.13, p<0.001, r^2=0.22). Longliners needed on average 108 min (51-188) to reach their fishing grounds: average between fisher variation was much lower (77-120 min), but with only 16% of the variation explained again with large within fisher variation ($F_{6,1289}$=41.02, p<0.001, r^2=0.16). Fishers with engines travelled significantly shorter, 46 min (5%-95% range: 20-103 min), than those with paddles and sails who used 70 min (30-135 min) to reach their fishing ground. However, only 14% of the variation in travel time was explained by propulsion type ($F_{1,1643}$=259.51, p<0.001, r^2=0.14). By comparison, the interviewed group of fishers, who reported the travelling time of their last two fishing days, travelled 75 min (90% range: 20-180). Of these groups, longliners travelled significantly longer (93 min) than gillnetters (57 min). In comparison, no significant difference was found between fishers using engines (68 min) and paddles and sail (90 min) ($F_{2,211}$=14.99, p<0.001, r^2=0.12; Type III error p=0.11 for the type of propulsion and p<0.001 for the gear type).

The group of interviewed fishers also were highly comparable to the group of logbook fishers in that they used the same boat types (Sesse), engines, and mesh sizes of gillnets - 94% of which were of sizes between 5-7 inch (127-178 mm) - and longline hook-sizes - 96% between hook-size 11 and 13 - numbers of hooks (average (sd): 700 (256)) and bait types. As none of the remaining longline fishers in the logbook survey had engines, propulsion was not further used explicitly as an explanatory factor. Still, as fishers were included as a random effect in the models explaining encounter rates and patch densities, this operational factor was accounted for indirectly.

Distance travelled, and the environmental factor location depth was highly collinear. A regression of $\log_{10}$(depth) for gillnet over region, season with log10(distance) as co-variate was significant ($F_{4,1769}$ = 1130, p<0.001, r^2 = 0.59). Gillnet fishers fished in deeper waters in the open lake region compared to the gulf region, irrespective of distance. Seasonality explained a mere <1% variation in location depth, where fishers were fishing in slightly deeper waters during the transitional short rain season. For gillnet fishers from the open lake region, the most common location depth at 5 km from the shore was 25 m (max. 48 m depth at 40 km), while their colleagues in the gulf were fishing at 13 m depth (max. 25 m depth at around halfway the gulf). Compared to fishers in the open lake region who headed more towards open waters, gillnet fishers from the gulf were fishing more often parallel to the shore at a distance from their homeport (Fig. 4.1). For longlines the relationship was also significant though less clear as distance explained less variation in depth of location while the difference between regions was not as pronounced as with gillnets ($F_{1318,6} = 55.7$, $p<0.001$, $r^2 = 0.20$). The most common fishing depth around the average of 7 km from the homeport for longline fishers from the open lake region was approximately 21 m, while their colleagues in the gulf were fishing at 17 m depth. Longline fishers were fishing at slightly deeper waters and, hence, further from the shore during the windy, dry season, accounting for 1.5% of the variation. In the remainder of the analyses, only the distance travelled will be considered and used as a proxy for the environmental factor location depth. The setting depth of the two gear types had limited overlap. Longlines were set about twice as deep (1-24 m; average (sd)=11 (5) m) as gillnets (1-15 m; 5 (3) m).

Random effects: clustering by fisher and size of Nile perch

Before discussing the full models for encounter rate and patch density, we first discuss the choice of random effects for these models, as these give insights into individual fishers' operational strategies. Clustering by fisher×size interaction for models examining encounter rates (model 4) led to a substantial reduction in AIC compared to the null model (intercept only). It accounted for gillnets and longlines, respectively, 34% and 44% of the variability (ICC, covariance parameter estimates: $p<0.01$) in the log-odds of catching Nile perch (Table 4.4). In the final model, which included size and interactions of size with other variables as fixed effects, the amount of variation explained by the random effect as expressed by the ICC was reduced to 16% and 23% ($p<0.05$), suggesting that the size of Nile perch took up a large amount of variability as a fixed effect. The fisher×size interaction can be understood as a variation in skills and operational strategies in the location choice of fishers and because of differences in the choice of mesh sizes and hook numbers. An in-depth examination of this random effect in the final model showed that for gillnet fishers most variation was found in the odds of catching small Nile perch that varied between 0.3 and 3, while those of large Nile perch varied between 0.7 and 6. However, in all cases but two, the odds were not significantly different from 1.

The two exceptions were fishers with significantly lower odds (0.3) of catching small Nile perch, indicating that they predominantly used larger mesh sizes or fished further from the shore where large Nile perch predominate, as shown below. Similar operational characteristics and apparent choice of hook sizes were found for longlines. For longlines, most variability between fishers again was found in the odds of catching small Nile perch. The odds ranged between

0.2 and 3, while the odds of catching the large Nile perched ranged between 0.9 and 6 and were not significantly different from 1, with three exceptions. The exceptions were a fisher with odds 6 and 0.3 for catching large and small Nile perch and another fisher with low odds (0.2) for catching small Nile perch. Choice of bait or hook size most likely were not causes of variation as these were accounted for as fixed effects. We checked this by including hook size and bait as random effects. Co-variance parameter estimates were non-significant when including hook size (θ=0.05, Z (2)=0.89, p=0.19) or bait as a random effect, the latter both on its own (θ=0.44, Z(4)=1.36 P=0.09) or in addition to the random effect fisher×size (θ=0.71, Z(18)=1.28, p=0.10). As the number of hooks, net size and soak-time were all accounted for as fixed effects, all other fixed effects related to the size category of Nile perch and interactions with the size category in encounter rates, therefore, now can be considered as characteristics of the environment and of gear-Nile perch interactions and thus are most likely not caused by specific differences in skills and operational characteristics of fishers.

We included a random effect for fisher for patch densities (model 5), which reduced AIC compared to the null model. However, the effect accounted for only 2% to 7% of the variability in patch density expressed as ICC in all models examined, non-significant in both longline weight and number models and just significant ($p<0.05$) in the two gillnet models. The variation or significance levels did not change in the final model, indicating that the fishers effect was fully accounted for. Although ICC estimates showed that fisher as a random effect could be removed for the longline models, it was kept in to make comparisons between models fully compatible.

Encounter rates: fixed effects determining the probability of catch

The final random intercept models examining encounter rates (model 4) included as fixed effects environmental (distance as a proxy for depth, setting depth, region, season), operational (distance as a proxy for travelling time, soak-time, hook-size, bait, number of hooks and size of nets) factors, Nile perch characteristics (size) and their two-way interactions. These were significantly different from the random intercept model only (Gillnets χ_{diff}^2 = 151.8, $p<0.001$; Longlines χ_{diff}^2 = 225.1, $p<0.001$). Both final models were only slightly over-dispersed. During the backward selection procedure, many interactions between the main effects were removed, and the main effects were soak time and hook size and their interaction. The impact of soak-time and hook size thus was only apparent in the catch densities and not in not the probability of catching Nile perch. Bait type was retained in the model and overrode the effect of hook size (Table 4.4). All further analysis in this section refers to table 4.4.

Table 4.4: Factors and interactions between factors determining encounter rates (probability of positive catch (P_c)) for gillnet and longline fishers. *** p<0.001, ** p<0.01, * p<0.05, ns= non-significant

	Gillnets						Longline					
AIC Null model	2323.5						2639.6					
AIC Final model	1830.3						1956.6					
Denominator DF	3577						2598					
Effect	df	F	p>f	Factor	Est.	p>χ^2	df	F	p	Factor	Est.	p>χ^2
Intercept					-0.30	ns					2.44	***
Season	2	4.34	*	Dry	-0.95	*	2	3.39	*	Dry	0.75	ns
				Long	0.03	ns				Long	0.39	ns
Region	1	0.25	Ns	Gulf	1.19	**	1	9.06	**	Gulf	0.22	ns
Size	1	32.32	***	<50	3.95	***	1	36.85	***	<50	-0.81	ns
Distance	1	12.95	**		0.26	**	1	0.81	ns		0.05	ns
Setting depth	1	3.66	Ns		0.26	**	1	5.02	*		0.01	ns
Season*size	-	-	-	-	-	-	1	13.38	***	Long, <50	-1.64	***
Region*Size	1	16.57	***	Gulf, <50	-2.07	***	1	17.66	**	Gulf, <50	-1.15	***
Distance(Season)	2	3.12	*	Dry	-0.08	ns	-	-	-	-	-	-
				Long	-0.19	*						
Distance (Region)	1	24.97	***	Gulf	0.28	***	-	-	-	-	-	-
Distance (Size)	1	26.04	***	<50	-0.32	***	1	11.45	**	<50	-0.13	**
Set. Depth (Size)	1	11.35	**	<50	-0.33	**	1	3.09	*	<50	0.05	ns
Residual					2.52						1.00	

Net size and number of hooks had small but significant effects on Pc in gillnets and longlines, respectively. Pc increased from 97% to almost 100%, with hooks increasing from 100 to 1000. In gillnets, it increased from 95% to close to 100% for large Nile perch, while for small Nile perch, it decreased slightly from 99% to 98% with an increase in net area from 100 to 10000 m^2.

Bait effects with their interactions were all significant but were dominated by the main size effect for longlines, where large Nile perch (*Pc* = 0.73) was 76 times more likely to be caught than small Nile perch (*Pc* = 0.01). Taking all effects into account, the four bait types had similar or higher *Pc* for large Nile perch (*Synodontis*, *Pc* = 0.73; Dagaa, 0.73; *Clarias*, 0.76-1; and haplochromines, 0.97-1). For some bait-types, *Pc* increased with increasing distance. However, confidence intervals for all estimates are large (Table 4.4): odds ratio estimates comparing the various bait types with each other at 7km distance and 7 and 20 km distance confirmed these differences but were invariably not significantly different from unity, highlighting the high variability around the estimates (Fig. 4.7). The analyses of the remaining factors all are with bait-type *Synodontis* as baseline.

The size category of Nile perch was the most dominant effect for both gears but with opposite main effects: for gillnets, it was 45 times more likely to catch a small Nile perch (*Pc* = 0.997) than a large Nile perch (*Pc* = 0.73), while for longlines it was over 200 times more likely to catch a large Nile perch (*Pc*=0.73) compared to small Nile perch (*Pc*<0.01). Spatial environmental factors, distance, setting depth and region all contributed to a lowering of AIC, but signals were less clear than size.

Spatial environmental effects with size changes were prominent in gillnets and, to a lesser extent, longlines. For gillnets size, distance and interaction effects of size with region, distance and setting depth, and distance with region were highly significant (Table 4.4). Overall odds for catching Nile perch increased with distance by 1%. Still, these were offset by a range of interaction effects that resulted in a different pattern for the open lake region than the gulf region. For small Nile perch, a regional effect led to an overall 2% lower probability of catch in the open lake region, but this difference was only observed at close distances to the homeport: the most dominant effect was the 17% decrease in odds per km distance for small Nile perch in the open lake that was offset by a 17% increase in odds over distance in the gulf. These effects led to a major difference between regions. Whereas in the gulf the Pc for small Nile perch increased from around *Pc* = 0.8-0.9 to close to *Pc* = 1 at further distances from the homeport, in the open lake region *Pc* = 0.8-0.96 in the first 10 km from the homeport decreased rapidly to almost zero at larger distances (Fig. 4.5). Spatial effects in relation to size for longlines were dominated by the difference in odds of catching large and small Nile perch, already discussed, the 37% overall lower probability of catch of Nile perch in the gulf to the open lake, and an interaction effect of size with setting depth. The 5% decrease in odds with distance affected both small and large Nile perch, leading to much-lowered encounter rates at larger distances for small Nile perch, comparable to gillnets in the open lake region (Fig. 4.6). With every meter increase in setting depth of gillnets, the odds of catching small Nile perch increased by 4% and of large Nile perch by 11%, leading to a slight effect of increased probabilities of catch for both size classes (Fig. 4.5). For longlines setting depth did not affect the Pc for large Nile perch. Still, the odds of catching small Nile perch per meter increased by 9% with every meter setting depth. However, here, the odds for setting depth and its interaction with size were not significantly different from 1, indicating that for longlines, the signal of setting depth for the size of the Nile perch was slight (Fig. 4.6).

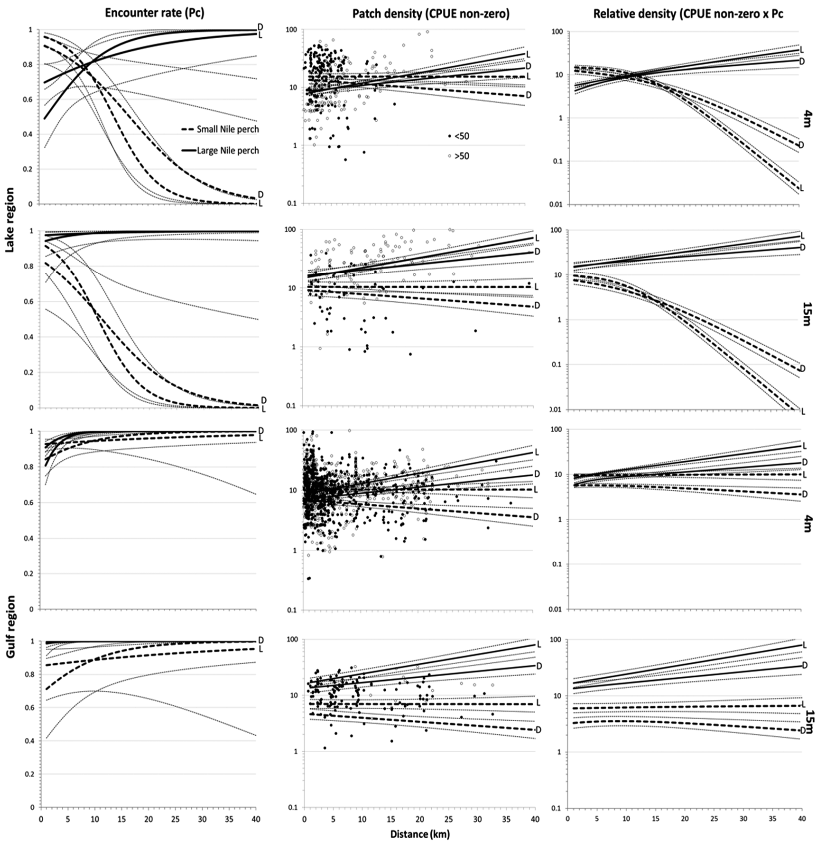

Figure 4.5: *Gillnet fishing encounter rate (P_c), patch density ($CPUE_{non-zero}$, kg·1200m^{-2}.10hr^{-1}), and relative density ($CPUE_{non-zero}$ x P_c, kg·12000m^{-2}.10hr^{-1}) by Nile perch size group (<50, ≥50cm) with distance from the shore at gear setting depths 4m and 15m in the Lake region (top two rows) and Gulf region (bottom two rows). The dotted lines are 95% confidence limits. L= long rain/stratified season, D= dry/mixing season.*

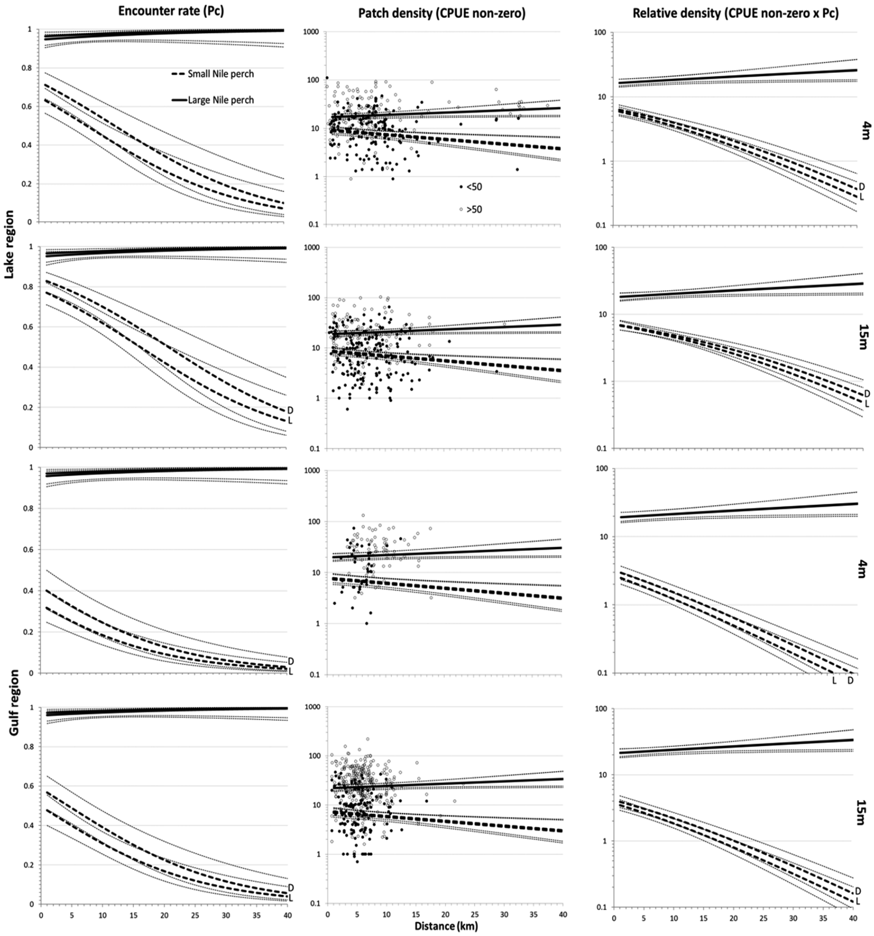

Figure 4.6: Longline fishing encounter rate (Pc), patch density ($CPUE_{non\text{-}zero}$, $kg \cdot 800hooks^{-1}.6hr^{-1}$), and relative density ($CPUE_{non\text{-}zero} \times P_c$, $kg \cdot 800hooks^{-1}.6hr^{-1}$) by Nile perch size group (<50, >50cm) with distance from the shore at gear setting depths 4m and 15m in the Lake region (top two rows) and Gulf region (bottom two rows). The dotted lines are 95% confidence limits. L = long rain/stratified season, D= dry/mixing season.

Overall, the spatial environmental effects lead to contrasting impacts for gillnets and longlines while the odds of catching Nile perch were lower in the gulf than in the open lake, the opposite was for gillnets. Longlines had lower odds of catching small Nile perch overall than gillnets, whereas, for gillnets, the odds of catching the two sizes were not significantly different from 1. The most conspicuous effect for both gears was the higher odds of catching large Nile perch at larger distances from homeport (Fig. 4.7).

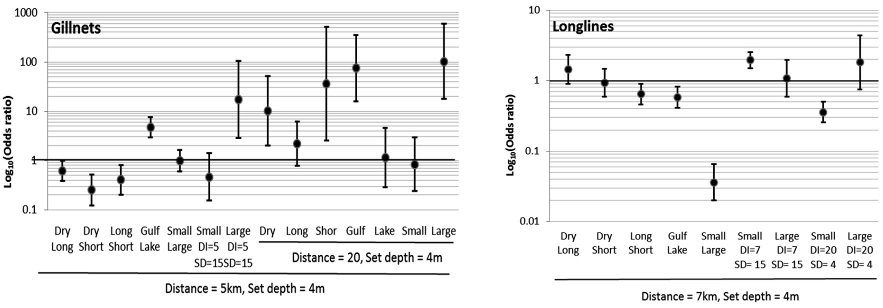

***Figure 4.7**: Odds ratios (Log10(odds ratio)) of encounter rates (probabilities of catch) of Nile perch related to region (lake, gulf) season (long, short, dry), size (small Nile perch <50 cm, Large Nile perch ≥50cm), distance (km) and setting depth (m) of gillnets and longlines. Odds of encounter rates are calculated for or compared with the probability of catch at the average distance from the landing place that a gear type is employed (gillnets 5km, longlines=7m) and a setting depth of 4m. DI=distance (km), SD=Setting depth (m).*

Seasonal effects were not prominent and were unrelated to distance, setting depth or size of Nile perch for both gears. Only overall effects and differences between regions were observed. In general, for both gears and areas, slightly elevated catch probabilities were encountered during the transition period between stratified and mixed seasons (Fig. 4.7). However, in the gulf region, Pc was elevated during the stratified season and not significantly different from the transitional season. In the open lake again, the highest *Pc*'s were found during the transitional season, followed by the stratified and mixed seasons that were not significantly different (Fig. 4.5 and 4.6; Table 4.4).

Patch density: fixed effects determining positive catch rates

The final random intercept models examining patch densities (model 5) included the same environmental and operational factors as the previous model as fixed effects. After parameter selection based on minimising AIC, three of the four models of patch densities by weight and number were significant at p<0.001 based on a restricted log-likelihood deviance test of the nested null and full models. The model for patch density expressed in numbers for longlines had the lowest decrease in AIC, and the deviance test was non-significant (χ234=46.3, p=0.08), suggesting that an intercept only with a random fishers effect model would be the most parsimonious. We kept the parameter estimates of fixed main effects and their interactions after backward selection, confidence intervals and significance levels (Table 4.5). The size of the Nile perch again was the dominant effect in all models. The main differences between the two gears were found when including region and interactions with size. Gillnets caught patches of small Nile perch between around 13.5 kg.trip^{-1} in both open lake and gulf region and respectively 12 and 14 fish.trip^{-1}, so with individual sizes around 1 kg. Longlines caught between 12 kg.trip^{-1} (gulf) and 14 kg.trip^{-1} (open lake) of small Nile perch but in lower numbers (7–6 fish.trip^{-1}), so with individual sizes of around 2 kg. Gillnet densities for large Nile perch are between 4.6 kg.trip^{-1} (2 fish) in the open lake and 7.1 kg.trip^{-1} (5 fish) in the gulf; for longlines, the values are respectively 18 kg.trip^{-1} (3 fish) and 21 kg.trip^{-1} (3 fish). These numbers indicate that longlines overall target fish that are 2-3 times larger in weight than gillnets, and those overall patch densities in the two regions are comparable, if slightly higher, in the Gulf.

Besides region, the spatial factors distance from the homeport, setting depth and interactions of these with size and region, when present, were all significant, resulting in increased patch densities and size of large Nile perch, a slight decrease in patch densities for small Nile perch with increasing distance. Overall weight and number of large Nile perch in the open lake increased with increasing distance for both gillnets and longlines with respectively 3 kg.trip^{-1} (1.5 fish) and 2.4 kg.trip^{-1} (1 fish) per 10 km. The increase was lower in the Gulf region for both gears with 1.3 kg.trip^{-1} (0.6 fish) per 10 km. Patch densities of small Nile perch in the open lake region increased with increasing distance with 1.4 kg.trip^{-1} (0.9 fish) per 10 km. Still, they decreased slightly with distance from homeport for gillnets in the open lake and for longlines in both regions respectively, 0.3 kg.trip^{-1} (0.1 fish) and 4 kg.trip-1 (0.1 fish) per 10 km. Patch densities for large Nile perch slightly increased in weight and number with deeper net and line sets with respectively 1.9 kg.trip^{-1} (0 fish) and 0.5 kg.trip^{-1} (0.9 fish) per 10 m setting depth. Small Nile perch patch densities for gillnets decreased by 1.1 kg.trip^{-1} (1.5 fish) every 10m depth, indicating an increase in individual sizes for gillnets and a slight decrease for longlines. Seasonal effects in patch densities suggested generally slightly lowered patch densities during the dry mixed season compared to the long-rain stratified and short rain transitional seasons but were insignificant (Fig. 4.4 and 4.5). Interactions of seasons with size appeared in all models, with generally a slight increase in weight and decrease in numbers for the dry and rainy season compared to the short-rain, transitional season. Interactions of the season with the region, setting depth and distance were present in different models with very different effects partially cancelling each other.

In summary, patch densities showed similar patterns over distance for both gears and regions except for gillnets in the open lake region. Over 20 km, the distance around 90% of the longline and gillnet operations of all fishers, small Nile perch patch densities decreased by 20-46% in weight and 7-38% in number. In absolute terms, this represents a decrease in patch density over 20 km between 3–6 kg.trip^{-1} and 1–3 fish.trip^{-1}. Large Nile perch patch densities increased between 26–50% in weight and 4–19% in number. In absolute terms, this represents an increase over 20 km of between 4-6 kg.trip-1 and 0.1-1 fish trip^{-1}. The exception was for gillnets in the open lake region, where small fish patch densities increased over 20 km in weight. This represented an increase in patch density for small and large Nile perch, respectively, of 8 kg.trip^{-1} (4 fish.trip^{-1}) and 6 kg.trip^{-1} (91 fish.trip^{-1}). In general, over a 20 km distance, the average individual weight of small Nile perch in the gulf and open lake regions was between -250 and 220 grams, while the individual weight for large Nile perch increased in all cases between 380 and 1410 grams. In other words, at further distances, patch densities of small fish were less numerous, but individuals were smaller in the gulf and larger in the open lake area. In contrast, the patch densities of large Nile perch remained the same or increased somewhat, but individual fish were larger.

Factors determining relative biomass and density

Overall, the relative biomass (CPUEst*Pc, kg.trip^{-1}) for both longlines (Fig. 4.6) and gillnets (Fig. 4.5) had similar patterns in the gulf and open lake regions and at different depths, whereby large Nile perch CPUEst increased over distance from the homeport while small Nile perch decreased rapidly after a 10-15km distance, more prominent with gillnets. The exception was gillnets in the gulf region, for which relative biomass for small Nile perch remained the same or decreased slightly.

Size effects dominated spatial patterns of relative biomass and density of catch for both gears and regions (Fig. 4.5 and 4.6). Large Nile perch $CPUE_{ad}$ increased in both gears and regions. For longlines, over the first 20 km from homeport, this led to an average increase in catch rate from 19 kg.trip^{-1} to 24 kg.trip^{-1} in the gulf and from 16 to 21 kg.trip^{-1} in the open lake, where in all cases around 4 fish.trip^{-1} were caught. The average weight (length) of large Nile perch thus ranged between 4.5 kg (71 cm) to 5.7 kg (76 cm). Gillnets, on average, caught less large Nile perch in weight and more in number. Over the first 20 km, this increased from 9.2 kg.trip^{-1} (6 fish) to 15.4 kg.trip^{-1} (9 fish) in the gulf. A dramatic increase was observed in the open lake from 6.2 kg.trip^{-1} (3 fish) to 21.3 kg.trip^{-1} (11 fish). Large Nile perch in gillnets thus was smaller than those caught by longlines: the average weight (length) ranged between 1.6 kg.trip^{-1} (52 cm) and 2.1 kg.trip^{-1} (56 cm). Small Nile perch $CPUE_{ad}$ in all cases decreased. In long lines, this amounted to a decrease in catch rates in the gulf over 20 km from 1 kg.trip^{-1} (1 fish) to 0.3 kg.trip^{-1} (0.2 fish) gulf and in the open lake region from 3.4 kg.trip^{-1} (2 fish) to 1.2 kg.trip^{-1} (1 fish). This led to an average individual weight (length) range between 1.5kg.trip^{-1} (50cm) to 1.6 kg.trip^{-1} (52cm). In gillnets, small Nile perch catch rates in the gulf decreased from 5.7 kg.trip^{-1} (7fish) to 4.9 kg.trip^{-1} (6 fish) and in the open lake from 9.3 kg.trip^{-1} (9 fish) to 4.2 kg.trip^{-1} (5 fish). The average individual weight thus was 0.8kg (41cm) to 0.9kg (46cm), again smaller than caught by longlines.

Setting depth had a pronounced effect for large Nile perch on relative biomass and density. In gillnets, comparing 4 m and 15 m setting depth over 20 km distance increased to 2.5–5 kg.trip^{-1} (5-8 fish) in the gulf and 1–8 kg.trip^{-1} (4-10 fish) in the open lake. Small Nile perch decreased in catch rate with increasing setting depth between 1-2 kg.trip^{-1} and 1-2 fish, with limited seasonal effects. Differences were even more limited for longline catch rates that over the first 20km from homeport increased from 0.8 kg.trip^{-1} (0.5 fish) to 0 kg.trip^{-1} in the gulf and 2 kg.trip^{-1} (1fish) to 0 kg.trip^{-1} in the open lake. Catch rates in weight of small Nile perch did not change with increased setting depth in weight for large fish and only slightly increased in number. Seasonal effects suggested slightly elevated catch rates during the short, transitional, and long rain stratified seasons, with a stronger effect for gillnets and smaller Nile perch in weight and number. However, confidence intervals around CPUE estimates over distance for different seasons and setting depth overlapped, and estimates were non-significant from each other over the whole range examined. While the slopes were significant, the width of the confidence intervals also implied that the observed changes were detectable only over large distances, except for small Nile perch densities that showed a clear overall decrease over distance.

Long-term large-scale relative biomass changes: IFD predictions.

Over the period, total relative biomass was summed over the size categories and averaged over depth and season for each of the two fisheries increased over distance. Nearshore relative biomass for the two gears ranged between 15-20 kg.trip^{-1} and over the first 20 km distance from the homeport, covering 90% of all fishing operations, increased to 20-25 kg.trip^{-1}. At larger distances, expected catch rates increased to around 25-28 kg.trip^{-1} except for gillnets in the open lake region, which showed a larger increase (Fig. 4.8).

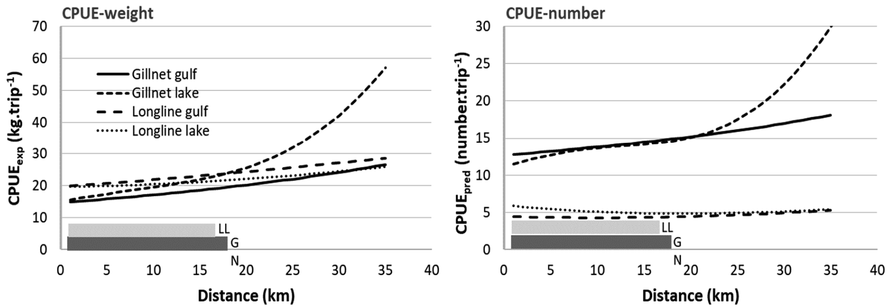

Figure 4.8: *Expected CPUE (kg. trip-1 (left)), number. trip-1 (right)) of Nile perch over the water column summed over large (>50 cm) and small (<50 cm) Nile perch and averaged over 4 and 15m setting depth and the three seasons for longline and gillnet fishers in the Gulf and Lake regions. Horizontal bars: 90% of the trip observations were within the range of distances from the homeport indicated for gillnets (GN, dark grey) and longlines (LL, light grey).*

The catch rate in numbers of fish was even more stable for gillnets in the first 20 km, increasing from 13 to 15 fish.trip^{-1} and for longlines hovering between 4-5 fish.trip^{-1}. Thus, average size differences over distance were also small and increased with distance from homeport between 0.1-0.3 kg for gillnets and 0.7-0.8 kg for longlines. Overall average Nile perch sizes for gillnets are 47-52cm and for longlines between 66-75 cm. Except for gillnets in the open lake at large distances from the homeport, total relative biomass estimates over distance thus were highly similar between the gulf and open lake regions and the two gears.

Discussion

The resource space of Nile perch fishers was determined by the travel distance, which ranged up to 39 km for both gears. It was centred around 3.5 km (gillnets) to 6.2 km (longlines) from the homeport (Fig. 4.1). Distances travelled. Location depths were highly collinear, meaning that travelling further meant fishing in deeper waters, while fishers mostly moved away from the shore. The exception was gillnet fishers in the gulf region, who travelled more alongshore. While resource spaces of longline and gillnet fishers overlapped, especially when gillnet fishers used outboard engines, there was limited interference between the two gears as gillnets were set overnight and longlines during the day. Furthermore, longlines generally were set twice as deep as gillnets. Finally, on average, the two gears targeted different size classes of Nile perch, with gillnets targeting overall smaller Nile perch than longlines.

Over the resource space up to around 15-20 km, where 90% of all fishing activities took place, the average total CPUE in weight increased slightly and in numbers was relatively stable over all locations and seasons. Fishers generally did not venture much further, and location choice appeared not strongly driven by expected higher catch rates away from the shore. This suggests that large daily variability in catch rates and the limited strength in other signals of fish distributional patterns that fishers received from the environment obscured the relatively small increase in total catch rates over distance. Other than the clear spatial patterns in size classes of Nile perch related to distance from the shore and depth, environmental signals had limited informational value for location choice. Environmental effects from region, season, and setting depth of gears were present but small and largely obscured by the high variation in encounter rates, patch densities and resulting catch rates, and random effects from different fisher strategies.

The high individual variability and the limited strength of environmental signals from the resource imply that fishers have a limited capacity to direct effort in space within this resource space (van Densen, 2001; van Oostenbrugge et al., 2002). Their distribution of the resource may be largely driven by operational constraints including costs such as available time and money (Salas and Gaertner, 2004). However, clear patterns in Nile perch size distribution existed to which the two gears reacted differently. We will first review these patterns and then discuss the resulting allocation effects in relation to the IFD predictions.

Of the environmental signals examined, the size of the Nile perch explained the most variability in encounter rates and patch densities, both as the main effect and in interactions with other environmental and operational effects. As described earlier, small Nile perch encounter rates decreased rapidly towards deeper waters (Katunzi et al., 2006; Taabu-Munyaho et al., 2013). In contrast, encounter rates with large Nile perch for both gear types and in both regions were always high and increased with increasing distance from the shore. Patch densities of Nile perch were hardly explained by any main effects except size, indicating that local variations in Nile perch densities within the area covered by a gear were not strongly driven by environmental or operational factors. For the Speke Gulf region gillnetters, encounter rates with small and large Nile perch remained high and increased with distance from homeport, while patch densities remained the same or increased. This was most likely a result of their more along-shore choice in fishing locations, and these fishers thus remained in areas with high encounter probabilities and overall stable catch rates of small Nile perch. Their increase in total catch rates over distance came mostly from large Nile perch, suggesting that at further distances from homeport along the shore, these fishers had less competition with other fishers targeting large Nile perch.

We expected larger Nile perch to be caught more in deeper, less heavily fished open lake areas (van Zwieten et al., 2016). Catch rates increased with increasing distance for both gears, especially for gillnetters in the open lake region. However, catch rates of large Nile perch in nearshore areas up to 20 km did not differ much between regions, though the average size of Nile perch increased with distance. Possibly, this indicates that fishing pressure on larger sizes was more evenly spread over the resource spaces of the Nile perch fisheries or that the gulf, with its higher fishing pressure, is more productive than the open lake area.

Seasonal effects driving Nile perch densities had equally limited informational value for daily fishing decisions. Generally, somewhat elevated Nile perch densities were present during the transitional, short-rain and the stratified, long-rain seasons. Increased densities of Nile perch higher in the water column during the stratified seasons have been observed in acoustic surveys and seasonally aggregated catch rates based on catch assessment surveys (Taabu-Munyaho et al., 2013), but in that case, the effect was not strong. This indicates that either the upward movement and resulting change in densities during stratification and in the transitional period during which turnover and mixing of waters takes place was not very strong or that, in our case, the stratification during the period of our research was not very strong (Cornelissen et al., 2015). Furthermore, no clear evidence for changes in setting depths or location was found over the seasons, indicating that individual fishers do not seem to change their fishing behaviour strongly in reaction to the effects of stratification on Nile perch and that effects may only visible when aggregated over large numbers of fishers.

The weak seasonal signal indicates no clear inshore spawning movement of Nile perch (Mkumbo 2002), while there is also no evidence for inshore nursery areas of targeted juvenile fish from 30 cm onwards. Both types of movement would increase patch densities during specific seasons in areas close to the shore, which was not the case. Though Nile perch is known to have higher densities of small juveniles of <30 cm close to the shore (Katunzi et al., 2006; Nyboer and Chapman, 2013), speculations about specific “spawning grounds” and “nursery areas” (Ligtvoet and Mkumbo, 1989) do not seem warranted, at least not for the areas covered in this study. The highly variable encounter rates and patch densities for both gears indicated that Nile perch was highly dispersed over space and did not appear in large groups that could be specifically targeted, as was also suggested by hydro-acoustic surveys (Goudswaard et al., 2004). Nile perch >30 cm, the lower size limit caught by fishers in this study, is a non-schooling solitary fish (Goudswaard et al., 2004). The high variation in patch densities and limited explanatory value of seasonal and spatial factors confirms the highly heterogeneous distribution of Nile perch found by Cornelissen et al. (2015).

The different patterns in encounter rates and patch densities of sizes of Nile perch for the two gears highlight different operational strategies resulting from their specific catch characteristics. Gillnets retain fish passively over a surface area, while longlines attract individual fish to bait on a hook (Bjordal, 2002). Mesh-sizes set by individual gillnet fishers ranged between 4 and 8 inches (101 – 203 mm stretched mesh), targeting Nile perch of 40 cm and 70 cm modal lengths (Msuku et al., 2011). Actual mesh sizes used varied almost daily, but the net set always included a range of small and large meshes. Except very close to the shore where smaller mesh sizes were used, on average, mesh sizes did not differ much over the distance from the home-port and by setting depth, indicating that fishers always targeted Nile perch over this size range.

Moreover, next to targeting a large size range, 11% of the catch weight consisted of several other species. This range of sizes and species caught in gillnets amounts to a bet-hedging fishing strategy. Increasing the fish portfolio over sizes and species decreases the catch variability in daily fishing outcomes (Schindler et al., 2015; van Densen, 2001).

In contrast, while the range of Nile perch sizes caught in our study by the different hook sizes 11-13 does not differ much from the reported modal lengths of 59-62 cm selected by these hook sizes (Msuku et al., 2011), their reported range in sizes caught of approximately 20-100 cm is high (Chitamwebwa et al., 2009). Chitamwebwa (2009) highlights that the choice of bait has an important effect on Nile perch sizes and shows the opportunistic character of Nile perch choices in the size of food relative to its size. With hook sizes 10-12, *Clarias* bait caught Nile perch with a dome shape, peaking at 60 cm but with a range of approximately 20-100 cm, whereas haplochromine bait caught the same size range but skewed with a peak at 40 cm. Most likely, the bait's condition and size also may impact the catch success (Kumar et al., 2015;

Sistiaga et al., 2018), possibly explaining the differences and high variability in the catch probability of the different bait types observed. That large Nile perch is caught by the relatively small hooks dominant in the fishery, which may be explained by the function of bait. Hook size had no significant effect on encounter rates with Nile perch, while there was a strong interaction between hook size and bait type. Bait type thus largely determines the catch characteristic of longlines as different bait types attract different species and sizes (Wraith et al., 2013) regardless of hook size.

Furthermore, larger fish have larger feeding ranges and thus may be more successful in competing for bait (Løkkeborg and Bjordal, 1992). We do not have the information to investigate these effects on daily outcomes further. However, for longlines, bet-hedging shifts to the choice of bait type in combination with small hook sizes and remaining relatively close to the shore. By doing so, longline fishers can still target large Nile perch using the attraction characteristics of the bait while also using the smaller, more productive size classes encountered closer to the shore.

While encounter rates more drove effort allocation than patch densities, daily patterns in encounters with patches of fish gave rise to an aggregated relative biomass related to the underlying biomass targeted by the two fisheries. Patterns in relative catch rates were similar for the two gears and between regions and coincided with what is known about the distributional patterns of Nile perch. Large, adult Nile perch occupies all open water habitats in the lake (Schofield and Chapman, 2000) and increases further offshore, is more common in deeper waters, and moves higher in the water column during the stratified season (Taabu-Munyaho et al., 2014), though the latter effect was small. As was the case for large Nile perch, smaller juvenile Nile perch were found at all depths in the lake but with higher densities in nearshore shallow waters (Katunzi et al., 2006), possibly because they are more tolerant to hypoxia (Robb and Abrahams, 2003) a condition found in shallow or nearshore habitats (Cornelissen et al., 2014).

Clear patterns of Nile perch size distributions thus exist, directing fishers' decisions in location choice. Although fishers are constrained by their daily movements from a single homeport and limited action radius due to time constraints and propulsion methods, violating the IFD assumption of free movement, overall catch rates within and over gears showed only a limited increase over distance. Thus, fishers largely appear to follow the prediction of the IFD theory of distribution over space such that resource outcomes are equalized (Gillis et al., 1993; Gillis and van der Lee, 2012). As a consequence of the IFD theory, patterns in effort allocation are predicted to follow the underlying size/productivity spectrum of Nile perch (Plank et al., 2017), which implies that spatial allocation of effort aggregated over all fishers and time will reflect the underlying productivity distribution of a resource. Other than size, Nile perch densities are only to a limited extent explained by other spatial and temporal environmental signal factors, indicating that these only have limited value in driving the location choice of fishers. Thus, fishers can then be expected to distribute themselves over the resource where renewal rates are highest if revenues per kg of fish do not differ much between sizes. Natugonza et al. (2016) estimated the P/B ratio of juvenile Nile perch in their study defined as <40 cm, at 3.5 year-1, while adult Nile perch (>40 cm) had a P/B=0.92 year-1. Productivity of 30-50 cm juvenile Nile perch, the main target in the fishery, thus is high, and this size range is within the 10 km distance from the shore where most fishing takes place.

As Natugonza et al. (2016) showed, current exploitation patterns in Lake Victoria are skewed to the least productive higher trophic level categories, including large Nile perch, with significantly less fishing occurring at the most productive lower trophic level categories, including small Nile perch. While enforcement up till recently has been weak, mesh size regulations still appear to form a constraint on the use of smaller mesh sizes, as attested by the distribution of mesh sizes over the open lake peaking at 6 inches (152mm) (Fig. 4.2). The decreasing mesh-size and hook-size frequencies respectively from 6 inches (152mm) and size >10 onwards suggests that Lake Victoria's fishing patterns were distributed proportionally to the productivity spectrum of the resources. Overall, fishing pressure was higher in the enclosed gulf compared to the open lake region (LVFO, 2017). Our starting point in contrasting open lake and gulf regions is that this would lead to lower catch rates and higher resource competition. At the same time, fishers would distribute over a larger resource space, which was not observed in this study. Despite the higher fishing pressure, catch rates in the gulf and open lake regions were highly similar. Fishing strategies and resulting fishing patterns may be optimised in a trade-off between operational costs and expected outcomes at locations where renewal rates of Nile perch are high. If the fishers of our study indeed are representative of the Nile perch fishery around the lake, as we suggest they are, this would mean that currently, a large part of the open lake and even the middle part of the gulf's surface and deeper waters are only lightly fished and thus could serve as a refuge for less productive large Nile perch. Current gear regulations, if enforced, force gillnet and longline fishers to focus on the lower productive adult Nile perch stock further from the shore and deeper in the water column. Without concurrent effort regulations to reduce the number of fishers this may be counterproductive and lead to overfishing of the large Nile perch size classes.

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Chapter 5

Bet-hedging strategies determine daily choices in effort allocation for Nile perch fishers of Lake Victoria.

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Peter, H.K. and van Zwieten, P.A.M. 2022. Bet-hedging strategies determine daily choices in effort allocation for Nile perch fishers of Lake Victoria. *Fisheries Research*, 2022, 253, 106363

Abstract

Small scale fishers experience high variability in daily catches within a resource space limited in extent by operational constraints, and biophysical factors affect daily choices in spatial effort allocation. We focus on the management consequences of the extent of the individual fisher's resource space and his options to handle risk arising from daily catch variability through a portfolio of sizes and species within that resource space. Gillnet and longline Nile perch fishers in south-eastern Lake Victoria, Tanzania, were provided with a GPS and recorded their position and daily catch and operations. Three different gillnet and longline fishing strategies could be discerned. All had bet-hedging characteristics, differing in the size of their resource space of an average of 120 – 141km2, distance from the shore fished and emphasis on the mix of sizes of Nile perch and other species caught. Daily choice of fishing locations did not relate to previous days' catch success. Still, fishers used the general inshore to offshore distributional patterns of small and large Nile perch in their daily choices of mesh and hook sizes. The mix of sizes and species reduced day-to-day catch variability due to a portfolio effect. Current mesh and landing size regulations based on classical arguments around growth overfishing interfere with these strategies and force individual fishers to specialise in size, species, and area. They must accept higher uncertainties by choosing their fishing locations further offshore or accepting a variable lower catch, leading to higher personal and occupational risk or ongoing management conflicts when disregarding regulations. Portfolio management of fished resources by compromising on mesh size regulations would make sense by allowing fishers to utilise a certain proportion of smaller mesh or hook sizes that are now illegal as part of their fishing strategies.

Introduction

Good fishery management requires accounting for the full dynamics of a fishery: fish stocks, fleet dynamics and individual fisher's behaviour (Béné and Tewfik, 2001; Hilborn, 1985). Failures in understanding strategies arising from individual fisher's decisions on effort allocation and aggregated fleet behaviour (Fulton et al., 2011; Opaluch and Bockstael, 1984; Salas and Gaertner, 2004; van Putten et al., 2012) may lead to management failures. Fishers target a range of sizes and fish species to reduce risk and often cannot readily adapt to changing regulatory and environmental circumstances (Aburto et al., 2009; Bavinck et al., 2018; Cardwell and Thornton, 2015; Kolding and van Zwieten, 2011). Here, we aim to uncover factors that shape fisher's daily choices in spatial effort allocation and how they cope with day-to-day catch variability, focusing on Nile perch fishers of Lake Victoria (Figure 5.1). What are the consequences of the limited spatial extent of an individual fisher's resource space and options to handle daily and long-term variation with a catch portfolio from that space (Anderson et al., 2017; Teh et al., 2012)?

The use of resource space can be understood by describing patterns in effort allocation and identifying their rationale (Béné and Tewfik, 2001). In North Atlantic fisheries, exploitation decisions of fishers and fleet dynamics were studied using detailed vessel distribution and movement data to examine interactions of vessels, fleets, and stocks. Answers were used to predict impacts on stocks, in parameter estimations, in stock assessments, and in the bio-economics of the spatial behaviour of fishers and fleets (Bourdaud et al., 2018; Gillis, 2003; Girardin et al., 2017; Hilborn, 1985; Poos and Rijnsdorp, 2007; van Putten et al., 2012). Predictions used data-driven random utility models or conceptual frames as ideal free distribution (Gillis, 2003; Rijnsdorp et al., 2000), optimal foraging (Rijnsdorp et al., 2011) or vessel trajectory analysis (Gloaguen et al., 2015; Vermard et al., 2010). Studies were often aided by detailed data on vessel positions and movements from Global Positioning Systems (GPS) or Vessel Monitoring Systems (VMS) (van Helmond et al., 2020).

A limited number of studies on effort allocation of small-scale, multi-species fisheries in tropical aquatic systems exist, focusing on territorial use and rights (Aburto et al., 2009), perceptions of patterns in local availability of fish (Pet-Soede et al., 2001; van Oostenbrugge et al., 2002), system approaches to elicit socio-cultural, economic, and biological drivers (Béné and Tewfik, 2001; Naranjo-Madrigal and Bystrom, 2019) and operational, environmental, and resource productivity factors (Peter and van Zwieten, 2018). Most small-scale fishers do not use GPS on fishing trips: spatial use studies generally are based on interviews, resource use mapping exercises or creel surveys (Pet-Soede et al., 2001; Siahainenia, 2016). These approaches have difficulties in accurately recording harvest locations (Close and Brent Hall, 2006). Small-scale fishers participating in our study were equipped with GPS, and their daily fishing locations and associated catches are known.

Fishing effort allocation: resource space, catch variability, portfolio effect

Small-scale fishers face several constraints. Catch variability causes financial risk (Cambiè and others, 2017), complicating strategic and tactical effort allocation decisions (Pavlowich and Kapuscinski, 2017). Their resource space, the area fished over their lifetime, is constrained by operational resources such as vessel size and propulsion mode. Limited storage space and refrigeration require that perishable fish land immediately after catch. With few possibilities to increase the scale of daily operations, fisher's resource space is thus restricted to an area around the landing site. This leads to a “friction of distance” problem – the trade-off between potential higher catches further offshore and costs and risks in travelling further from the homeport (Aburto et al., 2009; Caddy and Carocci, 1999).

Within the spatial constraints of daily fishing trips, fishers control factors such as distance to a fishing location, fishing time, gear types, gear numbers and gear operations. But they also face non-controllable factors (Christensen and Raakjær, 2006), as climate patterns and the distribution of targets over their resource space that may or may not be predictable. Predictability depends on the specific life-history characteristics of a species, including spatial behaviour of different life stages and the capacity of a fisher to discern and react to species-specific behaviour (Pet-Soede et al., 2001; van Oostenbrugge, 2003).

With a variable environment and limited predictability in stock distribution, fishers are expected to hedge bets to reduce uncertainty and risk (Boyce et al., 2002; Cambiè et al., 2017; Olofsson et al., 2009). In general, exploitation strategies available to small–scale fishers are: (1) to increase the quantity of their gear (invest in more of the same nets/hooks); (2) to increase the size range of the target species by increasing the number of different mesh or hook sizes used, or through active fishing methods; and/or (3) increase the number of species caught, depending on whether these species are found together (Jul-Larsen et al., 2003). The first strategy focuses on reducing risk by increasing the share of the resources taken by a fisher. The latter two are bet-hedging strategies that diversify catch over a range of species or sizes of fish to gain a more stable catch and potential income. This is the portfolio effect, a common strategy to reduce risk (Anderson et al., 2017; Lehman and Tilman, 2000; Matsuzaki et al., 2019; Sethi, 2010; Tilman et al., 1998).

In specific situations, strategies are influenced by the legality of fishing gears and methods, the level of actual enforcement of regulations, next to the price of fish and consumer preferences. The two bet-hedging strategies become increasingly tricky under limitations imposed by single-species fisheries management. Regimes focussing on single species catch optimisation force fishers to become specialised in sizes, species, and spatial areas (Aburto et al., 2009; Anderson et al., 2017), preventing them from using traditional means of risk management through diversification. In fishery systems worldwide, the ability of harvesters to maintain a diverse set of fishing strategies is vital for building adaptive capacity (Anderson et al., 2017; Beaudreau et al., 2019). A first step towards the development of management that accounts for fishers' risk-taking is by carefully categorising fishing activities, exploitation patterns and traditions to encounter variability and risk employed by small-scale fishers (González-Álvarez et al., 2016; Prestrelo et al., 2019, Tzanatos et al., 2012). Based on their spatial and observational constraints, portfolio management then recognises fishers’ options to choose among a diverse portfolio of sizes and species, accounting for risk resulting from uncertainty in the availability and abundance of species and sizes over their resource space (Hilborn et al., 2001).

The Lake Victoria Nile perch fisheries

Lake Victoria, the second largest freshwater lake in the world, supports one of the largest inland fisheries in terms of catch volume (0.8-1 million tons total, 240000 ton Nile perch), numbers of fishers (220,000) and landing sites (>1500) distributed along 3500km of coastline and over numerous islands (LVFO, 2017, Kolding et al., 2014b). Economically, Nile perch is the most important stock, intensively targeted and receiving the closest management attention. Nile perch are exported internationally as frozen fillets and traded regionally in fresh or processed (smoked, dried) form. Nile perch carcasses, heads, skins and swim bladders are important by-products (Kimani et al., 2018; Sadovy de Mitcheson et al., 2019). Freshwater fisheries in the region contribute between 0.4% (Kenya, Lake Victoria), 2.1% (Uganda, the whole country of which Lake Victoria contributes 40% of the catch) and 1.7% (Tanzania, Lake Victoria contributes 60% of the catch) of GDP (MLF, 2020, Onyango et al., 2021, UBOS, 2020). Lake Victoria Nile perch fisheries are increasingly crucial for regional trade and food security (Obiero et al., 2019; UNCTAD, 2017).

Nile perch can grow up to 2m, reach maturity in 2 years at around 60-70cm, is highly fecund (Ogutu-Ohwayo, 1988) and has a high population growth rate (Natugonza et al., 2016). A generalised solitary predator feeds on a wide range of prey and does not form (spawning) aggregations (Cornelissen et al., 2015; Goudswaard et al., 2006). At normoxic conditions, Nile perch can be found over the entire water column, with higher densities of small juveniles in riparian zones and sub-adults in inshore waters. Adult individuals are found inshore but dominate in offshore waters (Peter and van Zwieten, 2018; van Zwieten et al., 2016).

This study focuses on the longline and gillnet fisheries that target Nile perch (Sangara). The Nile perch fishery dominates in the number of fishers. It operates next to a large light fishery on *Rastrineobola argentea* (Dagaa) and smaller gillnet and beach seine fisheries, mainly targeting *Oreochromis niloticus* (Sato) in nearshore areas. Nile perch catch rates increase slightly over distance from the shore, but Nile perch fishers concentrate in areas with the highest fish productivity while catching both small and large Nile perch (Peter and van Zwieten, 2018). In nearshore waters, other species such as *Oreochromis niloticus*, *Clarias spp*., Synodontids, mormyrids and bagrids also appear in their catch. All fish species are landed and sold for consumption, with no discards.

The Nile perch fishery is managed under the authority of the three riparian countries, Kenya, Tanzania, and Uganda, coordinated by the Lake Victoria Fisheries Organization (LVFO). The main objectives of current management plans (LVFO, 2015a, b) are increasing revenues from Nile perch exports and raising catches to 300000 tons. To achieve these objectives, measures include limiting total effort and eliminating “undersized” Nile perch (<50cm) catches through mesh and hook size regulations, banning monofilament nets and beach seining, protecting nursery areas and a slot size (minimum and maximum landing size). While fishers view regulations as legitimate and justifiable, they consider using illegal gears necessary due to decreasing catch rates and sustaining livelihoods (Cepić and Nunan, 2017; Nunan et al., 2018). According to fisheries managers, the introduction of co-management in the 1990-ies has not changed the extent of illegal practices that are believed to threaten the sustainability of the fishery. Fishers generally disagree with this view (Nunan et al., 2018). Recently, enforcement efforts involving police and coast guards in Tanzania and the army in Uganda (Mpomwenda et al., 2022) have focussed on the “eradication” of illegal catches of undersized Nile perch by confiscating and burning boats and illegal gear, leading to the loss of livelihoods and, allegedly, lives (Jacobson, 2019; Mpomwenda et al., 2022). However, during our study, practically, there was no enforcement on illegal mesh and hook sizes.

To understand the distribution patterns of fishers over the resource (Peter and van Zwieten, 2018; Taabu-Munyaho et al., 2014), we will investigate the various strategies that individual Nile perch fishers employ to maintain catch rates. Nile perch fishers face a trade-off between fishing further offshore to catch legally sized large Nile perch with a higher value per specimen but low abundance and low productivity (Natugonza et al., 2016), leading to more variability in catches and income. Alternatively, with limited possibilities to invest in vessels, propulsion, and fishing gear, we propose that fishers may reduce variability in the catch, hence risk, by using the bet-hedging strategies discussed and opt to target different sizes of Nile perch and/or catch other species over a limited resource space. Thus, what are the Nile perch fishers’ daily effort allocation choices and responses towards day-to-day catch variability and the biophysical factors driving them, and how do the various emerging strategies lead to more stable outcomes? We aim to understand why current fishery regulations are often disregarded and what options portfolio management could offer in solving management conflicts.

2. Methodology

This study was conducted in the south-eastern part of Lake Victoria, in Tanzania, where around 49% of the lake's fishers are found (MLF, 2015) (Figure 5.1). Four landing sites in two regions were selected: Kayenze and Muluseni, located along the shallower Speke Gulf (Gulf region), and Muhula and Kome-Mchangani facing the deeper open lake (lake region) (Peter and van Zwieten, 2018). Site selection was based on our knowledge of the fishery in discussion with the Tanzanian Fisheries Research Institute staff and scientists who have worked in the region. All four villages had substantial longline and gillnet fisheries, daily access to traders, weighing scales, and fisheries officers responsible for enumeration and levy collection.

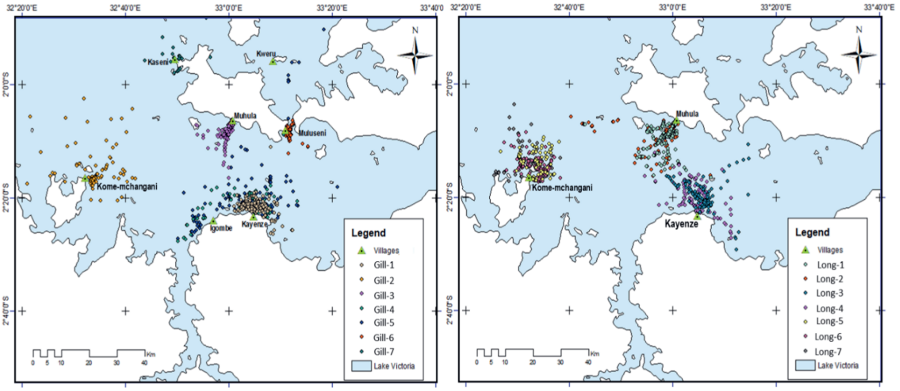

Figure 5.1*: Map of South-east Lake Victoria showing the four selected landing stations. Open lake: Muhula and Kome-Mchangani. Gulf: Kayenze and Muluseni. The map on the left shows daily fishing locations for individual gillnet fishers; the map on the right shows daily fishing locations for individual longline fishers over the research period.*

Ten gillnets and nine longline fishers targeting Nile perch using their fishing gear and operating each from the four landing sites were trained to record their daily operations and catch in logbooks (Ticheler et al., 1998) as well as the use of a handheld GPS device. Fishers were selected with the help of local fisheries officers and village leaders. Selection criteria were their experience in terms of years of active in and knowledge about Nile perch fishing, the type of gear used, the landing site, and their willingness to participate in the project. The selected fishers represented the gillnet and longline fishers of the lake, targeting Nile perch. Nile perch fisheries are highly homogeneous with respect to gear, vessel use, mode of propulsion, and general operational characteristics (Abila et al., 2000; Obiero et al., 2015). Nile perch fishers, use either gillnet (85% of the total number of nets employed in the fisheries of the lake) or longlines (100%) (LVFO, 2017, Peter and van Zwieten, 2018). They operate from wooden planked vessels - “Sesse” - that have a highly uniform design and form 83% of the vessel types on the lake. The mode of propulsion is pre-dominantly paddles and sails (67% of the vessels) or outboard engines (LVFO, 2017). All selected fishers had Sesse, operated mainly using paddles and sails and occasionally outboard engines. All used gillnets or longlines with a range of mesh and hook sizes comparable to the distribution of these gears in the lake (Peter and van Zwieten, 2018). Fishing operations were commonly carried out as day trips.

The logbooks captured catch data by species in number, weight, and beach price (revenue). Nile perch catches were distinguished into two size categories: <50cm (small Nile perch) and ≥50cm (large Nile perch) total length (TL). These size categories are based on (1) Nile perch fisheries regulations - the allowable size is ≥50cm TL - and (2) market preferences: large Nile perch is targeted for fillets for export, while small Nile perch is sold smoked and fresh both locally and regionally. The beach price per kilo of large Nile perch was variable but around the same as that of a kilo of small Nile perch (pers. obs. and logbooks). Other species caught were recorded with their number and total weight. Operational information captured was boat type and size; mode of propulsion (paddle, sail, outboard engine); travel time from the landing station to the fishing location and back (hr); soak time (hr); fishing location by name and GPS coordinate; number and size (length by depth, m) of gillnets used by mesh size; longline hook size, number of hooks and type of bait used; setting depth (m); daily operational costs of fishing including cost of fuel, bait, food, and miscellaneous costs (batteries, knives, plastic bags).

Data treatment and statistical analysis.

We reviewed data distribution, outlier detection and collinearity between explanatory variables (Zuur et al., 2010) (see Appendix). Seasons affect Nile perch distribution over the water column (Taabu-Munyaho et al., 2014) and fishing operations and were categorised as the short-rains season (October-January), long-rains season (February-May), and dry season (June-August) (Kizza et al., 2009; Wabwire et al., 2020). Figure 5.2 outlines the steps followed in the subsequent analysis of the logbook data. Two gillnet and two longline fishers did not collect sufficient data to analyse fishing strategies and were removed from the analysis.

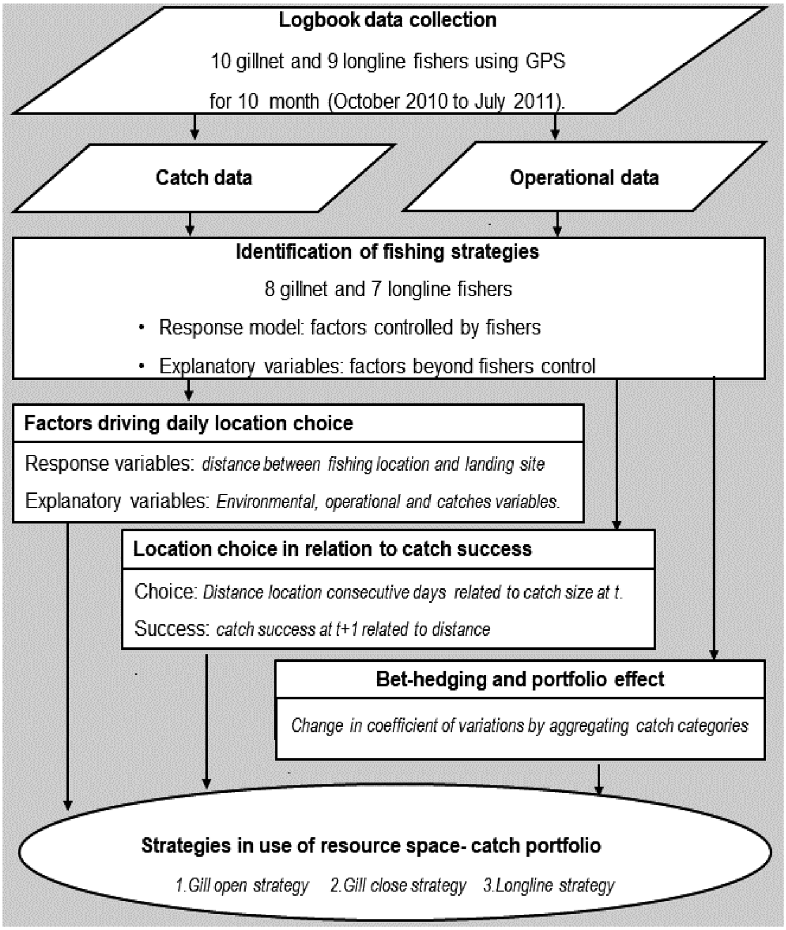

Figure 5.2: *Methodological framework of the steps in data inputs and outputs of the effort allocation analysis to determine daily choices and strategies for Nile perch fishery. Parallelograms indicate data input or output, and rectangles indicate an analysis, and oval outcomes of the analyses.*

Fisher's resource space

Recognising the potential bias from mapping fishing grounds based on singular GPS locations per trip (Close and Brent Hall, 2006), we approximated the size of the fishing grounds by defining the resource space for an individual fisher as the area (km2) encompassing 95% of the observations of daily georeferenced fishing locations. The convoluted polygon around fishing locations obtained by taking the shortest distance from one georeferenced fishing point to another was simplified to a logical regular polygon by connecting by sight the outer points around the area of observed fishing locations. When fishers used different homeports, the surface area encompassing 95% of the observations from each homeport was calculated separately and then summed.

Identification of fishing strategies

Fishing strategies within and between gears were identified by examining relationships between factors requiring daily fishing effort decisions controlled by individual fishers (response variables) and factors beyond their control (explanatory variables) using multivariate analyses. Detrended correspondence analysis (DCA) on log-transformed continuous variables was used to determine a suitable response model by removing redundant and non-significant explanatory variables and reducing cross-correlations. Next, we applied redundancy analysis (RDA) to examine the relationships between the response and explanatory variables by gear type and by combining the two gear types. Response variables were net sizes or hook numbers, soak time, travel time to fishing locations, distance to a fishing location, location depth, gear set depth and bait type (for longlines). Explanatory variables were daily catches in weight by Nile perch size class and other species, region, season, and propulsion. Analysis between gears was done by combining the two gears, leaving out all explanatory variables specific to a gear (mesh/hook size, total hooks, net sizes, and bait), and including the categorical variables region, gear, and season. Location depth (response variable) is a proxy for seasonally varying (explanatory variable) environmental factors, as depth is closely related to visibility (Secchi depth), oxygen concentration (higher in shallow waters), stratification, and temperature gradient over the water column. All are affected by seasonally varying climate (wind speed, wind direction, air temperature) patterns (Cornelissen et al., 2015). The emerging strategies were used in all subsequent analyses.

Fisher's daily decisions on location choice

To further examine location choice, and specifically, whether the size of the catch of Nile perch and other species is predictive of the decision to fish at a certain location, we analysed factors determining the distance from homeport to fishing locations, using a linear mixed modelling approach,

$$\log(Dist_{ij}) = (\beta_0 + Fisher_{0j}) + Strat_{ij} + R_{ij} + Seas_{ij} + \beta_1 Tt_{ij} + \beta_2 St_{ij} + \beta_3 Sd_{ij} + \beta_4 NPl_{ij} + \beta_5 NPs_{ij} + \beta_6 Oth_{ij} + \text{two-way interactions} + \varepsilon_{ij} \qquad (1)$$

Where, $Dist_{ij}$ is the distance (km) from homeport to fishing location by fisher i on the j-th fishing day, log-transformed to obtain a normal and homoscedastic distribution in the regression residuals; categorical variables are Strat = strategies as obtained through the multivariate analysis, R = region, Seas = season; continuous variables are Tt = travel time from home to fishing location, St = soak time, Sd = set depth, NPl = daily catch of large Nile perch (≥50cm), NPs = daily catch of small Nile perch (<50cm), Oth = daily catch of other species, $\beta0$ = the global intercept, Fisher0j = the random intercept per fisher, $\beta1$ - $\beta6$ = slope parameters, ε = residual error. Two-way interactions were possible between fixed effects and included the slope parameters for continuous fixed effects.

Fisher was modelled as a random intercept, as data clustering can be expected due to differences in fishers' skills and operational characteristics not accounted for by the fixed effects. The most likely model was obtained with a backward selection of variables from a full random intercept model by removing all non-significant fixed effects and interactions and minimising the Akaike Information Criterion (AIC). To avoid over-parameterisation, variables with significant parameter estimates close to zero were removed if this led to a decrease in AIC. The reduction in AIC was also used to compare a random intercept model with no fixed effects to an intercept only model with no random effects. The significance of the final model was compared to a random intercept model with no fixed effects through a Likelihood Ratio Test (deviance test). The contribution of the random effect to the total variability in daily distances covered by fishers was tested by examining the Intraclass Correlation Coefficient (ICC) calculated as $ICC= \theta/(\theta+\theta res)$ where θ = estimate of the covariance parameter (intercept) and θres the residual variability. The significance of the covariance intercept parameter estimate was tested using a Wald Z test. Bonferroni corrected least-square means tests were performed to compare the various categorical variables and their interactions.

Location choice and catch success.

Co-variation between the distance between successive fishing locations and the previous day's catch can be expected if fishers allocate their next day's fishing location based on the last day's catch success and return to the same location when the catch is good. If so, the change in the distance between fishing locations for consecutive days will be small, while, with low catches, fishers may prefer to test the waters in a different area. If this strategy is successful, then today's catch will be high, indicating the predictive value of a previous successful catch. If not, catch success will be indifferent to the distance between successive fishing locations or even positively related if previous fishing locations with high catches were to be avoided, e.g., due to local depletion. The expectation is that a change in distances between the fishing locations of the consecutive days t+1 and t will relate to today's (t) catch. Regression equation (2) was used to determine this relationship,

$$\Delta Distance_{ij} = (\beta_0 + Fisher_{0j}) + \beta_1 NPcatch_{(day\ t)ij} + Strat_{ij} + \beta_2\,(NPcatch_{(day\ t)ij} * Strat_{ij}) + \varepsilon_{ij} \qquad (2)$$

$\Delta Distance_{ij}$ = distance between fishing locations on consecutive fishing days on day *i* for strategy j, NPcatch(day t) = Nile perch caught in weight or number of today, and all other parameters and variables as in equation 1. Regression equation (3) was used to examine the relationship between the catch rate of day t+1 and the change in distance between consecutive fishing locations,

$$NPcatch_{(day\ t+1)ij} = (\beta_0 + Fisher_{0j}) + \beta_1 \Delta Distance_{ij} + Strat_{ij} + \beta_2(\Delta Distance_{ij} * Strat_{ij}) + \varepsilon_{ijk} \qquad (3)$$

Where $NPcatch_{(day\ t+1)ij}$ = Nile perch caught in weight or number on next ith day by strategy j. Other parameters and variables are in Equation 2. Catches in weight were log-transformed, and the model was performed using a Gaussian distribution with an identity link. To avoid the loss of zero catches, 1kg was added to the total weight of all NPcatch(day t+1). Nile perch caught in number was performed assuming a negative binomial distribution and a log-link.

Portfolio effect

To examine the portfolio effect, we compared the coefficient of variation (CV) of the daily catch by a strategy of respectively the catch of small Nile perch, large Nile perch, other species, all Nile perch and all species (total catch) in number and weight (Tilman et al., 1998). A higher CV implies lower stability.

XToolsPro, an extension of ArcGIS 10.1, was used to construct polygons to calculate the resource space of individual fishers. Multivariate analyses were executed with CANOCO 4.5 (ter Braak and Smilauer, 2002). Regression models were carried out using the GLIMMIX procedure (SAS/STAT software version 9.2 of the SAS system for Windows).

Results

Resource space and fishing operations

The resource space of individual fishers encompassing 95% of their fished locations on average approximated 130 km2 (CV=84%) (Figure 5.3, Table 5.1). Gillnetters (n=8) had a smaller (120 km2) and more variable (CV=127%) resource space then longliners (n=7, 141 km2, CV=14%). All fishers show occasional forays farther from homeport or in compass directions other than normal (Figure 5.3). Some fishers remain within one area (e.g., Figure 5.3C), while others' fish from different homeports (Figures 5.3A and 5.3D). In the lake region, the general shape of the resource space was more equidistant in all directions from the landing site. In the gulf, the resource spaces of gillnet fishers were more convoluted in shape and/or more parallel to the shore.

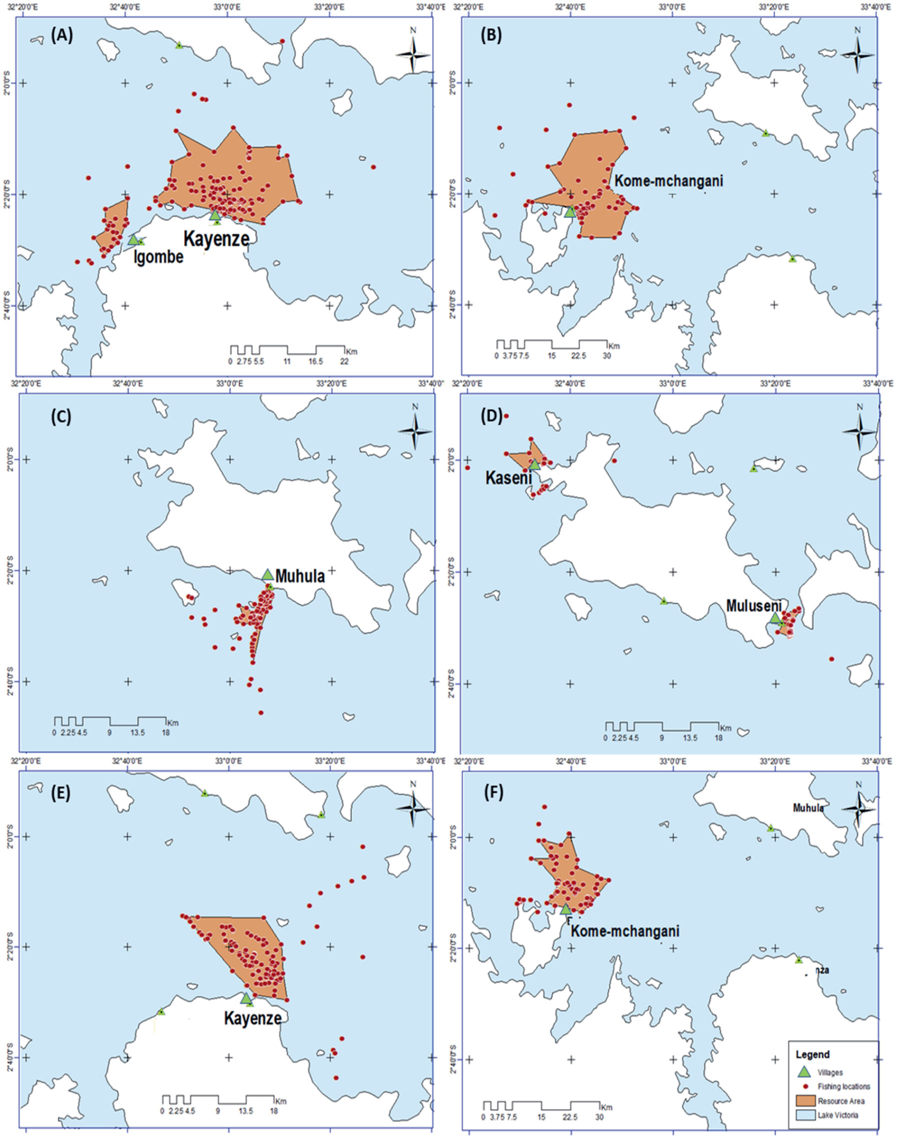

__Figure 5.3__: Fishers' daily fishing locations and 95% polygons around fishing locations to estimate the approximate size of their resource spaces. G2 and G4 fishers are representative of the gillnet offshore (Gill-open) strategy, G5 and G7 represent the gillnet inshore (Gill-close) strategy and L3 and L7 are representative of the longlines strategy (note the different scales).

All fishers fished close to the homeport: the maximum distance travelled was 38 km, with an average over the maximum distance observed of 27 km (CV=42%). longline fishers travel longer distances (average = 7km, SD = +5km, N = 2081, max=27 km, CV = 37%) compared to gillnetters (average = 5+5km, N = 1522, max=19 km, CV = 43%). Distances travelled by longliners were highly similar (CV = 65%), contrasting with a high variation in travel distances between gillnetters (CV = 112%). Some gillnetters remained close to the shore, while others chose to travel significantly further (F1512,7=104.3, p <.0001, r2=0.33) (Table 5.1).

Table 5.1: Characteristics of fishing strategies developed by artisanal fishers in Southeast Lake Victoria. G1-G8 = gillnet fisher, L1-L7 = longline fisher, E = engine; P = paddle/sail, in brackets number of days fishing.

Fisher	Propulsion	Days fishing	Strategy	Average distance (km)	Resource space (km²)	Mean (kg)	CV (kg)	Mean (no)	CV (no)
G1	E	271	Gill-open	5	72	17	59	16	66
G2	E (102), P (20)	122	Gill-open	7	395	22	48	22	49
G3	E	205	Gill-open	6	133	28	87	23	76
G4	E	275	Gill-open	9	312	38	68	13	83
G5	E (105), P(112)	227	Gill-close	4	17	37	78	10	76
G6	E (79), P (119)	198	Gill-close	1	7	40	93	17	115
G7	E (189), P (28)	217	Gill-close	2	17	37	81	12	111
G8	E	188	Gill-close	2	7	28	43	22	45
L1	P	239	Longline	7	151	19	70	24	70
L2	P	272	Longline	9	163	21	86	18	81
L3	P	177	Longline	9	113	32	77	21	79
L4	P	239	Longline	7	150	37	49	18	54
L5	P	212	Longline	7	124	34	68	17	77
L6	P	107	Longline	6	128	35	55	13	68
L7	P	151	Longline	8	160	25	76	15	71

Fishing strategies

The first two RDA axes of a redundancy analysis on gillnet fishing operations were significant (F = 78.8, p = 0.001, Monte Carlo test, 1000 replicates). Still, they only explained 22% of the variation in fishing operational data (Table 5.2). Four clusters of gillnet fishers could be distinguished (Figure 5.5): (1) fishers fishing further away from homeport in deeper locations; (2) fishers fishing further away from homeport but in shallower areas; and two clusters of individual fishers each respectively (3) fishing close to the homeport in shallow locations; or (4) in both shallow locations close to the homeport and deeper locations away from homeport. While the RDA on longliner fishing operations was significant (F = 3.67, p = 0.001), the first two axes explained only 1.3% of the variation in fishing operational data (Table 5.2). No clusters could be defined, implying that fishing strategies for this group of longline fishers were highly similar. An RDA on combined longline and gillnet fishing operations indicated a high overlap in strategies as the canonical axes were significant (F=130.3, p=0.001), explaining 18% of the variation in fishing operational data (Table 5.2). Three main clusters were (Figure 5.6):

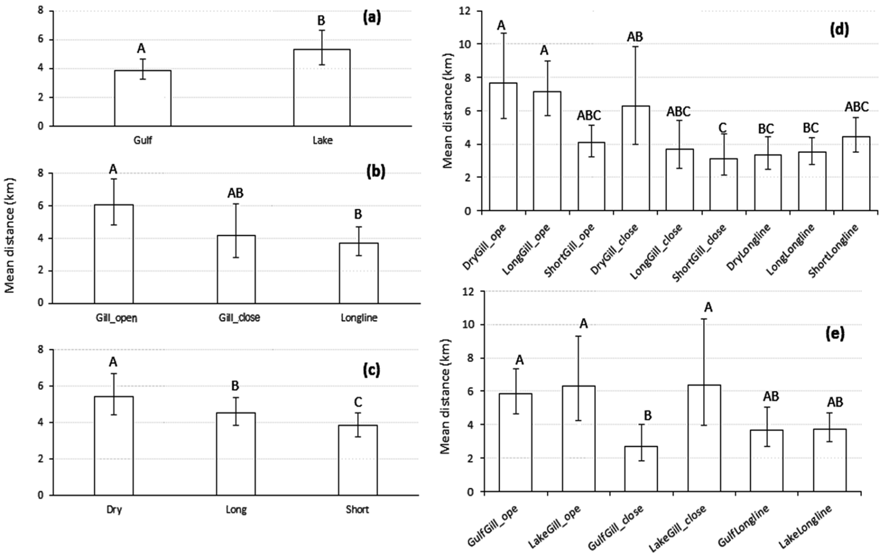

***Figure 5.4**: Average distances from homeport to fishing location by region (a), strategy (b), season (c), the interaction between season and strategy (d) and interaction between region and strategy (e). Error bars indicate 95% confidence intervals. Letters indicate groupings of significantly distinct categories (p<0.05) from Bonferroni adjusted t-tests on least-square means.*

Table 5.2: Results of redundancy analysis (RDA) on the relationship between response variables related to daily fishing operations and decisions (distance from homeport to fishing location, soaking time, fishing location depth, gear setting depth, travel time to fishing location, travel time back to homeport, total operation time and mesh/hook sizes) and the explanatory variables that related to environmental and biological variables for gillnetters, longliners and combined gears (season, region, propulsion and catches i.e. large Nile perch, small Nile perch, total other species). Axis 1 and axis 2 refer to the redundancy analysis and are assigned based on the amount of dispersion between variables.

Fishers	Axis 1	Axis 2
Gillnetters		
Eigenvalues	0.19	0.03
Fishing operation-environmental and biological correlations	0.60	0.36
Cumulative percentage variance of fishing operation data	18.6	22.1
Longliners		
Eigenvalues	0.01	0.002
Fishing operation-environmental and biological correlations	0.14	0.07
Cumulative percentage variance of fishing operation data	1.1	1.3
All fishers		
Eigenvalues	0.16	0.02
Fishing operation-environmental and biological correlations	0.52	0.34
Cumulative percentage variance of fishing operation data	16.2	18.0

(1) a longline cluster associated with targeting mainly but not exclusively large Nile perch at further distances with deeper sets and shorter soak times (longline strategy); (2) a gillnet cluster of fishers targeting small Nile perch, as well as other species, associated with shallower lake areas, closer to homeports, and longer soak times (gill-close strategy); (3) a gillnet cluster largely overlapping with the longline strategy, but where fishers targeted small and large Nile perch fishing further from homeport in shallow as well as in open waters (gill-open strategy) (Figure 5.4b and 5.4e). The three clusters, longline, gill-close, and gill-open, were considered strategies in subsequent analyses.

A strong negative correlation existed between the response variables soak time and distance (Figures 5.5 and 5.6), implying that fishers spent more hours fishing with shorter distances between homeport and fishing locations. On the other hand, distance was strongly correlated to the explanatory variable “large Nile perch”, indicating that fishers needed to travel long distances to catch more large Nile perch. With gillnetters, a negative correlation between the size of the net and soak time indicated that larger (or more) nets are used in areas further from the homeport with shorter soak times. These relations will be further explored in the next section.

Fisher’s daily location choices

The most parsimonious model explained distance from homeport through four sets of factors: individual (by strategy); controllable daily choices (travel time and related soak time; and setting depth); uncontrollable environmental and spatial factors (season, region) and catch (large and small Nile perch) (Table 5.3). Large and small Nile perch catch had highly significant parameter estimates but close to zero, indicating that catch success had a limited effect on location choice. Leaving these fixed effects out led to the best model according to the AIC criterion (Appendix 1). However, we retained Nile perch catch by size class as we aim to analyse the relation between location choice and Nile perch catch success. Interestingly, the daily catch of “other species” and its interactions with other variables dropped out of the models, indicating that the catch of these species did not affect location choice, implying that fishers do not actively target them.

Random effects and strategies

The random effect led to a substantial reduction in AIC compared to the null model and accounted for 45% of the variability (ICC, $p<0.01$) in distances from homeport to fishing locations. This aligns with earlier observations that travel distances and resource space varied between fishers. This effect was reduced to 5% of the variability in the full model (Table 5.3, ICC, $p<0.01$) due to the strong impact of the fishing strategy as a fixed effect, indicating that the three strategies accounted for most of the variation in travel distance between fishers.

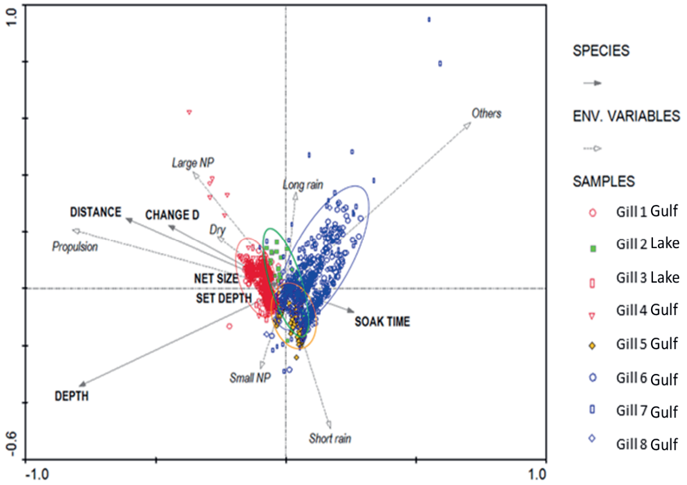

Figure 5.5*: Triplot of the first two axes in a redundancy analysis (RDA) indicating the relationship between drivers to gillnetter's daily choices (explanatory variables, dotted arrows: Long, Short, Dry = seasons defined as Dry: June to August, Long rain: February to May, Short rain: October to January; Others= catch of other species (kg), Small NP= catch of Nile perch <50cm (kg), and Large NP = catch of large Nile perch (kg), and fishers daily choices (response variables, black arrows: Depth, Set depth=gear setting depth, net size= total size of the net, Change D = distance between locations fished on consecutive fishing days, Distance= distance from homeport to fishing locations, and propulsion = mode of propulsion. Ellipses are fishers fishing strategies: Red - away from homeport, deeper locations; Blue - away from homeport, shallow locations; yellow - close to homeport, shallow locations, and Green - both far from homeport in deeper locations and/or close to homeport in shallow locations.*

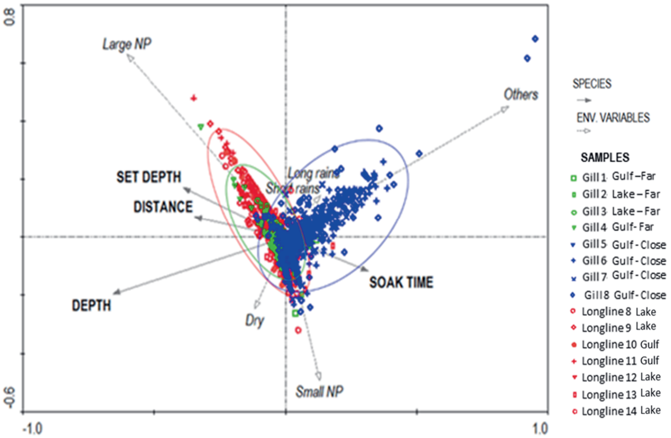

Figure 5.6*: Triplot of the first two axes in redundancy analysis (RDA) on combined gears, showing the relationship between drivers for longline and gillnet fishers' daily choices - Fixed factors, dotted grey arrows: Long rain season, Short rain season, Dry season, Others -Total catch other species, Small NP-small Nile perch, and large NP-large Nile perch), and fishers daily choices-variable factors, Grey arrows: Depth, Distances, Set depth and Soak time. Scatter samples showing fishers strategies gill-close (blue), gill-far (green) and longline (red).*

Fixed effects: daily choices

Daily choices in travel time and setting depth were positively related and increased with distance travelled, while soak time was negatively related to and decreased with distance travelled. These effects were reinforced in their interaction with strategies, specifically for longline and gill-open strategists who fished further from the homeport and more in open waters (Table 5.3). For the gill-close strategy, the soak time and travel time were not predictive of travel distance from homeport, but setting depth was strongly associated with travel distance. This indicated that gill-close strategists set their nets closer to the bottom than other strategies, where this association of travel distance with setting depth was less strong. Gill-open and longline strategists mostly set their gears in midwater.

Fixed effects environment

Travel distance in the lake was significantly higher, about 15%, than in the gulf (Figure 5.4a), mainly caused by the Gulf region's limited distance travelled by the gill-close strategy. Average distances travelled in the two regions did not differ much for each strategy, but longliners travelled shorter distances (Figure 5.4d). The two gillnet strategies travelled long distances in the dry season (July-August), during which strong southerly monsoon winds mixed the lake (MacIntyre et al., 2014). All strategies remained closer to homeport during the short-rain season (October-January) when stratification builds up, and Nile perch appears higher in the water column (Taabu-Munyaho et al., 2013). During the long-rains season (February-June), gillnet fishers travelled intermediate distances. Longliners had no significant seasonal changes in travel distances (Figure 5.4e).

Fixed effects: catch by size class

The catch of Small Nile perch catch was negatively related to travel distance, and that of large Nile perch was positively correlated. Still, as discussed, the effect was small, indicating that daily choices and environmental factors dominated decisions on travel distance rather than an expectation of the size of the catch of either size category (see Appendix). To better understand these results, we visualized the effect of the catch of different sizes of Nile perch on travel distance (Figure 5.7) by calculating these using the model parameter estimates over a range of catch sizes fixed on the average soak time, travel time, and setting depth for each of the three strategies. Logbook data indicate that for both size classes of Nile perch, 90% of the daily catches were smaller than 22-32kg, except for large Nile perch in longline catches, where 90% of the daily catch was smaller than 67kg per day. Over the catch range from zero to these maximum caches, expectations of daily catches had large confidence intervals and were not predictive for choices in travel distance, except for the longline strategy where higher catches of small Nile perch were indicative for distances closer to the shore (Figure 5.7).

Table 5.3: Parameter estimates of fixed effects, random effects and model diagnostics of fisher's daily distances from homeport to fishing location Wald test: Wald Z test covariance parameter, Only significant (Type 3) fixed effects are included in the model: *** $p<0.001$, ** $p<0.01$.. ns= not significant. The likelihood ratio test (deviance test) compares the final model with the random intercept model.

Model		**Daily distances (homeport to fishing locations)**			
			Confidence interval		
Fixed effect	**Effect**	Estimate	*Lower*	*Upper*	*P*
Intercept		0.86	0.64	1.08	<0.001
Strategy***	Gill-open	-0.15	-0.48	0.17	ns
	Gill-close	-1.69	-2.07	-1.31	<0.001
Season***	Dry	-0.12	-0.21	-0.03	<0.01
	Long	-0.09	-0.1313	-0.05	<0.001
Region**	Gulf	0.00	-0.14	0.13	ns
NP small***		- 0.00	0.00	0.00	<0.001
NP large**		0.00	0.00	0.00	<0.01
Travel time**		0.05	0.03	0.06	<0.001
Soak time**		-0.04	-0.07	-0.02	<0.001
Setting depth***		0.01	0.01	0.02	<0.001
Season*Strategy**	Dry - Gill-open	0.41	0.26	0.56	<0.001
	Dry - Gill-close	0.41	0.26	0.57	<0.001
	Long - Gill-open	0.34	0.27	0.41	<0.001
	Long - Gill-close	0.17	0.10	0.23	<0.001
Region*Strategy**	Gulf - Gill-open	-0.01	-0.25	0.23	ns
	Gulf - Gill-close	-0.37	-0.60	-0.14	<0.01
Soak time(Strategy)***	Gill-open	0.02	-0.01	0.05	ns
	Gill-close	0.09	0.06	0.13	<0.001
Setting	Gill-open	-0.01	-0.02	0.01	ns
	Gill-close	0.12	0.10	0.15	<0.001
Random effects		*Null model*	*Random intercept*	*Final Model*	
Fisher	N		15	15	
	ICC		0.45***	0.05*	
Diagnostics					
AIC		3127.3	1841.1	1519.22	
-2LL		3123.8	1837.1	1515.22	
Observation	N	2354	2354	2294	
Likelihood ratio test	X^2, df	358.8	34		<0.001

Region^1 = Lake region, Strategy^2 = Longline strategy, and Season^3 = Short rain season

Thus, previous catch success of Nile perch of either size class is not relevant to the choice of the fishing location, except when longliners choose to fish at a distance close to the homeport and add small Nile perch to their targeted sizes.

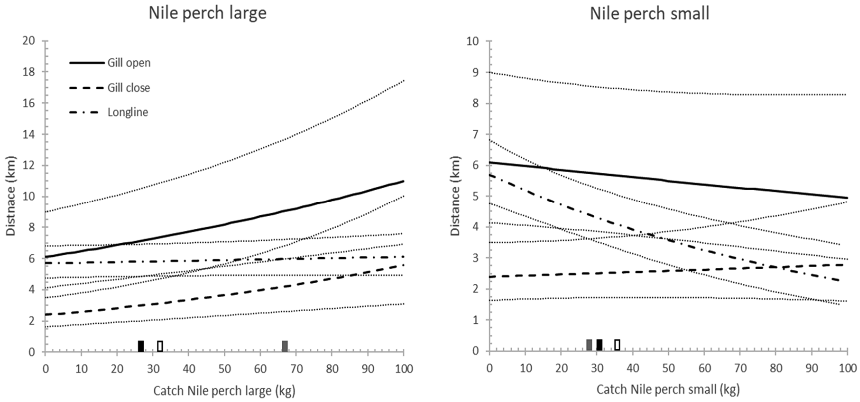

Figure 5.7*: Distance choices (km) as predicted by catch of large Nile perch (left) and small Nile perch (right) in weight for the gillnet offshore (Gill-open), gillnet inshore (Gill-close) and longline strategies, fixed at average soak time, travel time and setting depth for the three strategies. Grey lines are 95% confidence limits. The small boxes on the x-axis represent the 90% quantiles of the daily catch by size class of Nile perch of the longline (grey), gill-close (black) and gill-open (open) strategies. Note the different y-axes.*

Location choices and catch success

The overall mean distance between successive fishing locations was 1.2 km, where the mean distance of the gill-close strategy was significantly lower at 0.4 km (N=525, t=-4.1, p <0.001) compared to the gill-open strategy at 2.7 km (N=570, t=-4.1, p <0.001) and the longlines strategy at 1.3 km (N=947, t=-4.1, p=0.1). The mean distance between successive fishing locations significantly differed between the two gillnet strategies but not between the gill-open and longline strategies. Gill-close strategists fished close to the shore: distances between homeport and fishing locations and thus between the locations over consecutive days are expected to be short. The gill-open strategy had the highest mean distance; these fishers fished close and far from the homeport and, in most cases, parallel to the shore. A slight deviation in travel direction from the shore over a long distance led to a significant distance between consecutive daily catch locations. In contrast, longline fishing occurred approximately perpendicular to the shore from the homeport towards deeper offshore waters, which explains that the distance between successive fishing locations was not as high as that of the gill-open strategy. Thus, gill-close fishers often fished close to their previous day’s fishing location than gill-open fishers or longliners.

Next, we examined the expectation that fishers choose their next fishing location based on the previous day's catch success (Models 2 and 3). The variation explained by the individual fisher effect (ICC values) is between 10% and 18%, indicating that the random effect needed to be included (Table 5.4). The distance between successive days' fishing locations ($\Delta\text{Distance}_{t\rightarrow t+1}$) was significantly related to the previous day’s catch of Nile perch (NP-catch_{t}) both in weight ($p<0.01$) and number ($p<0.001$) (Table 5.4). According to expectation, the overall slope of this relation was negative in both cases and the interaction with the gill-close strategy. However, the parameter estimates of both the overall slope and the interaction with gill-close were not significantly different from zero, indicating a slight effect. Contrary to expectation, the interaction with the gill-open strategy resulted in a positive relation between NP-catch and ΔDistance, significantly different from the overall slope for the catch in number but not in weight, which suggested that in this case, higher catches lead to greater distances between consecutive fishing locations (Figure 5.8a).

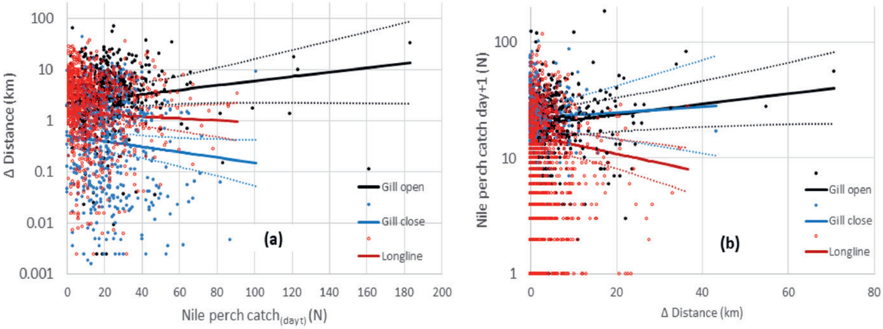

Figure 5.8: *(a) predicted distance between successive fishing locations from Nile perch catch (in number) at day t for three fishers’ strategies; and (b) Nile perch catch on day t+1 (in number) from a distance between consecutive fishing locations on day t+1 for the three fishing strategies. The dotted lines are 95% confidence limits.*

Table 5.4: Parameter estimates of fixed effects, random effects and model diagnostics of four models relating distance between successive fishing locations and catch testing the hypotheses that 1: shorter distance between successive fishing days leads to a successful catch on the next day, 2: today's catch success explains the choice of tomorrow's location for total daily Nile perch catch (NP catch) in number and weight, Wald Z test for covariance parameter. Change D, CD = distance between successive fishing locations: ns=not significant. Residual Log-likelihood ratio, § = p<0.001. All models are mixed effect models with a Gaussian link on log-transformed response variables except NP catch (day t-1) in number that uses a negative binomial distribution as a link function.

		Distance successive locations=NP catch $_{(day\ t)}$+ strategy+ interaction						**NP catch $_{(day\ t+1)}$ = Strategy+ distance successive location+ interaction**					
Model		**Total Nile perch (Weight)**			**Total Nile perch (Number)**			**Total Nile perch (Weight)**			**Total Nile perch (Number)**		
Fixed effects	*Effect*	*Est*	*Std error*	*P*	*Est*	*Std error*	*p*	*Est*	*Std error*	*p*	*Est*	*Std error*	*p*
Intercept		0.15	0.09	Ns	0.15	0.09	ns	1.4	0.04	**<0.001**	2.76	0.12	**<0.001**
NP catch$_{(t)}$	NP	-0.00	<0.01	Ns	-0.00	0.002	ns						
Strategy[1]	Gill-open	0.19	0.14	Ns	0.19	0.14	ns	-0.03	0.07	ns	0.20	0.20	ns
	Gill-close	-0.50	0.14	<0.01	0.45	0.15	**<0.01**	-0.18	0.07	**<0.05**	0.34	0.20	ns
Change D	CD							-0.01	<0.01	ns	-0.02	0.01	**<0.05**
Interactions	CD (Gill-open)							0.01	<0.01	**<0.05**	0.03	0.01	**<0.05**
	CD (Gill-close)							0.01	0.01	**<0.05**	0.02	0.01	**ns**
	NP (Gill-open)	0.01	<0.01	<0.05	0.01	0.003	ns						
	NP (Gill-close)	-0.01	<0.01	Ns	-0.00	0.003	ns						
Random effects		*0-model*	*intercept*	*Final model*	*0- model*	*intercept*	*Final model*	*0-model*	*intercept*	*Final model*	*0 model*	*intercept*	*Final model*
Fisher	N		15	15		*15*	15		15	15		*15*	15
	ICC		*0.15*	*0.04*		*0.18*	*0.14*		*0.15*	*0.12*		*0.18*	*0.14*
Diagnostics													
	AIC	5609.4	5330.5	5316.4	5609.4	5330.5	5314.2	1436.1	1202.8	1178.7	15883.7		
	-2ResLL	5605.4	5324.5	5300.4	5605.4	5324.5	5298.2	1432.1	1196.8	1194.7	15879.8	5019.7	4986.4
	Observation	2042	2042	2042	2042	2042	2042	2042	2042	2042	2042	2042	2042
Type III test of fixed effect													
	Strategy			Ns			ns			**<0.05**			ns
	Change D									**<0.01**			ns
	NP catch$_{(t)}$			**<0.01**			**<0.001**						
	Interactions			Ns			**<0.05**			**<0.05**			**<0.001**

Base level intercept [1]Strategy: Longlines

Whether a fishing tactic to fish close to a fishing location that earlier had a high catch in weight or number paid off was not observed for the three strategies, except for the longline strategy, which had a significant negative effect on the total number of Nile perch caught on day $_{t+1}$ (Table 5.4). Contrary to expectation, the next day's catch success in weight for the two gillnet strategies increased significantly at long distances from the previous day's fishing location. (Table 5.4, Figure 5.8b), suggesting that the average size of Nile perch caught is higher. This implied that more distant locations are also further offshore, where the probability of catching larger Nile perch would be higher. The expected negative effect between ΔDistancet□-t+1 and NP-catcht+1 for longliners was slight but indicated that they caught more fish at consecutive fishing locations near each other. There was no such effect on weight, likely resulting from fishing closer to the homeport at more inshore locations. Longliners chose locations travelling about perpendicular to the shore, and therefore, inshore locations were closer to each other than more offshore locations. As inshore areas had higher densities of smaller Nile perch, a larger number of fish caught did not lead to a significantly higher catch in weight.

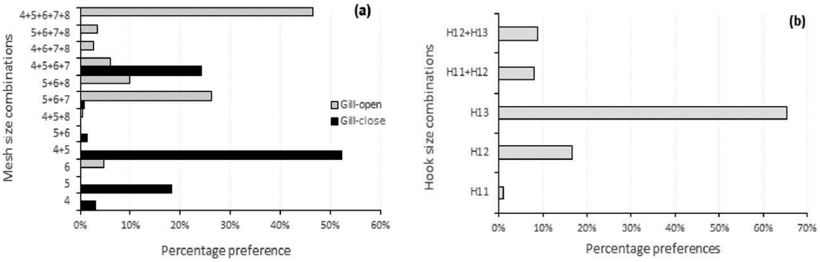

Figure 5.9: *Percentage preference use of (a) (combinations of) mesh sizes by gill-open and gill-close strategies and (b) of (combinations of) hook sizes by longline fishers.*

Bet hedging and portfolio effect.

We examined whether the two gillnet strategies differed in (combinations of) mesh sizes, indicating potentially different bet-hedging strategies. Fishers used seven different mesh sizes from 4 to 8 inches, catching Nile perch ranging from 20 to 100cm TL (Ogutu-Ohwayo et al., 1989). Of the 31 possible combinations remaining, if mesh sizes 5.5” and 6.5” were counted as 5” and 6”, 12 were used. Single mesh sizes were rarely used, limited to smaller mesh sizes.

Large mesh sizes (7” and 8”) were only used in combination with the smaller 4”, 5” and 6” meshed nets and predominantly by the gill-open strategists. The gill-close strategists used smaller mesh sizes (4 and 5 inches) (Figure 5.9a). Longliners mostly used a single hook size (Figure 5.9b), predominantly the smallest hook size 13. Larger mesh sizes (and hook sizes) are used farther away from the homeport (Peter and van Zwieten, 2018), indicating that these bet-hedging strategies targeted small and large Nile perch at further distances. The portfolio effect was visible in all strategies (Table 5.5). Daily catches of large Nile perch always had higher variabilities than of small Nile perch, the highest with the gill-close strategy. Combining small and large Nile perch reduced variability in total Nile perch catches, especially for longliners. Other species further reduced the variability in daily catch rates in the gill-close strategy but hardly impacted the catch variability of the other strategies. Thus, a more diverse species composition at nearshore shallower habitats is associated with smaller mesh sizes used by gill-close strategists.

Table 5.5: Coefficient of variation (CV) in catch rates for total daily catch and daily catch of the two Nile perch size categories combined, large Nile perch (≥50 cm), small Nile perch (<50 cm) and other species (others) for both weight (Wt) and number (No).

			Coefficient of Variation (CV) daily catch				
			Size and species categories			**Aggregations of categories**	
Strategy	**N**		**Nile perch <50cm**	**Nile perch >50cm**	**Other species**	**Nile perch all**	**Total**
Gill-open	261	**No**	56	62	404	51	51
		Wt	57	65	447	54	54
Gill- close	261	**No**	55	91	81	51	48
		Wt	54	71	85	49	45
Longline	263	**No**	85	61	447	59	59
		Wt	90	55	461	52	52

Discussion

Fishing operations and strategies

Small-scale fisheries are characterised by a high variation in daily catches taken from a limited individual resource space (Pet-Soede et al., 2001; Peter and van Zwieten, 2018; van Densen, 2001; van Oostenbrugge et al., 2002). Nile perch fishers of Lake Victoria deal with this condition through different behavioural choices. Three different strategies emerged from our analysis: (1) Gillnet fishers fishing close to the homeport, within a limited resource space, utilising mainly smaller mesh sizes, with a portfolio of smaller sized Nile perch of <50cm supplemented by Nile perch >50cm and by-catch of other species; (2) gillnet fishers fishing further from homeport within a larger resource space parallel to and further offshore, employing fleets of gillnets including large and small mesh sizes targeting both size-classes of Nile perch, and with limited by-catch. Fishers sometimes used engines, but this did not lead to further distances, only shorter travel times and hence longer soak times (Peter and van Zwieten, 2018); (3) longline fishers fishing in resource spaces perpendicular to the shore, utilising a limited range of predominantly smaller hook sizes using different bait types (Peter and van Zwieten, 2018). They generally use single hook sizes, probably because these catch a large size range of Nile perch, which showed no significant difference in the average size of Nile perch caught with larger hook sizes (Chitamweba et al., 2009; Medard Ntara, 2015; Peter and van Zwieten, 2018). Specific bait types did influence the size of the catch, but the choice of bait was highly dependent on availability and hence had no impact on the strategy followed (Medard Ntara, 2015; Peter and van Zwieten, 2018). Our study found no other longliner (Migonzo) strategies, possibly due to the limited sample size. A strategy not covered was daytime setting and hauling of longlines in shallow waters targeting smaller Nile perch, practised from January to May and farther offshore by larger operations (Medard Ntara, 2015). Other Nile perch fisheries, such as beach seines and small-seine light fisheries that capture Nile perch juveniles as by-catch were not covered. Whereas more strategies could have been discerned with a larger sample size covering more fishing methods, we can generalise our results given the nature of the resource and the operational constraints under which small-scale Nile perch fisheries function in Lake Victoria. Given these constraints, limitations in available resource space require fishers to reduce risk and uncertainty by employing bet-hedging strategies targeting a portfolio of species and sizes of Nile perch.

Resource space and competition for daily fishing locations

In homeport fisheries, distance comes at a cost, and a trade-off mediates location choice between an expectation of higher catch rates further offshore, interference with other fishers, and travel time (Aburto et al., 2009; Caddy and Carocci, 1999). Lake Victoria fishers predominantly utilise a limited resource space of approximately 120km2 (gillnetters) to 141km2 (longliners) around their homeport. Individual behaviour differs widely, ranging from residential fishers who always return to about the same place to roaming fishers who travel in many directions around a core area close to the landing site. Some fishers fish from different landing sites, but in that case, they appear to show similar behaviour in each landing site.

Extending our observations to the whole fishery, with around 50% of the fishing activities taking place within 6 km from the shore, a maximum spatial distribution extending to 16 km (Peter and van Zwieten, 2018) and using frame survey data for the total number of fishers per lake district (MLF, 2008), the density of longline and gillnet fishers was around 2.9 fishers per km2. This density implies that most of the gulf region is fully covered by the fishery, while much of the offshore regions of the open lake in Tanzania that contain few islands are exploited more lightly. Interference competition (Poos and Rijnsdorp, 2007) may be high, as Peter and van Zwieten (2018) suggested and likely plays a role in location choice. An indication is the different shape of the resource spaces in the gulf, where fishing is carried out from both sides, resulting in more convoluted spaces parallel to the shore, indicating spatial use competition, and the lake region, where fishing is carried out from the homeport leading to the semi-circular spaces observed, and competition will mainly occur with fishers from the same landing site. Competition for space between gillnetters and longliners may be limited: despite the extended size of nets (average 2 km length, 12000m2) and longlines (average 2.5-3km, 800 hooks) as longliners, on average, travelled further and set their gear about twice as deep as gillnetters (Peter and van Zwieten, 2018).

Location choices and catch success

Even though the probability of catching more profitable and legally sized large Nile perch offshore is higher (Peter and van Zwieten, 2018), fishers fish primarily within 2-7km from their homeport. Choosing locations close to homeport is because high catch variability in offshore areas increases the risk of unprofitable trips. Medard (2015) found fishers arguing that fishing offshore increased the costs of bringing fresh fish to the market in time. While other ecological, social and cultural factors may play a role (Naranjo-Madrigal and Bystrom, 2019), fishers avoid risk by covering at least daily costs (Abernethy et al., 2007; Sethi, 2010); this behaviour is also understandable from an information perspective (van Densen, 2001). Individual fishers gain limited information on Nile perch distributions from the signals obtained from their daily catch success within their resource space in relation to daily and seasonally changing environments. Catch success is nearly independent of previously fished locations, contrary to what was found in large scale fisheries (Vignaux, 1996) but similar to other small-scale fisheries (Pet-Soede et al., 2001) and targeting specific densities of Nile perch does not appear to be part of a daily fishing strategy.

Nevertheless, daily catches show some autocorrelation, most likely caused by the overall distribution of Nile perch size classes over the water column and from inshore to offshore rather than predictable aggregations or movements. Fishing patterns emerge from longer-term experience and, likely, from shared fishing experiences with other fishers operating from specific locations. The general distribution of densities of smaller Nile perch decreasing towards deeper offshore waters, as well as the slight increase in densities of larger Nile perch offshore, has been observed by several authors (Cornelissen et al., 2015; Goudswaard et al., 2011; Peter and van Zwieten, 2018; Taabu-Munyaho et al., 2013; van Zwieten et al., 2016). This distribution pattern appears to be steered predominantly by local abiotic factors such as visibility, oxygen concentration and temperature (Cornelissen et al., 2015), a general feature of the lake wide Nile perch distribution (Taabu-Munyaho et al., 2014).

Variability in daily catches, bet-hedging, and the portfolio effect

Theory suggests that adopting strategies that exploit various assets provides substantial benefits over strategies with lower diversity (Anderson et al., 2017; Edwards et al., 2004). Of the three general strategies available to reduce variability in catch (Jul-Larsen et al., 2003), the two bet-hedging strategies – exploiting multiple cohorts and increasing the number of species caught (van Oostenbrugge et al., 2002) were found in our study. Variability in catches of legally sized larger Nile perch was highest and increased with increasing distance from the shore (Peter and van Zwieten, 2018). Gillnetters reduced variability by using combinations of mesh sizes, focusing on large (fishing offshore) or small (inshore) mesh sizes, the latter with the bonus of catching a diverse array of species next to different size classes of Nile perch. While other species appear to be by-catch, this can exceed 30% of the daily catch. *Oreochromis niloticus* is sometimes valued higher than small Nile perch (Medard Ntara, 2015) and may also be important economically.

The third general strategy of reducing variability in daily catches by investing in more or more powerful gear (Jul-Larsen et al., 2003) is employed in Lake Victoria in a particular way but does not differ in essence from the gillnet strategies described: the difference is in the organisation of labour. As the labour cost is low (Medard Ntara, 2015), a way to obtain a more significant individual share of the total catch is to invest in more of the same existing small scale fishing vessel and gear technologies. Boat owners following this strategy own up to twenty boats, organise their operations in fishing camps outside main landing sites and have close links to transport and processing facilities for export (Medard Ntara, 2015). They generally use larger nets ranging from 4.5 – 7.2 km in length to 9 – 18 m depth per boat, but, like the gillnet strategies described, they include a range of mesh sizes. The same operational constraints apply as they perform day trips from a homeport using the same vessel types and propulsion modes. Resource spaces covered by these fishers are likely comparable to our sample of fishers, indicated by the spatial conflicts between these “packs of fishers” going out fishing in groups and other gillnet and longline fishers (Medard Ntara, 2015). Thus, bet-hedging by capturing a portfolio of sizes or species over a limited resource space again is the typical response to address risk.

Illegal fishing, objectives of management and portfolio management

Spatial behavioural choices and resulting fishing strategies are essential to understanding fishers’ operational responses to management regulations. The leeway of individual fishers to effectively diversify is limited by regulations and market forces (Anderson et al., 2017). Mesh and slot size regulations and a strong regulatory focus on production goals sustaining the export industry aim to constrain Nile perch fishers' choices and lead to continuous conflicts over their resource use (Jacobson, 2019; Kolding et al., 2014a). An unintended consequence of the enforcement strategies employed, focussing primarily on punishing illegal gear use, is decreased cooperative behaviour and increased individual exploitation rates. MacColl et al., (2018) claim that cooperative strategies to sustain the resource, an intrinsic motivation shared by many in the fishery (Cepić and Nunan, 2017; Mpomwenda et al., 2022), are crowded out by such extrinsic, regulatory induced motivations given the need to maintain individual livelihoods. Around Lake Victoria, this has led to corruption by allowing illegal gear through regular payments or payments when catching someone using illegal gear or landing undersized fish (Nunan et al., 2018), thus maintaining the fishing strategies described.

Abetted by science with its singular focus on growth overfishing and associated size-based regulations to maximise production based on a singular optimum size of fish forces individual fishers to take higher risks because they must become more specialised in sizes, species and areas (Hilborn et al., 2001, Kolding and van Zwieten, 2009). Mesh or hook size limitations force fishers to accept higher uncertainties in daily catches, drive their fishing locations further offshore, or accept a more variable lower catch, leading to higher personal and occupational risk. This is not necessary: because production is a decreasing function of fish body size, the distribution of fishing mortality over a range of sizes of fish will emerge as a result of fishers attempting to maximise their net profits by closely matching their effort to production (Plank et al., 2017). When size-selectivity results from the actions of many fishers operating independently, the aggregate fishing mortality will reflect this declining production at large sizes. Harvesting multiple size classes, which involves harvesting more biomass of juvenile Nile perch, will not lead to stock depletion, as juvenile sizes can withstand higher mortalities. Nile perch smaller than 50cm have higher productivity (Natugonza et al., 2016) and are currently underfished. Similar observations of the distribution of fishers over the production spectrum have been made in other small scale African freshwater fisheries where fishing on small fish sizes has not led to stock collapses (Kolding et al., 2015; Kolding and van Zwieten, 2014; Zhou et al., 2019).

Furthermore, Plank (2017) suggests that, given a size-structured Beverton and Holt yield-per-recruit model with decreasing natural mortalities over the body size of fish, the predicted yield from allowing fishers to choose what size of fish to target is only slightly lower than the theoretical maximum at a singular optimum size. The latter is comparable to the classic outcome of the Beverton and Holt (1957) theory, which forms the basis of current mesh size regulations and production objectives of Lake Victoria's Nile perch management. Thus, developing portfolio management of fished resources (Edwards et al., 2004) would make sense by compromising on mesh size regulations and allowing fishers to utilise a certain proportion of smaller mesh or hook sizes, which are now illegal but part of their fishing strategies. In this way, production objectives, both for international export and the underappreciated regional trade (Obiero et al., 2019; UNCTAD, 2017), and social goals of maintaining individual livelihoods can be reconciled. Understanding fisher exploitation behaviour towards biological fish production could inform the design of management systems where behavioural aspects and motivations underlying them (Nunan, 2020) are addressed where possible and appropriate.

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Appendix: mixed model selection

Variables used in the generalised mixed models were assessed for correlation to address possible multicollinearity. The table shows Pearson correlation coefficients testing Prob>|r| under H0: ρ=0. All correlations were significant at p<0.001. N_{obs} = 2354.

	Distance	NP small	NP large	Travel time	Soak time	Setting depth
Distance	1					
NP small	-0.13	1				
NP large	0.26	-0.17	1			
Travel time	0.23	-0.08	0.17	1		
Soak time	-0.41	0.14	-0.33	-0.33	1	
Setting depth	0.35	-0.10	0.30	0.28	-0.61	1

Variance inflation, tolerance and collinearity were assessed in a regression model (1) (see main text), retaining only the continuous variables. All tolerance values were<1 and VIF between 1 and 2. Collinearity analysis indicated that none of the eigenvalues approached zero in combination with a high condition index: the highest values were respectively 0.021 and 14.6.

Variable	DF	Parameter estimate	P	Tolerance	Variance inflation
Intercept	1	0.99	<.0001	.	0.00
NP small	1	0.00	0.61	0.95	1.06
NP large	1	0.00	0.04	0.81	1.24
Travel time	1	0.02	0.06	0.88	1.13
Soak time	1	-0.06	<.0001	0.57	1.76
Setting depth	1	0.01	<.0001	0.62	1.61

The next table includes the generalised mixed models evaluated to explain the travel distance. Model selection was based on the AIC criterion to arrive at the final model discussed in the paper. Only significant effects (main effects and interactions) and the random effect (re) were retained initially (model 5). To examine whether model five was over parameterised, we subsequently removed interaction effects one by one and examined the impact of the removal on the AIC criterion. The final model discussed in the main text retains the main effects of small and large Nile Perch (NP) catches. Though the most parsimonious model according to the AIC criterion does not include the catches of small and large Nile perch, we retained them as the aim of the model is to show the effects of these catches on the distance travelled.

N	Model	N par	AIC	-2LL	ICC	Removed interaction effects
1	Intercept only	1	3127.28	3123.28	0.45	
2	Intercept + random effect (re)	1	1841.05	1837.05	0.45	
3	Full model with interactions (+re)	96	1799.05	1803.05	0.05	
4	Main fixed effects model (+re)	14	1697.95	1701.95	0.1	
5	A model with significant fixed main effects and interactions only (+re)	40	1528.48	1524.48	0.05	
Models 6 – 17 start from model 5 with systematically removing interaction effects.						
6		31	1626.32	1622.32	0.04	Season (Strategy)
7		37	1576.84	1572.84	0.06	Setting Depth (Strategy)
8		37	1556.45	1552.45	0.06	Soak time (Strategy)
9		34	1531.73	1527.73	0.09	Strategy*Region
10		37	1525.56	1521.56	0.06	Travel time (Strategy)
11		39	1524.75	1520.75	0.05	NP Small*Soak time
12		39	1523.64	1519.63	0.06	NP Large* Soak time
13		38	1519.28	1523.28	0.05	Model 11 and NP Large*Soak Time
14	**Final model (+re)**	**35**	**1519.18**	**1515.18**	**0.05**	**Model 13 + Travel time (Strategy)**
15		34	1513.53	1509.53	0.05	Remove small NP from model 14
16		34	1507.50	1503.5	0.06	Remove large NP from model 14
17		33	1500.79	1496.79	0.05	Remove all NP catch from model 14


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Chapter 6

General Discussion

Overview

This thesis aimed to understand the combined influence of fisher’s effort allocation and eutrophication on Nile perch's size structure and distribution within the southern part of Lake Victoria. The research methodology comprises two key phases: firstly, closely examining the environmental and ecological drivers that shape fishing strategies within the Tanzanian context, and secondly, exploring the collective implications of effort allocation, fishing techniques, and oxygen levels on the interplay of size distribution and spatial occurrence of Nile perch. The study draws upon a diverse range of data sources, including primary data based on direct engagement with fishers, comprehensive frame surveys from 2000 to 2020, and acoustic data to determine patterns and trends within the realm of the Nile perch fishery. The synthesis of these multidisciplinary insights seeks to understand how the dynamics of effort allocation and eutrophication interact to shape the Nile perch's size structure and distribution in the southern part of Lake Victoria. This effort improves our scientific understanding of the ecosystem. It provides insights for developing strategies to ensure the survival of Nile perch populations in the face of changing environmental conditions due to fishing pressure, nutrient loading and climate change.

Ecological Balance

I found that fishers were concentrated at an average distance of 5 km and 7 km from their homeport for gillnet and longline fishers, respectively (Figure 6.1a & b) (Peter and van Zwieten, 2018), with some of them sailing up to 40km even. These findings can be extrapolated to the rest of the lake. If the fishers in our study are indeed representative of the Nile perch fishery around the lake, as I suggest they are, this would mean that a large part of the open lake, and even the middle part of the gulf's surface and deeper waters, is not or is only lightly fished. Consequently, offshore deep waters have less or no fishing activity. Due to this reduced fishing pressure, offshore waters emerge as sanctuaries for all Nile perch, particularly as reservoirs for larger individuals. However, the Nile perch population's response stimulates fishers to venture beyond their usual homeport areas. Opting for offshore locations significantly heightens the likelihood of capturing larger Nile perch, as large Nile perch densities are higher in offshore waters (Peter and van Zwieten, 2018; van Zwieten et al., 2016). The choice to fish inshore with limited pressure offshore may be strategically beneficial, as part of the mature stock of Nile perch remains only lightly fished, thus saving a part of the spawning population. Consequently, the central parts of the lake may act as a refuge, and the fishery avoids recruitment overfishing. By their current spatial effort allocation, fishers may thus contribute to the long-term sustainability of the Nile perch populations.

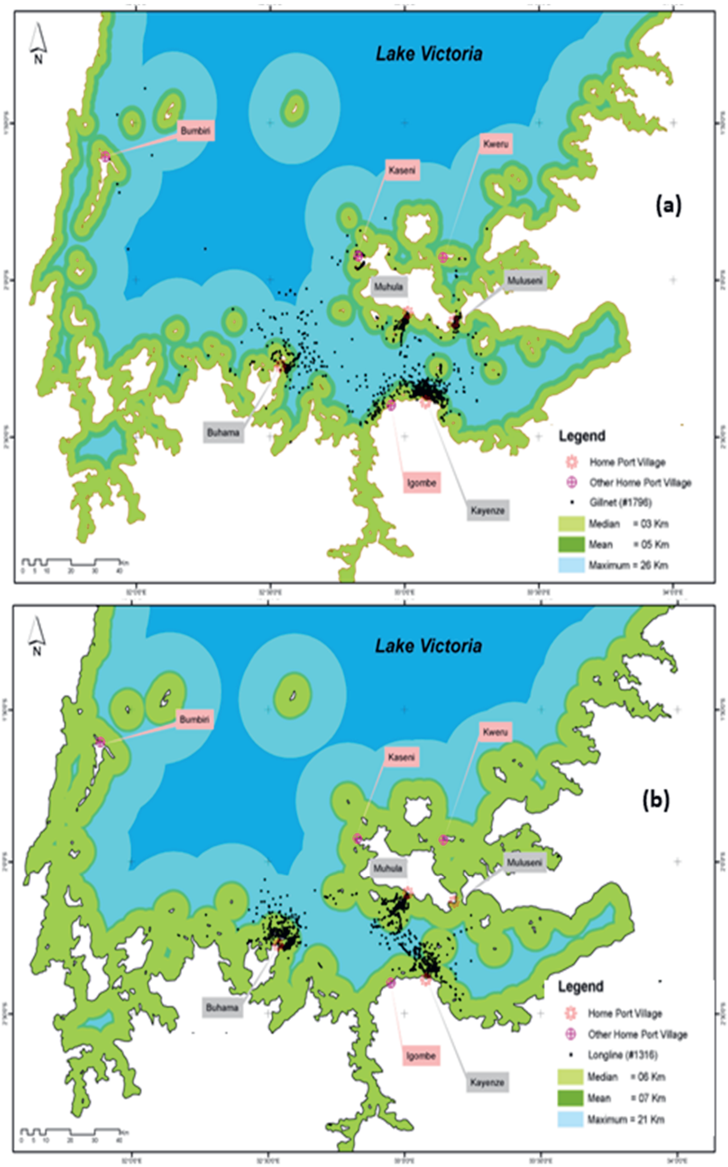

Figure 6.1: Map of the southern part of Lake Victoria showing the distance from homeports with the concentration of fishing effort from gillnet (a) and longline (b) fishers. Where light green is the median distance from the homeport to the fishing grounds, dark green is the average fisher's distance from the homeport to the fishing grounds, light blue is the maximum distance fishers can move from the homeport to fishing grounds, and dark blue is the area with less or no fishing effort.

Fishers' behaviour and drivers to daily choices

In small-scale fisheries, operational factors, environmental factors, and resource productivity influence the distribution of fishers across a resource. These constraints limit the area over which fishers can allocate their effort. In Lake Victoria, gillnet and longline fishers target Nile perch and share some resource space (Peter and van Zwieten, 2018). Gillnet fishers tended to fish closer to the shore compared to longline fishers. However, their resource space overlapped significantly at a 39km maximum distance from homeports (Peter and van Zwieten, 2018). Furthermore, they respond differently to Nile perch size changes, with gillnets targeting smaller Nile perch than longline fishers. In the next paragraphs, I will delve into a detailed discussion for further insights into their strategies and implications.

How do fishers deal with the shifts within the context of Nile perch fishery and the size distribution of Nile perch in the lake? Changes in ecology, environment, economic factors, management practices, and the demographic situation around the lake directly impact fishers' effort allocation. Before the 1980s, the lake ecology was home to hundreds of endemic haplochromine fishes (Hecky et al., 2010; Kaufman 1992; Witte et al., 1992). Commercial fishing was limited to traditional table fish species: tilapiines*, Bagrus, Clarias, Labeo, Protopterus, Mormyrus*, and barbs, such as *Labeobarbus* (Kudhongania et al., 1992). The fish community changed after the 1980s. It became simpler as only economically significant species dominated its biomass: Nile perch (*Lates niloticus* L.), Nile tilapia (*Oreochromis niloticus L.*), and Dagaa (*Rastrineobola argentea*) (Kolding, 2008; Kudhongania et al., 1992; Natugonza et al., 2022).

Regarding gear use, fishers have strategically adjusted the sizes of the mesh and hooks they use, primarily driven by changes in the composition of their catches. An interesting point to consider is the motivation behind these shifts. In the 1990s, most fishers relied on gillnets with a mesh size of 8 inches (Mkumbo, 2002; Schindler et al., 1998). However, as time progressed, a noticeable transformation emerged. There was a definitive transition towards utilising smaller mesh sizes, notably ≤5 inches, and more recently, an average increase to a larger mesh size of 6 inches. Additionally, Nile perch fishers in Lake Victoria joined the gillnet panel with the same mesh sizes from two to six panels deep (Mkumbo, 2007), an approach reported by Mpomwenda et al. (2022), to extend their nets' depth.

The reasons for the changes mentioned above are multifaceted. The shift from larger to smaller mesh sizes could be attributed to an alignment with the size of the catch. On the other hand, the shift to a larger mesh size might have resulted from law enforcement and specific market demands. Fish processing factories are permitted to process only Nile perch exceeding 50 cm in total length, and a recent fish maw market prioritises the largest Nile perch specimens. This combination of regulatory pressure and market dynamics appears to influence fishing practices. This insight invited me to explore the underlying factors that prompted these changes, offering a more comprehensive understanding of the dynamics shaping fishing practices over time.

With regard to environmental aspects, a variable environment and limited predictability in stock distribution, fishers are expected to bet-hedge to reduce uncertainty and risk (Boyce et al., 2002; Cambiè et al., 2017; Olofsson et al., 2009). Broadly, exploitation strategies available to small–scale fishers are: (1) enhancing their equipment's quantity (investing in more nets/hooks), (2) broadening the spectrum of targeted species by employing various mesh or hook sizes or using dynamic fishing techniques, and (3) capturing a greater variety of species, or sizes which depends on the presence of these species and sizes in the same areas (Jul-Larsen et al., 2003). Although I found marked changes in the preferred gear used for Nile perch (from gillnet to longline), I also found that fishers combined different mesh sizes when gillnet was used. A combination of mesh sizes diversifies catch over a range of species or sizes of fish to gain a more stable catch and potential income. This combination of mesh size is the so-called "portfolio effect", a common strategy to reduce risk (Anderson et al., 2017; Lehman and Tilman, 2000; Matsuzaki et al., 2019; Sethi, 2010; Tilman et al., 1998).

In the context of longlines, I did not find evidence of such a portfolio strategy – fishers did not combine different sizes of hooks. Interestingly, this observation seemingly contrasts with our earlier findings whereby gillnets used combinations of different mesh sizes. However, when considering a broader range of hook sizes and baits used, it becomes evident that mitigating risk is still in play. According to Chitamweba et al. (2009) and Msuku et al. (2011), hook sizes 11-13 did not yield significant differences in fish sizes, suggesting that a single hook size is sufficient. Nevertheless, it's important to note that the condition and size of the bait impact the catch's success (Kumar et al., 2015; Sistiaga et al., 2018).

Our results indicate that with hook sizes 10-12, Nile perch caught with *Clarias* as bait ranged from 20-100 cm, with a peak at 60 cm, while those captured with haplochromines as bait had the same size range but skewed towards 40 cm. Although longline fishers do not mix hook sizes, they employ a portfolio strategy by using different bait to catch fish across various fish sizes to achieve a more stable catch.

Regarding the economic aspect, the primary market for Nile perch consists of fish factories, which are exclusively permitted to purchase Nile perch measuring ≥50 cm in total length. Simultaneously, a substantial regional market exists for dried and smoked juvenile Nile perch (Medard Ntara, 2015). At the same time, the fish maw market requires larger fish to obtain sizable bladders. These factors have prompted fishers to adopt larger mesh sizes and incorporate larger bait to capture larger Nile perch (≥ 50cm TL). Additionally, fishers equipped with the means to invest in large fishing vessels and outboard engines are encouraged by the prospects of an international market. However, even those with limited capacity who catch fish smaller than 50cm can still find a market within the region.

Restrictive preconditions of my research

With regard to nutrient loading, my study was constrained by time limitations. Because of this, I could only gather data on dissolved oxygen and Chlorophyll-a over two years. During my study, the lake appeared to be in good condition as dissolved oxygen was relatively high for the entire water column. This good condition encompassed depths of up to 50 meters with a dissolved oxygen level of $3mgL^{-1}$, a critical threshold for Nile perch (Akiyama et al., 1977; Hecky et al., 1994; Kishe, 2004). Given the abundant oxygen presence throughout the lake, I could not find evidence for our hypothesis that hypoxia patches impact the Nile perch size distribution. Therefore, a comprehensive exploration of nutrient loading and its ecological implications becomes essential to assess the long-term environmental influence on Nile perch thoroughly. Also, under this fully oxygenated condition, Nile perch densities were mainly determined by food availability. The question remains whether this finding would hold under more stressful environmental conditions. Therefore, continued research on the factors influencing Nile perch populations in Lake Victoria remains advisable.

Chapter 2 of this thesis explores historical changes in effort allocation among Nile perch fishers, specifically focusing on the interplay of mesh size and hook size. However, our analysis faced limitations due to the dataset I utilized, derived from the Frame survey data spanning 2000 to 2020. This dataset had gaps in specific years, resulting in missing information. Additionally, the sampling of various hook sizes began in 2008 for longlines. Consequently, it was more feasible to discern trends and shifts with gillnets than with longlines. A significant constraint was the resolution of the data, which was limited to the district level. Future research at a landing station level would provide valuable insights. Despite these constraints, this chapter contributes to our broader understanding of how fishers adapt to changing conditions and employ diverse strategies.

In Chapter 3, my goal was to investigate the distribution of Nile perch in the lake and evaluate its correlation with physico-chemical factors. I hypothesised that juvenile Nile perch would predominantly inhabit shallow inshore waters, while adult individuals would be more prevalent in the deeper offshore areas. I assumed that physico-chemical factors and food availability influence Nile perch distribution.

I further found a strong and positive correlation between Nile perch densities and their potential food sources under the specific conditions of this study. However, it's important to note that our primary dataset was collected over only two years, encompassing the dry and wet seasons. While it could be argued that incorporating data from a lake-wide survey might have improved the comprehensiveness of my conclusions, it's noteworthy that my results align with those of a lake-wide survey conducted by Taabu-Munyaho et al. (2013). They also observed higher Nile perch densities in inshore waters during the stratified season when food was abundantly available. The timing of our study could be questioned. During our sampling period, the lake was in good condition, with oxygen present throughout the water column, and there were variations in the lake's oxygen levels throughout the water column in different years. Initiating a long-term monitoring study on the factors affecting Nile perch over the same area could provide insights that enable a more in-depth understanding of what influences Nile perch.

Implications of Our Research: Lake Victoria and Beyond

Our research revealed valuable information concerning the complex dynamics of Nile perch fishing practices in the southern region of Lake Victoria, alongside their intricate interactions with environmental shifts. These findings hold broad-ranging implications across various domains.

Fisheries Management and Regulation

Our study reveals a shift in gear preference as fishers moved from gillnets to adopting longline fishing strategies. This strategic evolution underscores the remarkable adaptability of fishers in response to changing conditions. While mesh size control is subject to strict regulation, our findings unveiled a comparatively lenient or non-existent enforcement regarding hook sizes. These nuanced differences underscore the complexities of the regulatory framework governing fishing practices.

The fishing industry's evolving preferences and enforcement strategies emphasise the necessity for adaptable regulations. Collaborating closely with fishers, particularly at the outset of the legislative process, can facilitate the development of rules that consider fisher's specific gear, net, and hook preferences, together with their limitations and strategies. This collaborative approach strikes a balance between preserving fish populations' health and sustaining the economic well-being of fishing communities, ensuring that decision-makers account for the issues that directly impact them.

Regulations can be more effective by acknowledging the evolving fishing methods. This can help to maintain a balanced relationship between the environment and the needs of fishing communities. Adapting rules to these changes recognises the creative problem-solving of fishers and allows for regulations that suit their real experiences. By doing so, the management of Nile perch fishing can achieve a sustainable balance, safeguarding the ecosystem and the livelihoods of those who depend on it.

Small-scale fisheries

As Kolding and van Zwieten (2011) highlighted in their study, the global concern regarding open access to resources and the fishing of undersized and immature fish is a fundamental basis for modern fisheries management. This modern fisheries management is rooted in the concept that fish should be allowed to reproduce before being caught. It also emphasises that fish should not be caught before maturity. Selective fisheries management aims to protect fish stocks by targeting the larger and more mature fish for fishing while allowing smaller fish to grow and reproduce. Fishing mortality thus generally increases with fish age, unlike the decrease in natural mortality from predation. However, this strategy could alter the maturity age and potentially affect the natural mortality pattern of fish populations.

Our results show that fishers harvest large and smaller Nile perch as it becomes available and accessible in their conditions, irrespective of the formal regulations. The fishery regulation in Lake Victoria follows the modern fisheries management of giving fish a chance to reproduce before being caught by following a traditional approach of single-species management. Like other African lakes, the fishery in Lake Victoria, global lakes and marine fisheries in the least developed countries are primarily conducted by small-scale fishers (Kolding and van Zwieten, 2011). Nearly 90% of the world's 120 million fishers are estimated to be engaged in small-scale fisheries (Kolding et al., 2014). Small-scale fisheries (SSF) are characterised by a diversity of gears, target species, size and higher spatio-temporal variation (Tzanatos et al., 2005). Thus, small-scale fishers fish across a broad range of species, trophic levels, stocks, and sizes within an ecosystem.

Some authors suggest that the unselective fishing pattern employed by small-scale fisheries (SSF) serves as a practical illustration of the ecosystem approach to fisheries (EAF), which upholds species and size compositions – a foundational principle of the concept of Balanced Harvest (BH). Natugonza et al. (2022) noted the historical alignment of Lake Victoria's fishing practices with Balanced Harvest in the past, and our study identified similar practices: gillnet fishers unknowingly employ a Balanced Harvest strategy in their daily fishing activities. This BH is shown by the bet-hedging technique observed, where fishers strategically utilise multi-mesh sizes in their gear. This approach enables them to catch a diverse Nile perch sizes spectrum and various species within Lake Victoria, aligning with the characteristic patterns of BH.

However, in recent years, the BH practice in Lake Victoria has faded (Natugonza et al., 2022). These authors attribute this to the overexploitation of the less productive groups, such as the big Nile perch, Nile tilapia, and other demersal groups. In contrast, highly productive groups, especially small Nile perch and dagaa, are underexploited together with the commercial collapse of native species. To safeguard the fisheries of Lake Victoria, particularly the economically vital Nile perch species, which significantly impacts the well-being of those relying on Lake Victoria's fisheries, the current selective fishing management approach needs to be reconsidered. The existing approach primarily focuses on protecting Nile perch, particularly the smaller ones, while potentially overlooking the importance of other sizes and species essential to the Nile perch fishery. A more effective approach would be to adopt a management strategy that ensures balanced harvesting, similar to the methods employed by fishers who use multiple mesh sizes, including mesh size that may currently be illegal, and have the flexibility to employ various baits in longline fishing. This inclusive approach aims to maintain a thriving Nile perch population while preserving the ecosystem's health.

Nonetheless, it's crucial to recognise that every lake and fishery possesses distinct characteristics. Therefore, our research's specific outcomes and suggestions may not be immediately relevant to other lakes without additional research and analysis. However, van Zwieten et al. (2003) found a diversity of fishing methods used in Lake Mweru, which complemented each other in a way that different parts of the fish community were exploited, which can be regarded as a sort of BH. Fisheries management worldwide primarily focuses on implementing measures such as minimum size regulations and gear restrictions to manage the selective targeting of specific segments within the fish community (Kolding et al., 2014). These measures are virtually essential for almost every fishery globally. I suggest revisiting the approach towards a balanced harvesting strategy, where moderate fishing pressure is spread across a wide range of species, maintaining a minimum spawning population biomass for sustainable recruitment.

Sustainability and Conservation

Our research highlighted a clear shift toward the use of smaller hook sizes. With the expanding bait fishery enabling Nile perch fishers to access various bait types and sizes (Medard, 2015), the latter can now capture a wider range of Nile perch sizes. This transition reflects the adaptability of Nile perch fishing practices rather than a deliberate choice of primarily targeting smaller Nile perch. Conversely, a trend has emerged in gillnet fishing, where larger mesh sizes are now employed alongside mixed mesh sizes. This strategy signals an intention to capture fish of varying sizes, similar to the approach observed in longline fishing. It has the potential to balance the goals of resource conservation and supporting the economic well-being of fishing communities. However, it faces challenges related to regulations governing the fishery in Lake Victoria and aligns with regulations in many other regions, emphasising selectivity through gear-size limits (Garcia et al., 2012; Kolding et al., 2014).

Policymakers worldwide have implemented various fisheries strategies and regulations, such as specifying limits on the types and sizes of fish caught, regulations regarding fishing gear, and controlling when and where fishing occurs (Garcia et al., 2012). These measures aim to mitigate the negative environmental impacts of fishing while continuing to provide economic and food benefits to communities. However, selective fishing may have unintended adverse social and biological consequences (Kolding and van Zwieten, 2011; Zhou et al., 2010). These consequences can counter international agreements that aim to restore fish stocks to sustainable levels for harvesting, known as maximum sustainable yield (MSY). Selective fishing practices may hinder progress towards achieving this goal (Garcia et al., 2012).

To ensure the long-term health of the Nile perch population, it is essential to customise fishing regulations to safeguard both young and adult Nile perch. Establishing catch limits for fish at various life stages prevents overfishing and facilitates the recovery of the fish population. This approach aligns with responsible fishing practices and contributes to maintaining a diverse Nile perch population. Ultimately, it benefits the broader Lake Victoria ecosystem.

I advocate for fishing regulations that protect the entire size range spectrum of Nile perch (approaching balanced harvest theories), promoting the long-term well-being of the Nile perch population. The suggested regulation could include permitting, to a limited extent, the use of mesh sizes that are currently illegal (smaller mesh sizes) to enable fishers to practice their bet-hedging strategy. However, further research is needed to determine what percentage of smaller mesh sizes should be allowed. Implementing catch limits for fish at different life stages prevents overfishing and aids in the fish population's recovery. This approach can be in harmony with responsible fishing practices and fosters the preservation of a diverse Nile perch population, ultimately benefiting the wider Lake Victoria ecosystem.

Regulatory Innovation and Adaptive Practices

The interrelationship between fishers' strategies and the environmental dynamics in the southern region of Lake Victoria provides a basis for an innovative approach to regulatory strategies. Our investigation unveils how fishers capably adapt to changing conditions, as demonstrated by the shifts in gear preferences from gillnets to longlines and the evolving mesh size and hook size choices. These adaptive practices underscore the complex decision-making process that guides fishers' actions and strategies.

Furthermore, our study uncovers the practice of fishers within a single fleet employing various mesh sizes during fishing, which also involves using smaller mesh sizes. This versatile strategy within fishing operations highlights the flexibility and ability to navigate the dynamics in fishing conditions.

Our research shows that adapting regulations to fit the needs of fishers not only makes the rules more acceptable but also makes enforcement more effective. I suggest considering innovative approaches like allowing smaller mesh or hook sizes, which are currently restricted. This approach recognises that various factors influence fishermen's choices, such as market demand, fish behaviour, and the environment. Allowing fishers some flexibility in their gear choices while staying within certain limits encourages them to follow the rules based on real-world fishing practices. This flexible approach will bridge the gap between regulations and the changing realities of fishing, benefiting both fishers and Lake Victoria's ecosystem. Our study highlights the potential for regulations to evolve alongside fishermen's strategies, ultimately promoting a more sustainable and adaptable fishing industry.

Conclusions

From this thesis, the following main conclusions can be drawn based on the different studies I carried out.

- Nile perch fishers on Lake Victoria distribute themselves according to the underlying productivity distribution of the resource within the constraints of their available resource space.
- Fishing pressure is mainly exerted in nearshore lake areas, typically within an average distance of up to 7km from the homeport, while offshore areas are lightly fished. Consequently, offshore areas serve as a refuge for Nile perch, particularly the larger individuals.
- Nile perch fishers on Lake Victoria employ bet-hedging strategies by combining mesh of different sizes in their daily fishing activities to reduce uncertainty and risk.
- The daily choice of fishing locations did not exhibit a significant relationship with the catch success of the previous days, suggesting that the previous day's catch success is not a driver of fishers' daily choices.
- From 2000 to 2016, the dominant and preferred mesh sizes remained consistently around 5-6 inches, while hook sizes ranged from 8 to 10. However, starting in 2016 and continuing to the present, the preferred mesh size shifted to 6 inches.
- Nile perch densities correlated strongly and positively with their possible food items.
- A noticeable shift in fishing dynamics is observed: fishers increasingly favour longlines over gillnets. As the current regulatory emphasis has primarily been on mesh size, there's an urgent requirement to extend this focus to include the sizes of the hooks used.

Recommendations

- Acoustic studies on small areas are important to design proper management of the Nile perch fishery. Different parts of the lake differ significantly regarding available space for Nile perch, nutrient loading, and fishing pressure. I recommend special attention to different parts of the lake, e.g., gulfs, during the acoustic surveys.

- The study highlights the role of food availability in determining Nile perch densities. I recommend continued research on the factors influencing Lake Victoria's Nile perch food availability for better conservation and management of the Nile perch fishery.
- I recommend focusing on total fishing effort management – e.g., determining where fishing effort should be allocated from inshore areas to deep offshore fishing grounds - instead of primarily focusing on size-related regulations.
- I recommend considering a portfolio management approach for fished resources, which involves a measured relaxation of mesh size regulations. Adapting management strategies to align with this evolving gear preference is needed for effective fisheries regulation. This management approach could permit fishers to strategically incorporate a defined proportion of smaller, currently prohibited, mesh sizes into their fishing strategies, useful for balanced harvesting.
- Based on my findings, I propose enhancing Frame survey data for effective fishery management. I recommend incorporating precise geospatial coordinates along with fishing ground names in the data collection process to achieve this. Such an addition would enable a comprehensive understanding of the (changes in) spatial and temporal distribution of fishing efforts. These enhancements would facilitate more strategic decision-making in fishery management, contributing to the preservation of Lake Victoria's ecosystem and the sustainability of the fishing industry.
- The continuous rise in fishers and fishing vessels emphasises the essential requirement for comprehensive management in Lake Victoria. As the lakeside population expands, more individuals are expected to join fishing activities. Just as gear sizes are regulated, prioritizing the control of total effort is needed to ensure the sustainable management of the Nile perch fishery.

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Appendices

Summary

Acknowledgements

About the author

List of scientific publications

WIAS Training and Supervision Plan (TSP)

Summary

The ecological sustainability of fisheries is a global concern that requires a comprehensive understanding of the factors influencing fishing practices. Over the past three decades, efforts have been made to identify challenges in fisheries and propose interdisciplinary solutions. While catch data provide insights into the status of fisheries, they do not offer a complete picture of fishing patterns, such as where and how fishing efforts are distributed, and selection patterns occur. To gain a deeper understanding of the dynamics and trends in fishing activities, it is important to examine developments in fishing efforts, including the number of fishers, types of gear used, and gear configurations.

This research focuses on Nile perch fishery from Lake Victoria, which is commercially significant and plays a vital role in the economies of riparian countries, i.e., Kenya, Tanzania and Uganda. Nile perch is distributed throughout the entire lake, often linked to spatial variations in environmental conditions, particularly hypoxia and food availability.

Operational and environmental factors constrain the available resource space for gillnet and longline fishers when targeting Nile perch in the Speke Gulf and open waters of southern Lake Victoria. These factors also influence their encounter rates with patches of fish, resulting in distinct distributional patterns specific to their gear types.

Small-scale fishers, including Nile perch fishers from this study, experience substantial variability in daily catches within their limited resource space from the operational constraints. Environmental factors further impact their daily choices in allocating spatial fishing efforts. To mitigate uncertainty and risks from the high variability in their daily catches within these resource spaces, Nile perch fishers on Lake Victoria employ bet-hedging strategies, which involve using meshes of different sizes in their daily fishing activities.

The **Choice to Catch: Effort Allocation Strategies and Drivers of Nile Perch Fishers in Lake Victoria** study aims to untangle how fishing pressure, characterised by effort allocation, and nutrient loading due to eutrophication interact to shape the size structure and distribution of Nile perch in Lake Victoria, Tanzania. Specifically, in this study, I will assess changes in fishing pressure, fishing patterns, and the effects of nutrient loading (eutrophication) on the distribution and size structure of Nile perch populations. The goal is to understand to which extent the size structure of the Nile perch stocks is determined by the fishery or by ecological (eutrophication) factors of the lake.

The following two research questions were addressed:

1. Which physical and short-term ecological factors drive the fishing effort allocation and fishing patterns in the southern part of Lake Victoria, Tanzania?
2. How do effort allocation, fishing, and lowered oxygen levels impact the Nile perch size structure and distribution?

Chapter 1 I briefly give the background of Lake Victoria, the history and current statistics on fishing efforts, environmental biological changes, and the diversity of fish species in Lake Victoria. Details on effort allocations and eutrophication are also explained in this chapter. Regarding the effort allocation, I have stated that it is not random but expected to be based on fishers' knowledge of the distribution of the targeted species, the density of fishers, and the fishing costs. As eutrophication results from increased nutrient levels, we infer that in the case of Lake Victoria, their primary sources are agricultural activities, deforestation, swamp clearance, and urban pollution. The shallow nature of Lake Victoria makes eutrophication a matter of significant concern for both fisheries and environmentalists.

In **Chapter 2**, we used the historical data from past frame surveys (2000-2020) collected from recognised landing sites around the lake. We used the data to assess the changes in fishing patterns and pressure along the study area. Data reveals changes in fishing dynamics whereby the number of fishers and fishing vessels has increased from 2000 to 2020. In Tanzania alone, fishers increased from approximately 55,000 in 2000 to 100,000 fishers in 2020. In the study, I also found a shifting preference in the gear used from gillnets to longline. Predominant gillnet mesh sizes were (5-6 inches) and hook sizes (8-10), which remained constant from 2000 to 2016, and from 2016 to the present, mesh sizes changed to 6” and hook sizes to ≥10. We further observed that there is no congestion in the market for Nile perch: dried, smoked or fresh – apparently, all captured Nile perch can be sold. In such a situation, the nominal fishing effort (number of fishers, vessels, and gear) may continue to increase until the biological limitations of the Nile perch populations may be reached. Focusing on total effort – e.g., through licensing - instead of size-related regulations may be more appropriate.

In **Chapter 3**, we utilised hydroacoustic techniques to examine how Nile perch is distributed in the south-eastern region of Lake Victoria. We aimed to gather detailed insights into how Nile perch distribution relates to living (biotic) and non-living (abiotic) factors in this area. We hypothesised that juvenile Nile perch would predominantly occupy the shallow, nearshore waters, while adult Nile perch would be more prevalent in the deeper, offshore waters. We based this assumption on factors like size differences, physico-chemical conditions, and food availability, all of which we believed played a role in shaping Nile perch distribution.

Our findings in this chapter underscored a strong positive correlation between Nile perch densities and the presence of their potential food sources. Additionally, we observed that dissolved oxygen levels, which were consistently above the critical threshold of $3mgL^{-1}$ for Nile perch, did not significantly influence Nile perch densities. This study highlights the critical role of food availability in determining Nile perch densities. It emphasises the need for ongoing research into the various factors that impact Nile perch populations within Lake Victoria.

In **Chapter 4,** we studied the fishing effort allocation, analysing the factors driving fishers' daily fishing choices. The strategies deployed by individual Nile perch fishers to remain in the fishing activities against the background of high variability in daily catches were investigated. Variability in daily catches puts fishers at risk of losing their capital. Operational and environmental factors limited available resource space of gillnet and longline fishers targeting Nile perch in the Speke Gulf and open lake of southern Lake Victoria and drove their encounter rates with patches of fish, resulting in gear-specific distributional patterns.

Gillnet and longline fishers distributed themselves over the size-productivity spectrum of Nile perch. Still, they reacted differently to patterns in the size distribution of Nile perch: gillnetters focused more on numbers of productive juveniles between 30-60cm at an average 5km distance (59min travel time) from homeport and longliners on larger sized 40-80cm Nile perch deeper in the water column at 7km (108min travel time). If our sample of fishers are representative for most of the Nile perch fishers, then fishing pressure is mainly exerted on nearshore lake areas and offshore areas are lightly fished.

The chapter pointed out that current gear regulations, if enforced, force gillnet and longline fishers to focus on the lower productive adult Nile perch stock further from the shore and deeper in the water column. Without concurrent effort regulations to reduce the number of fishers, this may be counterproductive and lead to overfishing of the large Nile perch size classes.

In **Chapter 5,** we focused on small-scale fishers targeting Nile perch. Small-scale fishers experience high variability in daily catches within a resource space, which is limited in extent by operational constraints, and biophysical factors affect daily choices in spatial effort allocation. We aim to uncover factors that shape fisher's daily choices in spatial effort allocation and how they cope with day-to-day catch variability. The question in this chapter was what are the consequences of the limited spatial extent of an individual fisher's resource space and options to handle daily and long-term variation with a catch portfolio from that space? Gillnet and longline Nile perch fishers in south-eastern Lake Victoria, Tanzania, were given a GPS to record their position, operations and daily catch. Three different gillnet and longline fishing strategies were determined. Daily choice of fishing locations did not relate to previous days' catch success. In particular gillnet fishers used a bet-hedging strategy combining different mesh sizes in a single fleet. From such a strategy, they can catch Nile perch of different sizes and other species. The mix of sizes and species reduced day-to-day catch variability due to a portfolio effect. Current mesh and landing size regulations based on classical arguments around growth overfishing interfere with these strategies and force individual fishers to specialise in size, species, and area.

In **Chapter 6**, we brought together the key findings from all the studies in this thesis. We discussed them in the context of the factors driving effort allocation and the strategies employed by Nile perch fishers in Lake Victoria. This chapter marks the end of the thesis, restating the conclusions and offering the last set of recommendations.

Acknowledgements

One significant thing to do before concluding this thesis is to reflect and express my heartfelt gratitude to all those who, in one way or another, played a role from the beginning to the completion of this exceptionally long journey. To all of you, my deepest gratitude, even when it may be challenging to mention everyone by name.

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At a time when I had lost hope and direction on how to reignite the progress of my study after a pause, I turned to the Western Indian Ocean Marine Science Association (WIOMSA) for a travel grant, and I was extended a helping hand. WIOMSA support is something I will always hold close to my heart. Without the support, this story would have remained unfinished. My **daughter Chloe-Ella** and **son Ty**, I welcomed you into my life while already immersed in my PhD studies, and your arrival was the missing piece that made everything fall into place. Even when I was often separated from you, your innocent inquiries, 'Mom, have you completed your teacher's work?' and your simple requests for my attention have been constant reminders of the patience and understanding you bring into my life. I am forever grateful and will always cherish these moments. I love you so much, my kiddos.

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About the author

About the author

Happy Kokwenda Peter, a proud Tanzanian, developed a passion for science at a young age, which led her to pursue a scientific education during her secondary and high school years. Although her mother strongly encouraged her to pursue a degree in medical science after completing high school, Ms. Peter had different aspirations. She sought a path that diverged from the conventional choices made by many. Despite having little prior knowledge of the subject, Ms. Peter decided to enroll in a diploma program in Fisheries. This decision turned out to be one of the best choices she ever made, and she completed her studies with a First-Class distinction. The experience opened her eyes to the world of fisheries and ignited her desire to delve deeper into the field. Following her diploma, in 1999 she embarked on a bachelor's study in Marine Science and Microbiology. During her studies, she undertook a project that involved an experimental investigation into the mass mortality of mangrove *Heritiera littoralis* at Rufiji Delta after an El Niño event. Her dedication to research and her passion for aquatic ecosystems continued to grow. Upon completing her bachelor's degree in 2003, she joined an internship with the Coral Reef Conservation Project (CRCP) in Mombasa, Kenya. This experience further fueled her curiosity about aquatic environments and ecosystems. Ms. Peter started her career as a research officer at the Tanzania Fisheries Research Institute (TAFIRI) in 2003 where she continues to work to date. Her thirst for knowledge remained unfulfilled, prompting her to pursue a Masters' degree at the Free University of Brussels (VUB), Belgium, in Ecological Marine Management with a specialisation in Marine Pollution and Risk Management. She graduated with the highest distinction in 2007. Her initial decision to study fisheries at the diploma level proved instrumental, as it provided her with a broad foundation in various aspects of fisheries, including gear technology, fishing techniques, fish processing, marketing, engineering, and navigation. Her hunger for in-depth knowledge continued, prompting her to seize the opportunity to pursue a PhD that seamlessly integrated her passion for science, her expertise in fisheries, and her experiences gained during her internship and MSc studies. Her PhD research centred on Nile perch fisheries in Lake Victoria, investigating how fishing pressure, effort allocation, and nutrient loading due to eutrophication influence the size structure and distribution of Nile perch in the Victoria-Tanzania region. She embarked 2008 on this academic journey as part of the project "Exploitation or Eutrophication as Threats for Fisheries? Disentangling social and ecological Peter's of ecosystem changes in Lake Victoria (SEDEC)." Her educational and professional journey reflects her consistent dedication to advancing the understanding of aquatic ecosystems and their sustainable management. Currently, Ms. Peter is involved in a project that uses remote sensing technology to help fishers access potential fishing areas in Tanzania under the Global Monitoring for Environmental Security and Africa (GMES & Africa) program. The project is co-financed by the European Commission and the African Union Commission.

Contact: happypeter2000@yahoo.com

List of scientific publications

Andrea S. Downing, Egbert H. van Nes, John S. Balirwa, Joost Beuving, P.O.J. Bwathondi, Lauren J. Chapman, Ilse J. M. Cornelissen, Iain G. Cowx, Kees P. C. Goudswaard, Robert E. Hecky, Jan H. Janse, Annette B. G. Janssen, Les Kaufman, Mary A. Kishe-Machumu, Jeppe Kolding, Willem Ligtvoet, Dismas Mbabazi, Modesta Medard, Oliva C. Mkumbo, Enock Mlaponi, Antony T. Munyaho, Leopold A. J. Nagelkerke, Richard Ogutu-Ohwayo, William O. Ojwang, **Happy K. Peter**, Daniel E. Schindler, Ole Seehausen, Diana Sharpe, Greg M. Silsbe, Lewis Sitoki, Rhoda Tumwebaze, Denis Tweddle, Karen E. van de Wolfshaar, Han van Dijk, Ellen van Donk, Jacco C. van Rijssel, Paul A. M. van Zwieten, Jan Wanink, F. Witte, Wolf M. Mooij. Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's ecosystem services. *Ecology Society* 19(4).

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WIAS Training and Supervision Plan (TSP)

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EDUCATION AND TRAINING (minimum 30 credits)	
The Basic Package	**3 ECTS**
WIAS Introduction Course	2008
WGS Scientific Integrity course	2012
Disciplinary Competences *(minimum 2 courses)*	**15 ECTS**
Preparing own PhD research proposal	2008
Statistics for life science	2008
Fisheries acoustic training course (Norway)	2010
Research methodology I: From Topic to proposal	2009
Lake Victoria SEDEC workshops	2009
Professional Competences *(minimum 2 courses)*	**8 ECTS**
Techniques for Writing and Presenting a Scientific Paper	2008
Information Literacy including introduction to ENDNOTE	2008
Project and timemanagement	2011
English academic writing II	2009
Presentation Skills *(max 4 credits)*	**2 ECTS**
31st congress of the international society of Limnology, South Africa	2010
6th World Fisheries Conference, Scotland	2012
Teaching competences *(max 6 credits)*	**6 ECTS**
Masters (Minor) student supervision	2009-2012
Masters (Major) student supervision	2009-2012
Education and Training Total (minimum 30 credits) *	**34 ECTS**

**One ECTS credit equals a study load of approximately 28 hours*

A

Colophon

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