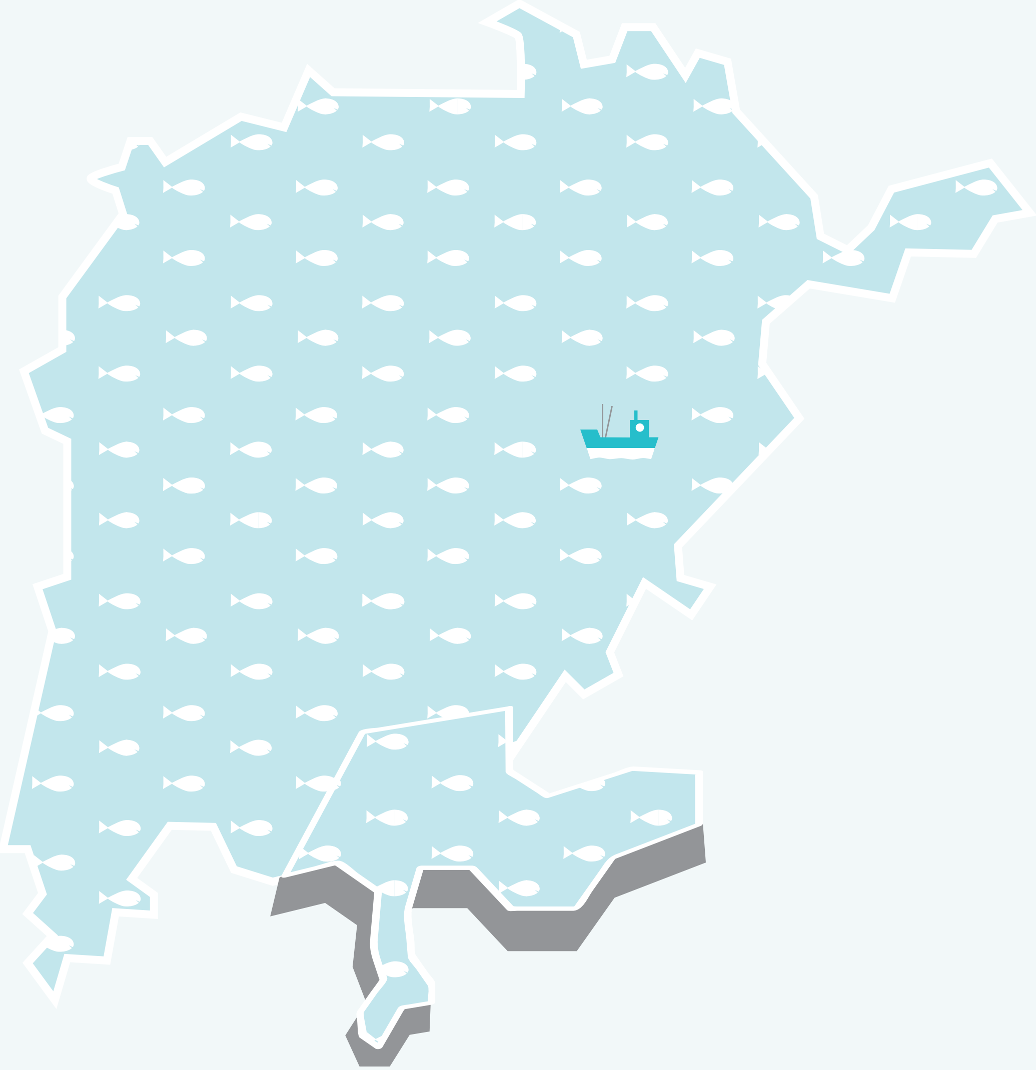
EUTROPHICATION, NILE PERCH AND FOOD-WEB INTERACTIONS IN SOUTH-EAST LAKE VICTORIA.



Ilse J. M. Cornelissen

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EUTROPHICATION, NILE PERCH AND FOOD-WEB INTERACTIONS IN SOUTH-EAST LAKE VICTORIA

Ilse J. M. Cornelissen

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr. A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Monday 9 November 2015
at 11 a.m. in the Aula

Ilse J.M. Cornelissen
Eutrophication, Nile perch and food-web interactions in south-east Lake Victoria,
164 pages

PhD Thesis, Wageningen University, Wageningen, NL (2015)
With references, with summary in Dutch and English
ISBN: 978-94-6257-566-0

Voor Jacob en Annabel

Abstract

Cornelissen, I.J.M (2015). Eutrophication, Nile perch and food-web interactions in south-east Lake Victoria. PhD Thesis, Wageningen University

The increasing eutrophication, the introduction of Nile perch (*Lates niloticus)* and the increasing fishing pressure has changed Lake Victoria tremendously the last century. Since the 1960s, eutrophication increased primary production, enabling an increase in fish production. However, eutrophication also created hypoxia pockets, which reduced the available habitats for fish. In addition, the endemic haplochromines declined, whereas the introduced Nile perch boomed in the 1980s. The Nile perch boom and increased fish production resulted in the largest freshwater fisheries of the world. However, it is unclear whether fish production can still increase with further eutrophication as maximum primary production rates may have been reached. Fish stocks fluctuate since the 1980s and in order to manage these, it is important to understand how eutrophication and fisheries affect the Nile perch population. The present study investigates the bottom-up effects of eutrophication on the Nile perch and food-web dynamics in south-east Lake Victoria. We analysed the level of eutrophication along an eutrophication gradient in the Mwanza Gulf. Phytoplankton biomass varied spatially and seasonally and was limited by nutrients in deep water and by light in shallow water. Fish distributions were dynamic, with environmental factors depth and temperature influencing Nile perch size structure and distribution patterns similarly on small and large spatial scales. Although prey densities of haplochromines and *Caridina nilotica* shrimp did not explain Nile perch distributions, ontogenetic diet shifts and composition were related to prey densities, suggesting an opportunistic feeding behaviour of Nile perch. Small Nile perch however, showed some preference to shrimp and Nile perch preferred haplochromines above Dagaa *(Rastrineobola argentea)* and juvenile Nile perch as fish prey. On a food-web level, the base of the food web was spatially and seasonally highly dynamic. The onset of rains caused a spatial differentiation in littoral/benthic and pelagic carbon sources, affecting the whole food web. Trophic levels of fish were related to the spatial variation in diet compositions. Although a large heterogeneity was found in water quality, fish distributions and food-web structure, bottom-up processes affected the food web similarly. Despite the ongoing nutrient load in Lake Victoria, water quality has improved since the 1990s. Climate forcing through increasing wind speeds increased visibility and oxygen levels. Global climate change will therefore be an important driver of the water quality and fish distributions of Lake Victoria.

Contents

Chapter 1

General introduction

The sustainability of Lake Victoria's resources is of utmost importance for the livelihood of 1.3 million people in East Africa, who use the lake for food and generating income (Witte *et al.*, 1999; Njiru *et al.*, 2005). However, profound changes in the ecosystem and limited understanding of the main drivers make it difficult to manage its resources in the future. In this chapter an overview of Lake Victoria's ecosystem and the main drivers of changes in its food web are given. The main factors influencing Lake Victoria's food web are eutrophication, the introduction of Nile perch *(Lates niloticus,* L.*)* and the increasing fisheries pressure. Finally, an overview of the objectives and outline of the thesis will be given.

The Lake

In terms of surface area, Lake Victoria is the largest tropical freshwater lake in the world, covering a surface area of 68,800 km$^{2.}$ It is situated across the equator in East Africa at an altitude of 1350 m. The lake is shared by Kenya (6% by area), Uganda (43%) and Tanzania (51%) and it lies in a shallow basin on a plateau between the western and eastern branches of the East African Rift System (Tiercelin and Lezzar, 2002). Lake Victoria is well known for its high diversity in cichlid fish and their mass extinction in the 1980s (Witte *et al.*, 1992b). During this period, Nile perch, an introduced species, boomed and dominates the food web since then. With the Nile perch boom, fishing pressure increased tremendously and developed into the largest freshwater fishery of the world (Kolding *et al.*, 2008; Kolding *et al.*, 2014). The lake's resources have always attracted people, but since the Nile perch upsurge, the human population increased rapidly (Kolding *et al.*, 2014). This has led to environmental degradation of the shorelines and eutrophication of the lake (Kolding *et al.*, 2008; Kolding *et al.*, 2014). Lake Victoria's food web is now primarily driven bottom-up by eutrophication and top-down by the increasing fishing pressure.

The increasing eutrophication

Since the 1960s, extensive deforestation, biomass burning, agriculture and urbanization led to an increased input of nutrients into the lake by mainly atmospheric deposition and run-off from the land (Lindenschmidt *et al.*, 1998; Tamatamah *et al.*, 2005). Presently, this accounts for more than 90% of the external phosphorus and nitrogen load into the lake (Scheren *et al.*, 2000). Since the 1960's, phosphorus and nitrogen influx to the water column and sedimentation rates have been doubled (Bootsma and Hecky, 1993; Hecky, 1993; Lung'ayia *et al.*, 2001; Hecky *et al.*, 2010). This eutrophication resulted in increased primary production and a 3-5 fold increase in phytoplankton biomass between 1960s and 1990s (Hecky, 1993; Hecky *et al.*, 2010). Algal biomass in inshore areas increased relative to the open water. At present chlorophyll concentrations tend to be 1.5-5 times higher than in offshore waters (Lung'ayia *et al.*, 2001; North *et al.*, 2008; Sitoki *et al.*, 2010; Ngupula *et al.*, 2011) and in both habitats, chlorophyll concentrations are high during periods of stratification (Silsbe, 2004).

Furthermore, visibility decreased (Lung'ayia *et al.*, 2001; Hecky *et al.*, 2010), which led to light limitation of photosynthesis and primary production in the northern part of Lake Victoria (Silsbe *et al.*, 2006). Also the composition of the phytoplankton changed: the diatom-dominated community was replaced by a cyanobacteria-dominated community (Hecky, 1993; Kling *et al.*, 2001; Verschuren *et al.*, 2002).

Global climate change has increased the strength of the thermal stratification of the water column (Hecky, 1994). The increasing stability resulted in a reduced water mixing and lower oxygen concentrations in the water column (Hecky, 1993). In addition, higher primary production rates in the surface waters caused increased sedimentation rates of phytoplankton and detritus, which in turn resulted in an increased hypoxic layer in the hypolimnion (Bootsma and Hecky, 1993; Hecky, 1994; Silsbe, 2004). This hypoxia occasionally triggered massive fish kills in the 1980s when hypoxic water suddenly welled up (Ochumba, 1990; Kaufman, 1992; Wanink *et al.*, 2001). The increase in anoxic conditions stimulated denitrification, decreasing the availability of nitrates for phytoplankton. As a consequence, N:P ratios decreased vertically in the water column from 16:1 in the mixed layer to 8:1 in hypolimnetic waters, favouring N-fixing cyanobacteria (Hecky, 1993; Guildford and Hecky, 2000; Lung'ayia *et al.*, 2000; Haande *et al.*, 2011). Cyanobacteria are potentially toxic and less nutritious for herbivores such as zooplankton (de Bernardi and Giussani, 1990). As a consequence the phytoplankton shift towards cyanobacteria may have led to a change in zooplankton composition, shifting from large herbivorous cladocerans to small omnivorous cyclopoids (Wanink *et al.*, 2002). The shift towards 'inedible' cyanobacteria thus decreased the efficiency of energy transfer from primary producers to primary consumers.

The Nile perch upsurge

To boost the fishery, Nile perch was repeatedly introduced into Lake Victoria in the 1950s and 1960s (Pringle, 2005; Goudswaard *et al.*, 2008). Nile perch numbers remained low until 1979, when a sudden upsurge was observed in the northern part of the Lake (Hughes, 1983). A similar upsurge was observed in 1983 in the Mwanza Gulf in the south-east of the Lake (Goudswaard *et al.*, 2008). The then dominating endemic haplochromine cichlids declined rapidly (Witte *et al.*, 1992b). *Caridina nilotica* (Roux), an atyid shrimp, which occurred in low numbers before the Nile perch upsurge, also increased (Goldschmidt *et al.*, 1993; Budeba and Cowx, 2007b). Similarly, numbers of Dagaa (*Rastrineobola argentea,* Pellegrin), a small cyprinid, and Nile tilapia *(Oreochromis niloticus,* L.) increased as well (Cowx *et al.*, 2003). As a consequence, the food web changed from a diverse haplochromine-dominated food web, to a simplified one, dominated by Nile perch, *Caridina,* Dagaa and Nile tilapia.

After its introduction, Nile perch fed mainly on haplochromines (Gee, 1969; Mkumbo and Ligtvoet, 1992), but since the decline of haplochromines, its diet shifted to *Caridina* shrimp, Dagaa and juvenile Nile perch (Hughes, 1986; Mkumbo and Ligtvoet, 1992). However, since the 1990s, a recovery of pelagic zooplanktivore and detritivore haplochromines is observed in Lake Victoria (Witte *et al.*, 2000; Witte *et al.*, 2007a). Haplochromines are again an increasingly important prey for Nile perch, suggesting that Nile perch prefers haplochromines as a food source (Kishe-Machumu *et al.*, 2012).

Developments in Lake Victoria's fisheries

The profound changes in Lake Victoria's ecosystem provided new opportunities for more than 1.3 million people to make a livelihood in the fishing industry (Witte *et al.*, 1999; Njiru *et al.*, 2005). It provided employment, income and export earnings to the riparian communities. During the 1960-1980s, the fisheries sustained a production of around 100,000 ton yr^{-1} (Fig. 1) (Kolding *et al.*, 2014). The commercial fishery was primarily for tilapia, haplochromines and a few other valued native species. The markets were all national or, at best, regional within eastern and central Africa. From the late 1980s and early 1990s onwards, the fisheries produced over 500,000 tons of fish per year, primarily Nile perch (fluctuating around 300,000 tons per year), Dagaa and tilapia (Fig. 1) (Kolding *et al.*, 2014). Fishing effort increased from 40,000 fishers in 1960 to 200,000 in 2010 (Kolding *et al.*, 2014). The changes in the fishery of Lake Victoria resulted in a flourishing international export industry of Nile perch, and a regional industry of Dagaa and tilapia (Budeba and Cowx, 2007a; Njiru *et al.*, 2008a; Njiru *et al.*, 2008b).

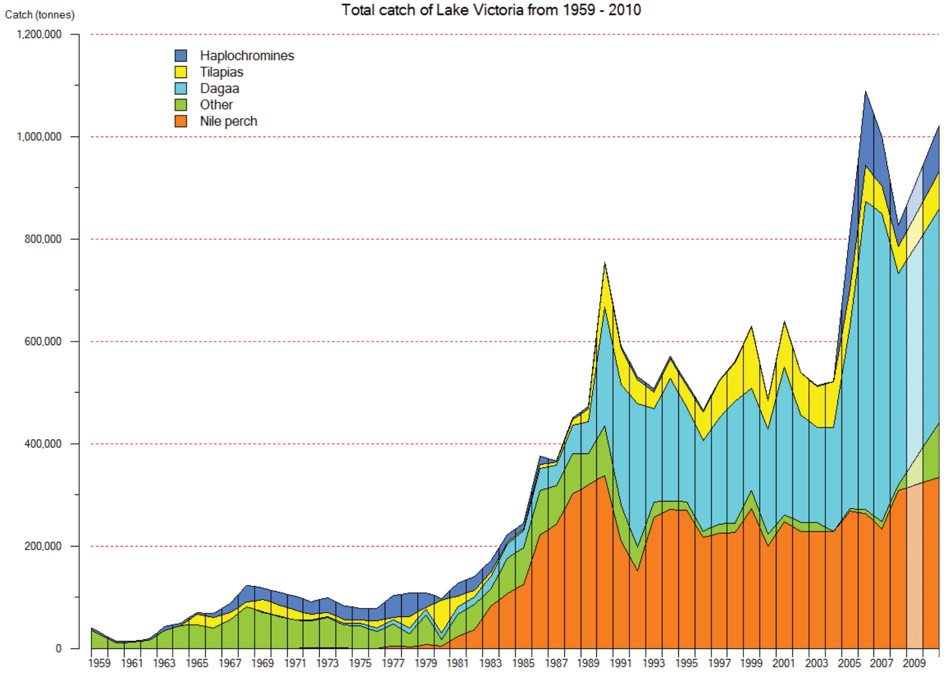

Figure 1: Total annual catches from 1959-2009 from Kolding *et al.* (2014)

Since the beginning of the Nile perch fishery, there were concerns that the Nile perch stock was being overexploited and might collapse when fishing intensity was not reduced (Mkumbo, 2002; Balirwa *et al.*, 2003; Njiru *et al.*, 2005; Matsuishi *et al.*, 2006). Recent studies report a decline of Nile perch biomass in the Lake (Getabu *et al.*, 2003; Ngupula and Mlaponi, 2010) and a recovery of Nile perch's main prey, haplochromines (Witte *et al.*, 2000; Witte *et al.*, 2007a; Kishe-Machumu *et al.*, 2012). In addition, many fillet factories, which were thriving in the 1990s are now working on a 50% capacity and a number of them are closed down, because of the low supply of legally-sized Nile perch (Ntara, 2015). This feeds the concern of overexploitation and of a Nile perch stock being only top-down driven by fisheries. However, Kolding *et al.* (2008) argued that there is no proof for a decline in Nile perch stocks and that here are no signs of overfishing. Their main hypothesis was that the increased Nile perch catches were supported by an increased primary and secondary production, driven by the continuing eutrophication, allowing fishing pressure to intensify without depleting Nile perch stocks. It is expected however, that the increase in fish production with continued eutrophication cannot continue and might eventually lead to stock collapse. Maximum levels of primary production might have been reached already as a result of self-shading by algae (Silsbe *et al.*, 2006). This would lead to lower Nile perch production if the fishing pressure would further increase. Furthermore, eutrophication will lead to the previously described deleterious effects of hypoxia, fish kills, and reduction of the habitat area of Nile perch and other organisms (Kolding *et al.*, 2008). Therefore, continued increasing eutrophication could present a much graver risk to the resource base and thus to livelihoods of Lake Victoria's coastal population than fishing pressure. However, it is still not clear to what extent eutrophication compensates for the increasing fishing pressure, and what this means for the type and direction of fisheries management.

Disentangling the main drivers of eutrophication and fisheries was the basis for the interdisciplinary and integrative SEDEC-programme (Disentangling the Social and Ecological Drivers of Change in Lake Victoria). The programme consisted of four collaborating projects, studying Lake Victoria from a socio-economic, fishery, ecological and modelling perspective to determine the main factors driving the system and in particular Nile perch. Two projects focussed on the top-down drivers, studying the socio-economic impact on the fisheries (Ntara, 2015) and the impact of fisheries on Nile perch stocks (H.K. Peter, in prep.). This study focussed on bottom-up processes, e.g., how environmental factors, via the food web, affected Nile perch. The fourth project combined knowledge from the different fields into a model study to understand how Lake Victoria's ecosystem is driven (Downing, 2012).

Thesis objectives and outline

The general objective of this study was to investigate the nature and extent of (further) eutrophication and its bottom-up effects on the higher trophic levels of the food web in Lake Victoria, focussing on Nile perch. The Mwanza Gulf in the south-east of Lake Victoria was selected as the main study area (Fig. 2b). The Mwanza Gulf has been extensively studied for the evolution of haplochromines (Witte and van Oijen, 1990). It was also the location where the extinction of haplochromines, upsurge of Nile perch and later the recovery of haplochromines was first documented (Goldschmidt *et al.*, 1993; Witte *et al.*, 2000; Goudswaard and Witte, 2008; Witte *et al.*, 2008; Kishe-Machumu *et al.*, 2012). The Gulf has a natural eutrophication gradient from the mouth of the gulf in the north (the lake side), to the end of the gulf in the south (Fig. 2b). This natural gradient is caused by its increasing depth towards the mouth of the Gulf, which automatically increases the mixing depth, resulting in an increase in visibility and decrease in phytoplankton biomass. Effects of eutrophication such as hypoxia and phytoplankton blooms have been previously reported in the Mwanza Gulf (Wanink *et al.*, 2001; Kayombo and Jorgensen, 2005; Goudswaard *et al.*, 2011). Therefore, the Gulf is excellent to study bottom-up effects of eutrophication on the food web. A part of the study was extended to the open, deep waters of Speke Gulf and Sengerema (Fig. 2c). The deepest station near the mouth of the Mwanza Gulf (station 6, Fig. 2b) corresponds in visibility to the open waters of these areas and is therefore considered representative for the open, less eutrophic waters of Lake Victoria.

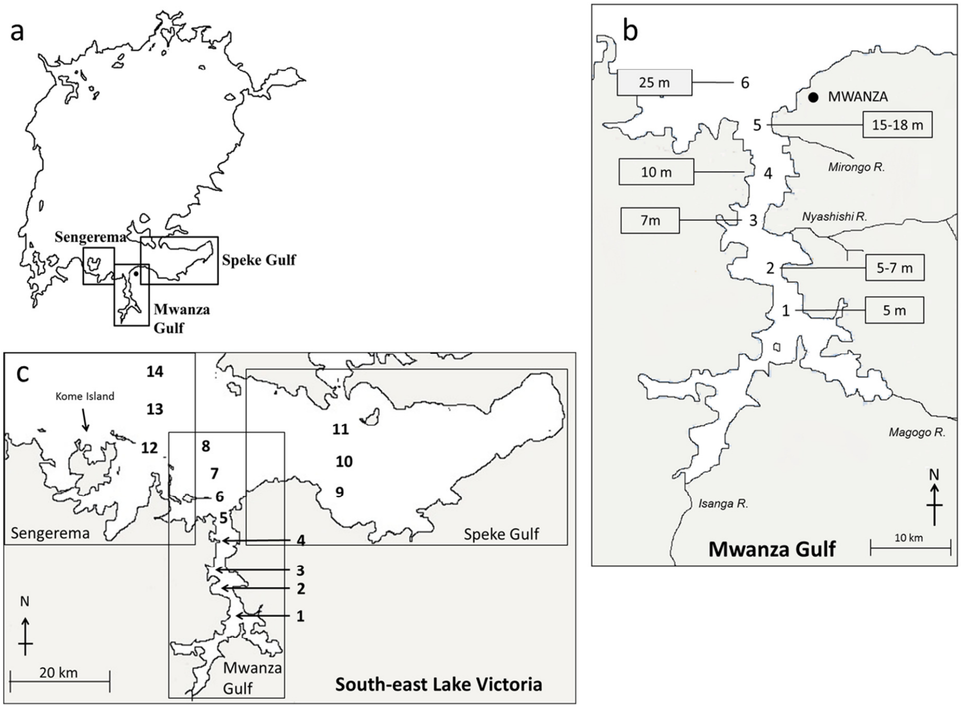

Figure 2: Maps of Lake Victoria: a) overview, b) Mwanza Gulf with locations of sampling stations, and c) south-east Lake Victoria showing the Mwanza Gulf, Speke Gulf and Sengerema area with locations of the sampling stations. Studies of chapters 2, 4 and 5 were conducted at sampling stations 1-6 in the Mwanza Gulf. The study in chapter 3 was conducted in the Mwanza Gulf (stations 1-8), Speke Gulf (stations 9-11) and the Sengerema area (stations 12-14) in south-east Lake Victoria.

Chapters 2–5 in this thesis analyse effects of eutrophication at different levels in the food-web. First, the water quality in the Mwanza Gulf was analysed to determine the extent of eutrophication **(chapter 2)**. The spatial and seasonal dynamics in nutrients, stratification, light attenuation and phytoplankton were studied in detail. We tested the hypothesis that nutrients and not light limited phytoplankton biomass.

The following two chapters describe the effects of abiotic and biotic environmental factors on Nile perch. In **chapter 3** we studied the size structure and distribution of Nile perch in a large region in south-east Lake Victoria in relation to abiotic environmental variables and prey densities. Distribution patterns were analysed on a small spatial and seasonal scale within the Mwanza Gulf (Fig. 2b) and on a larger spatial scale between three regions (Fig. 2c). We tested the hypothesis that the Nile perch size-structure and distribution patterns are determined by water quality and prey availability independent of geographical scale. In **chapter 4** we zoomed in on the direct interaction between Nile perch and its prey in the Mwanza Gulf. Spatial and seasonal variation in diet composition and ontogenetic diet shifts were studied by analysing stomach contents and stable isotope signatures. We investigated how diet compositions and diet shifts related to prey abundances, testing the hypothesis that haplochromines are the most preferred food type of Nile perch.

Chapter 5 focused on the spatial and seasonal variation in food-web structure in the Mwanza Gulf. Isotope-derived food-web indicators were used to quantitatively analyse spatial and seasonal variation in trophic diversity, shifts in primary food sources and trophic interactions between consumers. We tested the hypothesis that the base of the food web is highly dynamic and that changes at the basis affect higher trophic levels and food web interactions.

Finally, in the General discussion (**chapter 6**) the main findings of this study are discussed.

Chapter 2

Dynamics and limitations of phytoplankton biomass along a gradient in Mwanza Gulf, southern Lake Victoria (Tanzania)

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This manuscript is published in Freshwater Biology (2014) 59, 127-141

Abstract

We investigated how dynamics in phytoplankton biomass are driven through light and nutrient limitations in the Mwanza Gulf, Lake Victoria (Tanzania). We measured light attenuation, chlorophyll *a* and water quality parameters along a phytoplankton biomass gradient in the Mwanza Gulf at six sampling stations in three different seasons from August 2009 to March 2011. We found a higher rate of attenuation of photosynthetic available radiation (PAR) than in other gulfs of Lake Victoria which could only partially be explained by phytoplankton biomass, measured as chlorophyll *a.* Suspended particulate detritus strongly affected light attenuation, particularly in shallow water. In shallow water in the southern part of the Mwanza Gulf, nutrients were in excess and phytoplankton biomass was limited by light. In deeper water near the entrance of the gulf, light was not limiting when nitrogen probably was, as indicated by the N:P ratio. Low abundance of N-fixing phytoplankton species suggests that N-fixation was low in shallow water. Phytoplankton biomass was lower in Mwanza Gulf than in northern gulfs of Lake Victoria, but might increase in the future as a result of nutrient enrichment caused by an increase in intensive agriculture and rapid growth of the city of Mwanza.

Introduction

Lake Victoria has undergone major ecological changes since the 1960s. Its faunal composition changed with the introduction of Nile perch, *Lates niloticus* in the 1950s and 1960s, when the dominant endemic haplochromine cichlid fishes declined and hundreds of species went extinct (Witte *et al.*, 1992b; Goudswaard *et al.*, 2008). An important commercial fishery targeting Nile perch developed and peaked in 1990 with an estimated maximum total yield of 300,000 ton per year. Catches now fluctuate around 230,000 tons per year (Kolding *et al.*, 2008).

In addition to the Nile perch and its fishery, another major driver of change in Lake Victoria is eutrophication, which started gradually from the 1920s onwards and which was caused by an increasing human population around the lake and corresponding degradation of the shorelines (Hecky, 1993). As a result of the increasing nutrient load into the lake, phytoplankton biomass increased and the community shifted from dominance of diatoms to cyanobacteria (Hecky, 1993; Mugidde, 1993; Kling *et al.*, 2001; Verschuren *et al.*, 2002; Stager *et al.*, 2009; Sitoki *et al.*, 2010). The increased primary production fuelled the food web and increased lake productivity and fish catches (Kolding *et al.*, 2008; Hecky *et al.*, 2010). However, despite ongoing nutrient load into the lake, phytoplankton biomass has not increased since the 1990s (Silsbe *et al.*, 2006; Sitoki *et al.*, 2010) and is now supposedly light-limited in Lake Victoria in both shallow and deep water (Mugidde, 1993; Silsbe *et al.*, 2006; Cózar *et al.*, 2012). In shallow parts of Lake Victoria light becomes limited through self-shading when phytoplankton biomass is high and in deep water when the mixed depth is greater than the euphotic depth (Hecky, 1993; Guildford *et al.*, 2003; Mugidde *et al.*, 2003; Gikuma-Njuru and Hecky, 2005). Light limitation in shallow water may also be caused by resuspension of detritus and sediment and high concentrations of dissolved organic matter (Gikuma-Njuru and Hecky, 2005; Loiselle *et al.*, 2008). In inshore areas and bays, this organic matter originates mostly from allochthonous sources such as wastewater or run-off from cultivated shorelines whereas, in offshore areas, it originates mostly from decaying plankton (Machiwa, 2010).

When light conditions are good, nitrogen may become limiting in shallow parts of the lake (Guildford *et al.*, 2003), while in deep water nitrogen might become limited under anoxic conditions, stimulating denitrification, which usually occurs in stratified conditions during the rainy seasons (Guildford *et al.*, 2000; North *et al.*, 2008). In turn, nitrogen limitation favours nitrogen-fixing cyanobacteria (Guildford *et al.*, 2003), which now dominate the phytoplankton of Lake Victoria and are responsible for most of the nitrogen load into the lake (Kling *et al.*, 2001; Mugidde *et* *al.*, 2003). Phosphorus, on the other hand, has increased since the 1960s and is mostly in excess both in shallow and in deep parts of the lake (Hecky, 1993; Mugidde, 2001).

In contrast to the clear bottom-up effects of nutrient loading, no top-down regulation of phytoplankton biomass has been shown in *in situ* experiments, in which micro-crustacean grazing in shallow and deeper parts of lake Victoria apparently had little effect on chlorophyll *a* concentrations (Lehman and Branstrator, 1993). Moreover, the relative abundance of large-bodied grazers was very low and omnivorous cyclopoid copepods dominated the zooplankton of the Mwanza Gulf throughout the year (personal observations) and the rest of the lake (Mwebaza-Ndawula, 1994; Wanink *et al.*, 2002). Therefore, we assumed that limitation of phytoplankton growth by zooplankton is minimal and was not considered in this study.

Most studies on phytoplankton dynamics and limitations have been conducted in northern Lake Victoria, in eutrophic bays with high phytoplankton biomass (Mugidde, 2001; Gikuma-Njuru and Hecky, 2005; Silsbe *et al.*, 2006; Haande *et al.*, 2011). In general, the southern part of the lake has lower seasonal peaks in phytoplankton biomass, however, they occur two months later than in the northern part, possibly because of a lake-wide convective circulation of water (Cózar *et al.*, 2012). It is unclear whether the phytoplankton dynamics in the north, and their drivers, are the same for the whole of Lake Victoria. Furthermore, phytoplankton dynamics have rarely been studied for southern Lake Victoria. The few studies conducted have focussed on large spatial scales between Gulfs or depth strata covering half the lake (Shayo *et al.*, 2011; Ngupula *et al.*, 2012). Therefore, this study focussed on the dynamics of phytoplankton biomass and water quality on a small spatial scale in the Mwanza Gulf in southern Lake Victoria, covering a depth gradient from 3 m in inshore water in the south to 30 m in offshore water near the entrance of the Gulf. This depth gradient makes Mwanza Gulf an excellent area to study the spatial dynamics and limitations of phytoplankton biomass in detail.

To study the dynamics of phytoplankton biomass and growth limitation we examined spatial and seasonal dynamics of water quality parameters, light attenuation and chlorophyll *a* concentrations in the Mwanza Gulf from shallow inshore to deep offshore water. We addressed the following questions: 1) How does phytoplankton biomass vary in time and space? and 2) What are the factors driving this variability: is it light, nutrients, or a combination of both?

Methods

Study area

The Mwanza Gulf is located in the south of Lake Victoria (Tanzania) and is about 60 km long, 2.5-11 km wide and has a surface area of approximately 500 km² (Fig. 1) (Witte & van Densen, 1995). Its irregular shoreline is characterized by a vegetation of papyrus (*Cyperus papyrus*), reeds (e.g. *Phragmites australis*) and water hyacinth (*Eichhornia crassipes*), alternating with rock formations. The bottom consists of soft mud. The catchment area of the Mwanza Gulf is used mainly for agriculture (ranging from 62.9% in the north to 71.8% in the south). Bush land, formerly used for agriculture, covers around 20% of the catchment area. In the south 5.1% consists of natural habitats such as swamps and woodland, whereas this is only 0.7% in the north. Here, urban area covers 16.2% (Mwanza City; Fig. 1). Forests are absent around the Mwanza Gulf (Vlieghe, 2000).

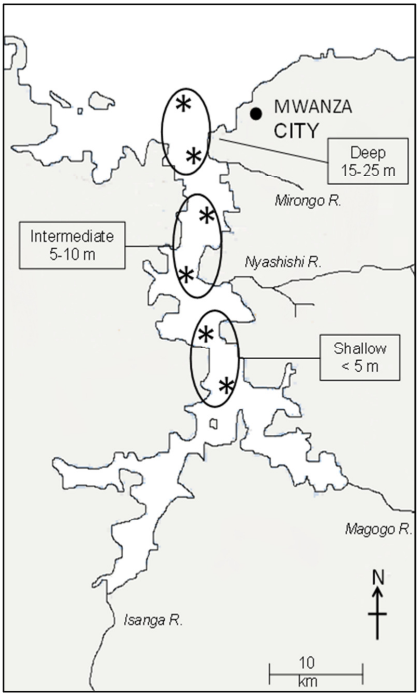

Figure 1: Map of the Mwanza Gulf with six sampling stations (asterisks). Stations were divided in three areas to facilitate data analyses: 1) Shallow=depth range of < 5 m, 2) Intermediate= depth range of 5-10 m and 3) Deep=depth range of 15-25 m.

Whereas most of the water flowing into the Gulf comes from surface run-off, forming seasonal streams during the rainy season, there are also some permanent rivers (Fig. 1). The Isanga River in the south is the largest with a mean annual discharge of 29.8 $m^3 s^{-1}$ and a catchment area of 6812 km². The Magogo River has a mean discharge of 8.9 $m^3 s^{-1}$ and a catchment area of 5207 km² (Myanza *et al.*, 2006). These rivers collect waste water from fish processing plants and a brewery. Towards the north, the Nyashishi River with a mean annual discharge of 1.7 $m^3 s^{-1}$ and a catchment area of 1565 km² flows into the gulf and in Mwanza city in the north, a small river (the Mirongo) collects waste water from the city and industrial plants before flowing into the lake. Compared to other gulfs in the lake, the Mwanza Gulf has weak river input and is poorly flushed (Machiwa, 2010).

Climate

There are three seasons in Lake Victoria based on the yearly monsoon cycles. There is a dry season from June-August when water temperature is low and strong southerly winds keep the water column well mixed, oxygenated and isothermal (Talling, 1966; Akiyama *et al.*, 1977). The short rains, from September-December, the water column gradually stratifies as the wind declines, rainfall increases and the surface layer of the water column warms up. During the long rains, from January-May, precipitation is high and stratification is strongest (Talling, 1966). However, both the onset and the timing of rainfall in the Lake Victoria basin are highly variable (Kizza *et al.*, 2009).

The Mwanza Gulf had similar seasons during the sampling period from 2009-2011, although during the short and long rains, from September 2009-May 2010, rainfall was twice as much as from September 2010-May 2011.

Data collection

Data were collected from August 2009 until April 2011 at six sampling stations along a north-south gradient in three areas (Fig. 1). Data from the six stations were pooled for analyses into three areas: shallow (< 5 m depth), intermediate (5-10 m depth) and deep water (10-25 m depth) (Fig. 1). In 2009-2010, sampling at all stations was done once per season, starting in August 2009 during the dry season and ending in May 2010 during the long rains. In 2010-2011, sampling was done three times per season, starting in June 2010 during the dry season and ending in April 2011 during the long rains. At each station three locations, separated ca. 500 m from each other, were sampled between 10:00 h and 14:00 h. To minimize direct littoral influences, sampling at each station was done at least 1.5 km from the shore. In May 2012 additional observations were carried out on dissolved organic matter fractions.

A hydrolab DS5 multiprobe (OTT Messtechnik GmbH & Co, Kempten, Germany) collected vertical profiles of temperature, conductivity and chlorophyll *a* from the bottom to the surface. A mounted spherical quantum sensor (LI-COR Biosciences, Lincoln, Nebraska, USA) measured photosynthetic active radiation. Water samples were taken on three occasions throughout the sampling period for calibration. Conductivity was calibrated by using standards with known conductivity and chlorophyll *a* by using extraction in 80% ethanol at 75^{o} C for 5 minutes (Moed and Hallegraef, 1978). Probe measurements were in general 1.5-2 fold lower compared to the extracted chlorophyll *a* analyses. Chlorophyll *a* measurements with the probe were corrected with the extracted calibration analyses of chlorophyll *a*.

At each station, Secchi depth was measured in triplicate with a 25 cm diameter black and white Secchi disk and was defined as the average depth at which the disk disappeared when lowering it in the water and reappeared when lifting it.

At each sampling station water samples were taken every metre over the euphotic depth by using a Van Dorn water sampler. Samples were pooled for analyses of the following nutrients: total phosphorus (TP), total nitrogen (TN); particulate fractions: particulate organic carbon (POC) and particulate inorganic matter (PIM); and dissolved fractions: dissolved organic carbon (DOC), chromophoric dissolved organic matter (CDOM) and humic acid (HA). Nutrients were analysed in the laboratory by a digestion and photometric method (Merck KGaA, Darmstadt, Germany). Water was filtered through a glass-fibre C filter (Whatman GmbH, Den Bosch, the Netherlands) and seston was used for analyses of POC and PIM. Particulate organic carbon (POC) was analysed with the standard loss on ignition method (American Public Health Association; APHA, 2005), whereby the organic fraction was calculated by the seston mass combusted for 1 hour at 550°C subtracted from the mass dried at 105° for 24 hours, and divided by 2.5 to get the carbon content. Particulate organic carbon (POC) contains carbon derived from mainly phytoplankton and detritus. Detritus was calculated by estimating the carbon content of chlorophyll by using a chlorophyll:dry mass ratio of 1:50 (Bailey-Watts, 1974) and a dry mass: carbon ratio of 2:1 (Winberg, 1971). This calculated C concentration was subtracted from POC to estimate the carbon concentrations of detritus. For estimating PIM, five unused filters were weighed after combustion at 550°C for 1 hour and the average mass was subtracted from that of the filters with seston after combustion.

Water for DOC, CDOM and HA was filtered through 0.22 μm pore filter and the filtrate collected for analyses. Dissolved organic carbon (DOC) was analysed by Chemical Oxygen Demand (COD) (American Public Health Association; APHA, 2005). Chromophoric dissolved organic matter (CDOM) and HA were determined by measuring the absorbance at 272 and 465 nm and calibrated gravimetrically (Mazzuoli *et al.*, 2003).

Pooled water samples from the euphotic zone were preserved in glutaraldehyde, and sent to the Netherlands Institute of Ecology for analyses with a phyto-PAM fluorometer (Walz, Germany) to differentiate between chlorophytes, diatoms and cyanobacteria. On 1 September 2010 and 4 April 2011 water samples from station 1, 3 and 6 were preserved with lugol and, after sedimentation, phytoplankton was generally classified to the genus or species and abundances estimated. Phytoplankton was counted as number of colonies, but the number of cells per colony was noted and all colonies were classified into size classes.

Estimating physical parameters

Water density was calculated using vertical profiles of temperature and conductivity (Chen and Millero, 1977). Thermal stability of the water column (N^2) was calculated according to the following equation (Langenberg, 2008):

$$N^2 = \frac{-g \, \Delta\rho}{\bar{\rho} \, \Delta z} \tag{1}$$

where N is the Brunt-Vaisälä buoyancy frequency, g is the gravitational acceleration (m s^{-2}), $\frac{\Delta\rho}{\Delta z}$ is the density gradient over a depth interval and $\bar{\rho}$ is the mean density over the water column (kg L^{1}).

Water temperature (T_{water}) was defined as the mean temperature over the whole water column. Mixed depth (Z_{mix}) was defined as the maximum change in temperature with depth over the water column. The euphotic depth (Z_{euph}) was defined as the depth at which 1% of the surface irradiance remains.

Analysis of spatial and seasonal dynamics

The spatial and seasonal effects on the dynamics of stratification, water quality and light associated parameters and phytoplankton data were analysed by Kruskal-Wallis tests because normality could not be achieved directly, or after log-transformations. In case of significant spatial or seasonal effects, *post hoc* pairwise comparisons were performed with adjusted levels for multiple comparisons using a Bonferroni correction.

Analyses of light conditions

The attenuation of photosynthetically active radiation (PAR: 400 – 700 nm wave length) is caused by optically active components in the water column and expressed by the attenuation coefficient K_{PAR}. K_{PAR} was estimated as the slope of the linear regression of the natural logarithm of PAR on depth of each vertical profile. Regression correlation coefficients of less than 0.9, and regressions with less than 15 observations within a single vertical profile, were excluded from further data analyses. In fresh water, light attenuating components consist mainly of phytoplankton biomass and background attenuation of other components such as coloured CDOM, inorganic sediments, suspended detritus and pure water (Morel, 1988):

$$K_{PAR}=(k_{Chl} \cdot Chl) + K_{bg} \tag{2}$$

where k_{Chl} is the specific light attenuation coefficient for phytoplankton (m^2 mg^{-1}) determined by the slope of linear regression of K_{PAR} (m^{-1}) on chlorophyll *a* concentration in the euphotic zone (Chl, in mg m^{-3}). K_{bg} is the background attenuation (m^{-1}), determined as the intercept with the K_{PAR}-axis of the same linear regression. To analyse the relationship between chlorophyll concentrations and K_{PAR} we performed regression analyses of K_{PAR} on Chl (with, or without $\log_e$ transformation, depending on the normality of the residuals). The residuals from these regression analyses indicate background attenuation, since the influence of chlorophyll *a* is excluded. These residuals were used to determine the influence of suspended detritus on K_{PAR}, by correlating them with suspended detritus concentrations ($C_{detritus}$). Since these residuals were not normally distributed, a non-parametric Spearman rank correlation was used. Similarly, K_{PAR} and PIM were also correlated with a Spearman rank correlation. Next, to test whether the relationship between K_{PAR} and chlorophyll *a* concentrations differed between areas, we also performed an analysis of covariance of K_{PAR}, with area as factor and Chl as covariate.

Solar irradiance was integrated over the mixed depth to determine the total integrated irradiance in the mixed layer by the following equation (Loiselle *et al.*, 2007:

$$Q_t = I_0 / (k_{Chl} \cdot Chl + K_{bg}) \cdot (1 - e^{-(k_{Chl} \cdot Chl + K_{bg}) Z_{mix}}) \tag{3}$$

where Q_t is the total integrated irradiance in the mixed layer (mol photon m^{-2} day^{-1} m) and I_0 is the incident irradiance just below the water surface.

Estimating maximum phytoplankton biomass under light limitation

We used a light limitation approach based on the carrying capacity of phytoplankton biomass developed by Loiselle *et al.*, (2007, 2008). This approach uses the calculated available irradiance (Q_t) and the chlorophyll *a* biomass per unit area (mg m^{-2}) to determine where light limitation occurs. Chlorophyll *a* biomass per unit area can be calculated when Chl concentration in mg m^{-3} is multiplied with Z_{mix}. When Q_t is plotted against chlorophyll *a* biomass per unit area, a linear regression of 10 data points with highest chlorophyll *a* over the Q_t range defines the carrying capacity for phytoplankton biomass under light limitation in a steady state (Fig. 2). The minimum irradiance to allow phytoplankton biomass is the intercept with the Q_t axis and the critical light requirement is the slope of the same linear regression. From this, we calculated the expected chlorophyll *a* biomass per unit area under light limitation:

$$W = Q_t - Q_{min} / \psi \tag{4}$$

where W is the expected depth integrated chlorophyll *a* biomass per unit area (mg m^{-2}), Q_{min} is the minimal light requirement for allowing phytoplankton biomass (mol photon m^{-2} day^{-1} m) and ψ is the critical light requirement (mol photon m^{-1} day^{-1} (mg m^{-2} chlorophyll *a* $)^{-1}$).

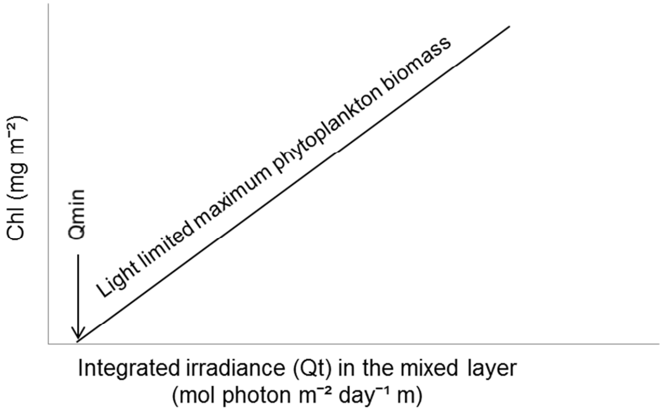

Figure 2: The relationship between daily depth integrated light irradiance and phytoplankton biomass per unit area (mg Chl *a* m^{-2}) under light limited conditions over the mixed layer. The line represents the maximum potential chlorophyll *a* concentrations when light is limited (upper limit), determined by regression of 10 sites with highest chlorophyll *a* concentrations. The intercept represents minimum light requirement (Q_{min}) for phytoplankton growth and the slope is the expected maximum phytoplankton biomass under light limitation.

By comparing the measured chlorophyll *a* (mg m^{-2}) with the expected light-limited maximum chlorophyll *a* (W), the relative degree of limitation by light and/or other factors was determined. Measured chlorophyll *a* located further from the expected W is probably limited by factors such as nutrients, so we calculated the distance between measured chlorophyll *a* and W. The latter is calculated by using a combination of equations 2, 3 and 4 for each measured chlorophyll *a* concentration. Note that the distance between measured chlorophyll *a* and W increases exponentially by using equation 3, because phytoplankton biomass cannot increase linearly with light, as phytoplankton itself will have a negative feedback on irradiance when increasing in biomass (Loiselle *et al.*, 2007, 2008). The distance is then plotted against P, N and detritus concentrations and correlations are tested with Pearson or Spearman rank, according to normality of the data, to investigate the potential role of nutrients and detritus dynamics in determining phytoplankton biomass. With increasing distance, chlorophyll is less likely to be limited by light and must be limited by another factor. A negative correlation between distance and nutrients or detritus suggests that nutrients or detritus might become limited when light conditions are good. A positive or no correlation might indicate a limitation by other factors not measured in this study.

Results

Spatial and seasonal dynamics

Variables associated with stratification and water column stability, such as T_{water} and N^2, differed between seasons but not between areas (Table 1). Highest temperatures and stability occurred during the short rains (September-December) (Table 1). Water column mixing was deepest during the dry season (June-August) and shallow during the short and long rains. This seasonal trend in mixing and temperature was observed in both shallow as well as deeper parts of the Gulf (Fig. 3).

Spatial and seasonal effects differed among water quality variables (Table 1). Total phosphorus (TP) concentration varied seasonally with a slightly higher concentration during the short rains (September-December) than the long rains (January-May). Total nitrogen (TN) concentration and TN:TP molar ratio showed a strong spatial pattern with decreasing values from shallow to deep water. TN also varied seasonally, with highest concentrations during the dry season and short rains and lowest during the long rains. From the particulate fractions, POC varied spatially with highest concentrations in shallow water and lowest concentrations in deep water, and seasonally with highest concentrations during the long rains. Particulate inorganic matter (PIM) was seasonally affected and showed the highest concentration during the long rains. From the dissolved organic matter fractions, both DOC and CDOM varied spatially. Dissolved organic carbon (DOC) concentration was lowest in deep water, whereas CDOM was highest in shallow water and lowest in deep water. Humic acid (HA) concentrations were very low and did not vary between areas.

Table 1: Summary table of means with *post hoc* pairwise comparisons and results of the Kruskal-Wallis tests of effects of area (shallow, intermediate and deep water) and season (dry period, short and long rains) on physical conditions, light associated parameters, nutrients and phytoplankton. Significance levels were corrected according to Bonferroni with *df*=2 except for seasonal effect on TP and TN:TP which significance level was at $P< 0.05$ with *df*=1. Mean values with different superscripts differ significantly. Abbreviations used: H=test statistic Kruskal-Wallis, NS=not significant, P=significance level, T_{water}=Water column temperature, N^2=buoyancy frequency, Z_{max}=maximum depth, Z_{mix}=mixed depth, Z_{euph}=euphotic depth, K_{PAR}=light attenuation coefficient, TN=total nitrogen, TP=total phosphorus, POC=particulate organic carbon, PIM=particulate inorganic matter, DOC=dissolved organic carbon, CDOM=chromophoric dissolved organic matter, HA=humic acid. DOC, CDOM and HA were sampled in May 2012.

		Area			Season			Area		Season	
		Shallow (<5m)	Intermediate (5-10m)	Deep (15-25m)	Dry	Long rains	Short rains	H	P	H	P
Stratification	T_{water} (°C)	24.75	24.98	24.94	23.92^{a}	24.98^{b}	25.74^{b}	2.19	NS	131.10	<0.001
	N^2 (10^{-3})	0.49	0.36	0.39	0.25^{a}	0.42^{ab}	0.56^{b}	2.29	NS	18.92	<0.001
	Z_{max} (m)	4.56^{a}	8.54^{b}	22.15^{c}	12.01	11.70	11.53	188.99	<0.001	0.71	NS
	Z_{mix} (m)	2.35^{a}	3.93^{b}	11.25^{c}	6.85^{b}	5.50^{a}	5.18^{a}	56.03	<0.001	19.76	<0.001
Water quality parameters (mg L^{-1})	TN	1.42^{c}	0.89^{b}	0.48^{a}	1.06^{b}	0.80^{a}	0.92^{b}	105.32	<0.001	8.65	0.013
	TP	0.08	0.08	0.07	–	0.07^{a}	0.09^{b}	2.23	NS	24.88	<0.001
	TN:TP molar	45.92^{c}	25.96^{b}	11.81^{a}	–	31.66	20.77	56.07	<0.001	1.21	NS
	PIM	17.66	30.71	86.22	13.81^{a}	79.95^{b}	43.56^{a}	4.44	NS	14.48	<0.001
	POC	11.76^{c}	8.03^{b}	5.64^{a}	7.17^{a}	10.94^{b}	7.32^{a}	40.96	<0.001	12.78	0.002
	DOC	1.03^{b}	1.24^{b}	0.32^{a}	–	0.86	–	11.97	0.003	–	–
	CDOM	1.91^{b}	1.21^{ab}	1.00^{a}	–	1.37	–	9.22	0.010	–	–
	HA	0.0023	0.0011	0.0012	–	0.0015	–	8.13	NS	–	–
Light-associated parameters	Z_{euph} (m)	2.77^{a}	3.52^{b}	5.57^{c}	4.83^{c}	3.38^{a}	3.62^{b}	91.02	<0.001	28.62	<0.001
	Secchi depth (m)	0.63^{a}	1.08^{b}	1.91^{c}	1.42^{c}	1.10^{b}	1.07^{a}	142.20	<0.001	17.17	<0.001
	K_{PAR} (m^{-1})	2.52^{a}	1.87^{b}	1.04^{c}	1.37^{a}	2.05^{c}	2.01^{b}	82.70	<0.001	17.73	<0.001
Phytoplankton (µg L^{-1})	Chlorophyll *a*	17.06^{c}	15.32^{b}	9.25^{a}	13.24	14.96	13.45	85.46	<0.001	0.472	NS
	Cyanobacteria	3.55^{c}	3.21^{b}	0.96^{a}	1.48^{a}	2.01^{a}	4.18^{b}	53.42	<0.001	31.81	<0.001
	Chlorophytes	0.09	0.00	0.00	0.03	0.02	0.04	6.02	NS	0.004	NS
	Diatoms	1.02^{b}	1.17^{b}	0.67^{a}	0.76^{a}	0.80^{a}	1.29^{b}	30.19	<0.001	39.66	<0.001

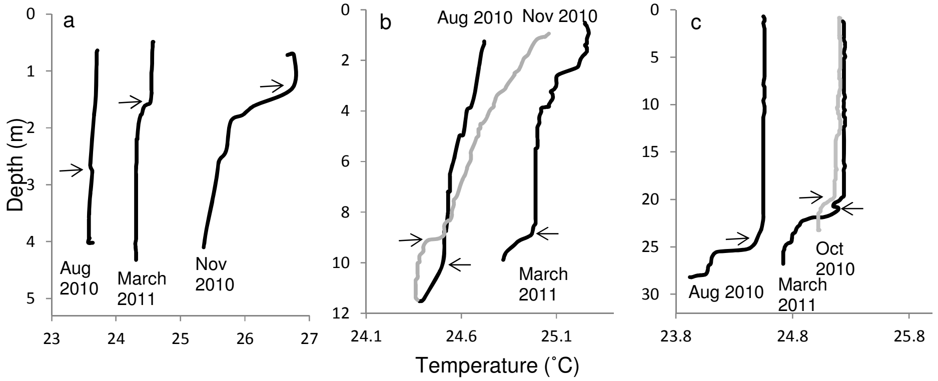

Figure 3: Temperature-depth profiles at three sampling stations of contrasting depths on one occasion each season in the Mwanza Gulf: a) at the most southern and shallow sampling station of 4-5 m depth; measurements were taken at 11:21, 10:15 and 11:58 hours, respectively, b) at an sampling station of intermediate-depth (10-12 m depth); measurements were taken at 11:31, 10:42 and 13:37 hours, respectively, and c) at the most northern and deep station of 25-30 m depth; measurements were taken at 9:13, 10:46 and 10:44 hours, respectively. Arrows indicate the mixing depths.

Chlorophyll *a* concentrations varied from shallow to deep water and to a lesser extent between seasons (Table 1). Total chlorophyll *a* concentration, as well as chlorophyll concentrations of the main taxonomic phytoplankton groups, all decreased with depth. Cyanobacteria and diatoms also varied seasonally, with highest concentrations during the short rains, whereas chlorophytes occurred only at very low concentrations in all areas and seasons. Phytoplankton density in September 2010 and April 2011 (stations 1, 3 and 6) showed very low abundances of N-fixing phytoplankton species (<4.5% of total abundance). N-fixing species found in September 2010 were *Anabaena spp*. and *Cylindrospermopsis africana*; in April 2011 *Anabaena spp., Cylindrospermopsis africana, C. cuspis, C. philippinensis, C. raciborskii* and *C. helicoidea.* On both occasions close to the date of phytoplankton sampling, N:P ratio was highest in shallow water (36.4 on 26 August 2010 and 71.1 on 1 April 2011) and lowest in deep water (24.5 on 27 August 2010 and 19.1 on 31 March 2011).

Light-associated parameters were all affected spatially and seasonally (Table 1). The light attenuation coefficient (K_{PAR}) decreased from shallow to deep water, following the chlorophyll *a* trend. Highest K_{PAR} values occurred during the long rains, although seasonal differences were less conspicuous than spatial differences. Euphotic zone depth and Secchi depth showed similar spatial trends with greatest values in deep water and during the dry season.

Light conditions in Mwanza Gulf

A power regression model best described the relationship between K_{PAR} and chlorophyll *a* concentration ($K_{PAR}=0.27 \cdot Chl^{0.71}$, $R^2=0.47$, F=67.94, P<0.0001, n=80: Fig. 4a). However, the high values of K_{PAR} and extent of the variation around the relationship suggested that background light attenuation (K_{bg}) was high and varied between areas (Fig. 4a). When using ANCOVA, with area as factor and chlorophyll *a* concentration as covariate, we indeed found a strong influence of both chlorophyll and area on K_{PAR} ($R^2=0.69$, F=55.03, P<0.0001, n=80: Fig. 4b). There was no interaction between chlorophyll and area (F=0.78, P=0.46, n=80) and the decreasing intercept from shallow to deep water indicates a decreasing influence of background light attenuation (K_{bg}) from shallow to deep water on K_{PAR} (Fig. 4b). The specific attenuation coefficient for chlorophyll *a* (k_{chl}) was 0.0357 (μg L^{-1}) m^{-1} (95% CL=0.016-0.055).

A high K_{bg} in shallow water can be caused, among other factors, by suspended detritus. There was a significant positive correlation between the suspended detritus concentration ($C_{detritus}$) with the residuals of K_{PAR} from the power regression ($r_s=0.27$, P=0.03), suggesting that detritus played a significant role in explaining the differences in light attenuation in Mwanza Gulf. However in the regression, only 12 % of the variance of residuals was explained (Fig. 4c), indicating that, in addition to chlorophyll and detritus, other light absorbers like PIM or CDOM could have contributed to light attenuation in the Mwanza Gulf. Particulate inorganic matter (PIM) was not significantly correlated with K_{PAR} (P=0.33) and, because of the limited data on the dissolved fractions, we could not directly test the influence of CDOM or DOC on K_{PAR}.

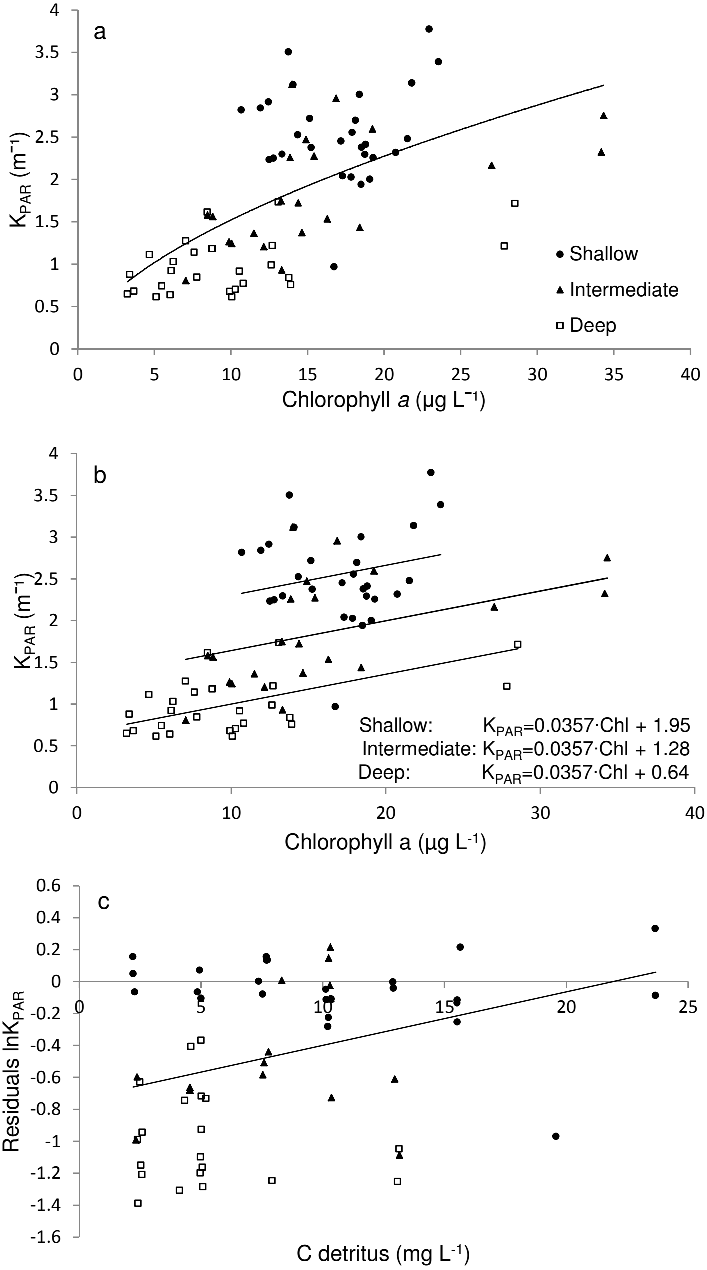

Figure 4: The relationship between chlorophyll *a* concentration and the light attenuation coefficient (K_{PAR}) in the Mwanza Gulf: a) Power regression of chlorophyll *a* concentrations versus K_{PAR} in Mwanza Gulf ($R^2=0.47$, n=80, $P<0.0001$), b) Linear regression of chlorophyll *a* versus K_{PAR} in Mwanza Gulf and c) Regression of detritus concentrations (mg C L^{-1}) versus residuals of $\ln K_{PAR}$ ($R^2=0.12$, n=61, $P=0.007$).

Limitation on phytoplankton biomass

Shallow and intermediate deep water was more light-limited than deep water and data points were in general located closer to the upper limit of chlorophyll *a* concentrations per unit area under light limitation (Fig. 5). The minimum light requirement to allow phytoplankton biomass was 9.01 mol photon m^{-2} day^{-1} m. The critical light requirement was 0.064 mol photon m^{-1} day^{-1} (mg m^{-2} chlorophyll *a* $)^{-1}$.

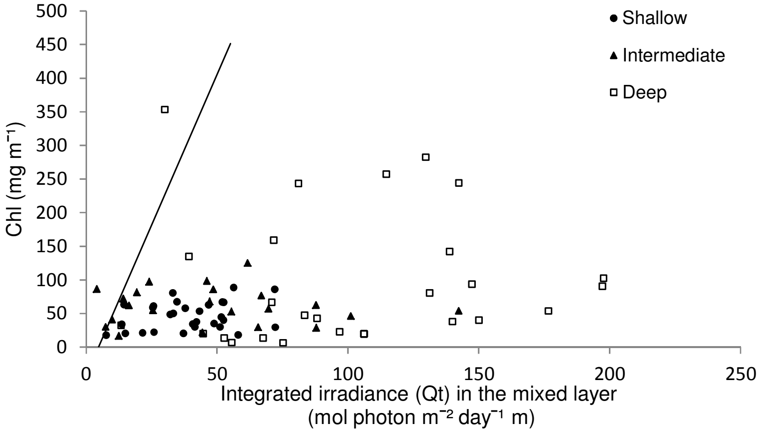

Figure 5: Chlorophyll *a* concentration per unit area and integrated light irradiance over the mixed layer in the Mwanza Gulf. The line represents the maximum potential chlorophyll *a* concentrations when light is limited (upper limit), determined by regression of 10 sites with highest chlorophyll *a* concentrations per unit area and lowest integrated irradiance (r^2=0.57, n=10, P=0.01). Sites close to upper limit are more light-limited than points far from the upper limit: n=80.

The calculated distance to the upper limit of chlorophyll *a* was plotted against nutrients and detritus (Fig. 6). A Spearman rank test showed a significant negative correlation of TN concentrations with distance from the upper limit (r_s=– 0.24, P=0.04). A negative correlation of detritus with distance was found (r_s=–0.21, P=0.04). Correlation between TP concentrations and distance was very weak and not significant (r_s=–0.08, P=0.61).

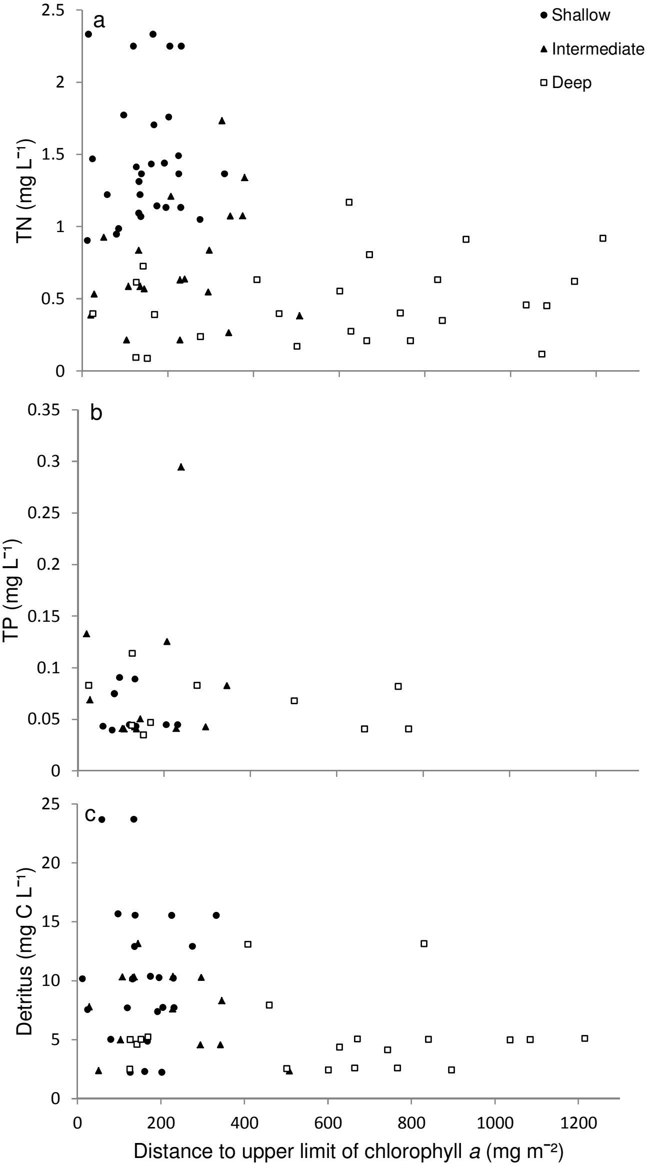

Figure 6: Distances between measured chlorophyll *a* concentrations and the calculated maximum concentrations under light limitation in relation to varying nutrient and detritus concentrations: a) total nitrogen concentrations (TN; n=76), b) total phosphorus concentrations (TP; n=34) and c) detritus concentrations (n=57).

Discussion

Spatial and seasonal dynamics

Stratification in the Mwanza Gulf varied among seasons, but the differences in mean mixed depth were not more than 2 m between seasons. This relatively weak effect of season suggests that stratification was not persistent throughout the rainy seasons. Lake Victoria has distinct diurnal rainfall and air convection patterns (Nicholson and Yin, 2002), which can build up and break down stratification on a daily basis. In the Mwanza Gulf, the water was mostly calm in the morning, but winds picked up in the afternoons (I.J.M. Cornelissen, personal observation), probably causing a break-down of the stratification built up the previous night. This diurnal break-up of the stratification was also observed in inshore waters of 15 m in Uganda (MacIntyre *et al.*, 2002).

The total nitrogen and phosphorus concentrations observed here were within the range reported by other authors for Lake Victoria at similar depths (TP: 0.03-0.15 and TN: 0.5-1.5 mg L^{-1}) (Mugidde, 2001; Gikuma-Njuru, 2008; Haande *et al.*, 2011; Ngupula *et al.*, 2011). Total phosphorus (TP) did not show a spatial trend, which also corresponds to other studies (Hecky, 1993; Mugidde, 1993). More than half of the P loading into the lake originates from atmospheric wet and dry deposition. Run-off is only of local importance (Tamatamah *et al.*, 2005). Total nitrogen (TN) concentrations were about three-fold higher in shallow than in deep water, resulting in higher TN:TP ratios in shallow water, corresponding to other studies in Lake Victoria (Mugidde, 2001; Gikuma-Njuru and Hecky, 2005).

In deep water, PIM probably originated from wastewater from Mwanza City and from river discharges, and from resuspension of sediment through turbulence in shallow water (Lung'ayia *et al.*, 2000; Machiwa, 2010). The high PIM concentrations observed during the long rainy season were probably caused by high land run-off into the lake and resuspension of sediment (Lung'ayia *et al.*, 2000). Particulate organic carbon (POC) concentration in our study was twofold higher inshore than offshore, which corresponds with spatial trends of particulate carbon in other studies in the Mwanza Gulf and in Ugandan water (Mugidde, 2001; Hecky *et al.*, 2010; Machiwa, 2010).

Chlorophyll *a* concentrations observed in the Mwanza Gulf fell in the same range as those measured by Shayo *et al.* (2011) in Mwanza Gulf and by Ngupula *et al.* (2012) in Tanzanian waters, but were in general two-threefold lower than in highly eutrophic gulfs in Uganda, such as Napoleon and Murchison Gulf (Lehman and Branstrator, 1994; Mugidde, 2001; Yasindi and Taylor, 2003; Silsbe *et al.*, 2006; Cózar *et al.*, 2007; North *et al.*, 2008; Okello *et al.*, 2010; Haande *et al.*, 2011). The decrease in chlorophyll concentration from shallow to deep water suggests that nutrients in shallow water were in excess, enabling a high chlorophyll concentration until light became limited. Deeper mixing than the euphotic depth and possible N limitation resulted in lower chlorophyll concentrations in deeper water. Similar to other studies on the Ugandan side of Lake Victoria, cyanobacteria were found to be the dominant phytoplankton group in all locations and throughout the study period (Okello *et al.*, 2010; Haande *et al.*, 2011). The very low concentration of chlorophytes also corresponds with other studies in Mwanza Gulf and Lake Victoria (Akiyama *et al.*, 1977; Lung'ayia *et al.*, 2000; Kling *et al.*, 2001; Gikuma-Njuru, 2008; Ngupula *et al.*, 2011).

Light conditions in Mwanza Gulf

Secchi depth was less strongly related to KPAR in Mwanza Gulf (R^2=0.75, n=99: Fig. 7), than in Ugandan waters (R^2=0.90, n=112: Fig. 7) (Silsbe, 2004). The relationship obtained paralleled that found for Ugandan waters, but our Secchi depths were consistently 20 cm greater than in Uganda at identical KPAR values. Since KPAR and Secchi depth measure different optical properties, *i.e.* KPAR measures attenuation of light in the visible wavelength range and Secchi measures clarity (Preisendorfer, 1986), KPAR-Secchi depth relationships differ between types of water. Koenings and Edmundson (1991) found a ten-fold range of KPAR-Secchi depth relationship between different types of lakes with either stained (high in CDOM concentrations), turbid (high in concentrations of suspended particles) or clear waters. Our KPAR-Secchi depth relationship can be classified in between clear and turbid waters. The wider 95% prediction intervals of our relationship compared with that for Uganda (Fig. 7) suggest that there is additional spatial variation in the sources of light absorption within the Mwanza Gulf.

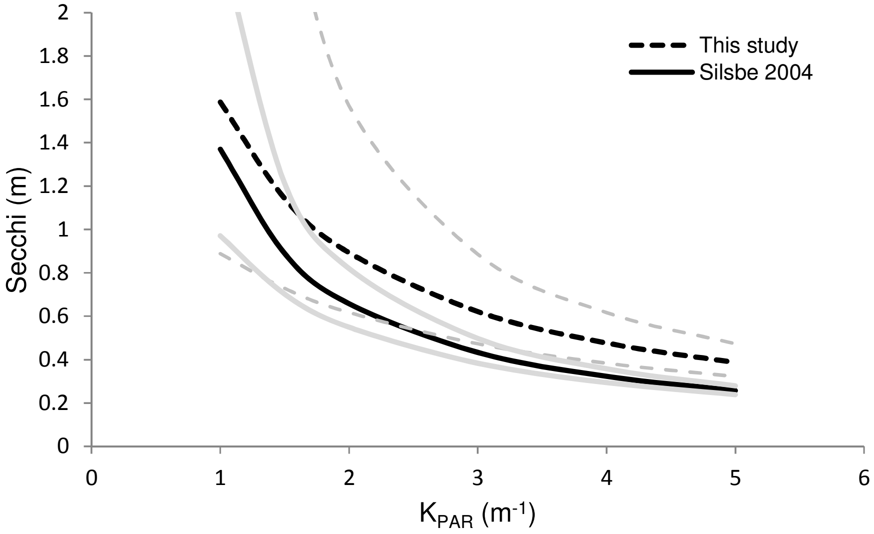

Figure 7: Regression of K_{PAR} and Secchi depth of this study in Mwanza Gulf and Silsbe (2004) in Ugandan waters. Grey dashed lines represent 95% prediction intervals of this study and grey lines represent 95% prediction intervals of the study of Silsbe (2004).

Morel and Prieur (1977) classified oceanic waters as 'case I' water, in which phytoplankton and detritus derived from phytoplankton contribute predominantly to the light attenuation in water, while in 'case II' waters sediments and CDOM play a dominant role in light attenuation. In our study K_{PAR} values were much higher in relation to the chlorophyll *a* range than in Ugandan and Kenyan waters (Silsbe, 2004; Loiselle *et al.*, 2008) and in oceanic case I waters (Morel, 1988), suggesting that light absorbers other than phytoplankton contributed to the light attenuation (background attenuation K_{bg}) and that the Mwanza Gulf might be considered as a case II water (Fig. 8). Loiselle *et al.* (2008), who found a similar relationship between chlorophyll and K_{PAR} as (Silsbe *et al.*, 2006), identified their study sites as case II waters. Our study showed high variation ($R^{2=}0.47$) between K_{PAR} and chlorophyll *a*, suggesting that the relative contribution of chlorophyll to light absorption varied spatially.

It becomes even more evident how strong the light attenuation by non-algal absoʳption in our study sites was, when we compare the integrated irradiance (Q_t) of Morel's type I waters (which have negligible non-algal absorption), with the Q_t in Mwanza Gulf at similar chlorophyll concentrations and surface irradiance. Our study shows that non-algal absorption removed 83, 78 and 67 % of the integrated irradiance in shallow, intermediate and deep water, respectively. This indicates that light limitation was caused by non-phytoplankton light absorbing properties rather than by self-shading of phytoplankton in the Mwanza Gulf.

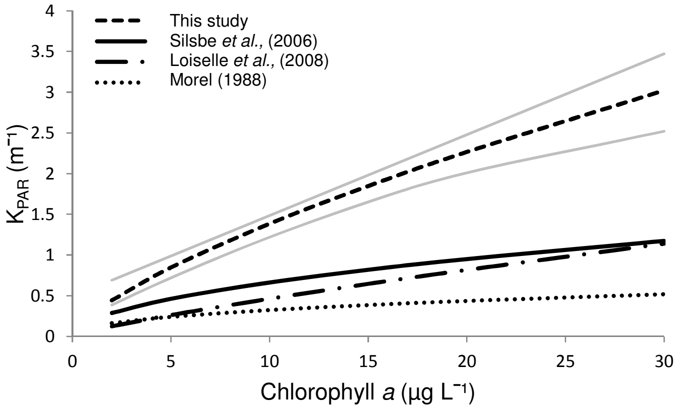

Figure 8: Regression of chlorophyll *a* concentrations and K_{PAR} of studies in southern Lake Victoria (this study), northern Lake Victoria (Silsbe *et al.*, 2006; Loiselle *et al.*, 2008) and oceanic waters (Morel, 1988). Grey lines represent 95% CL (this study).

In the Mwanza Gulf, besides phytoplankton, suspended detritus played an increasing role in PAR attenuation from deep to shallow water. In addition, shallow water had higher CDOM and DOC concentrations than deep water (Table I), which suggests that CDOM and DOC were probably of terrestrial origin (Loiselle *et al.*, 2007). Chromophoric dissolved organic matter (CDOM) concentrations were of similar magnitude as those in the Nyanza Gulf (Loiselle *et al.*, 2007). However, since chlorophyll *a* concentrations were much higher in the Nyanza Gulf, the relative contribution of CDOM to light attenuation could be of more importance in the Mwanza Gulf than in the Nyanza Gulf.

Limitations of phytoplankton biomass

The specific attenuation coefficient for chlorophyll *a* (k_{Chl}=0.036 µg L^{-1} m, 95% CL=0.016-0.055) was considerably higher and varied more than in Ugandan and Kenyan Gulfs (0.019 ± 0.002 (SD) µg L^{-1} m) (Loiselle *et al.*, 2008). The specific attenuation coefficient for chlorophyll *a* (K_{Chl}) of 414 data sets of temperate freshwater and marine waters ranged from 0.004-0.029 µg L^{-1} m (Krause-Jensen and Sand-Jensen, 1998). The coefficient depends on physiological state, photo-adaptation and historical light exposure of phytoplankton and can vary considerably within and between aquatic ecosystems with different taxonomic phytoplankton communities (Dubinsky and Berman, 1981). The high k_{Chl} coefficient in our study suggests that light attenuation was relatively fast at a relatively low chlorophyll *a* biomass and that light became limited at a low chlorophyll *a* biomass. Furthermore, we found that the minimal and critical light requirements for phytoplankton were similar and 7.5 fold higher than in Ugandan and Kenyan gulfs, respectively (Loiselle *et al.*, 2007). We also found that shallow and intermediate water were more light-limited (closer to upper limit for phytoplankton biomass) than deep water, because of higher background attenuation (K_{bg}) due to detritus and possibly CDOM. Although other studies confirm that, in general, phytoplankton growth in Lake Victoria is light limited, they suggest that this is due to self-shading when phytoplankton biomass is high, especially in shallow water and during periods of stratification (Guildford *et al.*, 2003; Gikuma-Njuru and Hecky, 2005). In the Mwanza Gulf, where biomass was much lower than in northern Lake Victoria Gulfs, self-shading is expected to play a smaller role.

Our results suggest that factors other than light might be limiting under specific local conditions. Nitrogen was probably limited in deep water when light was not limited. This is confirmed by the TN:TP ratio of 11.8, which is lower than the ratio of 20:1 at which N generally becomes limiting for phytoplankton growth (Guildford and Hecky, 2000). A possible cause for low N concentration might have been deoxygenation in deep water, enhancing denitrification (Hecky, 1993). The high TN:TP ratio of 46 in shallow water found in the present study indicates a tendency for P limitation besides light limitation (Guildford and Hecky, 2000). Through N-fixation, N could accumulate in the water column. Unfortunately, direct measurements of N-fixation were not available. However, based on the very low abundances of N-fixing phytoplankton species in September 2010 and April 2011, we infer that the concurrently measured high N:P ratios in shallow water were not caused by N-fixation. The high nitrogen content observed in this study in the Mwanza Gulf may be better explained by inputs from run-off from cultivated and urbanized land, river discharges and internal N loading through low denitrification rates in well oxygenated sediment and resuspension of sediments (Hecky, 1993; Lung'ayia *et al.*, 2001; Presing *et al.*, 2001). Furthermore, the slow flushing character and lack of extensive wetlands in connection with the Mwanza Gulf enable accumulation of N. The apparent lack of N-fixation is in contrast to other studies in Lake Victoria, in the Ugandan region, where N-fixation was high and considered an important N source (Hecky, 1993). N-fixation was especially high under optimal light conditions in shallow water with shallow mixed depths (Guildford *et al.*, 2003; Mugidde *et al.*, 2003). Possibly the low abundances of N-fixers we found might be an indication that light conditions in Mwanza Gulf were less optimal for N-fixers compared to other parts of Lake Victoria.

The degree of light limitation in our study was probably biased, since we estimated mixed depths from temperature profiles measured in the mornings when diurnal stratification was strongest. Complete mixing of the water column would probably occur once a day in the late afternoon, resulting in deeper mixed depths over much of the day. To demonstrate how much distances are affected by deeper mixing, we ran the light limitation analysis again with the original data, but assuming a 50% deeper mixed depths and using two alternative scenarios: (1) keeping the chlorophyll concentration per unit area over the mixed layer equal to the observed concentration per unit area, assuming that the concentration per unit volume below the observed mixed depth is zero and thus resulting in lower concentrations per unit volume over the simulated mixed depths, and (2) keeping the chlorophyll concentration per unit volume over the mixed layer equal to the observed concentration per unit volume, which resulted in higher concentrations per unit area with the simulated deeper mixed depths (Fig. 9).

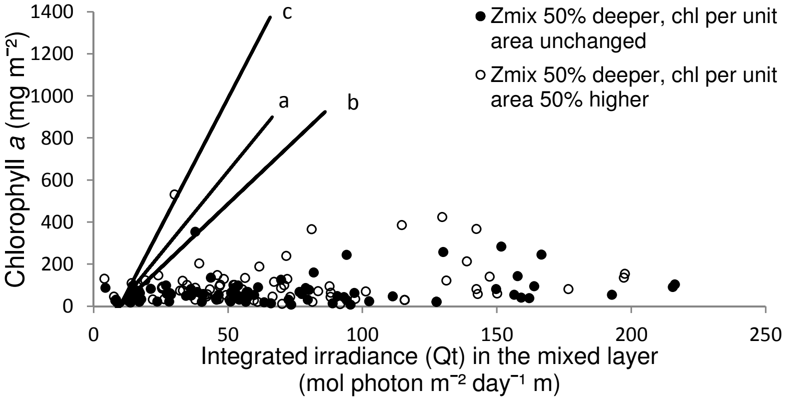

Figure 9: Chlorophyll *a* concentration per unit area and integrated light irradiance over mixed layer in Mwanza Gulf. The lines represent the maximum potential chlorophyll *a* concentrations when light is limited (upper limit). Three lines were calculated: a) based on the original data (for data points see Fig. 5), b) based on simulated data (black dots), assuming a Z_{mix} of 50% deeper than observed but with chlorophyll *a* concentrations per unit area equal to the observed values and c) based on simulated data (open circles), assuming a Z_{mix} of 50% deeper than observed, and with chlorophyll *a* concentrations per unit area 50% higher than observed Z_{mix} (i.e. assuming that the concentration chlorophyll per volume in the mixed depth remained equal).

According to scenario (1), distances increased with 5% on average (line b, black dots in Fig. 9), whereas in scenario (2) distances increased with 46% on average (line c, open circles). This means that if we assume a greater mixed depth than in our measurements, in both scenarios distances increase and, therefore, light limitation is less likely to occur than in our original calculations. Therefore, on a time scale of 24 hours, we most probably overestimated the importance of light limitation and thus underestimated the effect of other factors limiting phytoplankton biomass. Thus, our conclusions that other factors besides light might be limiting in the Mwanza Gulf are strengthened rather than diminished.

Several studies suggest that primary production in Lake Victoria might not increase further with eutrophication, because nutrients are in excess and light limits further phytoplankton biomass production (Silsbe *et al.*, 2006; Sitoki *et al.*, 2010). This may account for the highly eutrophic gulfs in the north with very high phytoplankton biomass, but our study shows that besides light, nutrients can be limiting in the Mwanza Gulf and phytoplankton production is likely to depend on specific local environmental conditions. A further increase in eutrophication could lead locally to higher chlorophyll *a* concentrations under optimal light and mixing conditions. However, this does not mean that primary production and lake productivity will continue to increase at a similar rate, because photosynthetic efficiency decreases with chlorophyll *a.* (Silsbe *et al.*, 2006). Eutrophication affects the whole of Lake Victoria, but its heterogeneous environment should be considered when assessing water quality and implementing measures to reduce eutrophication.

Acknowledgments

This work is part of the integrated project "Exploitation or eutrophication as threats for fisheries? Disentangling social and ecological drivers of ecosystem changes in Lake Victoria (SEDEC)", supported by the Netherlands Organisation for Scientific Research (NWO/WOTRO) grant number W01.65.304.00. We thank Koos Vijverberg for his supervision, advise and comments on this manuscript, and Andrea Downing for her comments and thoughts on this manuscript. We thank Theo Frank for his detailed analyses of the phytoplankton samples of Mwanza Gulf. We thank Klaas Gerber, Alex Mangassa, Gerardi Rajabu, Paulo and Emma for their valuable field assistance and support and all enthusiastic MSc. students involved in the data collection for this manuscript. Special thanks to the Tanzanian Fisheries Research Institute (TAFIRI) in Mwanza for providing laboratory space and use of field equipment during this research.

Chapter 3

Nile perch distribution in south-east Lake Victoria is more strongly driven by abiotic factors, than by prey densities

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This manuscript is published in Hydrobiologia (2015) 755, 239-255

Abstract

We studied the effects of environmental driving factors (maximum depth, visibility, oxygen, temperature and prey densities) on the distribution and diet composition of Nile perch (*Lates niloticus*) in south-east Lake Victoria from 2009-2011. We tested the hypotheses that (i) Nile perch distribution is regulated by the same environmental factors on a local scale (Mwanza Gulf) and on a regional scale (Mwanza Gulf, Speke Gulf and the open lake in Sengerema district), and (ii) driving factors act differently on different Nile perch size classes. Fish were sampled with gillnets. Nile perch densities were highest in the shallow part of the Mwanza Gulf and during the wet seasons, mainly caused by high densities of juveniles. The environmental driving factors explained Nile perch distributions on both regional and local scales in a similar way, often showing non-linear relationships. Maximum depth and temperature were the best predictors of Nile perch densities. Prey densities of shrimp and haplochromines did not strongly affect Nile perch distributions, but did explain Nile perch diet on a local and regional scale. We conclude that abiotic variables drive Nile perch distributions more strongly than prey densities and that feeding takes place opportunistically.

Introduction

Nile perch, *Lates niloticus* (L.), was repeatedly introduced in Lake Victoria in the 1950s and 1960s to boost the fisheries (Pringle, 2005). Its explosive population growth during the mid-1980s concurred with the decline in biomass and species numbers of haplochromine cichlids, a major prey of Nile perch (Witte *et al.*, 1992b). From that time onwards the Nile perch fishery thrived, peaking with an estimated annual yield of around 300,000 tons during the late 1980s after which it fluctuated around 250,000 tons (Kolding *et al.*, 2008; Kolding *et al.*, 2014).

Since the start of the fisheries concerns have been voiced that Nile perch stocks are declining and may collapse if fishing pressure will continue to increase (Mkumbo, 2002; Balirwa *et al.*, 2003; Getabu *et al.*, 2003; Ogutu-Ohwayo, 2004; Matsuishi *et al.*, 2006; Mkumbo *et al.*, 2007). However, stock assessments based on Nile perch catches and population size structure showed no signs of overfishing or long-term decline of the Nile perch stock, although, since the 1990s the stock shows short-term decadal fluctuations (Kolding *et al.*, 2008).

Besides fishing, water quality may play an important role in Nile perch distribution. The increasing eutrophication of Lake Victoria caused degradation of water quality, resulting in an increase in phytoplankton biomass. This led to changes in visibility and oxygen content of the water (Hecky, 1993; Hecky, 1994), while global climate change resulted in an increase of water temperatures in Lake Victoria with more than one degree since the 1920s (Sitoki *et al.*, 2010). In addition, it is hypothesized that prey density and availability may have profound effects on the size structure and distribution patterns of Nile perch (Goudswaard *et al.*, 2011; Downing *et al.*, 2013b).

Although Nile perch is considered a visual hunter, decreased visibility as such is not shown to affect Nile perch distributions, since it is found from clear to turbid waters. Nile perch is also a generalized predator, feeding on different types of prey of a large size range. This is an advantage when prey encounter rates decrease because of reduced visibility (Seehausen *et al.*, 2003; Hecky *et al.*, 2010). However, Nile perch is absent in turbid waters such as swamps when oxygen levels become critical (Chapman *et al.*, 2002).

Several studies showed the relationship of dissolved oxygen and Nile perch densities (Wanink *et al.*, 2001; Chapman *et al.*, 2002; Mkumbo, 2002; Balirwa *et al.*, 2003; Paterson and Chapman, 2009; Goudswaard *et al.*, 2011; Njiru *et al.*, 2012; Nyboer and Chapman, 2013; Taabu-Munyaho *et al.*, 2013). In Lake Victoria seasonal stratification of the water column results in decreased oxygen concentrations near the bottom, especially in deeper water. This hypoxia limits fish to utilize habitats and probably forces Nile perch to move up above the oxycline or to migrate to oxygenated shallow waters (Goudswaard *et al.*, 2011; Taabu-Munyaho *et al.*, 2013). Experiments showed that Nile perch was relatively intolerant to hypoxia (Schofield and Chapman, 2000). Therefore, hypoxic waters can act as refugia for hypoxia-tolerant haplochromine species in swamps, wetlands and deep water (Hecky, 1994; Chapman *et al.*, 2002; Paterson and Chapman, 2009; Njiru *et al.*, 2012) and for the freshwater shrimp *Caridina nilotica* (Roux) (Kaufman, 1992; Hecky, 1994; Njiru *et al.*, 2012), both important prey for Nile perch. Hypoxia also affects the size class distribution of fish, because it can limit physical growth and reproduction, resulting in a reduction of maximum fish size and length at maturity (Pauly, 1981; Pauly, 1984). Furthermore, large-sized Nile perch are affected more by low oxygen than small-sized Nile perch, because of their smaller gill surface area to biomass ratio (Njiru *et al.*, 2012). Sudden upwelling of anoxic waters caused incidental massive kills of large-sized Nile perch in Kenyan waters and in the Mwanza Gulf in the 1980s (Ochumba, 1990; Kaufman, 1992; Wanink *et al.*, 2001) and fish kills of Nile perch at smaller scales (i.e. individual fish floating dead or gasping for air rather than groups of fish) have been observed in 2009–2011 on at least 3 occasions during the breakdown of stratification (I.J.M. Cornelissen and H.K. Peter, personal observations).

The rise of the water temperature in Lake Victoria also resulted in higher stability of the water column (Hecky, 1993; Cózar *et al.*, 2012) and may also have affected Nile perch distribution. For instance, Getabu *et al.* (2003) observed high Nile perch densities in warmer, shallow waters. However, other studies observed a negative or no relationship between Nile perch densities and water temperature (Goudswaard *et al.*, 2011; Nyboer and Chapman, 2013; Taabu-Munyaho *et al.*, 2013).

In addition to abiotic environmental variables, prey abundance can affect Nile perch distribution and population size structure as well as their diets. A decline in prey abundance can decrease the condition factor of Nile perch (Ogutu-Ohwayo, 1999) and may decrease the size at maturity of fish (Pauly, 1984). A change in prey availability can affect the Nile perch's ontogenetic diet shift from invertebrates to fish and result in profound changes in mean population size and maximum size of Nile perch through changing growth and mortality rates (Downing *et al.*, 2013b). There are indications that Nile perch moves to habitats where its preferred prey is abundant. Goudswaard *et al.* (2011), for instance found that Nile perch stayed near the bottom in deep water where *Caridina* densities are high when oxygen conditions are favourable. He suggested that the distribution of *Caridina* may explain the distribution of Nile perch during the time when haplochromine populations were declining.

Most studies on the Nile perch stock in Lake Victoria focussed on whole lake dynamics over long periods and on the impacts of the Nile perch fisheries (Mkumbo, 2002; Getabu *et al.*, 2003; Mkumbo *et al.*, 2007). In addition, Nile perch distribution was generally studied in open waters of more than 15 m depth where most of the commercial Nile perch fishery is concentrated (Mkumbo, 2002; Getabu *et al.*, 2003). Little is known about how changes in abiotic factors as for instance caused by eutrophication or climate change will affect the Nile perch stock and at what scales such effects will become apparent. Therefore, there is a need to identify the environmental drivers of Nile perch densities and to identify the spatial and temporal scales at which such drivers are relevant.

We studied how Nile perch is distributed over a range of spatial and seasonal scales and related this to abiotic and biotic environmental variables. Three large regions in south-east Lake Victoria were selected: the Mwanza Gulf, the Speke Gulf and the waters near Kome Island (Sengerema district). In addition, we studied Nile perch distributions on a local, more detailed scale within the Mwanza Gulf. We tested the following hypotheses: (i) Nile perch distribution is regulated by the same environmental factors on both the regional and the local scale; (ii) Driving factors act differently on different Nile perch size classes.

Methods

Study area

Data were collected in south-east Lake Victoria at 14 sampling stations in the Mwanza Gulf, the Speke Gulf and near Kome Island in the Sengerema district, from here on referred to as Sengerema, (Fig. 1) from September 2009 – April 2011. The three regions differ in habitat: Mwanza Gulf has a strong coastal and littoral influence as the Gulf is narrow and shallow. Speke Gulf is wider and deeper and the stations sampled in Sengerema are deep and located in open water. Sampling stations were at least 8 km apart and at least 1.5 km from the shore. Maximum depth, water temperature and water quality parameters varied between stations during the study period (Table 1). The bottom at all stations mainly consisted of soft mud with occasional rocks at the Speke and Sengerema stations.

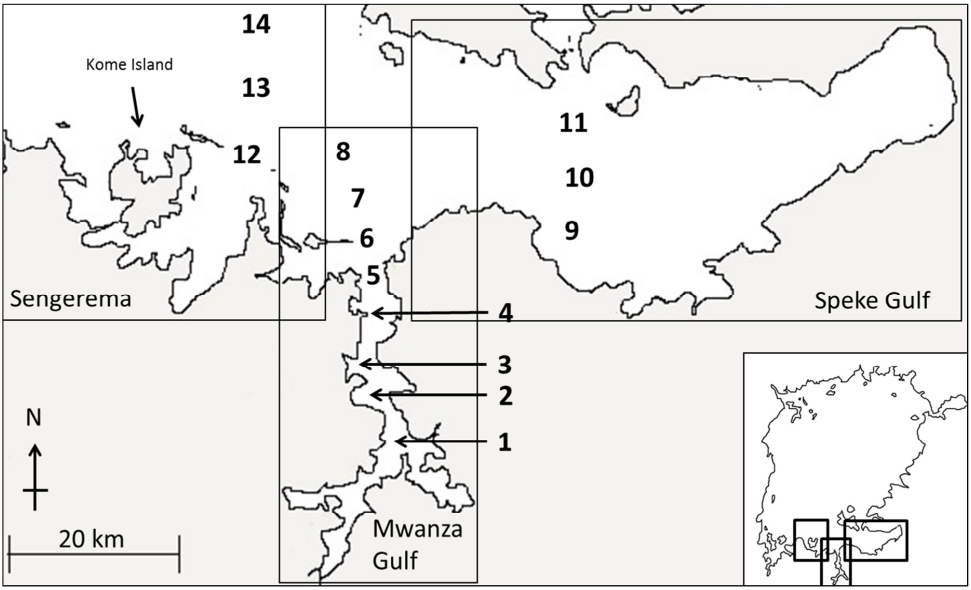


Figure 1: Map of south-east Lake Victoria with stations in the three regions: Mwanza Gulf (1-8) with a depth range of 5-44 m from station 1 to 8, Speke Gulf (9-11) with a depth range of 17-34 m from station 9 to 11, and Sengerema (near Kome Island) (12-14) with a depth range of 41-55 m from station 12 to 14.

Table 1: Maximum depths, average water temperature and means of water quality parameters measured at the sampling stations during the study period. Temperature and dissolved oxygen are means calculated over the whole water column. n=number of observations. For position of sampling stations see Fig. 1.

Region	**Station**	**n**	**Maximum depth (Dmax, in m)**	**Temperature of the water column (T, in °C)**	**Dissolved oxygen (DO, in mg L^{-1})**	**Visibility (SD, in m)**
Mwanza	1	9	5	24.5	7.1	0.63
	2	9	7	25.1	7.4	0.67
	3	9	8	24.8	6.8	1.02
	4	10	11	25.2	7	1.20
	5	9	18	24.9	6.1	1.73
	6	14	28	25.3	5.3	1.99
	7	7	39	24.7	5.6	1.90
	8	6	44	24.6	5.5	2.20
Speke	9	3	17	25	4.5	2.00
	10	3	29	24.6	4.9	2.00
	11	3	34	24.9	5.8	2.30
Sengerema	12	2	41	25	5.1	1.30
	13	3	50	24.9	5	1.40
	14	4	55	25.1	6.4	1.80

Mwanza Gulf, Speke Gulf and the waters in Sengerema are all commercially fished for Nile perch. The southern part of Mwanza Gulf, south of station 3, is officially closed for fishing from January to June, but this is not enforced and Nile perch is fished all year round. Here, Nile perch are fished on a relatively small scale and sold on local markets, whereas Nile perch caught in the open waters near the entrance of the Gulf, in Speke Gulf and in Sengerema generally are targeted for the international export market of frozen fillets (M. Medard, personal communication).

Climate

Seasons in Lake Victoria are based on the yearly monsoon cycles. In southern Lake Victoria, a dry season from June-August is characterized by strong southerly winds with minimal precipitation, low temperatures and a well-mixed, oxygenated water column (Talling, 1966; Akiyama *et al.*, 1977). From September-December, a transition to calm weather occurs with stratification gradually building up and precipitation increasing. From January-May precipitation and temperature are highest. Stratification is strongest from January-March (Talling, 1966), resulting in hypoxia near the bottom in waters of > 40 m depth (Hecky, 1994).

Data collection

Fish, prey organisms, water temperature and water quality variables were all sampled within ten days intervals at each station. Mwanza stations 1-6 were sampled 10–16 times from September 2009 until April 2011, stations 7 and 8 were sampled 6–7 times from June 2009 until April 2011. Stations 9-14 in Speke Gulf and in Sengerema were sampled 2–4 times between June 2009 and May 2010 (Table 2). Data from 2009-2011 were used for analyses on a regional scale between Mwanza Gulf, Speke Gulf and Sengerema, whereas data from 2010-2011 were used for analyses within Mwanza Gulf.

Nile perch > 5 cm standard length were collected using multifilament gillnet fleets consisting of panels with stretched mesh sizes ranging from 1 to 8 inch (25-203 mm) with increments of 0.5 inch (13 mm) for panels of 1 to 6 inch and with increments of 1 inch (25 mm) for panels of 6-8 inch (152-203 mm). Panels varied in surface area, from 58 m^2 for a panel of 1 inch mesh size to 1213 m^2 for a panel of 8 inch mesh size. Panels in the Mwanza Gulf were 5-7 m deep and panels in Speke Gulf and in Sengerema were 5-13 m deep. The total length of a fleet was approximately 600 m. Fleets were set in such a way that in the shallow stations (depth < 8 m) the whole water column was covered. At station 4 (depth=11 m) fleets were set at the surface and bottom, and at station 5-14 (depth from 17 to 55 m) fleets were set at the surface, middle and bottom of the water column (Table 2, Fig. 2). Gillnets were set in the afternoon at 6 pm and hauled the next morning at 6 am. All fish caught were weighed and standard lengths were measured at the laboratory of the Tanzanian Fisheries Research Institute (TAFIRI) in Nyegezi (near Mwanza City) or on location.

Table 2: Sampling frequency and fleet settings at stations during the study period. Abbreviations used: Dmax=Maximum depth (m); Gillnet fleet set at S=the surface; B=the bottom; and M=the middle of the water column. For position of sampling stations see Fig. 1.

Region	Station	Dmax (m)	Fleet setting	2009		2010				2011
				Jun-Sept	Oct-Dec	Jan-Mar	Apr-May	Jun-Sept	Oct-Dec	Jan-Mar
Mwanza	1	5	S	–	2	–	–	4	3	2
	2	7	S	–	3	–	3	4	3	3
	3	8	S	–	3	–	–	4	3	3
	4	11	S, B	–	2	–	3	4	1	–
	5	18	S, M, B	–	2	–	–	3	3	2
	6	28	S, M, B	1	2	–	4	–	3	5
	7	39	S, M, B	1	–	–	2	1	–	3
	8	44	S, M, B	1	–	–	2	1	–	2
Speke	9	17	S, M, B	1	–	1	1	–	–	–
	10	29	S, M, B	2	–	1	–	–	–	–
	11	34	S, M, B	2	–	1	–	–	–	–
Sengerema	12	41	S, M, B	–	–	2	–	–	–	–
	13	50	S, M, B	1	–	2	–	–	–	–
	14	55	S, M, B	2	–	2	–	–	–	–

Nile perch diets were analysed by dissecting the stomachs. Stomach fullness was classified into five categories: 0-1% (empty), 1-25 %, 25-50%, 50-75% and > 75% (full). The relative volume per prey category was estimated using the same five categories (Witte and van Densen, 1995). Preys were categorized as: odonate / ephemeropteran nymph, mollusc, *Caridina nilotica* shrimp, *Rastrineobola argentea* (Pellegrin) (a small cyprinid fish), haplochromine cichlids, Nile perch, other fish species, and unidentified fish remains.

A hydrolab DS5 multiprobe (OTT Messtechnik GmbH & Co, Kempten, Germany) collected vertical profiles of temperature and oxygen concentrations from the lake bottom to the surface during the day. Oxygen concentration was calibrated using the Winkler method (American Public Health Association, 2005). Secchi depth was measured in triplicate with a 25 cm diameter black and white Secchi disk and was defined as the mean depth at which the disk disappeared when lowering it in the water and re-appeared when lifting it.

Observations on the distribution of *Caridina* in the Mwanza Gulf were carried out in triplicate per station by hauling a 1 m^2 square lift net from bottom to surface. Samples were preserved in 5% formaldehyde solution and numbers were counted in the laboratory.

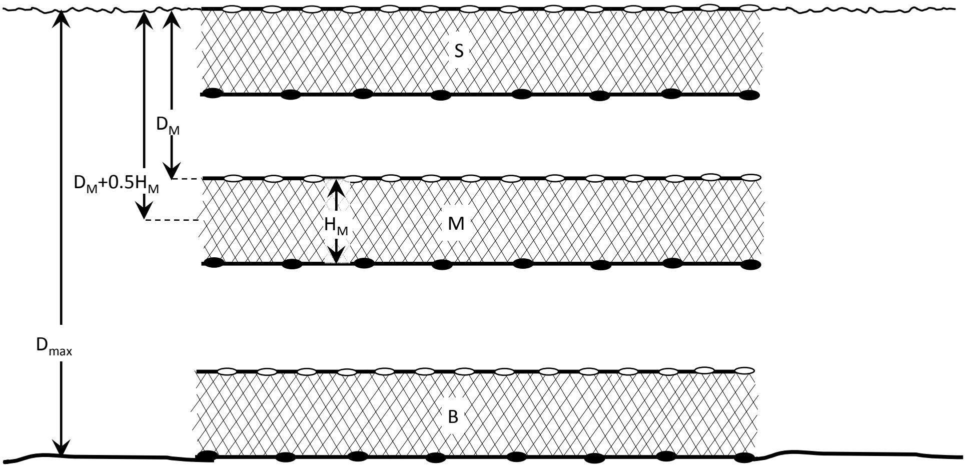


Figure 2: A schematic representation of the gillnet fleet sets. In deep stations fleets were positioned at the water surface (S), in the middle (M) of the water column at depth D_M and at the bottom (B). H_M, height of the nets of the middle fleet; D_{max}, depth of the water column.

Data analysis

Spatial and temporal distribution differences

CPUE was calculated in numbers per standardized fleet per hour (no·setting^{-1}). A standardized fleet was calculated as the mean surface area of one fleet (m^2). To enable comparisons between stations with different proportion of gillnet coverage of the water column, we estimated catch per unit effort (CPUE, no·setting^{-1}) over the whole water column, by interpolation for the part of the water column not covered by gillnets at stations deeper than 15 m. The mean value of the CPUE of the surface and middle panels was used to calculate the CPUE of the top part of the water column. This value was weighted for the depth of this part of the water column. Similarly, the mean value of the CPUE of the bottom part of the water column was calculated as the mean value of the middle and bottom fleet, weighted for the depth of this part of the water column. Total CPUE was the sum of the CPUE values of the top and bottom parts of the water column:

$$CPUE = \frac{CPUE_S + CPUE_M}{2} \cdot \frac{D_M + 0.5 \cdot H_M}{D_{\max}} + \frac{CPUE_M + CPUE_B}{2} \cdot \frac{D_{\max} - (D_M + 0.5 \cdot H_M)}{D_{\max}},$$

where $CPUE_S$, $CPUE_M$, and $CPUE_B$ are the CPUE values for the surface, middle and bottom fleet respectively, H_M is the height of the middle fleet, and D_{max} is the depth of the water column (Fig. 2).

Spatial effects on Nile perch size class distributions on a regional scale between Mwanza Gulf, Speke Gulf and Sengerema were analysed by Kruskal-Wallis tests, because normality of the residuals could not be achieved directly, or after transformation. Spatial and temporal effects on Nile perch size class distributions in the Mwanza Gulf were also analysed by Kruskal-Wallis tests. In case of significant spatial or temporal effects, *post hoc* pairwise comparisons were performed with adjusted levels for multiple comparisons using a Bonferroni correction (*df*=5, P=0.003 for spatial comparisons within the Mwanza Gulf and *df*=4, P=0.005 for temporal comparisons within the Mwanza Gulf and spatial comparisons on a regional scale).

Data of the residuals of prey densities of *Caridina* and haplochromines were not normally distributed and spatial effects were tested with Kruskal-Wallis tests and *post hoc* pairwise comparisons were corrected according to Bonferroni (*df*=5, P=0.003 for spatial comparisons within the Mwanza Gulf and *df*=4, P=0.005 for spatial comparisons on a regional scale). *Caridina* densities were only sampled in the Mwanza Gulf stations 1-6.

Multivariate analyses

We investigated variability in Nile perch distributions in relation to environmental factors by using multivariate analyses. Detrended correspondence analysis (DCA) on log-transformed data was used to determine the length of the environmental gradient, to choose the appropriate response model. For all analyses, the gradient length suggested that the response models could be either linear or unimodal. Subsequently we chose to use linear redundancy analyses (RDA) to explain Nile perch size class distributions by environmental variables on a local scale within the Mwanza Gulf and on a regional scale between Mwanza Gulf, Speke Gulf and Sengerema. Year was used as a co-variable. All multivariate analyses were carried out with CANOCO 4.55 (Biometris, Plant Research International, Wageningen, the Netherlands).

Generalized additive model (GAM) analyses

We used GAMs to investigate the relationships between Nile perch size class distribution and maximum depth, temperature, oxygen concentration, Secchi depth, and haplochromine and *Caridina* densities using the same data set as for the DCA. GAM is a non-parametric regression technique to model non-linear relationships and can be used with non-normally distributed data. We used the densities of Nile perch and haplochromines (CPUE in numbers per standardized fleet) for bottom, middle or surface sets in the water column. Means of temperature and oxygen were calculated over the depth at which a fleet of gillnets was set. Although densities of some Nile perch size classes were not normally distributed after log-transformations and some fitted a gamma distribution, GAM models fitted best with log-transformed Nile perch densities with a Gaussian error distribution and identity link function. Generalized cross validation (GCV) was used to choose the optimal degree of smoothing for each variable. We started with a model including all environmental variables as smooth, non-linear terms. When the degrees-of-freedom, estimated by GCV, of a variable was one, it was considered as a linear regression. Non-significant terms were excluded from the model. The model predicted densities of Nile perch for each smoothing and/or linear component (partial prediction). The partial prediction is the portion of the predicted response of Nile perch densities that is attributed to an environmental variable. Partial predictions were plotted against environmental variables to explore the nature of the relationships between Nile perch densities and environmental drivers. GAM analyses were carried out in R 3.1.0 (R Foundation for Statistical Computing, Vienna, Austria).

Logistic regression analyses

Nile perch diets were weighted for the fullness of stomachs to calculate the frequency of occurrence of prey. The diet category ‘fish’ consisted of haplochromines and unidentified fish remains. On average, 47% of the Nile perch stomachs were empty. Empty stomachs were excluded from further data analyses. To test the frequency of occurrence of prey in the diet as a function of Nile perch size classes, we used binomial logistic regression models with absence/presence of prey in the stomach. Binomial logistic regressions were then tested by using Wald tests. Non-parametric and logistic regression analyses were carried out in SAS 9.2 (SAS Institute, Cary, USA).

Results

Spatial and temporal distributions of Nile perch

Local scale

When comparing the CPUE over the whole water column on a local scale within the Mwanza Gulf, Nile perch size classes between 10 and 40 cm varied spatially with significantly higher densities at shallow stations 1-3 than in deeper water at 4-6 (Fig. 3). Small Nile perch of 5-10 cm varied seasonally with highest densities from November to February during the wet seasons and lowest densities from July-August during the dry season (Fig. 3).

Regional scale

On a regional scale, CPUE over the whole water column of Nile perch size classes between 5 and 40 cm were highest at the shallowest station of Mwanza (Mw1) and lowest in Sengerema (Fig. 3). Small-sized Nile perch of size classes between 5 and 20 cm were especially abundant in the Mwanza Gulf. Densities of Nile perch of 20-40 cm were similar between the medium and deep stations of Mwanza (Mw 2, 3) and Speke Gulf. Densities of Nile perch of > 40 cm were lowest at the medium deep stations of the Mwanza Gulf (Mw2) and similar in the other regions (Fig. 3).

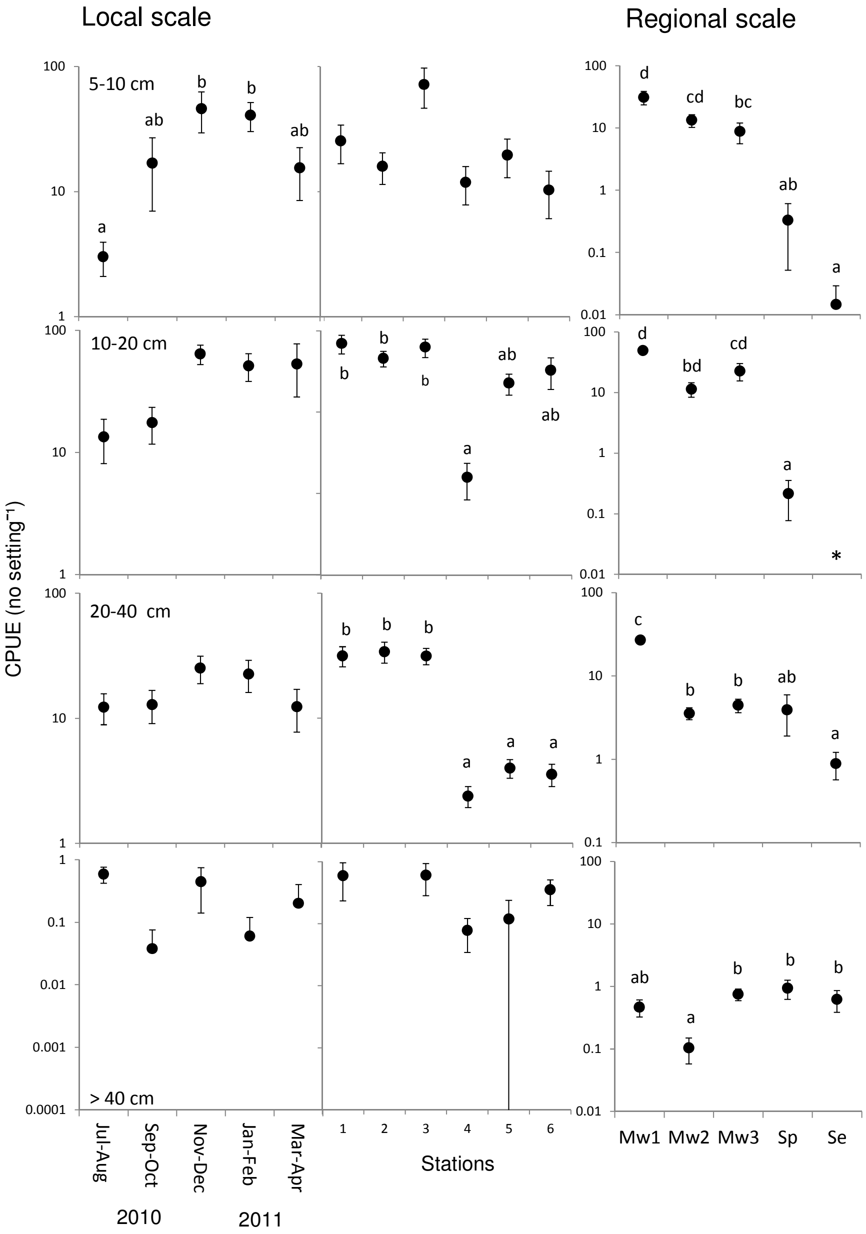


Figure 3: Mean Nile perch densities (CPUE of the whole water column) and standard errors of different size classes on a local scale in the Mwanza Gulf from 2010-2011 and on a regional scale in the Mwanza Gulf, Speke Gulf and in Sengerema from 2009-2011. Nile perch size classes were: 5-10 cm, 10-20 cm, 20-40 cm and > 40 cm. Abbreviations used for local scale: 1-6=Mwanza Gulf stations 1-6; and for regional scale: Mw1=Mwanza stations 1-3, Mw2=Mwanza stations 4-5, Mw3=Mwanza stations 6-8, Sp=Speke stations 9-11 and Se=Sengerema stations 12-14. For position of stations see Fig. 1. Identical letters above the means in the figure indicate non-significant differences between catches in a multiple comparison test ($p \geq 0.05$).

Factors determining Nile perch distributions

Local scale

On a local scale within the Mwanza Gulf, detrended correspondence analysis (DCA) showed a gradient length of the first ordination axis of 2.3, indicating either a linear or a unimodal relationship between the environmental gradient and Nile perch distributions. We chose a linear redundancy analysis (RDA) to relate Nile perch size class distributions to abiotic and biotic environmental factors (Fig. 4). The RDA ordination was significant for all axes (F=4.79, P=0.001, Monte-Carlo test, 1000 replicates) with the first two axes explaining 22.3 % of the variation. Generalized additive models (GAM) of Nile perch size class distributions and environmental factors showed both significant linear and non-linear regressions (Table 3, Fig. 5).

There was a strong spatial pattern in the RDA ordination, with a clear gradient between stations 1-6, correlating strongly with the maximum depth of the water column (Figs. 4a, c). The seasonal pattern was less conspicuous, with July-August (dry season) being most distinct from the rest of the year (Fig. 4e). This pattern was strongly correlated with low temperatures in the dry season. Densities of Nile perch of 20-40 cm were related to shallow stations of the Mwanza Gulf (Figs. 4a, c). GAM analyses showed that densities of Nile perch size classes of 5-10 cm, 20-40 cm and > 40 cm decreased with depth linearly and non-linearly respectively (Table 3, Fig.5). Partial predictions of densities of Nile perch of 10-20 cm versus maximum depth showed a quadratic-shaped pattern with minimum predicted densities at 10-20 m depth (Fig. 5).

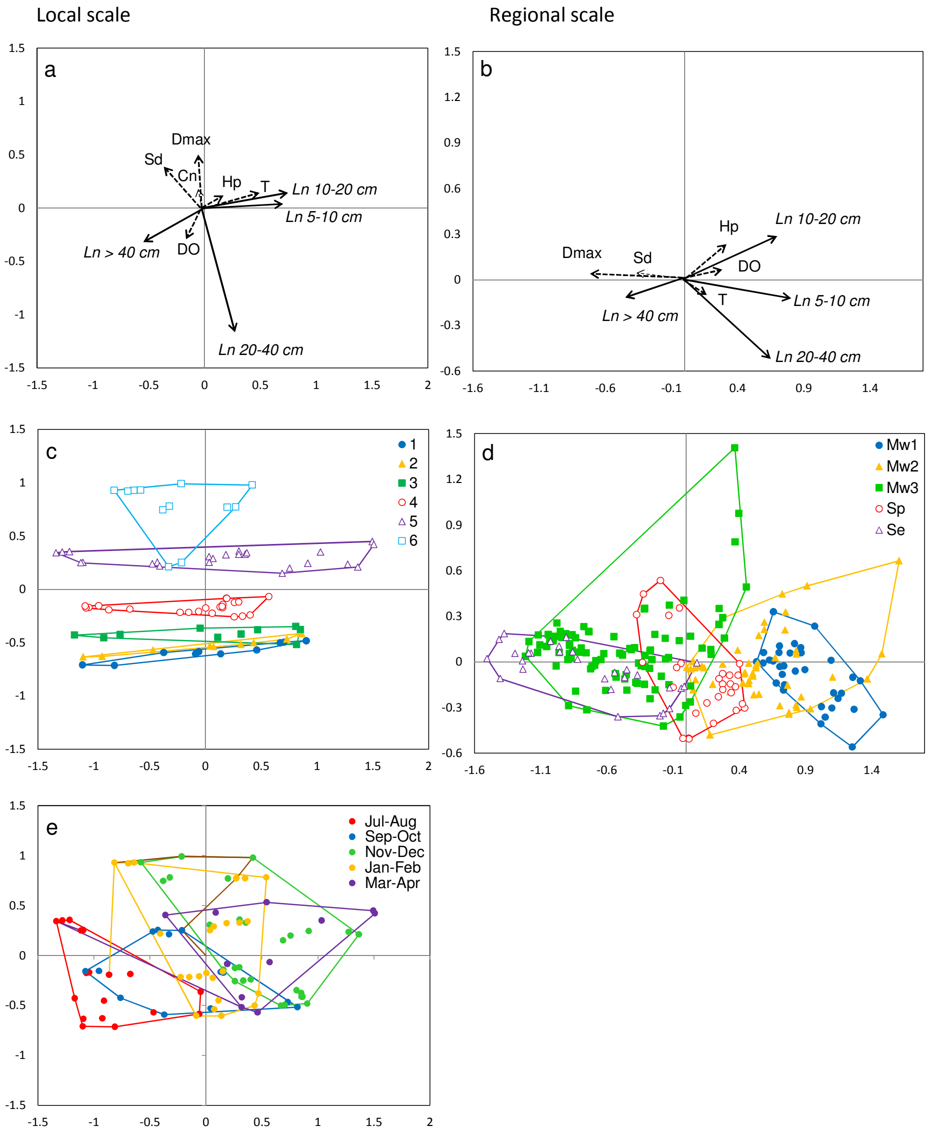


Figure 4: Spatial and seasonal distribution of Nile perch densities in relation to environmental factors on a local spatial scale within the Mwanza Gulf and on a regional spatial scale in the Mwanza Gulf, Speke Gulf and in Sengerema: a-b) RDA biplot of densities of Nile perch size classes in relation to environmental factors temperature (T), dissolved oxygen (DO), Maximum depth (Dmax), Secchi depth (SD), *Caridina* densities (Cn) and haplochromine densities (Hp). Abbreviations used for Nile perch size classes: Ln 5-10 cm, Ln 10-20 cm, Ln 20-40 cm and Ln > 40 cm, c-d) RDA scatter plot of spatial distribution of Nile perch densities. Abbreviations used for indicating Mwanza Gulf stations and regions see caption Fig. 3. For position of stations see Fig. 1. and e) RDA scatter plot of seasonal distribution of Nile perch densities in the Mwanza Gulf.

Table 3: General Additive Models (GAM) of non-parametric regressions between Nile perch densities and environmental variables on a local and regional scale. Models for each Nile perch size class included only significant variables. Significant P-values are in italics. Abbreviations used: F=test statistics, n.s.=not significant term and excluded from model (P ≥ 0.05), df=degrees of freedom

	Nile perch 5-10			Nile perch 10-20			Nile perch 20-40			Nile perch > 40		
	F	*P*	df	F	*P*	df	F	*P*	df	F	*P*	df
Local scale												
Maximum depth	4.25	*0.02*	2	9	*<0.0001*	2	3.05	*0.05*	2	18.80	*<0.0001*	1
Secchi depth	–	n.s.	–	4.11	*0.05*	1	3.08	*0.05*	2	16.13	*0.0001*	1
Oxygen	–	n.s.	–	–	n.s.	–	–	n.s.	–	–	n.s	–
Temperature	7.39	*<0.0001*	8	4.75	*0.0004*	5	–	n.s.	–	–	n.s	–
Caridina	–	n.s.	–	10.40	*0.002*	1	–	n.s.	–	–	n.s.	–
Haplochromines	–	n.s.	–	–	n.s.	–	3.51	*<0.006*	4	–	n.s.	–
Regional scale												
Maximum depth	47.39	*<0.0001*	3	22.97	*<0.0001*	9	15.62	*<0.0001*	7	23.95	*<0.0001*	1
Secchi depth	3.37	*0.0008*	8	5.95	*<0.0001*	8	–	–	–	2.36	*0.04*	4
Oxygen	2.19	*0.03*	6	5.02	*<0.0001*	7	7.82	*0.004*	1	–	–	–
Temperature	8.05	*<0.0001*	6	9.91	*<0.0001*	6	16.13	*<0.0001*	1	3.42	*0.008*	3
Caridina	–	–	–	–	–	–	–	–	–	–	–	–
Haplochromines	–	n.s.	–	3.32	*0.03*	2	–	n.s.	–	–	n.s.	–

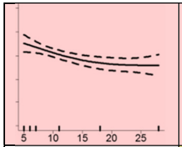
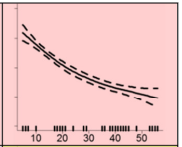
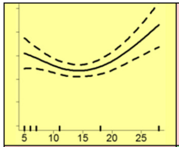
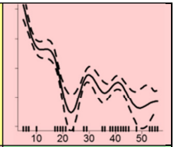
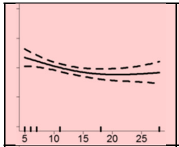
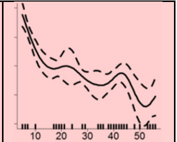
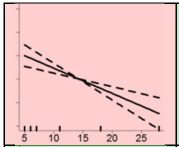
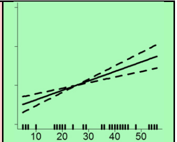
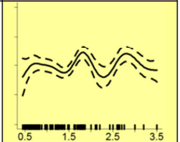
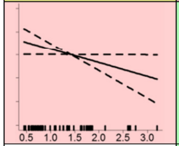
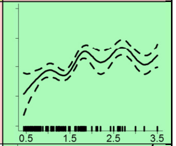
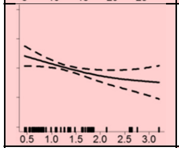
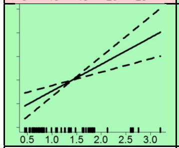
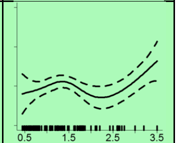
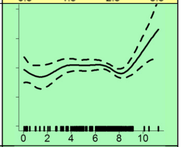
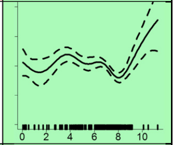
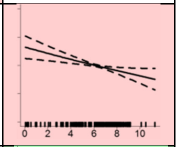
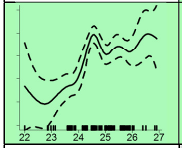
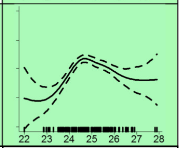
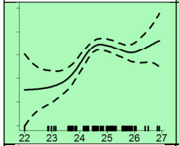
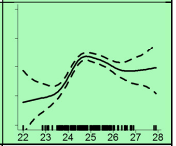
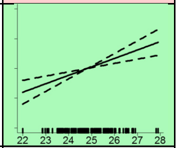
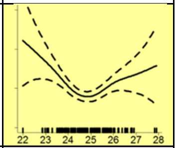
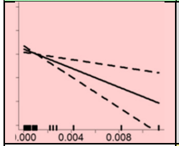
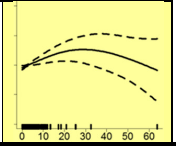
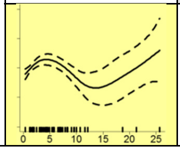
	Nile perch 5-10		Nile perch 10-20		Nile perch 20-40		Nile perch > 40	
	Local	Regional	Local	Regional	Local	Regional	Local	Regional
Dmax								
Sd	n.s.					n.s.		
DO	n.s.		n.s		n.s.		n.s	n.s.
T					n.s.		n.s.	
Cn	n.s.				n.s.		n.s.	
Hp	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.

Figure 5: Regressions of the significant linear and non-linear terms of the GAM models on a local and regional scale. Graphs indicate relationships between environmental variables (x-axis) and partial predictions of Nile perch densities (y-axis). Solid lines indicate the model fit and dashed lines the 95% confidence intervals. Colors indicate the nature of the relationship: green=increase, red=decrease and yellow=irregular, grey=model was not included because of lack of data of *Caridina* on a regional scale. Abbreviations used: n.s.=not significant term and excluded from model; dmax=maximum depth (m); Sd=Secchi depth (m); DO=dissolved oxygen (mg l^{-1}); T=temperature (°C); Cn=*Caridina* density (no. l^{-1}) and Hp=haplochromine densitiy (no setting^{-1}).

Visibility (Secchi depth) was closely correlated to maximum depth, although the influence of the former on the ordination was less strong (Figs. 4a). GAM analyses showed that visibility was negatively related to Nile perch size classes between 10 and 40 cm and positively, linearly related to Nile perch > 40 cm (Table 3, Fig. 5).

Oxygen concentration was influenced more or less equally by space and season with higher concentrations in shallow waters and in July-October (Figs. 4a, c, e). GAM analyses did not show any relationships between the observed oxygen concentrations and Nile perch densities (Table 3)

Temperature was positively related to the density of small Nile perch size classes between 5 and 20 cm (Fig. 4a). This was confirmed by the GAM analyses, showing a non-linear increase with maximum predicted densities at 24-25 °C (Table 3, Fig. 5).

Caridina densities were of minimal influence on the RDA ordination of Nile perch distributions in the Mwanza Gulf. (Fig. 4a). GAM analyses showed that *Caridina* densities were negatively and linearly related to densities of Nile perch 10-20 cm (Table 3, Fig. 5). *Caridina* densities increased with depth and were highest at station 6 and lowest at station 1 (Fig. 6a). The contribution of *Caridina* in the Nile perch diet was significantly related to the the size of Nile perch (Fig. 6d, $P < 0.05$, Wald test). The largest contribution of *Caridina* in the diet was found in Nile perch size classes between 5 and 20 cm and at stations 5 and 6. At station 1, the contribution of *Caridina* in the diet was low for all size classes.

Haplochromine densities also had a minimal influence on the RDA ordination (Fig. 4a). GAM analyses showed that Nile perch of 20-40 cm was related with an sinus-shaped pattern showing a local minimum at a density of ca. 10-15 haplochromines per standardised setting after which Nile perch densities increase with haplochromine densities (Fig. 5). Between stations in the Mwanza Gulf, no significant differences in haplochromine densities were found (Fig. 6b). The contribution of fish in the Nile perch diet was significantly related to Nile perch length at all stations (Fig. 6f, $P < 0.05$, Wald test). The largest contribution of fish in the diet was found in Nile perch size classes of > 20 cm, except for shallow waters in the Mwanza Gulf where Nile perches of all size classes predominantly fed on fish (Fig. 6f).

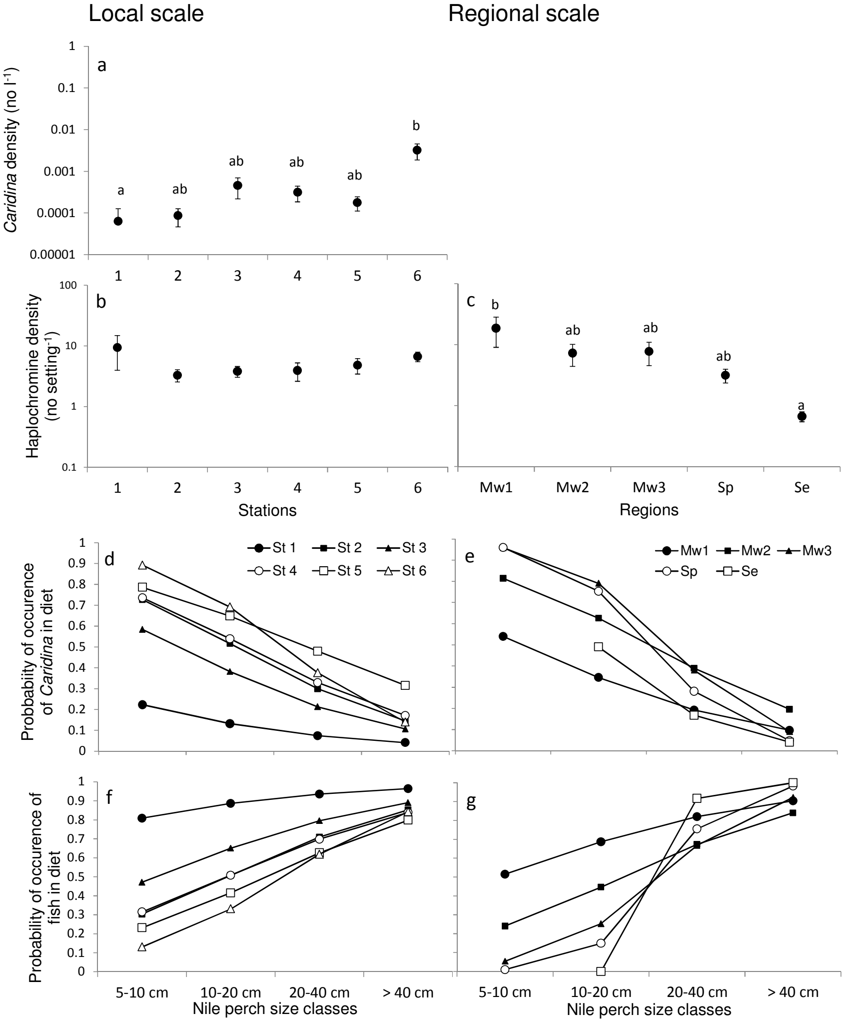


Figure 6: Spatial variation in prey density and diet composition of Nile perch size classes on a local scale in Mwanza Gulf and on a regional scale between Mwanza Gulf, Speke Gulf and in Sengerema: a) mean *Caridina* densities and standard errors. Identical letters above means and standard errors in figures a-c indicate non-significant differences between densities in a multiple comparison test ($p \geq 0.05$), b-c) mean haplochromine densities (CPUE) and standard errors, d-e) probability of occurrence of *Caridina* prey found in the diet of different Nile perch size classes and f-g) probability of occurrence of fish prey found in the diet of Nile perch size classes. Abbreviations used for indicating Mwanza stations and regions as in the caption of Fig. 3. For position of sampling stations see Fig. 1.

Regional scale

On a regional scale, detrended correspondence analyses (DCA) resulted in a gradient length of the first ordination axis of 3.6, which indicates either a linear or a unimodal relationship between the environmental gradient and Nile perch distributions. We chose linear redundancy analyses (RDA) to relate Nile perch size class distributions to environmental factors. The RDA ordination was significant for all axes (F=21.72, P=0.001, Monte-Carlo test, 1000 replicates). The first two axes explained 31.8 %. Generalized additive models (GAM) showed both significant linear and non-linear regressions between Nile perch densities and environmental factors (Table 3, Fig. 5).

Of all environmental factors, maximum depth influenced the RDA ordination most, primarily differentiating the shallower stations of Mwanza Gulf (Mw1, Mw2) from the deeper stations (Mw3) and Speke Gulf and Sengerema (Figs. 4b, d). Maximum depth was negatively related to Nile perch size classes between 5 and 40 cm (Fig. 4b). This was confirmed by GAM analyses, showing a non-linear decrease of densities of Nile perch size classes between 5 and 40 cm with depth (Table 3, Fig. 5). Densities of Nile perch > 40 cm linearly increased with depth (Table 3, Fig. 5).

Visibility (Secchi depth) was positively correlated to maximum depth, although its influence on the RDA ordination was less strong (Fig. 4b). GAM analyses showed an increase of densities of Nile perch of 10-20 cm and > 40 cm with visibility, of which Nile perch > 40 cm showed a sine-shaped function with increasing densities from 2 m visibility and up (Table 3, Fig. 5). Nile perch of 5-10 cm showed an irregular pattern with visibility (Fig. 5).

Oxygen concentrations were negatively correlated with depth, with the highest concentrations in the shallow waters of Mwanza Gulf (Figs. 4b, d). Oxygen concentration was positively related to the density of small Nile perch size classes between 5 and 20 cm and negatively with Nile perch > 40 cm in the RDA (Fig. 4b). GAM analyses confirmed a positive non-linear relationship between oxygen concentrations and densities of Nile perch size classes between 5 and 20 cm (Table 3, Fig. 5). Partial predictions showed an increase of Nile perch densities above an oxygen concentration of 8 mg l^{-1} (Fig. 5). In contrast, Nile perch 20-40 cm showed a negative linear relationship with oxygen concentration (Table 3, Fig. 5).

Temperature was positively related to the density of Nile perch size classes between 5 and 40 cm in the RDA and negatively to density of Nile perch > 40 cm (Fig. 4b). GAM analyses showed that temperature affected all Nile perch size classes (Table 3). Densities of Nile perch size classes between 5 and 20 cm showed positive non-linear relationships with maximum predicted densities at 24-26˚C (Fig. 5).

Densities of Nile perch of 20-40 cm showed a positive linear relationship with temperature and Nile perch > 40 cm showed minimum densities at a temperature of 25˚C (Fig. 5).

The inclusion of *Caridina* in the diet was negatively related to Nile perch length in all regions ($P < 0.006$, Wald test), except in Sengerema ($P=0.19$) (Fig. 6e). Nile perch of size classes between 5 and 20 cm fed predominantly on *Caridina,* except in shallow waters of the Mwanza Gulf (Fig. 6e: Mw1) where they had a larger proportion of fish in their diets.

Haplochromine densities were highest in the shallow water of the Mwanza Gulf and lowest in the deep water in Sengerema (Fig. 6c). RDA analyses showed that haplochromine densities were positively related to small Nile perch size classes between 5 and 20 cm and negatively related to large Nile perch of > 40 cm (Fig. 4b). GAM analyses showed a relationship between haplochromines and Nile perch of 10-20 cm, with increasing Nile perch densities up to 30 haplochromines per setting, after which Nile perch densities decreased with haplochromine densities (Table 3, Fig. 5). The contribution of fish in the diet was positively related to Nile perch length in the Mwanza Gulf and the Speke Gulf ($P < 0.006$, Wald test), but not in Sengerema ($P=0.93$) (Fig. 6g). The largest contribution of fish in the diet was found in Nile perch size classes of > 20 cm, except for the shallow waters in the Mwanza Gulf where Nile perch of all size classes predominantly fed on fish (Fig. 6g).

Discussion

Spatial and temporal distributions of Nile perch

Local scale

We found that local scale distributions of Nile perch differed from earlier distributions described in the literature. Highest densities of Nile perch occurred in shallow waters of < 10 m depth, while in bottom trawl surveys conducted from 1984-1990, highest densities were found in the deeper parts of the Gulf (> 12 m) (Goudswaard *et al.,* 2011). Haplochromines were absent in the Gulf by then and *Caridina* shrimp, occurring in high densities in waters of > 20 m, was the major prey of juvenile Nile perch up to 30 cm (Katunzi *et al.,* 2006).

The high densities of haplochromines in the Mwanza Gulf observed in our study confirm their recovery in the Gulf (Witte *et al.,* 2000; Witte *et al.,* 2007b; Kishe-Machumu *et al.,* 2012). Results of nightly experimental surface trawling (up to 3.5 m deep), carried out throughout all seasons in 2010-2011 in the Mwanza Gulf, confirm the high densities of haplochromines and Nile perch of < 5 cm in waters of < 7 m depth, both of which were three times higher than in deeper parts of the Gulf (I.J.M. Cornelissen, unpublished data). This suggests that the Mwanza Gulf is a well-suited habitat for small-sized fish. The now abundant haplochromines in shallow, inshore areas, as we found in the Mwanza Gulf, probably provide a good source of prey for juvenile Nile perch (Hecky *et al.*, 2010; Taabu-Munyaho *et al.*, 2013) and may increase survival and recruitment rates. The higher densities of juvenile Nile perch during the wet seasons in our study may be related to increased survival of recruits. We did not find evidence for increased spawning activity as we did not observe increased densities of mature Nile perch prior to the observed peak of juveniles. Seasonally higher densities in shallow areas can also be caused by Nile perch migrating from deeper waters during the wet seasons when the water column becomes stratified and hypoxic near the bottom (Taabu-Munyaho *et al.*, 2013). However, we only found seasonal variation in Nile perch densities of 5-10 cm and therefore we postulate that the seasonal variation is related to survival of recruits.

Regional scale

On a regional scale, Nile perch densities in the Mwanza Gulf were 10 and 40 times higher than in the Speke Gulf and Sengerema respectively. In contrast, during the Nile perch boom, from 1987-1990, Nile perch densities were homogeneous across the regions of Mwanza and Speke Gulf (Goudswaard *et al.*, 2008). More recent stock assessments through bottom trawling and catch assessments of Nile perch in the Tanzanian part of the lake from 1997-2002 showed that Nile perch aggregated on a very local and temporal scale in shallow and deep waters and at different depths of the water column (Mkumbo, 2002; Mkumbo *et al.*, 2007). However, on a large spatial scale, there was no consistent pattern in Nile perch densities between the east, west and south side of the Tanzanian part of the lake or between different depths up to 50 m (Mkumbo, 2002; Mkumbo *et al.*, 2007). In contrast, lake-wide acoustic surveys from 2007-2010 showed a seasonal spatial variation in Nile perch distributions, with higher densities in shallow waters and in the upper layers of the water column as a result of vertical and horizontal migrations related to oxygen (Taabu-Munyaho *et al.*, 2013).

The overall low Nile perch densities in Sengerema were mostly the result of very low densities of juvenile Nile perch, in contrast to the Mwanza Gulf, with relatively high densities of small Nile perch between 5-20 cm (about 2.5-9.5 months old recruits (Hughes, 1992a). Length-frequency distributions in the Tanzanian part of Lake Victoria showed that recruitment was higher in productive, sheltered, shallow bays (Mkumbo, 2002). Therefore we postulate that the productive shallow, sheltered habitats of the Mwanza Gulf may act as a nursery where larvae and juvenile Nile perch have higher survival rates than in Speke Gulf and in Sengerema.

Factors determining Nile perch distributions

Data on a regional scale was of a lower resolution than on a local scale because of lower sampling frequency in Speke Gulf and Sengerema during the study period. Yet, we found that most environmental drivers acted similarly on Nile perch densities on both scales despite spatial differences in densities (Table 3). This indicates that the resolution of the data was adequate to observe the main effects on Nile perch distribution patterns. In addition, environmental drivers acted similarly on Nile perch size classes, except on large Nile perch of > 40 cm (Table 3). On a local and regional scale, maximum depth best predicted Nile perch densities of all size classes. Depth can be considered as a habitat proxy, since it correlates strongly with other environmental variables such as oxygen content, temperature and visibility. In Lake Victoria oxygen and temperature decrease with depth, whereas visibility increases with depth (Hecky, 1994; Silsbe, 2004; Silsbe *et al.*, 2006; Cornelissen *et al.*, 2014). These and other habitat characteristics related with depth may have similar or contrasting effects on Nile perch densities and thus might explain the often non-linear nature between maximum depth and Nile perch densities. The decreasing densities of Nile perch with depth on a local scale and the increasing densities of Nile perch > 40 cm with depth on a regional scale we found in our study (Table 3), confirms the importance of shallow habitats for juvenile Nile perch (Mkumbo, 2002).

Surprisingly, on both local and regional scales, we did not find strong relationships between Nile perch densities and oxygen concentrations as was found in other studies in Lake Victoria (Wanink *et al.*, 2001; Mkumbo, 2002; Goudswaard *et al.*, 2011; Njiru *et al.*, 2012; Nyboer and Chapman, 2013; Taabu-Munyaho *et al.*, 2013). On a local scale we did not find any relationships between oxygen concentration and Nile perch density (Table 3), despite studies in the Mwanza Gulf during the 1980s that showed the importance of oxygen for explaining Nile perch distribution (Wanink *et al.*, 2001; Goudswaard *et al.*, 2011), especially in water deeper than 15 m (Wanink *et al.*, 2001). In our study in the Mwanza Gulf, low oxygen levels were seasonally related to the rainy season when stratification was strongest and spatially related to deep water. Most probably low oxygen conditions and hypoxia were less severe during our study in the Mwanza Gulf compared to the studies in the 1980s. In 1987-1988, persistent hypoxia near the bottom occurred over 3-5 months in waters as shallow as 6-20 m in the Mwanza Gulf (Wanink *et al.*, 2001), whereas during our sampling period, stratification in the Mwanza gulf was weak and probably fluctuating on a daily basis (Cornelissen *et al.*, 2014). This might also explain the apparent absence of the interaction between depth and oxygen concentration as described by Goudswaard *et al.* (2011). On a regional scale, oxygen concentration related positively with Nile perch densities of size classes between 5 and 20 cm. This positive relationship was only visible when oxygen concentrations were above 8 mg l^{-1} (Table 3). Such a threshold value seems very high as critical oxygen levels for Nile perch are much lower (i.e. are between 2.5-3 mg l^{-1}) (Kaufman and Ochumba, 1993; Wanink *et al.*, 2001). For fish of 20–40 cm, densities were even negatively related with oxygen. Most likely the relationship between small Nile perch and oxygen results from the high densities of small Nile perch in the shallow waters of the Mwanza Gulf, which happens to be more oxygenated than deeper waters.

We found that, both on a regional and local scale, densities of small Nile perch size classes between 5 and 20 cm increased with temperature with a local optimum between 24-26 ˚C. In Lake Nabugabo, a similar optimal temperature range for Nile perch > 20 cm (i.e. 25-26 ˚C) was found (Nyboer and Chapman, 2013). Except for large Nile perch > 40 cm, we found that, on a regional scale, temperature positively affected the densities of all Nile perch size classes. Temperature most likely affected densities indirectly through high recruitment and juvenile survival during the warmer, productive, wet seasons in the Mwanza Gulf. This seasonal effect of temperature on small Nile perch only, and the non-linear, positive nature of the relationship might be the reason why other studies found contrasting results with regard to the relationship between temperature and Nile perch densities (Getabu *et al.*, 2003; Goudswaard *et al.*, 2011; Nyboer and Chapman, 2013).

Visibility as measured by Secchi depth had less influence on Nile perch distributions than maximum depth on both regional and local scales. As visibility was strongly related to maximum depth, it probably did not directly relate to Nile perch densities.

Prey densities were not strongly correlated with Nile perch densities, indicating that prey densities do not drive Nile perch distributions and that Nile perch is an opportunistic predator. However, prey type and densities varied spatially and did influence Nile perch diet on a local and regional spatial scale, corroborating the opportunistic nature of Nile perch predation patterns. Nile perch of all sizes fed predominantly on haplochromines in shallow water of < 10 m in the Mwanza Gulf where haplochromine densities were high. This confirms that Nile perch is switching back to a haplochromine-based diet in these areas (Kishe-Machumu *et al.*, 2012). Larger-sized Nile perch of > 40 cm ate haplochromines regardless of their abundance. It seems that large Nile perch do not follow their prey into the Mwanza Gulf despite their preference for fish, as densities of large Nile perch were low in the Mwanza Gulf where densities of haplochromines were high. In deeper waters of the Mwanza Gulf (> 20 m), the whole of Speke Gulf and in Sengerema small Nile perch of size classes between 5 and 20 cm fed on *Caridina* shrimp. Within the Mwanza Gulf, high *Caridina* densities in deep waters were related to a high proportion of shrimp in the Nile perch diet. This indicates that small-sized Nile perch opportunistically prey heavily on shrimp when available at high densities, as suggested by Goudswaard *et al.* (2011). However, at lower shrimp densities within the Mwanza Gulf, small Nile perch accordingly ate less shrimp and more of the abundant haplochromines. Downing *et al.* (2013b) propose that growth and survival rates of Nile perch are affected by their specific diets of shrimp or haplochromines and that therefore diets may influence size distributions independent from fishery effects, thus affecting conclusions from size-based fishery assessments. However, strong, lake-wide effects on Nile perch size distributions because of specific diets are not to be expected, because of the high local variation in diets and prey densities and the opportunistic feeding habits of Nile perch. These will at most increase the variability in size at age of Nile perch cohorts.

Conclusion

We found that Nile perch distributions were heterogeneous on a local and regional scale. Maximum depth and temperature were the most important environmental drivers of Nile perch densities, acting similarly on both spatial scales. Relationships between diet and prey densities acted on smaller spatial scales and may influence growth and survival rates locally. This study emphasises the important role of habitat and season on Nile perch distribution patterns, especially of juvenile Nile perch. Changes and variation in environmental driving factors should be considered when interpreting developments in the Nile perch stock and the impact of fisheries when implementing management strategies.

Acknowledgments

This work is part of the integrated project “Exploitation or eutrophication as threats for fisheries? Disentangling social and ecological drivers of ecosystem changes in Lake Victoria (SEDEC)”, supported by the Netherlands Organisation for Scientific Research (NWO/WOTRO) grant number W01.65.304.00. We thank Koos (J.) Vijverberg for his supervision, advise and comments on this manuscript. We thank Andrea Downing for her comments. We thank Klaas Gerber, Alex Mangassa, Gerardi Rajabu, Paulo and Emma for their valuable field assistance and support and all enthusiastic M.Sc. students involved in the data collection for this manuscript. Special thanks to the Tanzanian Fisheries Research Institute (TAFIRI) in Mwanza for providing laboratory space and use of field equipment during this research.

Chapter 4

What drives ontogenetic diet shifts of Nile perch in south-east Lake Victoria?

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Abstract

We combined stomach content analyses with stable isotopes to analyse spatial and seasonal variation in ontogenetic diet shifts of Nile perch (*Lates niloticus*) and related these to their prey densities. Nile perch, *Caridina nilotica* shrimp and haplochromines were sampled in three seasons in the Mwanza Gulf in south-east Lake Victoria from 2009-2011. *Caridina* shrimp and haplochromine cichlids were the main prey of Nile perch. Despite high abundances of Dagaa (*Rastrineobola argentea*) and juvenile Nile perch in the Gulf, they contributed only little to the total diet of Nile perch. Ontogenetic diet shifts from shrimp to fish prey was a general phenomenon in the Mwanza Gulf, but the length of Nile perch at which the shift occurred varied spatially and seasonally, and was related to prey densities. Overall, the diet shift occurred at a standard length of 14.7 cm, but this varied from less than 5 cm in the most southern part of the gulf during the season of the long rainy season (with the lowest densities of *Caridina*), to more than 19 cm in the most northern part of the gulf in the season of short rainy season (with the highest *Caridina* densities). Nile perch showed a slight preference for *Caridina* shrimps above haplochromines. The recent recovery of the haplochromines in Lake Victoria could potentially lead to higher growth rates of Nile perch and with that to new balances between Nile perch and its prey.

Introduction

Many fish change their diet when increasing in size. Size-specific diet shifts are related to changes in morphology, prey availability, competition and predation risk (Werner and Gilliam, 1984; Wu and Culver, 1992; Luczkovich *et al.*, 1995; Wainwright and Richard, 1995; Kimirei *et al.*, 2013). When increasing in body size, an increase in mouth gape allows fish to ingest a larger range of prey types and sizes (Werner and Gilliam, 1984; Wainwright and Richard, 1995). In addition, prey availability may enforce or hinder ontogenetic diet shifts in predatory fish (Garcia-Berthou and Moreno-Amich, 2000; Galarowicz *et al.*, 2006). For instance, seasonal fluctuations in zooplankton can induce or delay an ontogenetic diet shift towards larger benthic invertebrates in yellow perch (*Perca flavescens*) (Wu and Culver, 1992). Ontogenetic diet shifts may also be habitat related, which is then often a trade-off between prey availability and predation risk (Werner and Gilliam, 1984). Many fish migrate to more productive habitats with a higher density of predators when they increase in size and become less vulnerable to predation (Cocheret de la Moriniére *et al.*, 2003; Nowak *et al.*, 2004; Kimirei *et al.*, 2013).

Nile perch (*Lates niloticus*, L.) is an opportunistic predator, feeding on a large variety of prey across lakes in East Africa (Hamblyn, 1966; Gee, 1969; Ogutu Ohwayo, 1990; Schofield and Chapman, 1999; Dadebo *et al.*, 2005; Katunzi *et al.*, 2006). In Lake Victoria, Nile perch of < 5 cm were reported to feed exclusively on zooplankton (Katunzi *et al.*, 2006). The diet composition of Nile perch > 5 cm is highly variable, often mirroring prey abundances and includes mainly *Caridina nilotica* (Roux), an atyid shrimp, insect larvae and fish (Mkumbo and Ligtvoet, 1992; Katunzi *et al.*, 2006; Budeba and Cowx, 2007b; Kishe-Machumu *et al.*, 2012). Nile perch also showed a strong long-term variation in diet composition (Hughes, 1986; Mkumbo and Ligtvoet, 1992; Budeba and Cowx, 2007b; Kishe-Machumu *et al.*, 2012). After its introduction, in the 1950s, Nile perch fed mainly on the dominant haplochromine cichlids (Gee, 1969), but with the decline of haplochromines in the 1980s, Nile perch mainly fed on the now abundant *Caridina* shrimp before switching to fish such as Dagaa (*Rastrineobola argentea, Pellegrin*) and juvenile Nile perch (Hughes, 1986; Hughes, 1992b; Mkumbo and Ligtvoet, 1992).

Since the 1990s, a recovery of haplochromines is observed in Lake Victoria (Witte *et al.*, 2000; Witte *et al.*, 2007a) and haplochromines are an increasingly important prey again for Nile perch, especially in shallow waters (Kishe-Machumu *et al.*, 2012; Cornelissen *et al.*, 2015). However, the scale on which haplochromines are important and how this affects its ontogenetic diet shift is unknown.

Previous studies on the ontogeny of Nile perch were mainly based on stomach analyses, giving detailed information on the diet composition at the moment the Nile perch was caught (Mkumbo and Ligtvoet, 1992; Budeba and Cowx, 2007b; Kishe-Machumu *et al.*, 2012). However, to investigate trophic interactions, stable isotopes are increasingly used, because these reflect the assimilation of prey following ingestion and, therefore, include the differences in assimilation efficiencies of the various food types ingested and integrate the dietary intake over a longer time span (Peterson and Fry, 1987). For this reason the isotope method is superior to the stomach content analysis method for estimation of a fish's trophic position. However, stomach content data give useful additional information about prey selection. In food-web studies these two methods are complementary and together give a more complete insight in food-web interactions (Peterson and Fry, 1987; Grey, 2001; Cocheret de la Moriniére *et al.*, 2003; Davis *et al.*, 2012; Dromard *et al.*, 2015).

Ontogenetic diet shifts are often detected by a changing signature of the stable isotopes of both carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). The $\delta^{13}C$ signature remains relatively stable when moving upwards in the food web and reflects the type of carbon source i.e. primary production at the base of the food web, whereas $\delta^{15}N$ values increase with each trophic level and reflect the diets of consumers in the food web.

We used stomach contents and stable isotopes to study spatial and seasonal variation in the ontogenetic diet shifts of Nile perch in the Mwanza Gulf, south-east Lake Victoria. We investigated how diet compositions and diet shifts related to densities of its two most important prey organisms, i.e. *Caridina* shrimps and haplochromines, to enable predictions about future individual growth, population density and biomass stocks of Nile perch in Lake Victoria.

Methods

Study area

Data were collected at 6 stations in three areas in the Mwanza Gulf in south-east Lake Victoria (Tanzania) (Fig.1). The Gulf is about 60 km long, 2.5-11 km wide, 3-25 m in depth. The shoreline at Mwanza City near the entrance of the Gulf is urbanized. The shoreline inside the Gulf is covered by papyrus (*Cyperus papyrus*), reeds (e.g. *Phragmites australis*) and water hyacinth (*Eichhornia crassipes*), alternating with rock formations. The bottom of the Gulf consists of soft mud.

Climate

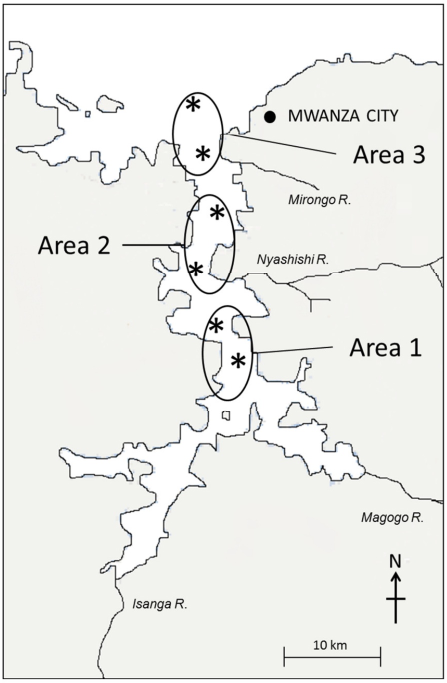

Figure 1: Locations of the six sampling stations in three areas in the Mwanza Gulf. Area 1 has a depth range of < 7 m, area 2 a depth range of 7-10 m and area 3 a depth range of 15-25 m.

Lake Victoria has a tropical climate based on the yearly monsoons. The weather is characterized by three seasons, a dry season, followed by two rainy seasons. Strong winds and low precipitation characterize the dry season, which is from June to August. The water column is well-mixed, isothermal and oxygenated during this season (Talling, 1966; Akiyama *et al.*, 1977). The short rainy season, from September to December, is characterized by increasing rainfall and temperature, warming up the surface water and gradually stratifying the water column. Rainfall increases further during the long rains from January-May, resulting in strong stratification of the water column (Talling, 1966). During the two years sampling period (2009-2011), corresponding seasons were generally similar in the Mwanza Gulf, but during the short and long rainy period from September 2009-May 2010, precipitation was twice as much as in the following year from September 2010-May 2011.

Data collection

Data were collected from September 2009-April 2011. The collection, processing and laboratory analyses of stable isotopes were performed according to (Cornelissen *et al.*, submitted – chapter 5). Stable isotope data of δ^{13}C values were corrected for lipids (Post *et al.*, 2007). For spatial and seasonal comparisons, we corrected δ^{15}N of Nile perch with a baseline for calculating trophic levels (Post, 2002; Cornelissen *et al.*, submitted – chapter 5). *Caridina* prey densities were estimated by hauling a lift net from bottom to surface according to Cornelissen *et al.* (submitted – chapter 5). Haplochromine prey densities were estimated by using gill nets according to

Cornelissen *et al.* (2015) and by surface trawling at night. Trawling was conducted with a 4 meter deep trawl net with a mesh size of 5 mm. In this way, small haplochromines of < 8 cm would be targeted, whereas gill nets were more targeted towards fish of > 8 cm. Trawling was done at station 1, 4 and 6 from 2010-2011. Trawling was done in a straight line with an average speed of 1 m s^{-1} for 20 minutes, three times at each station.

Diets of Nile perch < 5 cm were analysed by dissecting the stomachs. Stomach fullness was estimated as described in Cornelissen *et al.* (2015). Prey was categorized as: cladoceran, calanoid copepod, cyclopoid copepod, *Caridina* shrimp and insect larvae. Number of prey in stomachs was counted. To estimate the volume percentages of the different prey in stomachs, mean body size of prey, measured in the Mwanza Gulf during the study period, and known length-weight relationships of prey were used. Length-weight relationships of Hart (1980) and Leuven *et al.* (2008) were used for estimating a mean weight for *Caridina* shrimp. For zooplankton, length-weight relationships of Bottrell *et al.* (1976), Culver *et al.* (1985) and Watkins *et al.,* (2011) were used for estimating weight and volume percentages of cladocerans and copepods. Diets of Nile perch > 5 cm were analysed by dissecting the stomachs following the method of Witte and van Densen (1995). Diet compositions were used to calculate trophic levels of Nile perch (Adams *et al.*, 1983; Winemiller, 1990):

$$TL_i = 1 + \sum_{j=1}^{n} TL_j \left(f_{ij}\right)$$

where TL_i is the trophic level of Nile perch, TL_j is the trophic level of prey taxon *j*, f_{ij} is the volumetric fraction of the consumed food of Nile perch *i* consisting prey taxon *j*. Trophic levels of prey taxa were assigned according to their trophic guilds (vander Zanden *et al.,* 1997): gastropod=2, *Caridina nilotica*=2, dragon fly nymph=3, juvenile Nile perch=3, Haplochromine cichlid=3, fish of unknown taxa=3.

Data analyses

The effect of standard length on $\delta^{15}N$ and $\delta^{13}C$ stable isotope were analysed with linear regressions. The effects of areas, seasons and standard lengths on trophic levels of Nile perch were analysed by ANCOVA's, after which we separately analysed the effect of standard length on trophic levels of each area-season combination with linear regressions. When normality of residuals could not be achieved directly or after transformations, QQ-plots were assessed for outliers. All linear regressions of standard length versus $\delta^{15}N$ and isotope trophic levels showed outliers which were excluded from the dataset, except for the regression between standard length and trophic level of area 3 in short rains, which showed normally distributed residuals. Outliers were deleted from the dataset if the regression parameters were not considerably affected by the outliers. Maximum relative change in slope after deletion of outliers was 0.011 (from 0.019 to 0.30). The maximum percentage of outliers deleted from the dataset was 9% (4 outliers of 44 observations). Binomial logistic regressions were used to relate standard length of Nile perch with the occurrence of fish or *Caridina* in the diet. Parameter values were tested using Wald tests.

There are two diet shifts based on stomach analysis, the ontogenetic diet shift away from feeding on *Caridina* and the diet shift towards feeding on fish. We used the standard length at a probability of occurrence of 0.5 of both diet shifts as the lengths at which Nile perch ontogenetically shifts from *Caridina* to 'other prey' or towards fish.

Relationships between haplochromine densities (gill nets and trawls) and ontogenetic shift lengths from *Caridina* to 'other prey' were tested by linear regressions. The relationship between *Caridina* densities and ontogenetic shift lengths to fish were tested by a piecewise linear regression, which fit a 1-degree-spline with a knot point.

The piece-wise regression was analysed in R version 3.1.0 (R Core Team, 2014) using the SiZer package. Other calculations and statistical analyses were carried out in SAS 9.2 (SAS Institute, Cary, USA).

Table 1: Number of observations of stable isotopes values of Nile perch and prey organisms in the Mwanza Gulf. A total of 516 Nile perch and 290 prey organisms were sampled.

	Dry season			Short rains			Long rains		
	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
Lates niloticus	**77**	**92**	**31**	**73**	**61**	**43**	**51**	**50**	**38**
< 5 cm	–	–	–	–	–	–	7	–	–
5-10 cm	14	20	5	11	22	11	13	11	12
10-20 cm	23	28	7	19	15	8	9	10	6
20-40 cm	38	37	14	30	21	17	22	22	18
> 40 cm	2	7	5	13	3	7	–	7	2
Gastropod	4	2	1	–	5	5	10	7	8
Zooplankton	1	1	1	3	2	3	3	1	2
Caridina nilotica	6	6	5	–	–	2	4	4	5
Anisoptera nymph	3	3	–	–	–	–	–	–	1
Haplochromine 'detritivore' cichlid	12	13	2	–	–	3	12	23	28
Haplochromine 'zooplanktivore' cichlid	5	3	2	17	17	26	–	–	–
Haplochromine 'unidentified' cichlid	–	–	–	8	11	5	4	2	4
Haplochromine 'piscivore' cichlid	1	–	–	–	–	–	–	5	–
Rastrineobola argentea	–	–	–	–	–	–	5	10	5

Results

Ontogenetic diet shift of Nile perch

A total of 516 Nile perch were analysed for stable isotopes (Table 1). The smallest length class of Nile perch (< 5 cm) showed the most distinct isotopic signature with a low mean $\delta^{15}N$ value of 6 and an enriched mean $\delta^{13}C$ value of −13 (Fig. 2). Nile perch size classes of 5-10, 10-20, 20-40 and > 40 cm showed much higher $\delta^{15}N$ values, increasing with size from 8 to 9.3, all with similar mean $\delta^{13}C$ values of −17. A total of 98 invertebrate prey items were analysed for stable isotopes, including gastropods, zooplankton, *Caridina* shrimp and Anisoptera nymphs (Table 1). Mean $\delta^{15}N$ values of invertebrate prey ranged from 5-6.5 (Fig. 2). Invertebrates showed a large variation in $\delta^{13}C$ values, ranging from −15 to −19. A total of 197 haplochromine cichlid prey were sampled for stable isotopes, including three trophic groups which previously were identified by Witte and van Oijen (1990) as zooplanktivore, detritivore and piscivore species (Table 1). The unidentified haplochromines were, in retrospect, mainly zooplanktivores and detritivores. Mean $\delta^{15}N$ values of haplochromine groups were similar and ranged between 8-8.7 (Fig. 2). Mean $\delta^{13}C$ values ranged from −14.4 and −17.3, with piscivore haplochromines relatively enriched in $\delta^{13}C$ (−14.4) compared to the other groups (−16.2 to −17.3) (Fig. 2). A total of 20 samples were analysed for stable isotopes of Dagaa prey (Table 1). Dagaa showed a high mean $\delta^{15}N$ value of 9.3 and an enriched $\delta^{13}C$ value of −15 (Fig.2).

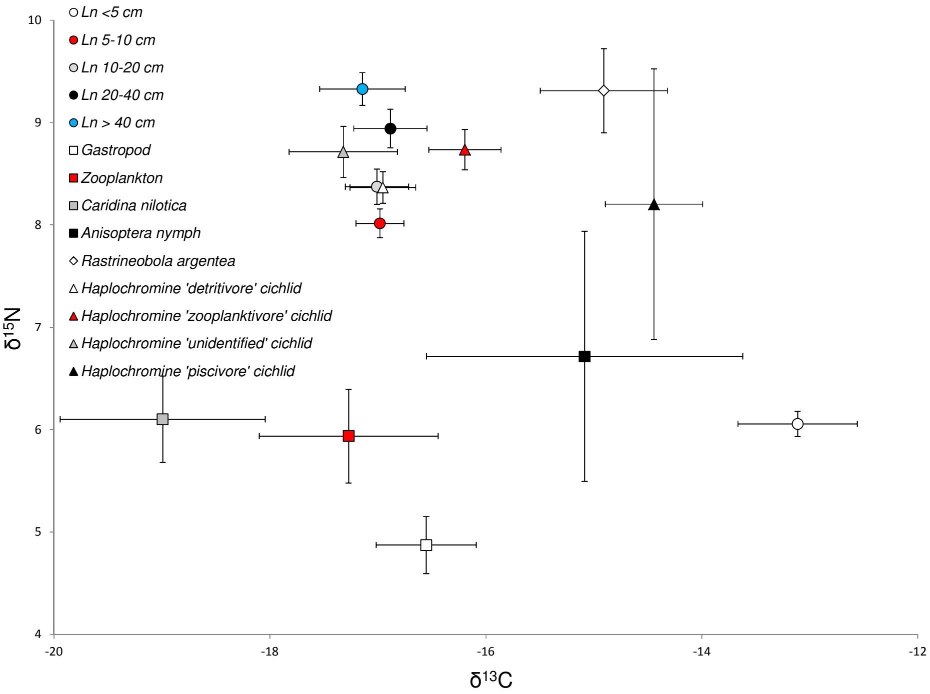

Figure 2: Mean $\delta^{13}C$ and $\delta^{15}N$ isotope values with standard errors of Nile perch and prey taxa in the Mwanza Gulf.

A total of 6697 stomachs of Nile perch were analysed for diet composition (Table 2). In 58% of the stomachs prey remains were found. The diet composition (%, volume) varied for the different size classes of Nile perch (Fig. 3). *Caridina* shrimp and insect larvae were the most dominant prey in Nile perch < 5 cm. *Caridina* shrimp were the most dominant prey in Nile perch size classes of 5-10 cm and 10-20 cm. Fish were the most dominant prey in Nile perch size classes of 20-40 cm and > 40 cm. Of the fish prey, haplochromine cichlids showed the highest contribution to Nile perch diet (8-68%), whereas juvenile Nile perch and Dagaa contributed less to the diet (< 13%). Dragonflies and gastropods contributed little to the diet of Nile perch size classes of > 5 cm (< 5.5%).

Table 2: Number of stomachs analysed for diet composition of Nile perch in the Mwanza Gulf. A total of 6697 stomachs were analysed.

	Dry season			Short rains			Long rains		
	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
Lates niloticus									
< 5 cm	91	49	15	–	–	–	–	–	–
5-10 cm	21	57	19	193	240	559	173	424	507
10-20 cm	95	108	13	346	285	1159	362	476	574
20-40 cm	78	88	20	113	94	144	116	122	105
> 40 cm	2	7	5	17	2	8	–	7	3
Total stomachs	**287**	**309**	**72**	**669**	**621**	**1870**	**651**	**1029**	**1189**
Full stomachs (%)	61.3	57.0	52.8	67.6	65.1	60.5	55.6	56.9	48.9

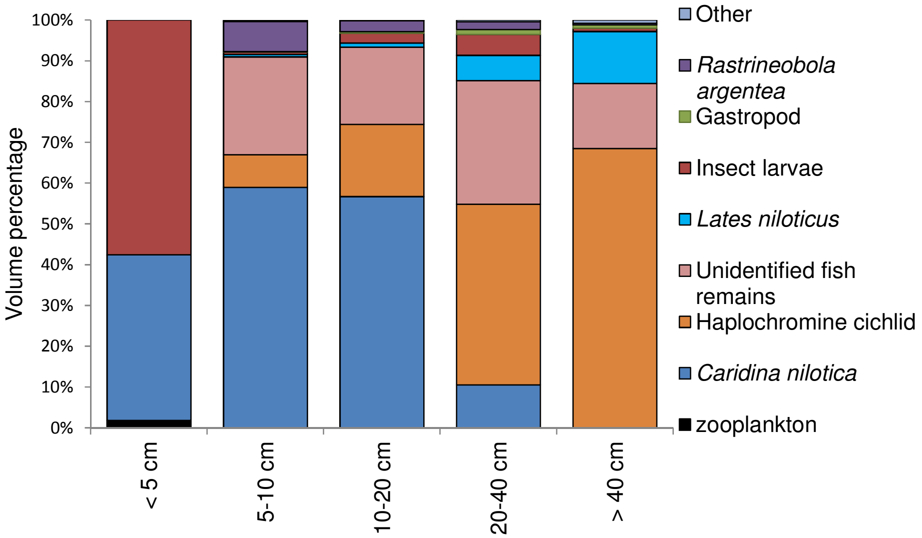

Figure 3: Mean diet composition (%, volume) of four size classes of Nile perch in the Mwanza Gulf. Insect larvae of Nile perch size classes > 5 cm were all classified as dragonfly nymphs

$\delta^{15}N$ increased significantly with length of Nile perch in the Mwanza Gulf, indicating an ontogenetic diet shift (Fig. 4a). $\delta^{13}C$ values did not relate to Nile perch length (Fig. 4b). Stomach content analysis showed that the diet contribution of fish increased with Nile perch standard length, whereas the diet contribution of *Caridina* shrimp decreased with Nile perch standard length in the Mwanza Gulf (Fig. 5). Overall, the ontogenetic diet shift of Nile perch to feeding on fish occurred at a standard length of 14.7 cm, while the shift away from feeding on *Caridina* occurred at a slightly larger standard length of 16.7 cm (Fig. 5).

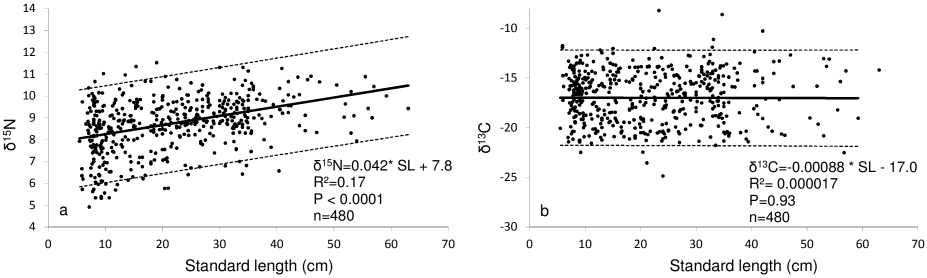

Figure 4: Linear regression between standard length of Nile perch and a) $\delta^{15}N$ isotope values and b) $\delta^{13}C$ isotope values of Nile perch in the Mwanza Gulf.

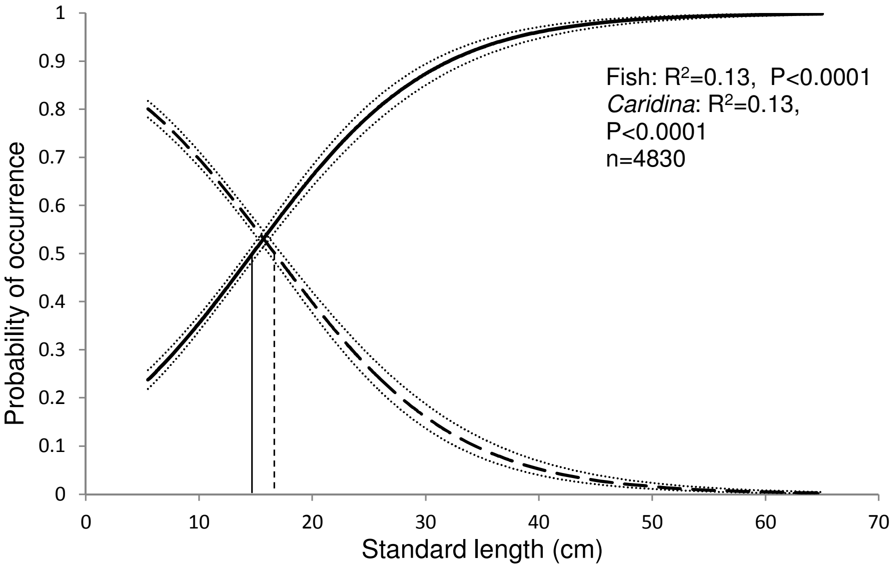

Figure 5: Relationship between standard length and probability of occurrence of fish (solid line) or *Caridina* shrimp (broken line) in diet of Nile perch in the Mwanza Gulf. Ontogenetic diet shift towards fish occurred at a Nile perch length of 14.7 cm (95% CI=14.2-15.2) and from *Caridina* to 'other prey' at 16.7 cm (95% CI=16.1-17.3).

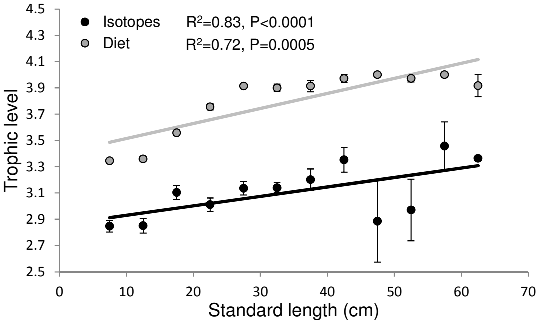

Figure 6: Mean and standard errors of trophic levels of 5 cm standard length intervals of Nile perch, estimated by $\delta^{15}N$ isotopes and stomach content analysis.

Both estimated '$\delta^{15}N$ isotope based trophic levels' and 'stomach content based trophic levels' increased similarly with Nile perch standard length, but differed significantly in intercepts (t=44.71, P < 0.0001) (Fig. 6). '$\delta^{15}N$ isotope based trophic levels' were c.a. 0.5 level lower than 'stomach content based trophic levels' (Fig. 6).

Spatial and seasonal variation in diet shifts of Nile perch

Areas and seasons had an effect on $\delta^{13}C$, but $\delta^{13}C$ was not related to Nile perch length (Table 3). Areas and seasons had a significant effect on the ontogenetic shifts in trophic levels based on both $\delta^{15}N$ isotopes and stomach contents (Table 3). Most effects of '$\delta^{15}N$ isotope based trophic levels' interacted except for the interaction between standard length and areas. In 'stomach content based trophic levels', only the effect of standard length and areas were interacting (Table 3).

Table 3: Effect of area, season and standard length on $\delta^{13}C$ and trophic levels of Nile perch. Trophic levels were estimated in two ways: based on $\delta^{15}N$ isotope values and on stomach contents.

		Isotopes				Stomach content	
		$\delta^{13}C$		Trophic level		Trophic level	
	df	F	P	F	P	F	P
Model	7	29.24	**<0.0001**	22.17	**<0.0001**	29.87	**<0.0001**
Area	2	69.64	**<0.0001**	13.34	**<0.0001**	14.16	**<0.0001**
Season	2	18.24	**<0.0001**	40.29	**<0.0001**	5.3	**0.007**
Area*season	4	15.15	**<0.0001**	5.23	**0.0004**	–	n.s.
SL	1	–	n.s.	115.99	**<0.0001**	171.17	**<0.0001**
SL*area	2	–	n.s.	–	n.s	7.52	**0.001**
SL*season	2	–	n.s.	18.24	**<0.0001**	–	n.s.
SL*area*season	4	–	n.s.	4.97	**<0.0001**	–	n.s.

Table 4: Linear regressions between standard length and the trophic level of Nile perch. Trophic levels were estimated for all area-season combinations in two ways: based on $\delta^{15}N$ isotope values, and on stomach contents.

		Dry season			Short rains			Long rains		
		Intercept	Slope	P	Intercept	Slope	P	Intercept	Slope	P
$\delta^{15}N$ trophic level	Area 1	3.14	0.0005	0.87	3.09	0.006	**<0.0001**	2.49	0.022	**<0.0001**
	Area 2	3.21	0.003	0.28	2.53	0.025	**<0.0001**	2.44	0.019	**<0.0001**
	Area 3	2.78	0.008	0.14	2.62	0.001	0.22	2.1	0.030	**<0.0001**
Stomach content trophic level	Area 1	3.62	0.009	**0.004**	3.49	0.009	**0.0006**	3.73	0.008	**0.02**
	Area 2	3.42	0.014	**0.004**	3.22	0.018	**0.01**	3.46	0.012	**0.001**
	Area 3	3.14	0.020	**0.010**	3.11	0.018	**0.0002**	3.32	0.014	**0.0003**

As most effects on trophic levels interacted, separate linear regressions between standard length and trophic levels of area-season combinations were used to investigate spatial and seasonal variation in trophic levels with size. '$\delta^{15}N$ isotope based trophic levels' were not related to Nile perch length in dry season and area 3 in short rains, whereas in other area-season combinations, '$\delta^{15}N$ isotope based trophic levels' increased with Nile perch length (Table 4). 'Stomach content based trophic levels' increased with Nile perch length in all areas and seasons (Table 4).

Ontogenetic diet shifts, expressed as the length at which Nile perch switched towards feeding on fish or away from feeding on *Caridina* were found in all area-season combinations except in area 1 in the long rains, where the diet shift apparently occurred at smaller Nile perch length than we sampled (Fig. 7a,b). In the dry season, lengths of diet shifts did not vary between areas (Fig.7a, b), while in the short rains, Nile perch shifted at smaller lengths in area 1 than in area 2 and 3 (Fig. 7a, b). In the long rains the pattern was similar, although the shifts occurred at even smaller lengths than in the short rains, even at lengths of < 5 cm in area 1. Nile perch shifted to fish almost always at a similar or larger length than when shifting from *Caridina* to 'other prey' (Fig. 8). This indicates that when Nile perch shifted to fish, they still fed on *Caridina*.

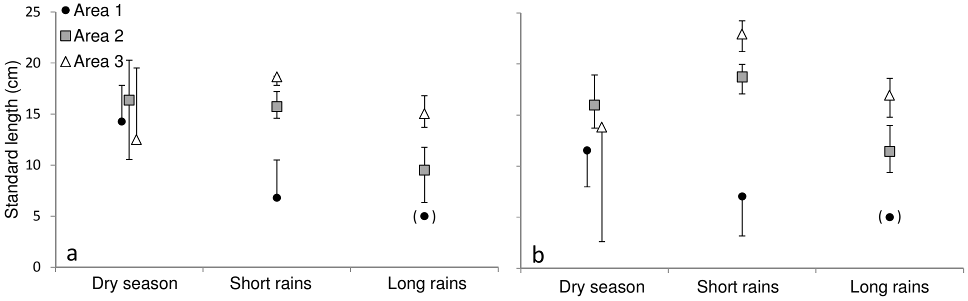

Figure 7: Spatial and seasonal variation in the length at which Nile perch ontogenetically shift its diet a) towards fish and b) from *Caridina* shrimp to 'other prey'. Error bars represent 95% confidence intervals. Ontogenetic length in area 1 in long rains was smaller than the length of Nile perch we recorded for stomach content analyses (< 5 cm) and is therefore displayed within brackets. Missing error bars indicates that confidence interval-lengths were not within the range of lengths measured for Nile perch in the Mwanza Gulf.

When relating the lengths at which Nile perch shifted away from *Caridina* with the densities of haplochromines, it was found that there was no relation with the haplochromine densities sampled by gill nets (Fig. 9a), but there was a significant decrease in shift length with increasing haplochromine densities based on surface trawling (Fig. 9b). In addition, Nile perch shifted towards fish at similar lengths (ca. 15 cm) for most of the range of *Caridina* densities, but at low densities (< 0.18 individuals L^{-1}) there was a steep decrease of shift length with decreasing *Caridina* densities (Fig. 9c).

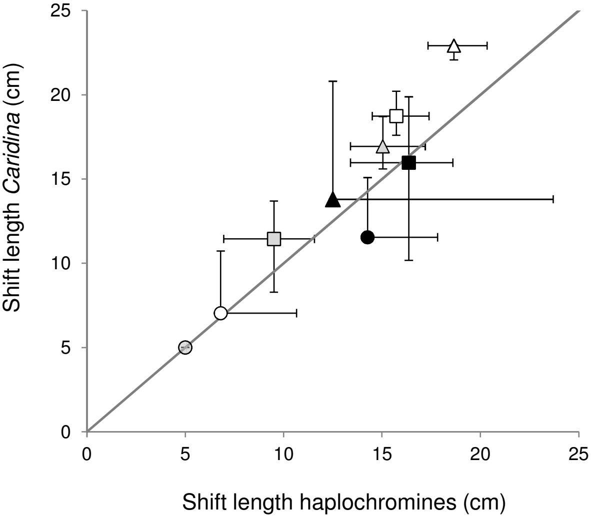

Figure 8: Ontogenetic diet shifts of Nile perch: length shifts towards fish related to length shifts from *Caridina* to 'other prey'. Error bars represent 95% confidence intervals. Missing error bars indicates that confidence interval-lengths were not within the range of lengths measured for Nile perch in the Mwanza Gulf. Areas are indicated by shapes: Area 1=circle, area 2=square and area 3=triangle. Seasons are indicated by shades: dry season=filled black, short rains=open and long rains=filled grey.

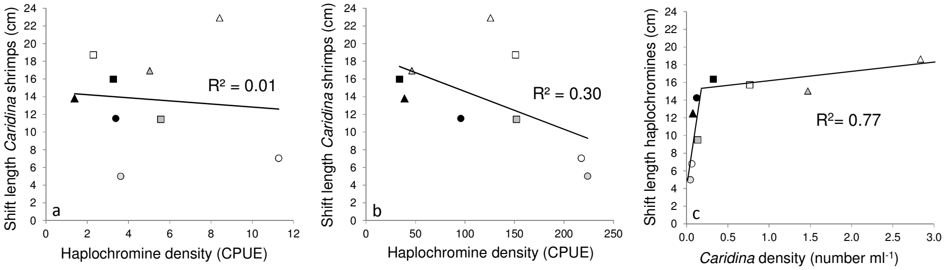

Figure 9: Nile perch diet shifts: relations between the lengths of diet shift from *Caridina* to 'other prey' and haplochromine densities sampled by a) gill nets and b) by surface trawling, and c) between the lengths of diet shift towards fish in diet and *Caridina* densities. Shapes and shades indicate areas and seasons as in Fig. 8.

Discussion

Trophic levels based on $\delta^{15}N$ stable isotopes were consistently 0.5 lower than trophic levels based on stomach content analysis, although both increased similarly with Nile perch length. There may be several reasons for this. One reason might be that the generally assumed increase of 3.4 ‰ $\delta^{15}N$ per trophic level, used for calculating the '$\delta^{15}N$ isotope based trophic levels' does not apply between Nile perch and its prey. The difference between Nile perch of > 5 cm and *Caridina* was 1.9 - 3.2 ‰ $\delta^{15}N$ and Nile perch showed similar $\delta^{15}N$ values as its haplochromine prey in this study. The 3.4‰ increase in $\delta^{15}N$ per trophic level is widely used on a food web level when averaged over multiple trophic pathways with many species (Post, 2002). However, the increase in $\delta^{15}N$ can vary greatly in single trophic transfers or between few feeding links (2-5‰ in (Post, 2002), −0.5-9.2‰ in DeNiro and Epstein (1981), and −0.5-3.3‰ in McCutchan Jr *et al.* (2003). Even species raised on different diets can have similar $\delta^{15}N$ enrichments and species raised on similar diets can have large differences in $\delta^{15}N$ enrichment (DeNiro and Epstein, 1981). Variations may partly be explained by differences in assimilation of $\delta^{15}N$ between types of prey. However, a diet on invertebrate prey results in less enrichment in $\delta^{15}N$ than other high-protein prey such as fish (McCutchan Jr *et al.*, 2003). Therefore, it is unlikely that this is the reason of the small enrichment in $\delta^{15}N$ between Nile perch and *Caridina* and the similar $\delta^{15}N$ values between Nile perch and haplochromines.

Most likely the discrepancy between isotopes and stomach contents may be explained by the difference in timespan covered by stomach contents versus stable isotope values (Wainright *et al.*, 1993; Vander Zanden *et al.*, 1997). The stomach content method gives a snapshot in time, whereas the isotope method gives an integrative value over a longer time period. A Nile perch might have spent considerable time outside the gulf, feeding on low trophic C*aridina* shrimp, and feed on higher trophic fish when it enters the gulf. This leads to a high fish contribution in stomach contents and therefore high 'stomach content based trophic levels' and low '$\delta^{15}N$ isotope based trophic levels'. Stable isotope analyses might therefore represent a larger area of Lake Victoria compared to the stomach analyses. Recent stomach analyses corroborates that Nile perch from open waters across the Tanzanian part of Lake Victoria feed mainly on *Caridina*, showing a diet shift towards haplochromines at a much larger total length > 50 cm (Ngupula and Mlaponi, 2010) than in the Mwanza Gulf (shift at total length of 17 cm).

The length of the diet shift of Nile perch towards fish was less strongly related to the haplochromine densities estimated by gillnets, than to the densities estimated by trawling. This is caused by the difference in selectivity between the two catching methods. Gill nets were highly selective towards the larger-sized detritivore haplochromines (mean length of 8 cm) (see Table 2, Cornelissen *et al.* (submitted – chapter 5). Surface trawling was more selective towards smaller sized haplochromines (mean length of 5 cm). As Nile perch of < 40 cm mainly feed on small sized fish prey of < 8 cm (Hamblyn, 1966), trawling catches probably give a better estimate of relative prey densities of haplochromines than gillnet catches. It is therefore not surprising that the trawling catches resulted in a stronger relationship between fish diet and haplochromine densities.

Stable isotope values of $\delta^{15}N$ and $\delta^{13}C$ of Nile perch length classes of > 5 cm were in the same range as in other studies from Lake Victoria and Lake Albert (Campbell *et al.,* 2003; Campbell *et al.*, 2005). The small difference between $\delta^{15}N$ values of Nile perch and *Caridina* and the similar $\delta^{15}N$ values between Nile perch and haplochromines suggest a heavy reliance on *Caridina.* The low $\delta^{15}N$ of Nile perch < 5 cm in our study agrees with a diet of mainly herbivorous and omnivorous zooplankton found in stomach contents (Katunzi *et al.*, 2006). However, our stomach contents showed a diet of mainly insect larvae and *Caridina,* which would give higher $\delta^{15}N$ signatures. As isotopes and stomach contents were sampled in different seasons (isotopes in long rains and stomachs in dry season), this discrepancy might be explained by a seasonal variation in feeding on zooplankton, *Caridina* shrimp and insect larvae. The enriched $\delta^{13}C$ values of Nile perch < 5 cm were within the range of taxa of food organisms sampled in that area and season (Cornelissen *et al.*, submitted – chapter 5).

$\delta^{15}N$ values increased with Nile perch length, suggesting an ontogenetic diet shift. This was corroborated by stomach content analyses, which showed an ontogenetic diet shift from a *Caridina* diet towards a fish diet with increasing Nile perch length. $\delta^{15}N$ values increased less steeply with Nile perch length than observed in northern Lake Victoria, but more steeply than in Lake Albert (Slopes: Our study=0.04, Napoleon Gulf=0.06, Winam Gulf=0.05, Lake Albert=0.02) (Campbell *et al.*, 2005). The differences in rate of change in $\delta^{15}N$ with other waters indicate that ontogenetic diet shifts of Nile perch are variable. $\delta^{13}C$ values did not change with Nile perch length in our study and were mid-ranged within the food web, corresponding with Nile perch in Lake Albert (Campbell *et al.*, 2005). This indicates that Nile perch is largely omnivorous throughout its juvenile life until reaching a size of at least 60 cm. $\delta^{13}C$ values significantly increased with length in the northern gulfs of Lake Victoria (Campbell *et al.,* 2003, 2005), which might be explained by the increase of littoral-based tilapia in their diet with size (Campbell *et al.*, 2003). The intercepts of the relations between $\delta^{15}N$ and $\delta^{13}C$ and Nile perch length differed from those in northern Lake Victoria and Lake Albert, suggesting that the food chain of Nile perch between the Mwanza Gulf, the northern Gulfs and Lake Albert is fuelled by different primary production sources at the base of the food web.

Caridina shrimp and haplochromines were the main prey of Nile perch based on stomach content analyses, corresponding with a recent study on Nile perch diet in the Mwanza Gulf (Kishe-Machumu *et al.*, 2012). Furthermore, the occurrence of Dagaa in diet and cannibalism was low (Kishe-Machumu *et al.*, 2012). This contrasts with diet studies from the 1980s in the Mwanza Gulf during the Nile perch boom, when cannibalism was high and Dagaa a common diet item in Nile perch stomachs (Katunzi *et al.*, 2006). The importance of *Caridina* shrimp in the diet decreased with Nile perch length, whereas the importance of fish in the diet increased with length. However, the ontogenetic diet shift of Nile perch towards a fish diet occurred at smaller lengths than observed in 2006 and 2008 in the Mwanza Gulf. The overall diet shift now occurred at 14.7 cm standard length, which equals 17.2 cm total length (I.J.M. Cornelissen, unpublished data), versus 20 cm total length in the earlier study (Kishe-Machumu *et al.*, 2012). Moreover, the shift occurred in specimens as small as 5 cm (and probably even smaller) in some parts of the Gulf, indicating the large flexibility in the feeding behaviour of Nile perch.

There was a clear spatial and seasonal differentiation in ontogenetic diet shifts in the Mwanza Gulf. In the dry season, neither the isotope-based trophic levels increased with Nile perch length, nor was there significant spatial differentiation in the length at which diet shifts occurred. In the short and long rains however, isotope-based trophic levels significantly increased with length and there was a clear spatial differentiation in the lengths at which diet shifts occurred. Apparently, in the dry season, Nile perch was more flexible in its diet than during the rains. These seasonal and spatial trends are in line with what was found on a food-web level in the Mwanza Gulf and tropical estuaries where the trophic structure was strongly influenced by the rainy seasons (Abrantes *et al.*, 2014; Cornelissen *et al.*, submitted – chapter 5).

The seasonal and spatial trends in diets and shifts of Nile perch were strongly related to the densities of haplochromine and *Caridina* prey. At very low *Caridina* densities, Nile perch switched to fish at a very small size, while at higher *Caridina* densities Nile perch fed on *Caridina* up to a size of ca. 15 cm before switching to fish. When switched to fish, Nile perch mostly kept feeding on *Caridina* when present. Small Nile perch preferred *Caridina* even at low densities, only feeding on fish when *Caridina* densities became very low. This is in contrast to other studies on Nile perch diets, which suggest a preference towards haplochromines (Mkumbo and Ligtvoet, 1992; Chapman *et al.*, 2003; Kishe-Machumu *et al.*, 2012). We agree that Nile perch prefer haplochromines above juvenile Nile perch and Dagaa as fish prey, as contribution of these prey items to Nile perch diet were low in this study, despite high abundances of Dagaa and juvenile Nile perch in the Gulf (Cornelissen *et al.*, 2015, IJM Cornelissen, unpublished data).

Since diet shifts of Nile perch affect its individual growth and survival rates, it will therefore also influence its population dynamics (Werner and Gilliam, 1984; Downing *et al.*, 2013b). Downing *et al.* (2013b) report that Nile perch grows faster on a fish-dominated diet and suggest that a delay in ontogenetic diet shift towards fish increases the vulnerability of Nile perch to fishing pressure. Furthermore, a haplochromine-based diet reduces cannibalism, which may positively affect recruitment and therefore Nile perch stock (Kishe-Machumu *et al.*, 2012). However, a further recovery of haplochromines may also negatively affect Nile perch recruitment by haplochromines feeding on Nile perch eggs and competing for food with juvenile Nile perch. This may lead to a stable state of the food web with haplochromines and Nile perch co-existing at a new balance (van de Wolfshaar *et al.*, 2014).

Acknowledgments

This work is part of the integrated project "Exploitation or eutrophication as threats for fisheries? Disentangling social and ecological drivers of ecosystem changes in Lake Victoria (SEDEC)", supported by the Netherlands Organisation for Scientific Research (NWO/WOTRO) grant number W01.65.304.00. Thanks to Hans Hoogveld, Nico Helmsing and the Netherlands Institute of Ecology (NIOO) for the analyses of stable isotopes. Special thanks to Klaas Gerber, Alex Mangassa, Gerardi Rajabu, Paulo and Emma for their valuable field assistance and support, and to the Tanzanian Fisheries Research Institute (TAFIRI) in Mwanza for providing laboratory space and use of field equipment during this research.

Chapter 5

Seasonal and spatial food-web shifts in the Mwanza Gulf, Lake Victoria: a quantitative stable isotope study

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Abstract

Stable isotope analyses and derived community metrics were used to quantitatively analyse spatial and seasonal variation in the food-web structure of the Mwanza Gulf, Lake Victoria. Primary producers, invertebrates and fish were sampled in three seasons and three areas from 2009-2011. $\delta^{15}N$ and $\delta^{13}C$ signatures of fish taxa, including Nile perch, indicated omnivorous diets with a heavy reliance on invertebrates. This in contrast with the large diversity of specialized feeders, observed in the lake before the Nile perch upsurge in the 1980s. Carbon sources varied seasonally and spatially, affecting the whole food web up to the highest trophic levels. With the onset of rains, carbon sources became spatially differentiated, indicating a strong littoral/benthic influence in shallow waters, and pelagic influence in open waters. Trophic levels were more strongly related to space than to seasonal dynamics. The food-web structure and interactions varied on small spatial and seasonal scales. Isotopic spatiality and seasonality in food-web structure was previously reported for (sub)tropical estuaries, rivers and coastal lagoons, but not for tropical freshwater systems such as Lake Victoria.

Introduction

The food web of Lake Victoria underwent major ecological changes, including eutrophication (Hecky, 1993; Hecky, 1994) and changes in the fish community. The decline of the endemic haplochromines (Witte *et al.*, 1992b) and the following upsurge of the introduced Nile perch *(Lates niloticus,* L.) in the lake in the 1980s changed the food web from a complex multispecies system, to a food web with a few dominating species. During the explosive population growth of Nile perch, there was also an increase in population numbers of the atyid shrimp *Caridina nilotica* (Roux), the small cyprinid fish Dagaa (*Rastrineobola argentea*, Pellegrin), and the exotic Nile tilapia *(Oreochromis niloticus,* L.) (Ogutu-Ohwayo, 1990; Witte *et al.*, 1992a; Goldschmidt *et al.*, 1993; Goudswaard *et al.*, 2006). From the 1980s onwards, the Lake's fishery thrived, dominated by Nile perch as economically most important fish, and Dagaa and tilapia as second and third most important target species (Wanink, 1999; Cowx *et al.*, 2003; Njiru *et al.*, 2005).

The former complex food web with specialists occupying every niche in the lake (Witte and van Oijen, 1990; van Alphen *et al.*, 2003) has been replaced by a simpler food web, dominated by omnivorous feeders (Ojwang *et al.*, 2010), opportunistically switching between available food sources. Traditional diet analyses showed that during the Nile perch boom, Nile perch preyed heavily on the endemic haplochromines and, when haplochromines declined, they switched their diet to the increasingly abundant *Caridina* shrimp, their own juveniles and Dagaa (Hughes, 1986; Mkumbo and Ligtvoet, 1992; Katunzi *et al.*, 2006). Since the 1990s, a recovery of some pelagic haplochromine species was observed in the Mwanza Gulf in the south of Lake Victoria (Witte *et al.*, 2000; Witte *et al.*, 2007a; Kishe-Machumu *et al.*, 2012) and Nile perch is observed to switch to haplochromines again (Kishe-Machumu *et al.*, 2012; Cornelissen *et al.*, 2015). Other abundant species of Lake Victoria also changed their diets. The recovered haplochromines, tilapia, Dagaa and *Brycinus sadleri* (Boulenger), formerly specialist feeders in phytoplankton, detritus and zooplankton are now including larger invertebrate prey and even fish in their diet (Wanink, 1998; Wanink and Witte, 2000; Katunzi *et al.*, 2003; Wanink and Joordens, 2007; Kishe-Machumu *et al.*, 2008).

On a lake-wide scale, the increasing eutrophication facilitated the explosive population growth of Nile perch and increased fish production in Lake Victoria (Kolding *et al.*, 2008). However, even though the food web simplified and Nile perch boomed, the Lake still displayed great spatial heterogeneity in limnology and fish distributions (Getabu *et al.*, 2003; Silsbe, 2004; Taabu-Munyaho *et al.*, 2013). In the

Mwanza Gulf, water quality and other abiotic factors varied on a spatial and seasonal scale (Cornelissen *et al.*, 2014). Nile perch distributions were primarily driven by these abiotic factors and not by the availability of particular prey species (Goudswaard *et al.*, 2011; Cornelissen *et al.*, 2015). Since Nile perch opportunistically feeds on prey which is available in its abiotic-driven, distribution range, also their diets vary spatially and temporally (Cornelissen *et al.*, 2015). This indicates that the spatial and temporal variability in water quality and other abiotic factors at the base of the food web likely also affect the food-web interactions at higher trophic levels in Lake Victoria. In this study we aim at systematically and quantitatively investigating this spatial and temporal variability in food-web interactions and food-web structure using stable isotopes.

Most studies in Lake Victoria focused on stock assessments and diet studies of a few commercial species, giving limited and 'snapshot' information on the organization of the food web and trophic interactions. Combined carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes provide information on food sources, trophic interactions and food-web structure of entire communities, covering a longer integrated timespan (Peterson and Fry, 1987; Hesslein *et al.*, 1993). However, only few isotopic studies on the food-web structure of Lake Victoria, using stable isotopes, have been conducted and studies were limited to two Gulfs in the northern part of Lake Victoria (Branstrator *et al.*, 2003; Campbell *et al.*, 2003; Ojwang *et al.*, 2010). Carbon stable isotope values stay relatively constant between consumers throughout the food web (Post, 2002; McCutchan Jr *et al.*, 2003), but vary between sources of primary productivity at the base of the food web (France, 1995). Primary producers from the pelagic zone show more negative values and primary producers from the benthic/littoral zone showing more positive values (France, 1995; Hecky and Hesslein, 1995). Carbon stable isotopes are therefore useful for identifying primary sources in a food web. Nitrogen stable isotopes increase each trophic level up the food web and give information on consumer's diets and their relative trophic position (Peterson and Fry, 1987; Post, 2002).

In addition to identifying the trophic signature of individual organisms and species, community-wide metrics can be used to quantify trophic structure on a food-web level of entire communities in a number of diagnostic metrics (Layman *et al.*, 2007). This is especially useful for comparing food webs across space and time (Jackson *et al.*, 2011; Jackson *et al.*, 2012). The metrics reflect two aspects of a community in $\delta^{13}C$ - $\delta^{15}N$ space: the extent of spacing of the entire community or population in $\delta^{13}C$ - $\delta^{15}N$ space and the dispersion of individuals in $\delta^{13}C$ - $\delta^{15}N$. The first indicates niche space and trophic diversity. The second gives information about trophic redundancy. The quantitative use of community metrics have so far been used to compare different communities between ecosystems or to study the effect of invasive species on a food web (Jackson *et al.*, 2012; Abrantes *et al.*, 2014), but we use it here for the first time to detect small-scale shifts within a food-web structure. The metrics allow us to draw conclusions about food-web functioning in the Mwanza Gulf in southern Lake Victoria, which is already shown to be highly variable in water quality, primary production and fish densities in time and space (Cornelissen *et al.*, 2014, 2015).

Methods

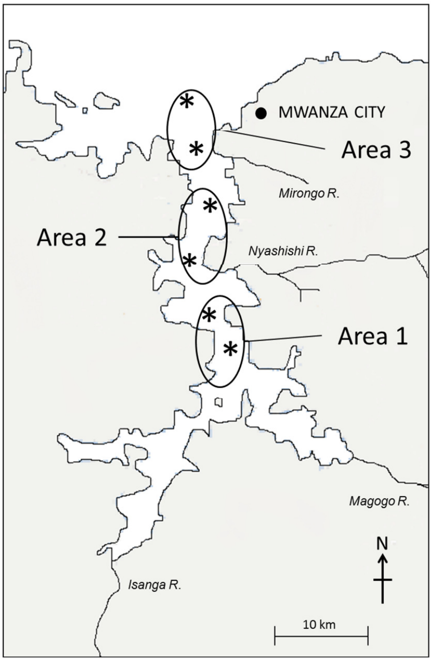

Figure 1: Map of the Mwanza Gulf with six sampling stations (asterisks). Stations were divided in three areas: 1) shallow=depth range of <7 m, 2) intermediate=depth range of 7–10 m and 3) deep=depth range of 15–25 m.

Study area

Data for isotopes were collected at 6 sampling stations in three areas in the Mwanza Gulf (Fig. 1). The Mwanza Gulf is located in southern Lake Victoria in Tanzania and is about 60 km long, 2.5-11 km wide, 3-25 m in depth, and covers a surface area of approximately 500 km^2 (Witte and van Densen, 1995). The south of the Gulf at station 1 is shallow and narrow with a depth of < 7 m and circa 3 km wide, whereas station 6 is located in the open lake outside the Gulf with a depth of 25 m (Fig. 1). Mwanza City is located in the north near the entrance of the Gulf (Fig. 1). The shoreline there is completely urbanized, while inside the Gulf it is characterized by a mixed vegetation of papyrus (*Cyperus papyrus*), reeds (e.g. *Phragmites australis*), and water hyacinth (*Eichhornia crassipes*) and by rock formations. The bottom of the Mwanza Gulf consists of soft, fine-grained mud.

Climate

The climate in Lake Victoria is characterized by three seasons, based on the yearly monsoon cycles. In the dry season, from June to August, strong southerly winds and low precipitation keep the water well-mixed, isothermal and oxygenated (Talling, 1966; Akiyama *et al.*, 1977). In the short rainy season, from September to December, winds decline and rainfall increases, warming up the surface layer of the water column, which becomes gradually stratified. In the long rainy season, from January-May, precipitation is high and stratification of the water column becomes strong (Talling, 1966). During the sampling period from 2009-2011, the Mwanza Gulf had similar seasons, although in the long rains of 2010, there was twice as much rainfall as in the long rains of 2011.

Data collection

Biological samples were collected from September 2009-April 2011. Fish were caught using gill nets and surface trawling at night. Fish were classified to species level, except for haplochromines, which were classified as one group from 2009-2010 and classified into trophic guilds in 2010-2011. Invertebrates and algae were collected during the day. *Caridina* shrimp and gastropods were collected by hauling a 1 m^2 square lift net from bottom to surface. Zooplankton was collected by hauling a 150 µm net from bottom to surface and preserved in a 50 ml jar. After zooplankton was settled at the bottom of the jar, zooplankton was transferred to 2 ml tubes with a pipette. Water for phytoplankton was taken at every meter of the euphotic zone by a Van Dorn water sampler and then pooled. Phytoplankton was then collected by filtering the euphotic water over 80 µm mesh plankton gauze and concentrating it over 30 µm mesh gauze. The residue was preserved in 2 ml tubes. Epiphyton was collected by scraping off algae from rocky substrates and aquatic plants and placed and preserved in 2 ml tubes.

In fish > 5 cm standard length, ca. 0.5 cm^3 of skinned dorsal muscle tissue was collected. Fish < 5 cm were entirely skinned and filleted. Fish tissue was rinsed in distilled water before preservation. Gastropods were kept in regularly refreshed, distilled water for 24 hours to allow for emptying their digestive tracts from food particles, after which their shells were removed and body tissue was preserved. *Caridina*, insects, epiphyton and phytoplankton specimens were preserved entirely. Algae, invertebrates and fish taxa were preserved in 70% ethanol, stored at −20°C and shipped to the laboratory of the Netherlands Institute of Ecology (NIOO) in the

Netherlands for further sample preparation and analyses. There, samples were freeze-dried and homogenized with stainless steel balls (4 mm in diameter) in 2 ml Eppendorf tubes. Of each sample, 300-500 μg of tissue powder was weighed before $\delta^{13}C$ and $\delta^{15}N$ isotope analysis. Stable isotopes of samples collected in 2009 were analysed with an Elemental analyser (Eurovector), interfaced with a Conflo 2 device for continuous flow and an IRMS (Delta XP Advantage, Thermo, Germany). The samples collected in 2010-2011 were measured with an Elemental analyser Flash2000 (Thermo) interfaced with a Conflo 4 and an IRMS (Delta XP Advantage, Thermo, Germany). The isotope ratios were measured against reference standards of carbon and nitrogen by using USGS40 L-glutamic Acid C5H9NO4, with $\delta^{15}N$ of −4.5 and $\delta^{13}C$ of −26.389. The differences between isotopic ratio (R) of samples and the standard were calculated as:

$$\delta^{13}\text{C or }\delta^{15}\text{N}=\left[\left(R_{sample}-R_{standard}/R_{standard}\right)\right]\times 1000$$

where $R={}^{13}CO_2:{}^{12}CO_2$ or $R={}^{15}N_2:{}^{14}N_2$

Data analyses

Lipid correction

Variation in lipid content in tissues among organisms may introduce a bias in the observed $\delta^{13}C$ values. Our data indicated that correction for lipids was necessary as part of the samples showed higher C:N ratios than 3.5% and $\delta^{13}C$ end members differed less than 10-12‰ in $\delta^{13}C$ (Post *et al.*, 2007). Samples with very low N contents caused unrealistically high C:N ratios and ratios higher than 10 were excluded from the dataset.

We applied *a posteriori* mathematical normalisation of $\delta^{13}C$ values using the lipid-correction equations given by Post *et al.,* (2007). We corrected for both autotroph and consumer values. The corrections ($\delta^{13}C$) rely on % carbon values (%C) and carbon to nitrogen ratios (C:N).

For autotrophs (phytoplankton and epiphyton):

$$\delta^{13}\mathrm{C}_{\mathrm{corrected}}=\delta^{13}\mathrm{C}-3.02+0.09\times\%\mathrm{C}\ (\text{where }\%\mathrm{C}<40\%)$$

$$\delta^{13}\mathrm{C}_{\mathrm{corrected}}=\delta^{13}\mathrm{C}-5.83+0.14\times\%\mathrm{C}\ (\text{where }\%\mathrm{C}>40\%)$$

For consumers (invertebrates and fish):

$$\delta^{13}\mathrm{C}_{\mathrm{corrected}} = \delta^{13}\mathrm{C} - 3.31 + 0.99 \times \mathrm{C{:}N}$$

Baseline correction for trophic levels

For spatial and seasonal comparisons of the food web in the Mwanza Gulf, we corrected $\delta^{15}N$ with a baseline for calculating trophic levels (TL). As samples were collected in shallow, littoral waters inside the Gulf and in open pelagic waters near the entrance, we used a two-end-member mixed model with a littoral and pelagic source for calculating trophic levels (Post, 2002). The $\delta^{15}N$ baseline was identified by the two-end-member organisms in $\delta^{13}C$, which represent the littoral (baseline 1) and pelagic baseline (baseline 2). We used primary consumers as end members and identified end members for each area and season, as baselines varied over time and space. Trophic levels were calculated as:

$$\mathrm{TL} = \lambda + (\delta^{15}\mathrm{N}_{\mathrm{sc}} - [\delta^{15}\mathrm{N}_{\mathrm{b1}} \times \alpha + \delta^{15}\mathrm{N}_{\mathrm{b2}} \times (1 - \alpha)])/\Delta_{\mathrm{n}}$$

where λ is the trophic position of the baseline organism, $\delta^{15}N_{sc}$ is measured $\delta^{15}N$ of the consumer of interest, $\delta^{15}N_{b1}$ is measured $\delta^{15}N$ of baseline 1, $\delta^{15}N_{b2}$ is measured $\delta^{15}N$ of baseline 2, Δ_n is the enrichment in $\delta^{15}N$ per trophic level. We used 3.4‰ as enrichment (Post, 2002). The letter α represents the proportion of nitrogen derived from baseline 1 and can be estimated as:

$$\alpha = (\delta^{13}C_{sc} - \delta^{13}C_{b2})/(\delta^{13}C_{b1} - \delta^{13}C_{b2})$$

where $\delta^{13}C_{sc}$ is measured $\delta^{13}C$ of the consumer of interest, $\delta^{13}C_{b1}$ is measured $\delta^{13}C$ of baseline 1, $\delta^{13}C_{b2}$ is measured $\delta^{13}C$ of baseline 2. Lipid and trophic level corrections were carried out in SAS 9.2 (SAS Institute, Cary, USA).

Food-web metrics

Isotopic signatures of organisms (Table 1) were plotted in a bi-space with $\delta^{13}C$ and trophic level (TL) as axes. We used 8 diagnostic community metrics (Table 3) based on the $\delta^{13}C$ and trophic level isotope data to reveal spatial and seasonal differences in food-web structure. Sample sizes of species in our data varied greatly (Table 1) and application of the metrics to the whole community could bias our results, with the species most sampled − in this case Nile perch − influencing the metrics most. Therefore, we chose to combine species into trophic groups with more similar sample numbers to minimize this potential bias (Table 1). The trophic group 'invertebrates' included zooplankton, gastropods, *Caridina* shrimp and insect taxa (Table 1). 'Haplochromines' included mainly pelagic zooplanktivore and detritivore species (Table 2). The haplochromines caught before 2010 and classified as one group, were in retrospect also almost exclusively detritivore and zooplanktivore species (I.J.M. Cornelissen, personal observations). The group 'Other fish' was excluded from the metric analysis because this group included species with very different ecology, such as herbivores, detritivores, omnivores and piscivores. Also, the number of observations of each fish species in 'Other fish' varied too much between areas and seasons to analyse overall spatial and seasonal patterns.

The metrics nitrogen range (dNr), carbon range (dCr), mean core niche area (SEAc) and trophic diversity (CD) give information on the total isotopic space used in $\delta^{13}C$-trophic level bi-space by a group. The metrics nitrogen range (dNr) and carbon range (dCr) indicate the total carbon or nitrogen range used by a trophic group and are calculated as the difference between the lowest and highest values of trophic level or $\delta^{13}C$ within a trophic group (Layman *et al.*, 2007). The mean core niche area (SEAc) is a measure of the core trophic diversity and is expressed as the standard ellipse area. It is calculated from the variance and covariance between $\delta^{13}C$ and trophic levels, containing about 40% of the data points (Batschelet, 1981). It is insensitive to sample sizes and is even corrected when sample sizes are small (Jackson *et al.*, 2011). Mean $\delta^{13}C$ and mean trophic level (TL) represent the centre of the mean core niche area. Trophic diversity (CD) is calculated as the mean Euclidean distance of each individual to the $\delta^{13}C$ –trophic level centroid, and is a metric of average degree of trophic diversity (Layman *et al.*, 2007).

The metrics packing density (MNND) and trophic evenness (SDNND) give information on the dispersion of isotopic signatures in the bi-space and are related to the trophic redundancy. MNND is calculated as the mean of nearest neighbour distance between individual data points and measures the density of data point-packing (Layman *et al.*, 2007), with high values indicating that the isotope signatures are widely spread in isotopic bi-space. This suggests a decreased trophic redundancy and that individuals differ in trophic ecology. SDNND indicates how evenly (low value) or clustered (high value) the isotope signatures are spread in isotopic bi-space (Layman *et al.*, 2007). Clustering means that organisms of different clusters differ in carbon sources or diets.

Table 1: Trophic groups of taxa in the Mwanza Gulf used for spatial and seasonal analysis of community metrics. Number of observations per taxa in the Mwanza Gulf are indicated. Total number of observations of trophic groups are in bold. Areas are indicated as: area 1=A1, area 2=A2 and area 3=A3.

			Dry season			Short rains			Long rains		
Trophic group	Taxa	Common name	A1	A2	A3	A1	A2	A3	A1	A2	A3
			1	**1**	**2**	**0**	**0**	**0**	**3**	**2**	**1**
Algae	Phytoplankton		–	–	–	–	–	–	2	1	–
	Epiphyton		1	1	2	–	–	–	1	1	1
			15	**12**	**7**	**4**	**8**	**10**	**19**	**12**	**16**
Invertebrates	Zooplankton		1	1	1	3	2	3	3	1	2
	Gastropods	Snail	4	2	1	–	5	5	10	7	8
	Caridina nilotica	Shrimp	6	6	5	–	–	2	4	4	5
	Trichoptera nymph	Caddisfly nymph	–	–	–	1	–	–	–	–	–
	Baetis nymph	Mayfly nymph	1	–	–	–	–	–	–	–	–
	Zygoptera nymph	Damselfly nymph	–	–	–	–	–	–	1	–	1
	Anisoptera nymph	Dragonfly nymph	3	3	–	–	–	–	1	–	–
	Ephemeroptera nymph	Mayfly nymph	–	–	–	–	1	–	–	–	–
Haplochromine cichlids	Haplochromine cichlids		**18**	**16**	**5**	**8**	**11**	**8**	**33**	**47**	**58**
Lates niloticus	*Lates niloticus*	Nile perch	**77**	**92**	**31**	**73**	**61**	**43**	**51**	**50**	**38**
			17	**11**	**2**	**31**	**11**	**15**	**23**	**21**	**17**
Other fish	*Labeo victorianus*	Ningu	–	–	–	1	1	1	–	–	–
	Oreochromis niloticus	Nile tilapia	1	–	2	1	8	–	–	–	–
	Synodontis afrofischeri	Marbled squaker	–	–	–	–	–	2	1	–	–
	Synodontis victoriae	Victoria squaker	1	4	–	3	–	–	5	17	14
	Rastrineobola argentea	Dagaa	–	–	–	–	–	–	5	10	5
	Barbus sp.	Barb	–	–	–	–	–	–	6	–	–
	Brycinus sadleri	Sadlers robber	9	7	–	17	–	7	10	4	3
	Schilbe intermedius	Butter catfish	2	–	–	8	–	1	–	–	–
	Clarias gariepinus	African catfish	3	–	–	–	1	1	–	–	–
	Bagrus docmak	Silver catfish	–	–	–	–	–	–	1	–	–
	Mormyrus kannume	Elephant-snout fish	–	–	–	–	1	–	–	–	–
	Protopterus aethiopicus	Marbled lungfish	1	–	–	–	–	3	–	–	–
	Caecomastacembelus frenatus	Longtail spiny eel	–	–	–	1	–	–	–	–	–

Table 2: Percentages of haplochromine trophic guilds caught with surface trawls and gill nets in the Mwanza Gulf from 2010-2011. The group 'Unidentified' refers to small-sized haplochromines which could not be identified and 'Other' were piscivore or gastropod shell crushing haplochromines.

	Trawls	Gill nets
Detritivores	43.5	78.7
Zooplanktivores	52	16.3
Unindentified	4.3	2.6
Other	0.2	2.4
Total number of haplochromines	2611	454

For statistical testing metrics were bootstrapped, because normality of residuals could not be achieved directly, or after transformations. We used 10,000 replications and a minimum of 7 observations to perform the bootstrap analysis. The calculated bootstrapped estimates of the variance of the means were used to compare 95% confidence levels of metrics to indicate differences between areas and seasons of trophic groups (see Table 3 in Results).

An additional analysis on the community metrics was performed to summarise the overall dynamics in food-web functioning. For that purpose the values of the metrics in Table 3 were adjusted for significant differences. Values of each metric in Table 3 that were indexed with the same letter form an interval of values that are not significantly different. For each of these intervals the mean value was calculated from the individual values of the interval. Next, if a metric value belonged to several intervals, the adjusted value of the metric was calculated by taking the mean of the interval means. Missing values were interpolated using the mean of the values of the same season and area. This resulted in an adjusted Table 3 in which values that were not significantly different had the same value (Suplementary table S1). A principal components analysis (PCA) was performed on the standardized and centred data of the adjusted Table 3.

Metrics were calculated in R version 3.1.0 (R Core Team, 2014), using the SIBER analyses (Jackson *et al.*, 2011) within the SIAR package (Parnell *et al.*, 2013). PCA analysis was conducted with CANOCO 4.55 (Biometris, Plant Research International, Wageningen, The Netherlands).

Results

The number of fish sampled varied between 38 and 128 for the nine different area-season combinations (Table 1). In general, haplochromines and Nile perch were the most dominant taxa caught in the Mwanza Gulf (7–49% and 32–82% of total numbers respectively). Mean $\delta^{13}C$ isotope ratios in the Mwanza Gulf ranged from −21 (*Caecomastacembelus frenatus)* to −14 (*Bagrus docmak)* (Fig. 2). The variation in the $\delta^{13}C$ isotope ratios caused taxa to overlap, although algae and invertebrates, at the base of the food web, showed larger variation around means than fish taxa (see error bars in Fig. 2). Phytoplankton was most variable in $\delta^{13}C$ values, with standard errors ranging from −21.1 to −14.7.

Mean $\delta^{15}N$ values ranged from 4.8 (gastropods) to 10.0 (*B. docmak)* in the Mwanza Gulf (Fig. 2). Phytoplankton showed large variation in mean $\delta^{15}N$, with standard errors ranging from 3.8 to 7.2. Of the fish, *Schilbe intermedius,* Nile perch, haplochromines, *Brycinus sadleri* and *Mormyrus kannume* had similar $\delta^{15}N$ values of ca. 8.5. Dagaa, *Synodontis victoriae, B. docmak* and *C. frenatus* showed the highest $\delta^{15}N$ values (ca. 10) and Nile tilapia the lowest (5.2).

Mean core niche areas (SEAc), represented as standard ellipses in Fig. 2, were larger for invertebrates and algae than for fish. Mean core niches of fish (haplochromines, Nile perch and other fish) showed great overlap amongst each other, but less with algae and invertebrates.

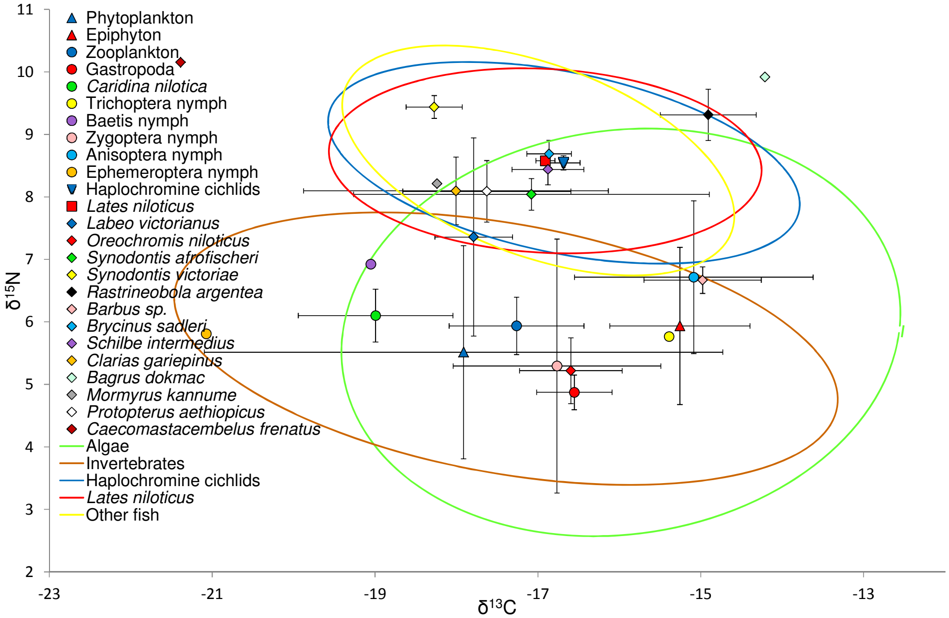

Figure 2: Mean $\delta^{13}C$ and $\delta^{15}N$ values with standard errors of taxa found in the Mwanza Gulf. Symbols represent trophic groups of taxa (algae=triangles, invertebrates=circles, haplochromine cichlids=reversed triangle, Nile perch=squares and other fish=diamonds. Ellipses represent mean core trophic niches of trophic groups (algae=green, invertebrates=brown, haplochromine cichlids=blue, Nile perch=red and other fish=yellow. Taxa of trophic groups are listed in Table 1.

Seasonal and spatial dynamics in food-web structure

We observed large seasonal and spatial shifts along the $\delta^{13}C$-axis in the position and size of mean core niches of trophic groups in the Mwanza Gulf (ellipses in Fig. 3). In the dry season, mean core niche sizes were relatively large and niches were largely overlapping in position between areas (Fig. 3a, d, g). This was related to relatively large carbon ranges in this season (dCr, Table 3). In the following short rains, a strong spatial differentiation of niches occurred along the $\delta^{13}C$ axis for trophic groups (Fig. 3b, e, h). Seasonal mean $\delta^{13}C$ values were very different between area 1 and areas 2 and 3 for most trophic groups. In area 1 mean $\delta^{13}C$ values increased from dry season to short rains and then remained similar into the long rains (Fig. 4a, c, e). Area 2 and 3 showed the opposite with mean $\delta^{13}C$ values decreasing from dry season into the short rains. When going into the long rains values increased again (Fig. 4a, c, e). Therefore, the largest spatial differences in $\delta^{13}C$ values were found in the short rains, with the highest mean $\delta^{13}C$ values in area 1 and the lowest in area 3. Because of this differentiation, niches showed no or minimal overlap in the short rains (Fig. 3b, e, h and mean δ¹³C values, Table 3). This was enhanced by the relatively small mean core niche areas and by the small carbon ranges (SEAc and dCr, Table 3). A similar, spatial effect was visible in the following long rains, but less strong (Fig. 3c, f, i). Niches were also more overlapping, because of the relatively large niche areas and large carbon ranges (SEAc and dCr, Table 3).

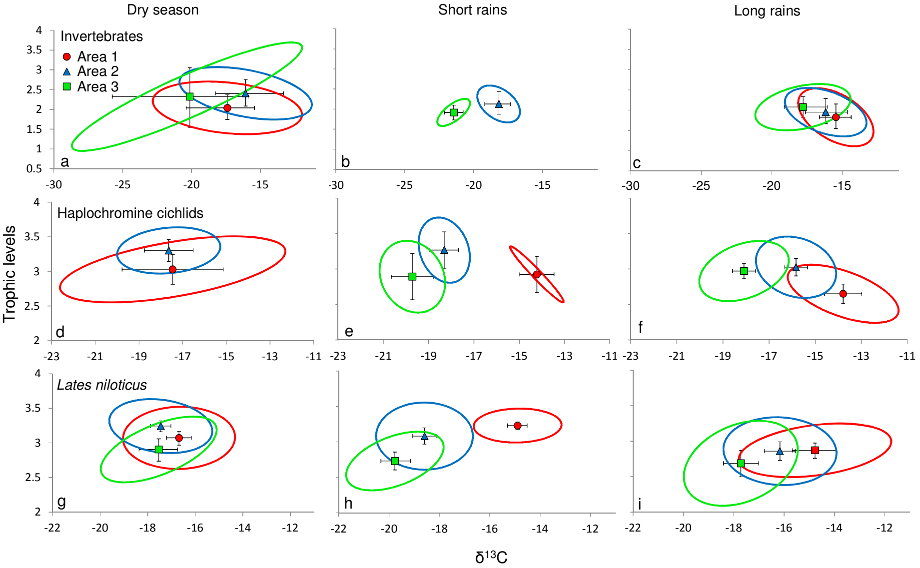

Figure 3: Spatial and seasonal variation of mean $\delta^{13}C$ values, trophic levels and mean core population isotopic niche (ellipses) of a-c) invertebrates, d-f) haplochromines and g-i) *Lates niloticus*. Error bars represent 95% confidence intervals. Means were bootstrapped. For location of sampling stations and the three areas see Fig. 1.

Along the trophic-level axis, positions of trophic niches were spatially and seasonally largely overlapping (Fig. 3a-i). However, for all trophic groups lowest nitrogen ranges were observed in the short rains (dNr, Table 3). Furthermore, mean trophic levels varied spatially and seasonally for trophic groups (Fig. 4b, d, f and mean TL, Table 3), except for invertebrates. Unlike for the $\delta^{13}C$ values there was no overall dominant pattern in trophic levels, except for Nile perch having the lowest trophic levels in area 3 in all seasons (Fig. 4f, Table 3).

Table 3: Food-web metrics of trophic groups in the Mwanza Gulf. Abbreviations used: dNr=nitrogen range, dCr=carbon range, SEAc=mean core niche area, mean $\delta^{13}C$=mean $\delta^{13}C$, mean TL=mean of trophic level, CD=trophic diversity, MNND=packing density, SDNND=trophic evenness. Metrics were bootstrapped. Letters indicate differences based on 95% confidence intervals.

		Dry season			Short rains			Long rains		
		Area 1	Area 2	Area 3	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
Invertebrates	dNr	1.96^{bc}	1.68^{bc}	2.82^{bc}	–	1.05^{ab}	0.85^{a}	2.09^{c}	1.59^{ab}	1.59^{bc}
	dCr	15.85^{b}	12.77^{b}	18.04^{b}	–	3.39^{a}	2.92^{a}	8.94^{b}	7.38^{b}	10.76^{b}
	SEAc	8.74^{bc}	7.51^{c}	9.07^{bc}	–	1.50^{ab}	0.73^{a}	4.52^{bc}	4.05^{bc}	4.86^{bc}
	Mean $\delta^{13}C$	-17.39^{ab}	-16.07^{ab}	-20.13^{abc}	–	-18.17^{b}	-21.44^{c}	-15.45^{a}	-16.18^{ab}	-17.78^{ab}
	Mean TL	2.04^{a}	2.41^{a}	2.32^{a}	–	2.13^{a}	1.92^{a}	1.83^{a}	1.95^{a}	2.08^{a}
	CD	0.83^{c}	0.69^{bc}	1.08^{c}	–	0.39^{ab}	0.33^{a}	0.74^{bc}	0.58^{ac}	0.77^{c}
	MNND	0.34^{a}	0.28^{a}	0.61^{a}	–	0.24^{a}	0.16^{a}	0.20^{a}	0.23^{a}	0.22^{a}
	SDNND	0.25^{a}	0.27^{a}	0.39^{a}	–	0.15^{a}	0.13^{a}	0.24^{a}	0.20^{a}	0.17^{a}
Haplochromine cichlids	dNr	1.53^{acd}	0.91^{bc}	–	0.80^{ac}	1.10^{ab}	1.15^{ab}	1.49^{ad}	2.32^{d}	2.06^{d}
	dCr	17.91^{b}	6.64^{b}	–	2.34^{a}	2.91^{a}	3.27^{a}	8.30^{b}	7.26^{b}	10.06^{b}
	SEAc	5.54^{bc}	2.17^{b}	–	0.23^{a}	1.29^{ab}	1.52^{ab}	2.35^{bc}	2.16^{bc}	2.31^{c}
	Mean $\delta^{13}C$	-17.47^{bc}	-17.64^{c}	–	-14.22^{a}	-18.31^{c}	-19.72^{c}	-13.79^{a}	-15.83^{b}	-18.09^{c}
	Mean TL	3.03^{bc}	3.30^{c}	–	2.92^{abc}	3.26^{bc}	2.89^{abc}	2.65^{a}	3.02^{b}	2.97^{bc}
	CD	0.61^{d}	0.37^{a}	–	0.56^{c}	0.55^{ac}	0.43^{ac}	0.49^{abc}	0.49^{ac}	0.50^{bc}
	MNND	0.20^{a}	0.13^{a}	–	0.12^{a}	0.16^{a}	0.24^{a}	0.14^{a}	0.15^{a}	0.11^{a}
	SDNND	0.18^{ab}	0.11^{a}	–	0.15^{ab}	0.20^{ac}	0.17^{ac}	0.12^{a}	0.25^{bc}	0.12^{a}
Lates niloticus	dNr	2.40^{c}	2.22^{c}	1.79^{ac}	1.26^{a}	1.83^{bc}	1.50^{ab}	1.31^{a}	2.02^{bc}	2.15^{c}
	dCr	9.26^{cd}	10.90^{cd}	8.82^{bcd}	8.11^{ac}	6.93^{a}	7.07^{ab}	13.63^{d}	10.34^{cd}	7.75^{ac}
	SEAc	3.20^{bc}	2.54^{abc}	2.73^{abc}	1.25^{a}	2.77^{bc}	2.09^{ab}	3.24^{bc}	3.21^{bc}	3.85^{c}
	Mean $\delta^{13}C$	-16.68^{c}	-17.45^{c}	-17.54^{cde}	-14.89^{a}	-18.59^{ef}	-19.77^{f}	-14.77^{ab}	-16.17^{bd}	-17.72^{ce}
	Mean TL	3.07^{bd}	3.24^{de}	2.90^{ab}	3.23^{ce}	3.08^{be}	2.73^{a}	2.87^{ab}	2.86^{ab}	2.69^{a}
	CD	0.43^{b}	0.48^{b}	0.57^{bcd}	0.26^{a}	0.60^{c}	0.55^{bc}	0.48^{b}	0.63^{cd}	0.74^{d}
	MNND	0.09^{ab}	0.09^{b}	0.16^{cef}	0.06^{a}	0.12^{be}	0.12^{be}	0.10^{bd}	0.14^{cdef}	0.18^{f}
	SDNND	0.11^{ab}	0.10^{ab}	0.15^{b}	0.07^{a}	0.08^{ab}	0.09^{ab}	0.08^{ab}	0.12^{ab}	0.14^{ab}

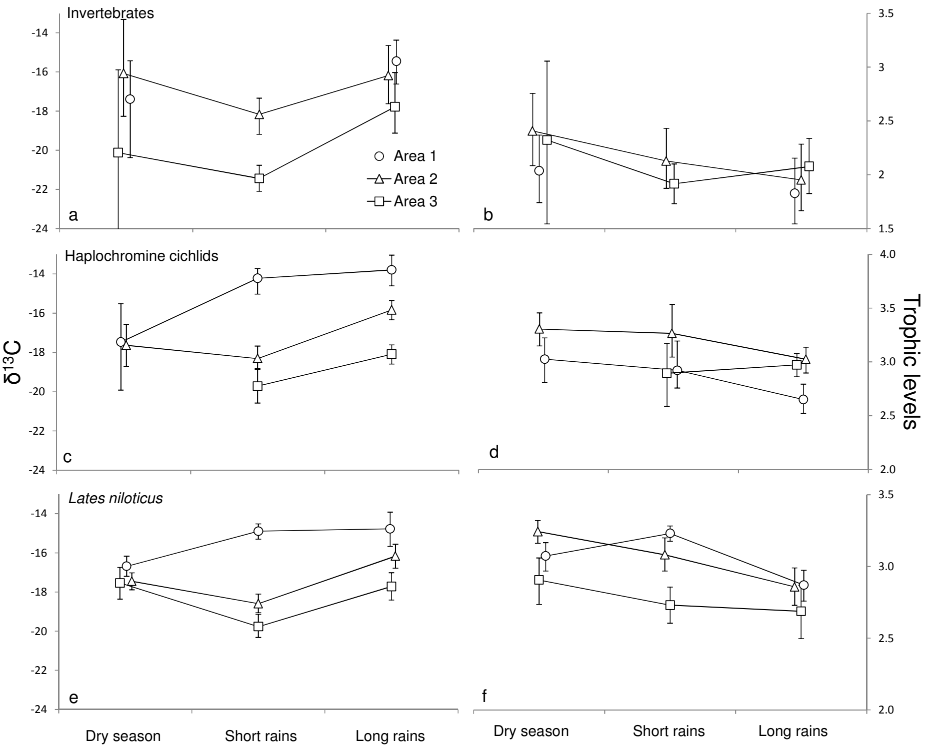

Figure 4: Seasonal shifts in δ^{13}C values and trophic levels of trophic groups in three different areas in the Mwanza Gulf. For location of sampling stations and the three areas see Fig. 1.

The dispersion metrics packing density (MNND) and trophic evenness (SDNND), did not vary greatly on a spatial and seasonal scale (Table 3).

The PCA explained 31.4 % of the variance in the metrics on the first axis and 21.7 % on the second (Fig. 5). Areas were clearly different, mostly along the second axis, with area 1 being the most distinct (Fig. 5a). Overall differences between seasons were clearest along the first axis, with the short rains distinct from the other two seasons (Fig. 5b). Area differences were mostly related to δ^{13}C –signature of all groups, with areas 2 and 3 having the strongest negative mean δ^{13}C values (Fig. 5c). Seasonal differences were mostly associated with metrics related to the total isotopic space (dCr and SEAc), which were overall higher in the dry season and long rains than in the short rains (Fig. 5c).

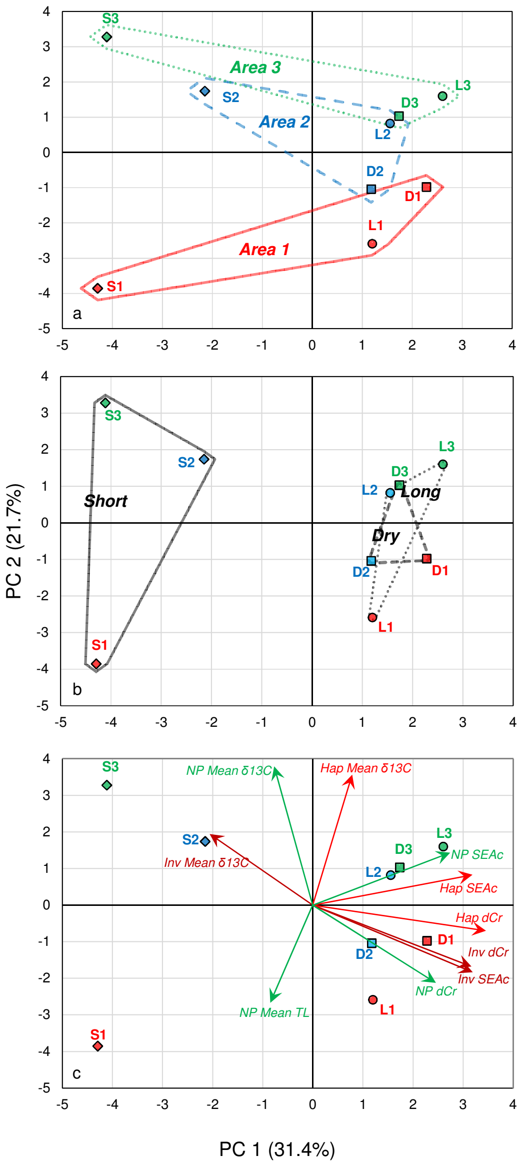

Figure 5: Principal Component Analysis (PCA) of the significantly different isotope metrics of a) areas, b) seasons and c) of trophic groups. Symbols indicate areas (area 1=red, area 2=blue, area 3=green) and seasons (dry season (D)=squares, short rainy season (S)=diamonds, long rainy season (L)=circles). Trophic groups are indicated with coloured vectors (invertebrates=brown, haplochromine cichlids=red, Nile perch=green). Only metrics were depicted. For illustration purpose, metrics dNR, CD, SDNND and MNND were not depicted in the Fig. as they did not show overall spatial or seasonal trends. For location of sampling stations and the three areas see Fig. 1.

Discussion

This study showes that the community metrics, which were so far used to compare between entire communities from different ecosystems, or to compare between populations with similar feeding ecology (Jackson *et al.*, 2012; Abrantes *et al.*, 2014), are also applicable to identify small spatial and seasonal variation in niches of species or trophic groups and in food-web functioning.

Invertebrates and algae formed the broad carbon base of the food-web structure of the Mwanza Gulf, with large variations, narrowing down towards fish at the top of the food web with smaller variations (Fig. 2). In addition, most fish were positioned mid-range between the carbon ranges of algae and invertebrates. The mid-range positioning and relatively small variations of fish in the food web indicates omnivory at higher trophic levels and fish consuming a wide variety of carbon sources in different proportions (Hecky and Hesslein, 1995; Bearhop *et al.*, 2004).

The food web consisted of two main trophic levels: primary producers/invertebrates and fish. Most fish were similar in $\delta^{15}N$, indicating similar omnivorous diets. This is in contrast with the large diversity of specialized feeders, based on stomach and gut analyses, observed in the lake before the Nile perch upsurge (Witte and van Oijen, 1990; van Alphen *et al.*, 2003). Many abundant fish species, for instance Nile tilapia, *Brycinus sadleri*, Dagaa and haplochromines, that were originally known as phytoplankton, zooplankton or detritus feeders, extended their diets with larger invertebrates, such as insects, *Caridina* shrimps, and even small fishes (Wanink, 1998; Wanink and Witte, 2000; Katunzi *et al.*, 2003; Njiru *et al.*, 2004; Wanink and Joordens, 2007; Kishe-Machumu *et al.*, 2008).

Lake Victoria's top predator, Nile perch, showed relatively low $\delta^{15}N$ values in the food web of the Mwanza Gulf. If we assume an enrichment of 3.4‰ per trophic level (Post, 2002), $\delta^{15}N$ values of Nile perch corresponded with an invertebrate-based diet and was low for a mixed invertebrate-fish or a piscivore diet. Other stable isotope studies also found relatively low positions of Nile perch in the food web (Campbell *et al.*, 2003; Ojwang *et al.*, 2010). This was explained by the high occurrence of cannibalism and dependence on invertebrates during the time when haplochromines were scarce and supported by stomach analyses (Campbell *et al.*, 2003). However, recent diet studies of Nile perch in the Mwanza Gulf revealed that haplochromines and *Caridina* both dominated the diet and that cannibalism was not regularly observed (Kishe-Machumu *et al.*, 2012; Cornelissen *et al.*, 2015). The similar $\delta^{15}N$ signatures we found in Nile perch and haplochromines do not suggest a consistent predator-prey relationship between these two taxa. This large discrepancy between trophic positions based upon stomach contents and based upon isotope values cannot be explained by differences in digestion rates or feeding frequencies between fish and invertebrate prey, or between prey fish of different size (Kionka and Windell, 1972; Hart and Connellan, 1984; Chapman, Mackay and Wilkinson, 1989; He and Wurtsbaugh, 1993). As Nile perch in our study was caught at night and Nile perch exhibits a diel feeding pattern of consuming more shrimps during the day and more fish at night (Mkumbo and Ligtvoet, 1992; Goudswaard *et al.*, 2004), we probably overestimated the contribution of fish in its diets and, therefore, also its trophic position. Furthermore, isotopes cover a integrated timespan of weeks compared to the timespan of days in diets. A Nile perch sampled in the Gulf may have been feeding on haplochromines there, resulting in higher proportion of fish in stomach analyses, but may have been feeding previously on *Caridina* shrimps outside the Gulf where *Caridina* densities are higher and where *Caridina* is still a major prey in Nile perch diets (Ngupula and Mlaponi, 2010; Cornelissen *et al.*, 2015). Both explanations support the idea that Nile perch isotope signatures correspond more to an invertebrate dependence and that haplochromines are a less important food source for Nile perch than is suggested by stomach content analyses alone (Campbell *et al.*, 2003).

We observed high $\delta^{15}N$ values for Dagaa, which were higher than in Nile perch and haplochromines. In contrast, former isotope studies revealed that Dagaa and haplochromines had similar trophic levels and that both include invertebrate and insect prey in their diet (Wanink and Witte, 2000; Campbell *et al.*, 2003; Ojwang *et al.*, 2004; Kishe-Machumu *et al.*, 2008; Ojwang *et al.*, 2010). Despite the relatively high $\delta^{15}N$ values for Dagaa compared to Nile perch and haplochromines, values were within the range of other studies, which were explained by Dagaa's diet of *Caridina* and lakeflies (Campbell *et al.*, 2003; Ojwang *et al.*, 2004; Ojwang *et al.*, 2010). $\delta^{13}C$ values of Dagaa were more enriched than of haplochromines (-14.9 of Dagaa vs -16.3 of haplochromines), which was also found in the Napoleon Gulf and Kenyan waters of Lake Victoria (Campbell *et al.*, 2003; Ojwang *et al.*, 2004). This indicates that in the Mwanza Gulf Dagaa relied on a more littoral-based diet than haplochromines.

After the Nile perch upsurge in the late 1980s, the Lake Victoria food web became less diverse with *Caridina* shrimp, Dagaa, Nile tilapia, zooplanktivorous and detritivorous haplochromine cichlids and Nile perch dominating the food web. When comparing our estimates of isotopic trophic positions, most taxa in our study correspond with the estimates in 2000 and 2005 in Lake Victoria (Table 4) (Matsuishi *et al.*, 2006; Downing, 2012). Therefore, the overall trophic structure of the food web seems unchanged since 2000. Nile perch in our study, however, showed considerably lower trophic levels (Table 4). The higher trophic levels observed in 2000 and 2005 for Nile perch, were solely based on stomach content analyses and are therefore probably overestimates.

Table 4: Observations of trophic positions of main taxa in the Tanzanian part of Lake Victoria (LV) and the Mwanza Gulf (MW) according to different authors. Trophic positions for Lake Victoria (Matsuishi *et al.*, 2006) and Mwanza Gulf from 2005 (Downing, 2012) were based upon stomach contents and estimated by ECOPATH, and for the Mwanza Gulf from 2009-2011 were based upon $\delta^{15}N$ stable isotope values (this study).

Taxa	LV 2000	MW 2005	MW 2009-2011
	Matsuishi *et al.*, 2006	Downing, 2012	This study
Zooplankton	2	2.1	2.2
Caridina nilotica	2.3	2.4	2.1
Oreochromis niloticus	2.6	2.2	2.1
Haplochromine cichlids	3	3.2	3
Rastrineobola argentea	3.1	2.9	3.3
Lates niloticus (juvenile)	3.5	3.6	3
Lates niloticus (adult)	3.9	4.2	–

Seasonal and spatial dynamics in the food-web structure

We found large seasonal changes in carbon sources of the Mwanza Gulf food web. The dry season showed large core niches, meaning that trophic diversity was high in this season (SEAc, Table 3). This was mainly caused by large carbon ranges (dCR), which ‘flattened’ the niches (ellipses in Fig. 3). Furthermore, during the dry season niches overlapped greatly between areas (Fig. 3). This indicates that during the dry season, consumers were omnivores, using a mixture of carbon sources regardless of their location in the Gulf. This can be explained by the low precipitation and strong winds during the dry season, resulting in complete mixing of the water column. This resulted in low phytoplankton biomass and relatively clear waters (Silsbe, 2004; Cornelissen *et al.*, 2014), leading to a mixed carbon environment at the base of the food web with phytoplankton, benthic algae and detritus as main sources.

In the following short rainy season, a large spatial differentiation in carbon sources was observed for most trophic groups (Fig. 3). This spatial differentiation of carbon sources was probably caused by the increased run-off from the land into the Gulf, the effect of which is greatest in area 1, deep inside the Gulf and decreases towards area 3 in the open water outside the Gulf. The extreme negative $\delta^{13}C$ values found in the open water outside the Gulf indicate that isotopic composition of consumers here were mainly influenced by pelagic phytoplankton (France, 1995; Hecky and Hesslein, 1995; Keough *et al.,* 1996; Schindler *et al.*, 1997).

The more positive δ^{13}C values inside the gulf in shallow water indicate an increased effect of littoral/ benthic influence and/or increased primary production (France, 1995; Casey and Post, 2011). Littoral primary producers such as macrophytes, benthic algae and increased phytoplankton growth rates often seen in shallow inshore areas, all have enriched δ^{13}C values. The dominant macrophytes, sedges (*Cyperus papyrus)* and reeds *(Phragmites spp.)*, fringing the shores in the Mwanza Gulf have a typically enriched δ^{13}C of -12.7 to -11.9 in Lake Victoria (Campbell *et al.*, 2003; Machiwa, 2010), but their δ^{13}C is more enriched than we found for consumers. Therefore, these macrophytes are unlikely to be a major source of carbon for consumers in the Gulf, which is consistent with other studies in a satellite lake of Lake Victoria (Hecky and Hesslein, 1995; Mbabazi *et al.*, 2009) and temperate and arctic lakes (Hecky and Hesslein, 1995; Keough *et al.*, 1996). Water hyacinth *(Eichhornia crasspes)*, another common macrophyte in the Mwanza Gulf, has generally a more negative δ^{13}C range in Lake Victoria than we found for trophic groups in shallow water (-27.8 to -27.2, (Campbell *et al.*, 2003; Machiwa, 2010) and is therefore unlikely to be a major carbon source. In eutrophic water, like the Mwanza Gulf, phytoplankton production often causes light-limitation for the benthic primary production pathway in the food web (Vadeboncoeur *et al.*, 2003). Therefore, benthic algae are probably of minimal influence on the food web.

High primary productivity and high N-fixation with associated phytoplankton blooms also result in an enrichment of δ^{13}C (Mugidde, 2001; Casey and Post, 2011). δ^{13}C levels of consumers in shallow water during the short rains were within the δ^{13}C range of phytoplankton. The higher phytoplankton biomass in shallow water during rainy seasons suggests higher primary productivity (Cornelissen *et al.*, 2014) and therefore phytoplankton might have contributed to an enriched δ^{13}C in shallow water. N-fixation rates were low in the Mwanza Gulf and N-fixing bacteria are unlikely to be a major carbon source for consumers in the Mwanza Gulf (Cornelissen *et al.*, 2014).

The long rains showed a similar spatial shift in carbon sources as short rains, but trophic diversity of niches was larger, showing large overlaps, indicating a more mixed use of carbon sources by consumers. The long rains seemed to represent a transition period where carbon sources start to diffuse over the Gulf, before becoming mixed in the dry season.

Trophic levels could be explained by the spatial differences found in diets of trophic groups. Trophic levels of haplochromines differed spatially and were relatively high in area 2. The spatial variation in isotopic trophic levels can be explained by stomach analyses. The higher isotopic trophic levels found in area 2 corresponded with a relatively large contribution of fish in the stomach contents (Table 5). The spatial variation in isotopic trophic levels and diets confirms that the former zooplanktivore and detritivore haplochromines now have a broad diet, including larger prey, such as invertebrates and even fish (Katunzi *et al.*, 2003; Kishe-Machumu *et al.*, 2008).

Table 5: Spatial differences in diets of haplochromines in the Mwanza Gulf, sampled at areas 1, 2 and 3 (2009-2011). Diet composition are in percentages of biovolume (n=75).

Diet items	Area 1	Area 2	Area 3
Phytoplankton	21	23	27
Detritus	15	4	2
Zooplankton	20	13	29
Insects	23	22	6
Caridina nilotica	0	2	18
Fish	21	36	18

The decrease in trophic position of Nile perch from shallow to deep water in the Mwanza Gulf during the short rainy season was probably caused by the seasonal high abundance of *Caridina* in deep water and the corresponding high occurrence of *Caridina* in their diets (Cornelissen *et al.*, 2015). In shallow water, small Nile perch shifted from *Caridina* to fish at a much smaller size than in deep water (Cornelissen *et al.*, 2015), leading to a higher position of the Nile perch in shallow water.

In our study, dispersion metrics did not vary greatly on a spatial and seasonal scale, but often seemed positively related to trophic diversity and niche area. Isotopes of trophically diverse groups were more widely spread in isotopic space, because of large variation in carbon sources and diets. In other studies, high values of dispersion metrics also appeared to correspond generally to a high trophic diversity and large niche area (Cooper and Wissel, 2012; Jackson *et al.*, 2012; Abrantes *et al.*, 2014).

We were the first to investigate spatial and seasonal changes in food-web structure in the Mwanza Gulf in a quantitatively way by using stable isotopes. A study in the north of Lake Victoria showed differences in carbon sources on a much larger spatial scale between two widely separated Gulfs, but overall food-web structure between the Gulfs were similar (Campbell *et al.*, 2003). The differences in carbon source were explained by the differences in hydrology and morphology between the two Gulfs. Our results are clearly different, in the Mwanza Gulf seasons have a much larger influence on carbon sources and act on much smaller spatial scales, affecting the whole food web to the highest trophic levels. Isotopic spatiality and seasonality in food-web structures were previously also found in (sub)tropical estuaries, rivers and coastal lagoons where hydrologic seasonality and spatiality is strong (Jepsen and Winemiller, 2002; Vizzini and Mazzola, 2003; Abrantes *et al.*, 2014), but so far not in tropical freshwater systems as Lake Victoria. In addition to the temporal and spatial variation in food-web structure, we also found, based on isotopic signatures of the fish taxa, that during the study period (2009-2011) most taxa had omnivorous diets with a heavy reliance on invertebrates, including Nile perch, which predominantly fed on invertebrates and only sparsely on haplochromines. This is in sharp contrast with current stomach content analyses, which most likely overestimate the proportion of fish in their diets, but, even more compellingly, with the large diversity of specialized feeders observed in the lake before the Nile perch upsurge in the 1980s.

Acknowledgments

This work is part of the integrated project "Exploitation or eutrophication as threats for fisheries? Disentangling social and ecological drivers of ecosystem changes in Lake Victoria (SEDEC)", supported by the Netherlands Organisation for Scientific Research (NWO/WOTRO) grant number W01.65.304.00. Thanks to Hans Hoogveld, Nico Helmsing and the Netherlands Institute of Ecology (NIOO) for the analyses of stable isotopes. Special thanks to Klaas Gerber, Alex Mangassa, Gerardi Rajabu, Paulo and Emma for their valuable field assistance and support, and to the Tanzanian Fisheries Research Institute (TAFIRI) in Mwanza for providing laboratory space and use of field equipment during this research.

Supplementary table

Table S1: Adjusted significant spatial and seasonal differences used for the Principal Component Analysis.

		Dry season			Short rains			Long rains		
		Area1	Area2	Area3	Area1	Area2	Area3	Area1	Area2	Area3
Invertebrates	dNr	1.83	1.83	1.83	1.58	1.49	1.16	1.83	1.49	1.83
	dCr	12.29	12.29	12.29	7.72	3.16	3.16	12.29	12.29	12.29
	SEAc	5.75	5.75	5.75	4.01	3.43	1.12	5.75	5.75	5.75
	Mean δ13	17.31	17.31	19.05	18.18	17.31	20.79	17.31	17.31	17.31
	Mean TL	2.09	2.09	2.09	2.09	2.09	2.09	2.09	2.09	2.09
	CD	0.78	0.69	0.78	0.61	0.52	0.43	0.69	0.61	0.78
	MNND	0.29	0.29	0.29	0.29	0.29	0.29	0.29	0.29	0.29
	SDNND	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23
Haplochromine cichlids	dNr	1.44	1.16	1.44	1.16	1.16	1.44	1.44	1.71	1.71
	dCr	10.03	10.03	8.24	2.84	2.84	2.84	10.03	10.03	10.03
	SEAc	2.68	2.32	2.30	1.01	1.49	1.89	2.32	2.32	2.32
	Mean δ13	17.45	18.25	18.05	14.01	18.25	18.25	14.01	16.65	18.25
	Mean TL	3.06	3.06	3.03	2.94	3.06	2.94	2.82	3.06	3.06
	CD	0.61	0.47	0.51	0.50	0.49	0.49	0.49	0.49	0.49
	MNND	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16
	SDNND	0.17	0.15	0.16	0.17	0.17	0.17	0.15	0.19	0.15
Lates niloticus	dNr	2.07	1.99	1.82	1.47	1.99	1.69	1.47	1.99	1.99
	dCr	9.89	9.89	9.24	8.20	7.47	7.70	10.59	9.89	8.20
	SEAc	2.95	2.69	2.69	2.15	2.95	2.49	2.95	2.95	3.08
	Mean δ13	17.15	17.15	17.42	15.28	17.95	19.77	15.28	16.12	17.65
	Mean TL	3.06	3.16	2.88	3.16	3.06	2.81	2.88	2.88	2.81
	CD	0.50	0.50	0.57	0.26	0.61	0.54	0.50	0.61	0.64
	MNND	0.09	0.10	0.14	0.08	0.12	0.13	0.11	0.14	0.15
	SDNND	0.10	0.10	0.11	0.10	0.10	0.10	0.10	0.10	0.10

Chapter 6

General discussion

The increasing fishery on Nile perch *(Lates niloticus,* L.*)* in Lake Victoria since its explosive population growth created a fear of overfishing and stock collapse (Kitchell *et al.*, 1997; Schindler *et al.*, 1998; Mkumbo, 2002; Balirwa *et al.*, 2003; Getabu *et al.*, 2003; Matsuishi *et al.*, 2006; Mkumbo *et al.*, 2007). Management strategies to sustain Nile perch stocks were therefore mainly focused on regulating the fishery (van der Knaap *et al.*, 2002; Matsuishi *et al.*, 2006; Kolding *et al.*, 2008; Msuku *et al.*, 2011; Kolding *et al.*, 2014). However, besides the top-down effects of the fishery, the changing environment around the lake has led to eutrophication and its resulting bottom-up effects in the food web. Extensive deforestation, burning, agriculture and urbanization due to the rapid growth of the human population within the catchment area, led to an increased input of nutrients into the lake by mainly atmospheric deposition and run-off from the land (Scheren *et al.*, 2000; Tamatamah *et al.*, 2005). The increasing phosphorus and nitrogen load resulted in increased phytoplankton production, stratification and hypoxia near the bottom in deep waters (Hecky, 1993; Hecky, 1994; Lung'ayia *et al.*, 2001; Verschuren *et al.*, 2002). Recently, eutrophication has been slowly acknowledged as a potential threat for Nile perch (Kolding *et al.*, 2008; Hecky *et al.*, 2010). Unfortunately, the bottom-up effects of eutrophication via the food web are poorly understood.

The key objective of the SEDEC (Disentangling Social and Ecological Drivers of Ecosystem Change) programme, in which the present study was incorporated, was to disentangle eutrophication and fishery effects on the food web of Nile perch. Our research assessed the effect of eutrophication through the food web on Nile perch and whether this leads to decreasing stocks of Nile perch or even a stock collapse in the future. For that purpose, the Mwanza Gulf (south-east Lake Victoria) was selected as the target area for this study because it shows an increasing eutrophication gradient from offshore into the gulf.

Because *Caridina nilotica* (Roux), an atyid shrimp, was known to be the main prey of Nile perch, we initially focused only on a simplified food web with *Caridina* as prey and Nile perch as top predator (Fig. 1), (Hughes, 1986; Hughes, 1992b; Mkumbo and Ligtvoet, 1992; Katunzi *et al.*, 2006). However, it soon became clear that haplochromines had become important again as prey and were therefore included in this study as well. To study the effect of eutrophication on Nile perch, we investigated the Mwanza Gulf ecosystem at the following levels (Fig. 1):

1. The water quality and phytoplankton level **(chapter 2)**
2. The fish level, studying the distribution of Nile perch **(chapter 3)**
3. The food-web level, studying the direct interaction between Nile perch and its prey **(chapter 3 & 4)**
4. The community level **(chapter 5)**

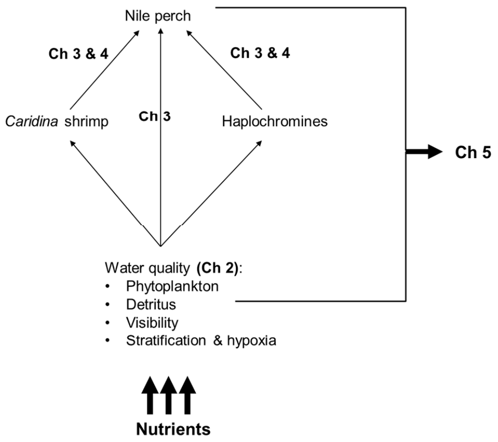

Figure 1: Schematic overview of this thesis.

In this chapter, the findings of this research are summarized and discussed. Implications of the findings are addressed as well their limitations and suggestions for future research.

Eutrophication of the Mwanza Gulf

The Mwanza Gulf showed an increased eutrophication gradient from offshore waters at the entrance of the gulf towards waters deep inside the Gulf **(chapter 2)**. Spatial and seasonal variation in nutrients was in line with other studies in Lake Victoria (Mugidde, 2001; Silsbe *et al.*, 2006; Gikuma-Njuru, 2008; Haande *et al.*, 2011; Ngupula *et al.*, 2011). Stratification of the water column varied seasonally and spatially, but strong long-term stratification was not observed and fluctuated on a daily basis **(chapter 2)** as reported in a shallow bay in north Lake Victoria (MacIntyre *et al.*, 2002). This is in contrast with previous studies in the Mwanza Gulf and other parts of Lake Victoria, where long-term stratification during the wet season was observed (Kaufman, 1992; Hecky, 1993; Wanink *et al.*, 2001). In our study, phytoplankton was limited in light, whereas nutrients were in excess inside the Gulf **(chapter 2)**. Light limitation was caused by both phytoplankton and suspended particulate detritus.

Phytoplankton was dominated by cyanobacteria, but N-fixating species were generally low in abundance. These findings differ with other gulfs in Lake Victoria, where phytoplankton was found to be limited by mainly self-shading and N-fixation was high (Hecky, 1993; Kling *et al.*, 2001; Mugidde *et al.*, 2003; Gikuma-Njuru and Hecky, 2005; Silsbe *et al.*, 2006; Haande *et al.*, 2011). In our study, deeper mixing depths and limitation in nitrogen resulted in lower phytoplankton biomass in deeper water near the entrance of the Gulf **(chapter 2)**. Other studies showed a similar eutrophication gradient from off to inshore areas with a 2-5 fold lower phytoplankton biomass in offshore than inshore areas (Hecky, 1993; Silsbe, 2004; North *et al.*, 2008; Haande *et al.*, 2011).

There is no doubt that eutrophication took place in Lake Victoria since the 1920s, but the question is whether it is still ongoing? The increase in nutrients resulted in increased stratification, hypoxia and phytoplankton biomass and decreased visibility (Bootsma and Hecky, 1993; Hecky, 1993; Hecky, 1994; Lung'ayia *et al.*, 2001). From the 1980s onwards, nutrients were still increasing in the lake (Lung'ayia *et al.*, 2001; Hecky *et al.*, 2010), but since then water quality seems to have stabilized. Chlorophyll concentrations and visibility remained similar in inshore and offshore areas since the 1980s and some scientists claim therefore an improvement in water quality (Sitoki *et al.*, 2010). A similar historical trend is observed in the Mwanza Gulf (Fig. 2): there was a strong decrease in visibility between 1974 and 1987, but the visibility in 2005 and 2010 was considerably higher than in 1987. This indicates that visibility has improved in the Mwanza Gulf since 1987, was stable between 2005 and 2010, and is now only slightly lower than in 1974.

Hypoxia near the bottom is another effect of increased eutrophication by increased sedimentation of phytoplankton and detritus when the water column is stratified (Bootsma and Hecky, 1993). Persistent hypoxia of large deep-water areas in the Lake reduces the available habitats for fish (Kaufman and Ochumba, 1993; Wanink *et al.*, 2001; Verschuren *et al.*, 2002; Kolding *et al.*, 2008). From the mid-1970s until the beginning of the 1990s, the climate in Lake Victoria was characterized by relatively low wind stress, causing increased stratification and hypoxia (Kolding *et al.*, 2008). In the Mwanza Gulf, wind speed dropped since the 1980s, with lowest recorded wind speeds in 1991, after which it increased to higher levels than before the 1980s (Kolding *et al.*, 2008; van Rijssel, 2014). In 1988-1989, hypoxia was reported to last for 3-5 months in the Mwanza Gulf in waters less than 20 m deep (Wanink *et al.*, 2001), and Nile perch distributions were strongly influenced by hypoxia (Goudswaard *et al.*, 2011). In 1988 a massive kill of Nile perch was observed after a sudden upwelling of hypoxic waters (Wanink *et al.*, 2001). At that time, massive fish kills were also frequently observed in other parts of the Lake (Ochumba, 1990). In this study, stratification fluctuated on a daily basis **(chapter 2)**, resulting in relatively well oxygenated water **(chapter 3)**. Lake-wide oxygen levels improved too (Sitoki *et al.*, 2010). I conclude that the increased wind stress since 1990s probably resulted in deeper mixing and decreased stratification, which improved visibility and oxygen conditions to levels before 1987.

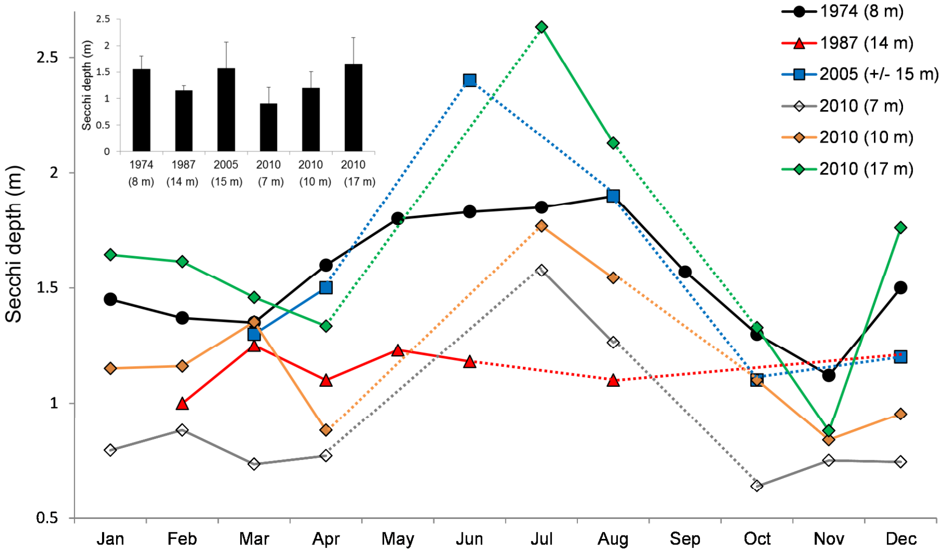

Figure 2: Monthly visibility in the Mwanza Gulf in 1974, 1987, 2005 and 2010. Bars represent mean transparencies with standard deviation. Total depth is indicated within brackets. Data from 1974 and 1987 are from Witte *et al.* (1999), data from 2005 is from Shayo *et al.* (2011) and data from 2010 is from this study.

The position of Nile perch in the food web

Nile perch distributions were mostly driven by depth and temperature in south-east Lake Victoria and affected size-classes differently **(chapter 3)**. Densities of small Nile perch were mostly positively correlated with the warm wet seasons, whereas medium-sized Nile perch were positively correlated with shallow depths. Oxygen levels did not influence Nile perch as long-term hypoxic conditions and stratification did not occur. This is in contrast with previous studies, where Nile perch stayed above the oxycline or moved into inshore normoxic areas during seasonal stratification (Mkumbo, 2002; Goudswaard *et al.*, 2011; Taabu-Munyaho *et al.*, 2013). Visibility did not drive Nile perch distributions. The high densities of haplochromines and juvenile Nile perch in the Mwanza Gulf suggest that the Gulf is well-suited for small fish.

Direct interactions between Nile perch and prey organisms indicated a highly opportunistic feeding behaviour of Nile perch **(chapter 3 & 4)**. However, small Nile perch showed a slight preference towards *Caridina* shrimp above haplochromines, whereas haplochromines were preferred as fish prey above Dagaa *(Rastrineobola argentea,* Pellegrin*)* and juvenile Nile perch **(chapter 4)**. Nile perch distributions were not driven by prey densities of *Caridina* shrimp and haplochromines **(chapter 3)**, but diet composition and diet shifts were related to prey densities **(chapter 4)**. Nile perch shifted from *Caridina* shrimp to fish at a small size in the Gulf, whereas in open waters, where *Caridina* was most abundant, this diet shift occurred at a larger Nile perch size. The high haplochromine densities and their abundant occurrence in Nile perch diet confirm the recovery of haplochromines in the Mwanza Gulf (**chapter 3 & 4**, (Kishe-Machumu *et al.*, 2012). However, the recovery of haplochromines is restricted to shallow areas like the Mwanza Gulf and possibly to other shallow gulfs (Taabu-Munyaho *et al.*, 2013). The overall heavy reliance on *Caridina*, as indicated by stable isotopes and by diet analysis, demonstrates the importance of *Caridina* prey in the Lake **(chapter 4 and 5).**

The food web in the Mwanza Gulf varied on a spatial and seasonal scale up to the highest trophic levels **(chapter 5)**. Littoral and pelagic based carbon sources were spatially mixed in the Mwanza Gulf during the dry season. However, with the onset of rains, carbon sources differentiated and the food web in the Mwanza Gulf became strongly influenced by littoral sources and high primary production. At the same time the food web in the offshore waters was mainly influenced by pelagic sources. This spatial differentiation concurred with a decrease in trophic diversity in food-web structure in the Mwanza Gulf. Trophic levels indicated an omnivorous diet for most fish species. Trophic levels of Nile perch and haplochromines varied according to variation in diet compositions. The overall food-web structure has not changed since the Nile perch boom in the 1980s, but the food-web structure in the Mwanza Gulf is highly dynamic on small spatial and seasonal scale.

The heterogeneity in the Mwanza Gulf and Lake Victoria

The most consistent finding of this research is the large spatial and seasonal heterogeneity in the water quality and in each level in the food web of the Mwanza Gulf. Water quality varied on a spatial and seasonal scale according to depth and seasons as described in other studies (Mugidde, 1993; Kling *et al.*, 2001; Silsbe *et al.*, 2006; Haande *et al.*, 2011). This heterogeneity was also observed in the distribution of Nile perch, Nile perch's trophic interactions and food web. The spatial and seasonal heterogeneity affecting the whole food web is an important finding and should be taken into account when considering measures aimed at management of fish stocks in Lake Victoria.

We chose the Mwanza Gulf as study area to investigate the effect of eutrophication on Nile perch through the food web. During the course of this research, the question was raised how representative the Mwanza Gulf is for Lake Victoria as a whole. Although the gulf is eutrophic, this study showed that its food web is highly influenced by littoral sources and its shallow depth. Neither of these influences is present in offshore waters which form the largest part of Lake Victoria.

The high productivity and Nile perch densities in the Mwanza Gulf indicate that shallow areas are important habitats for (juvenile) fish. These areas are also important for local fisheries and thus for the livelihood of people around the lake as most fishing is restricted in near distance from the shore (Peter, H.K. personal communication). Is the Mwanza Gulf representative for other gulfs in Lake Victoria? In Lake Victoria five gulfs are regularly studied for water quality (Fig. 3). Phytoplankton biomass in waters less than 20 m deep in the northern Napoleon Gulf and Murchinson Bay was 2.5 fold higher than in the southern and eastern gulfs, Nyanza Gulf, Speke Gulf and Mwanza Gulf (Fig. 4). This indicates that in Lake Victoria, inshore habitats vary in water quality. The northern Gulfs are more sheltered from winds because of the many islands in the gulfs, resulting in stronger stratification of the water column and therefore higher phytoplankton biomass (Kolding *et al.*, 2008). The Mwanza Gulf is relatively open with a minimum width of 3 km and only few islands and has therefore a more mixed water column. Morphometry of inshore areas and gulfs seems to be an important factor for the primary production rates (Silsbe *et al.*, 2006). In addition, monsoon winds and lake-wide convections create warmer waters and stronger stratification with higher phytoplankton biomass in the northern part of Lake Victoria and cooler, more mixed waters with lower phytoplankton biomass in southern Lake Victoria (Cózar *et al.*, 2012; MacIntyre, 2012).

Studies on Nile perch distribution in gulfs of Lake Victoria are limited to two gulfs: Mwanza Gulf and Speke Gulf. We showed that Nile perch densities and size structure varied considerably within and between these two gulfs **(chapter 3)**. Therefore, also on a small and large spatial scale, fish populations are quite heterogeneous, with the more eutrophic Mwanza Gulf harbouring the highest fish densities. However, environmental factors driving Nile perch distributions acted similarly on both spatial scales, within the Mwanza Gulf and between gulfs and open waters in south-east Lake Victoria **(chapter 3).** This indicates that despite large spatial heterogeneity in water quality and fish distributions, bottom-up processes driving the food web are similar, which makes the Mwanza Gulf a good representative for studying these processes in Lake Victoria.

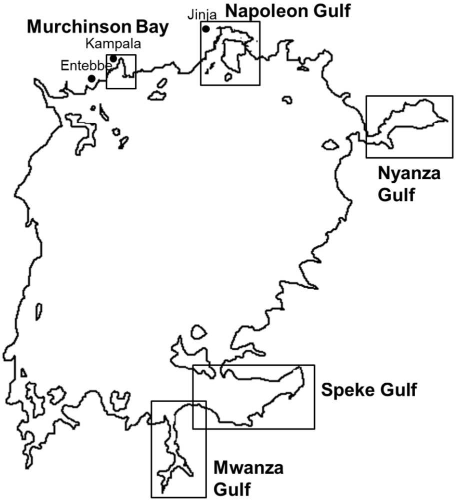

Figure 3: Map of Lake Victoria with frequently studied Gulfs and Bay.

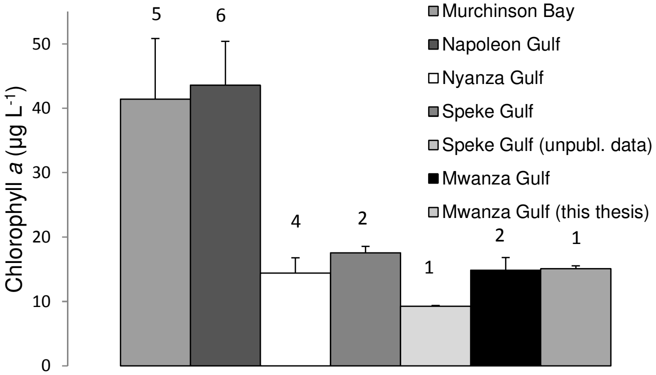

Figure 4: Chlorophyll concentrations of the studied Gulfs and Bay. Number of studies is indicated above the bars. Error bars represent standard deviations. Data from Murchinson Bay was from 2001-2005 (Silsbe *et al.*, 2006; Cózar *et al.*, 2007; Okello *et al.*, 2010; Haande *et al.*, 2011 and acoustic Lake Survey), Napoleon Gulf was from 1989-2003 (Lehman and Branstrator, 1994; Mugidde, 2001; Yasindi and Taylor, 2003; Silsbe *et al.*, 2006; North *et al.*, 2008; Okello *et al.*, 2010), Nyanza Gulf from 1984-2006 (Mavuti and Litterick, 1991; Lung'ayia *et al.*, 2000; Gikuma-Njuru, 2008 and acoustic Lake Survey), Speke Gulf from 2005 (Shayo *et al.*, 2011 and acoustic Lake Survey, Speke Gulf from 2009-2010 (H.K. Peter, unpublished data), Mwanza Gulf from 2005 (Shayo *et al.*, 2011 and acoustic Lake Survey) and Mwanza Gulf from 2009-2011 (this thesis).

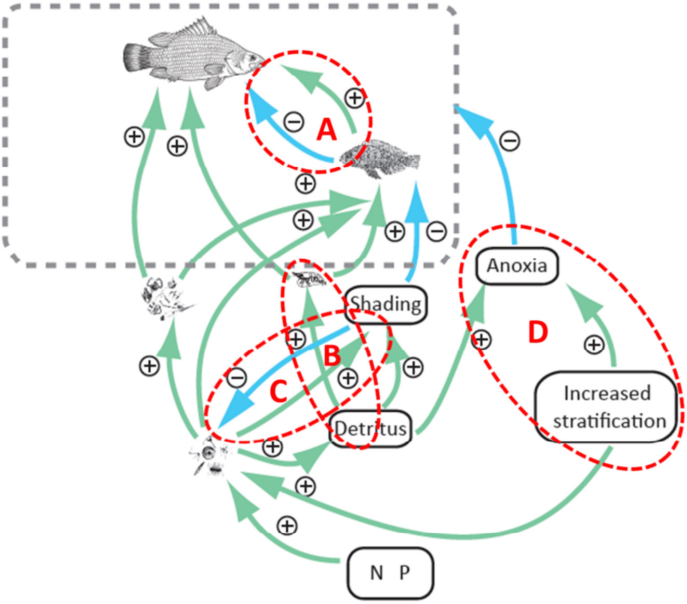

Figure 5: Ecological interactions in Lake Victoria, adjusted from Downing *et al.* (2014). Interactions indicate A: haplochromines positively affecting growth and negatively affecting recruitment of Nile perch, B: detritus as important food source for *Caridina,* C: phytoplankton limitation by self-shading and D: the effect of stratification on oxygen levels.

Is further eutrophication a threat for Nile perch and the Lake Victoria ecosystem?

In the following paragraphs, I will discuss the main interactions in the ecosystem of Lake Victoria in terms of future ecological developments and priorities for further research (Fig. 5).

The recovery of haplochromines and their increasing importance in Nile perch's diet affect Nile perch in two opposite ways (Fig. 5, Ellipse A,). Firstly, Nile perch grows faster on a haplochromine-based diet than on a *Caridina*-based diet (Kaufman and Schwarts, 2002; Downing *et al.*, 2013b), which will make the Nile perch stock more resilient to fishing mortality (Downing *et al.*, 2013b). Secondly, juvenile haplochromines may have a negative effect on the recruitment of Nile perch by predation on eggs and larval competition for food (Goudswaard *et al.*, 2008; Kolding *et al.*, 2008; van de Wolfshaar *et al.*, 2014). A reduced recruitment by haplochromines may counterbalance the reduced recruitment caused by cannibalism as observed in the Nile perch-dominated system from the 1980s and 1990s (Kishe-Machumu *et al.*, 2012). If the recovery of haplochromines continues, the effect on Nile perch will be two-fold: negative through recruitment suppression, and positive as a nutritious food source. The future of Nile perch and haplochromine stocks will depend (among other things) on the balance of these two factors.

Stratification and hypoxia have been the main focus by limnologists in Lake Victoria, as hypoxia is a direct physical threat for Nile perch and other life in Lake Victoria. This thesis demonstrated that detritus concentrations were high in the Mwanza Gulf. However, so far the detritus cycle in Lake Victoria is poorly understood (Downing *et al.*, 2012). This in spite of the importance of detritus as a food source for *Caridina*, an important food-web component, and for the development of hypoxia through sedimentation (Fig. 5, Ellipse B). The increased biomass of *Caridina* in Lake Victoria probably compensated for the declining detritivorous haplochromines and may have maintained detritus-processing rates (Downing, 2012). *Caridina* might be important for controlling accumulation of detritus and therefore hypoxia. It is suggested that *Caridina* is decreasing in biomass, caused by being caught as bycatch in the Dagaa fishery and because of pollution (Ngupula and Mlaponi, 2010). The long-term trends in *Caridina* biomass are however unknown in Lake Victoria. If a new regime shift towards increased stratification and high phytoplankton biomass occurs in Lake Victoria, it might benefit *Caridina,* because of increasing detritus accumulation. However, food quality of detritus may decrease, as decaying phytoplankton blooms often consist of toxic cyanobacteria. It is unknown what the effect of detritus quality is on *Caridina* (Goudswaard *et al.*, 2006).

The main hypothesis of the SEDEC programme was that the increasing eutrophication and primary production facilitated the increasing fish production and in particular the Nile perch stock (Kolding *et al.*, 2008; Hecky *et al.*, 2010). However, it was expected that with further eutrophication, nutrients would become available in excess and phytoplankton production would become light-limited so that further eutrophication would not lead to further increased productivity (Kolding *et al.*, 2008) (Fig. 5, Ellipse C). Clearly the latter stage was not reached in the Mwanza Gulf, although other studies indicate this was the case in some highly eutrophic northern gulfs (Mugidde, 1993; Silsbe, 2004; Hecky *et al.*, 2010).

We believe that the relatively low-eutrophic status and the improvement of water quality since the 1990s in the Mwanza Gulf are based on climatic forcing (Kolding *et al.*, 2008; MacIntyre, 2012) (Fig. 5, Ellipse D). A drop of wind speeds, changing wind direction and increasing differences between surface and bottom water temperatures resulted in increased stratification and coincided with a decrease in water visibility and oxygen levels in the Mwanza Gulf in the 1980s (Kolding *et al.*, 2008; van Rijssel, 2014). The increased wind speeds after 1990s probably weakened stratification and increased visibility in the Mwanza Gulf again. In other words, the increased mixing after the 1990s might have counter-acted the effect of ever-increasing nutrient loads in the Mwanza Gulf. Therefore the 'water quality' in terms of high water transparency and low chlorophyll concentrations improved since the 1990s (Sitoki *et al.*, 2010), but a new episode of decreased wind speeds and decreased mixing might cause a new, sudden shift in the ecosystem, resulting in algal blooms, anoxia, and decreased fish stocks (van Zwieten *et al.*, in review). In general, global climate change towards warmer temperatures affect tropical lakes most, with increasing stratification of the water column (Kraemer *et al.*, 2015). Together with changes in wind speed and lake levels, these factors will determine the future environment of Lake Victoria. In some way the absence of strong algal blooms and hypoxia during the SEDEC-years may have misled us: in the meantime the continued nutrient loading works as an invisible "assassin", which will "kill" the ecosystem as soon as environmental circumstances allow it.

Limitations and recommendations

Two aspects of the Nile perch-haplochromine interaction are not understood well and should be investigated in depth (Fig. 5, Ellipse A). The counteracting effect of haplochromines on Nile perch (negative effect on recruitment and positive effect on Nile perch growth) is important in the present situation of recovering haplochromines and increasing haplochromines in the Nile perch's diet. However, how strong these effects are on the Nile perch stock, is unknown. Although we found fish eggs in stomachs of several adult haplochromines, it was never thoroughly analysed whether juvenile haplochromines also prey on fish eggs (Goudswaard *et al.*, 2008). Simple research on the diet of juvenile haplochromines should give more insight on the predation rates on Nile perch eggs and competition between haplochromine and Nile perch larvae (Table 1). Experimental work on Nile perch feeding on *Caridina* versus haplochromines might give accurate values on growth rates. This information can then be used for models to predict future Nile perch stocks.

Although investigating and understanding a food web's detritus cycle is an incredibly difficult task, future research should undertake small steps to unravel the energy transfer and importance of detritus in Lake Victoria's food web. *Caridina* is a major link between detritus and higher trophic levels (Fig. 5, Ellipse B). So far a first step was taken to investigate this link by analysing the diet of *Caridina* and its growth in Lake Victoria by simple, replicable experiments (Hart, 2001; Hart *et al.*, 2003)

(Table 1). Repeating those experiments under varying levels of eutrophication would give insight in the variation in growth rates and relation to food quantity and quality of detritus in the Lake.

Table 1: Overview of research done and suggestions for future research

	Interaction	Models	Fieldwork / time series analysis	Experiments
A	Nile perch – haplochromine interactions	Downing *et al.* (2013a), Downing *et al.* (2013b), van de Wolfshaar *et al.* (2014), van Zwieten *et al.* (in review)	Kolding *et al.* (2014); Cornelissen *et al.*, (in prep.), Kishe-Machumu *et al.* (2012): predation by NP To be done: stomach contents of juvenile haplochromines	To be done: Growth experiments of Nile perch on different diets
B	Detritus – *Caridina*	To be done: developing a model which predicts detritus-processing rates based on the detritus-*Caridina* food chain	Hart (2001) and Hart, Campbell L.M and Hecky (2003): In situ experiments on diet and growth	To be done: Growth experiments of *Caridina* with varying water quality
C	Phytoplankton – shading interactions	To be done: PC-Lake models	(Cornelissen *et al.*, 2014)	Lehman and Branstrator (1993), Guildford *et al.* (2003) To be done: Enclosure experiments on nutrient and light limitations
D	Climatic forcing – anoxia and stratification interactions	To be done: stratification models based on morphology and climatic changes in temperature and wind speed (Kraemer *et al.*, 2015)	Kolding *et al.* (2008), van van Zwieten *et al.* (in review). To be done: effect of morphometry on water quality	Not applicable

This thesis elucidated the limitations of phytoplankton biomass in a present state in the Mwanza Gulf (Ellipse C, Fig. 5), but experimental work may be useful to predict when maximum primary production rates are reached in Lake Victoria. So far, experimental work on phytoplankton growth is limited to two studies (Lehman and Branstrator, 1993; Guildford *et al.*, 2003) (Table 1). Preliminary results of phytoplankton-limitation experiments conducted during this research showed that under the right light conditions, present nutrient concentrations are limiting phytoplankton biomass. Increasing nutrient load will further increase phytoplankton biomass under the right mixing and light conditions. Information on limitations in phytoplankton growth experiments might be used for eutrophication models such as PC-Lake (Janse, 2005) to predict future environmental conditions in Lake Victoria (Table 1).

It is very important to investigate the influence of climate change on the eutrophication in Lake Victoria (Table 1). Global temperature increase and changes in wind patterns are key factors shifting the Lake towards a potential eutrophied, turbid system. In large lakes eutrophication affects inshore areas most, depending on morphometry, whereas offshore areas are more gradually affected (Beeton and Edmondson, 1972). Therefore, the effect of morphometry on stratification and water quality should be further investigated to understand spatial variation in water quality and hypoxia. The information on morphometry, wind changes and temperature are useful in models to predict eutrophication in Lake Victoria (Kraemer *et al.*, 2015) (Table 1).

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Summary

Lake Victoria has undergone major changes during the last century. The main drivers of these changes are the increasing eutrophication, the introduction of Nile perch *(Lates niloticus)* and the increasing fishing pressure. Since the 1960s, eutrophication increased primary production, enabling a strong increase in fish production. However, eutrophication also created hypoxia pockets, which reduced the available habitats for fish and occasionally led to mass fish kills. In addition, Nile perch, which was first introduced in the 1950s and 1960s, boomed in the 1980s, after which Lake Victoria turned into a simplified food web. The high diversity of endemic haplochromines declined whereas Nile perch, tilapia, endemic Dagaa (*Rastrineobola argentea)* and *Caridina nilotica* shrimp became dominant. The Nile perch boom and the increased overall fish production resulted in the largest freshwater fisheries of the world. However, it is unclear whether primary production can still increase further or that it has already reached a maximum. Fish stocks fluctuate since the 1980s and in order to manage these, it is important to understand how eutrophication and fisheries affect the Nile perch populations via the food web. The present study aimed at understanding the bottom-up effects of further eutrophication on the Nile perch and food-web dynamics in general.

We chose the Mwanza Gulf in the south-eastern part of the lake to study the food web along an eutrophication gradient from deep, offshore waters to inshore waters in the Gulf. We analysed the level of eutrophication along the gradient and the limitations of phytoplankton growth **(chapter 2)**. We concluded that inside the Gulf, nutrients were in excess and phytoplankton production was light-limited, which can be partially explained by the phytoplankton biomass and the high suspended detritus concentrations in the water. Outside the Gulf, light was not limited, but nutrients were. The relatively low phytoplankton biomass compared to other parts of Lake Victoria was explained by a higher frequency of complete water-column mixing which was caused by a relatively low stability of stratification.

In **chapter 3**, Nile perch size-structure and distributions were related to environmental factors, such as depth, temperature, visibility, oxygen and prey abundance at different spatial scales. Nile perch distributions were mainly driven by depth and temperature, but the effect was also dependent on the size class of the Nile perch. Small Nile perch was driven by temperature, while larger Nile perch were mostly driven by depth. Abiotic factors explained Nile perch distributions and size-structure in a similar way on a small spatial scale within the Mwanza Gulf and on a regional scale (Mwanza Gulf, Speke Gulf and Sengerema). Prey densities of *Caridina* shrimp and haplochromines did not explain Nile perch distributions, but diet composition varied on a spatial scale. Nile perch fed on *Caridina* in open waters and

haplochromines in inshore waters, which suggest an opportunistic feeding behaviour.

To further investigate the diet interactions of Nile perch, we analysed ontogenetic diet shifts using stomach contents and stable isotopes **(chapter 4)**. Results showed that the length at which Nile perch switches from *Caridina* to fish prey, varied spatially and was highly related to prey densities of *Caridina* and haplochromines. Small Nile perch had a slight preference towards *Caridina*, only shifting to fish when *Caridina* was present at very low densities. Nile perch preferred haplochromines above Dagaa and juvenile Nile perch, which were also abundant in the Gulf. The recent recovery of haplochromines and their increasing importance in the Nile perch diet might create a new balance of co-existence between Nile perch and its prey species.

Finally, we used stable isotopes and derived community metrics to analyse the food-web structure of the Mwanza Gulf **(chapter 5)**. Fish taxa in the Mwanza Gulf showed a highly omnivorous diet with a heavy reliance on invertebrates. The base of the food web, i.e. the carbon source, varied on spatial and seasonal scale and affected the whole food web. The onset of the rains caused a spatial differentiation in carbon source, with a strong littoral/benthic/high primary production influence in shallow waters and pelagic influence in deep waters. The food web during the rains was characterized by a low trophic diversity. The dry season was characterized by mixed carbon sources and higher trophic diversity. Trophic levels of Nile perch and haplochromines varied spatially according to spatial variation in diet compositions. We conclude that the food-web structure and trophic interactions in the Mwanza Gulf are highly dynamic.

Although we found a large spatial heterogeneity in water quality, fish distributions and food-web structure, bottom-up processes affect the food web similarly, which makes the Mwanza Gulf an excellent area to study the effects of eutrophication. Maximum primary production rates in the Mwanza Gulf are not reached yet, despite the ongoing nutrient load in Lake Victoria. Climate forcing through increasing wind speeds was the main cause for the improved water quality in terms of visibility and oxygen levels since the 1990s. This means that if global warming continues and the extent of stratification would increase in the future, Lake Victoria may shift back to a more turbid and hypoxic state.

Samenvatting

Het Victoriameer is sterk veranderd gedurende laatste eeuw. De voornaamste redenen zijn de toenemende eutrofiëring, de introductie van Nijlbaars *(Lates niloticus)* en de toenemende visdruk. De eutrofiëring leidde tot een verhoogde primaire productie sinds de jaren 60 van de vorige eeuw, waardoor de visproductie sterk toenam in het meer. De eutrofiëring leidde echter ook tot een laag zuurstofgehalte in de diepere waterlagen, waardoor het habitat van vis gereduceerd werd en incidenteel zelfs grote vissterfte veroorzaakte in het meer. De in 1950-60 geintroduceerde Nijlbaarspopulatie groeide explosief vanaf de jaren 80, waarna het voedselweb van het Victoriameer sterk vereenvoudigd werd. De diverse, endemische haplochromine cichliden vedwenen nagenoeg, terwijl Nijlbaars, tilapia, Dagaa (*Rastrineobola argentea)* en *Caridina nilotica* garnalen dominant werden in het voedselweb. De explosieve Nijlbaarsgroei en de algehele toegenomen visproductie resulteerden in 's werelds grootste zoetwater visserij. Het is echter niet duidelijk of de primaire productie nog steeds stijgt, of dat er een maximum is bereikt. De visstand in het meer fluctueert sinds de jaren 90 en om deze op een goede wijze te beheren, is het belangrijk om grip te krijgen op hoe eutrofiëring en visserij de Nijlbaarspopulatie beïnvloeden via het voedselweb. Dit proefschrift onderzoekt de bottom-up effecten van verdere eutrofiëring op de Nijlbaars en het voedselweb.

We hebben de Mwanza Golf in het zuid-westen van het meer geselecteerd om het voedselweb langs een eutrofiërings-gradient van het diepe, open water naar het littorale, ondiepe water in de golf te bestuderen. In **hoofdstuk 2** hebben we de mate van eutrofiëring langs de gradient in de golf en de limitaties van fytoplanktongroei geanalyseerd**.** We concludeerden dat in het ondiepe water in de golf nutrienten in overvloed waren en dat productie van fytoplankton lichtgelimiteerd was. Dit werd ten dele verklaard door de fytoplanktonbiomassa en de hoge concentratie van gesuspendeerde detritus in het water. Buiten de golf was er geen sprake van lichtlimitatie, maar waren vooral nutrienten limiterend. The relatieve lage fytoplanktonbiomassa in vergelijking met andere delen van het Victoriameer werd verklaard door een hogere frequentie van complete menging van de water kolom, veroorzaakt door een relatief instabiele stratificatie.

In **hoofstuk 3** onderzochten we de relatie tussen de lengteverdeling en verspreiding van Nijlbaars en omgevingsfactoren zoals diepte, temperatuur, troebelheid, zuurstofgehalte en prooidichtheid op verschillende ruimtelijke schalen. De verspreiding van Nijlbaars werd vooral beïnvloed door diepte en temperatuur, maar het effect was ook afhankelijk van de lengteklassen van Nijlbaars. Kleine Nijlbaarzen werden vooral door temperatuur beïnvloed, terwijl grotere Nijlbaarzen vooral door diepte werden beïnvloed. Abiotische factoren verklaarden de verspreiding en lengteverdeling van Nijlbaars op dezelfde wijze op lokale ruimtelijke schaal in de Mwanza Golf en op regionale schaal (Mwanza Golf, Speke Golf en Sengerema). Prooidichtheden van *Caridina* garnalen en haplochromine cichliden konden de verspreiding van Nijlbaars niet verklaren, maar de dieetsamenstelling varieerde op een ruimtelijke schaal. Nijlbaarzen aten vooral *Caridina* in het open water en haplochrominen in het ondiepe water in de golf, wat een opportunistisch fourageergedrag suggureert.

Het dieet van Nijlbaars werd verder onderzocht door ontogenetische verschuivingen in het dieet te analyseren met behulp van maaginhouden en stabiele isotopen (**hoofdstuk 4).** We vonden dat de lengte waarbij Nijlbaars van *Caridina* naar visprooi switcht, ruimtelijk varieerde en sterk gerelateerd was aan prooidichtheden van *Caridina* en haplochrominen. Kleine Nijlbaarzen hadden een lichte voorkeur voor *Caridina* en switchten alleen naar vis wanneer *Caridina* in zeer lage dichtheden voorkwam. Nijlbaars prefereerde haplochrominen boven Dagaa en juveniele Nijlbaars die ook abundant waren in de golf. De recente terugkeer van haplochrominen en hun toenemende invloed in het dieet van Nijlbaars zou tot een nieuw evenwicht kunnen leiden van co-existentie tussen Nijlbaars en zijn prooisoorten.

Tot slot hebben we met behulp van stabiele isotopen en afgeleide community metrics de voedselwebstructuur van de Mwanza Golf geanalyseerd **(hoofdstuk 5).** De vis taxa in de Mwanza Golf hadden vooral een omnivore dieetsamenstelling , waarvan invertebraten een grote invloed hadden. De basis van het voedselweb, (de koolstofbron), varieerde in ruimte en seizoenen en beïnvloedde het gehele voedselweb. Het begin van de regens veroorzaakte een ruimtelijke differentiatie van koolstofbronnen, met een sterk littoraal-benthische invloed in het ondiepe water in de golf en pelagische invloed in het diepe, open water. Tijdens de regenseizoenen werd het voedselweb gekarakteriseerd door een lage trofische diversiteit. Het droge seizoen werd gekarakteriseerd door gemengde koolstofbronnen en hogere trofische diversiteit. De trofische niveaus van Nijlbaars en haplochrominen in het voedselweb varieerde in ruimte, overeenkomstig met ruimtelijke verschillen in dieetsamenstelling. Wij concluderen dat de voedselwebstructuur en trofische interacties sterk dynamisch zijn in de Mwanza Golf.

Ondanks dat we een grote ruimtelijke heterogeneiteit in waterkwaliteit, visverspreiding en voedselwebstructuur gevonden hebben, beïnvloeden de bottom-up processen het voedselweb op dezelfde wijze in de ruimte. Dit maakt van de Mwanza Golf een geschikte locatie om de effecten van eutrofiëring te bestuderen. Maximale primaire productie is nog niet bereikt in de Mwanza Golf, ondanks de toenemende nutriententoevoer in het Victoriameer. Klimaatverandering door toenemende windsnelheden was de voornaamste reden voor de verbeterde waterkwaliteit sinds 1990 als het gaat om troebelheid en zuurstofgehaltes. Dit betekent dat als de aarde verder opwarmt en de stratificatie van de waterkolom stabieler wordt in de toekomst, het Victoriameer weer terug kan veranderen in een meer troebele en hypoxische staat.

Acknowledgements

I was only able to complete this PhD with the help of others. I am grateful for the enthusiasm of people involved in this research and take this opportunity to thank them.

This PhD was part of the SEDEC (disentangling the social and ecological drivers of ecosystem change in Lake Victoria) programme. I would like to thank Paul van Zwieten, for leading this project, for your logistic support and your contributions to the Nile perch distribution paper. Also thanks to the SEDEC scientific committee for their advice.

I am deeply grateful to my daily supervisors Leo and Koos, whose influence was immense during my PhD. You are a supervising dream-team, you were always on the same page with your feedback and complemented each other. Leo, thanks for your straightforward and smart advice, you are a true teacher. Your feedback always motivated me to dig deeper. Thanks for always having time to skype or phone, even in evenings or weekends. Koos, thanks for your valuable guidance and your to-the-point-and–practical feedback on papers and in the field. Thanks for your huge help in the field and lab. I always looked forward to your visits in Mwanza: working late in the limnolab, enjoying sunsets and drinks at Gonza or eating the best grilled chickens at Nyegezi's street corner.

I would like to thank my promotors Ellen van Donk and Johan Verreth for their advice and contribution to the papers. Johan, thanks for your great involvement and support, especially this last year. The numerous skype-dates helped me to focus and kept me motivated to stick to the ultimate deadline for submitting this thesis.

Happy, Andrea and Modesta, thanks for joining me in this PhD-adventure, for your support and the productive cookie-discussions. Modesta, thanks for your support during my time in Tanzania, without you, I would have probably ended up homeless or in jail. Also, Christmas, birthdays and new years were not lonely thanks to you and your lovely, warm family.

Andrea, you inspired me in so many ways! Thanks for your valuable discussions and great ideas, your enthusiasm and creativity are endless! We also became good friends since we first met at AFI. We had some crazy adventures, from swimming with sharks and hippos, Monty-python-Jacuzzi-nights to our 'biltong' road trip through Africa. Thanks for coming over to celebrate with me and for being my paranimph.

I would like to thank Egid Katunzi and the staff of TAFIRI for facilitating my field work in Mwanza. Godfrey, thank you for your keen interest in this research, your help and supply for building the ponds and for introducing me to the lovely people of Sweya. Many thanks to Emma, Rajabu, Mangassa, Abel and (in memory of)

Paulo, for all your crazy, hard work with me in the field and at TAFIRI. Even with stormy weather and leaking raincoats, we had great fun on the Lake. I really appreciate you for bringing me into your homes and families and for the good times after working hours at Gonza. Nawatakia wote bora! Mama Lucy, thank you for the best chapatis in Mwanza to keep us running and focussed on the Lake all day. Mashafi, thanks for being a friend and for introducing me to Gonza. Salome, thanks for helping me at home, so I could entirely focus on my fieldwork, but above all, thank you for your warm personality and great company.

I would like to thank MSc. students André van den Beld, Benedicto Kashindye, Jeroen Demmer, Christian Hazenoot, Papius Tibihika and Quincy de Bruijn for working together with me on this project in the Netherlands and in Mwanza. You all helped me a lot and it was great fun. André, thanks for the sightseeing tours up the Mwanza hills and for your excellent baking skills, the pepernoten and arretjescake were a welcoming change in my daily diet of chapatis, beans and rice.

Greg Silsbe, thanks for your huge contribution to the first paper on phytoplankton dynamics, your comments and advice improved the paper tremendously.

To my Wageningen office-mates, Konrad, Monica, Julia, Bob, An, Grace, Happy, Catarina, Gonçalo, Pascal, Christos, Vasco, Mirjam, Stefan, Saravanan, Andre, Marit and Mahmoud, thanks for all the fun at the office and the lovely PhD dinners. Konrad and Monica, thanks for the gezellige cigarette breaks and company!

I would like to thank some persons for their huge practical support. Ronald Booms, thank you for helping to purchase and ship all laboratory and field equipment to Tanzania and for keeping me supplied with chemicals during my field work there. Helene, Linda, Gera and Eugenia, thanks for all the office-support and your company at the office. I like to thank Theo Frank for identifying and analysing phytoplankton, a most difficult and time-consuming job (for which I tried and failed miserably). Nico Helmsing and Hans Hoogveld, thanks for analysing the huge bulk of stable isotope samples. Thanks to Suzanne Wiezer for the numerous phytopam-analyses. Kenneth van Lith, thanks for helping me at the lab in Wageningen. I would like to thank Mr. Kessy for his help in analysing water samples in Mwanza. In memory of Frans Witte, who taught me all about haplochromines and trawling and who shared his great stories on the old Mwanza and Lake Victoria with me.

I also want to thank my best friends Floor, Barbara and Chris for their support all these years. It was nice to have a life besides this PhD. Thanks Barbara for your always useful advice and for being my paranimph. Chris, it comforted me that I was

not the only one working late evenings and during weekends these last couple of years.

Thanks to my parents and sister for your confidence and huge support. You always believed that I could do anything I want, even if I did not believe it myself. Thanks to my parents, Marlienke, Klaas and Tjalling and Tineke for taking care of the children when I needed time to work.

And lastly, I don’t know where to begin with expressing my gratitude to you, Klaas. In all these years you supported me both mentally and practically in each step of this long journey. We’ve survived being apart for two years when I was in Mwanza. The times you were ‘on holiday’, visiting me in Tanzania, you worked most of the time in the lab or in the field. Even gutting fish while you hate the smell of it did not scare you off, you always came back. When I went back to Holland you supported me whenever you could from taking care of the children, checking and formatting papers to keeping me motivated and sane. I love you, you’re the best!

Curriculum vitae

Ilse J.M. Cornelissen was born in 1977 in Lichtenvoorde, the Netherlands. After high school, she studied Biomedical Chemistry at Hogeschool Ijsselland in Deventer. Because she was more interested in biology than chemistry, she switched after two years in 1998 to study Biology at the University of Nijmegen. She wanted to go abroad to do her MSc. thesis, so she went to Zanzibar to study juvenile reef fish ecology in mangroves. After her graduation in 2003, she worked as an assistant teacher at the University of Nijmegen. From 2005 to 2006, she went back to the tropics to work for a NGO as an assistant research coordinator in Tanzania. As part of a marine programme, she trained volunteers to monitor reefs and fish in and around marine parks in Tanzania. Furthermore, she implemented an environmental education programme at primary schools at Mafia Island. Back in the Netherlands, she worked for a pharmaceutical company before she started her PhD in 2008 at Wageningen University, where she studied Nile perch and the food web of Lake Victoria in Tanzania.

Training and supervision plan

Training and Supervision Plan — Graduate School WIAS

Name PhD student	Ilse Cornelissen
Project title	Eutrophication, Nile perch and food-web interactions in south-east Lake Victoria
Group	Aquaculture and Fisheries

The Basic Package — 3 ECTS

WIAS Introduction Course
Course on Ethics and the public role of life scientists

Scientific Exposure — 10 ECTS

International conferences

31st Congress of the International Society of Limnology (SIL), Cape Town, SA, 15-20 Aug 2010

Netherlands Annual Ecology Meeting (NAEM), Lunteren, the Netherlands, 7-8 Feb 2012

14th European congress of Ichthyology, Liege, Belgium, 3-8 July 2012

Seminars and workshops

Scientific workshop SEDEC programme Lake Victoria, Wageningen, 15-16 Jan 2009

Scientific workshop SEDEC programme Lake Victoria, Mwanza,Tanzania, 19-20 May 2010

Presentations

Presentation at Scientific workshop SEDEC Programme Lake Victoria, Wageningen, 15-16 Jan 2009

Oral paper at 31st Congress of the International Society of Limnology (SIL), Cape town, 15-20 Aug 2010

Presentation at Scientific workshop SEDEC Programme Lake Victoria, Mwanza, 19-20 May 2010

Poster at Netherlands Annual Ecology Meeting (NAEM), Lunteren, 7-8 Feb 2012

Oral paper at 14th European congress of Ichtyology, Liege, Belgium, 3-8 Jul 2012

In-Depth Studies **6 ECTS**

Disciplinary and interdisciplinary courses
Research Methodology I: from topic to proposal
Statistics for Life Sciences

Statutory Courses **4 ECTS**

Laboratory Animal Science
Subtotal Statutory Courses

Professional Skills Support Courses **3 ECTS**

Techniques for Writing and presenting a scientific paper
Project and time management
Career assessment

Research Skills Training **6 ECTS**

Preparing own PhD research proposal

Didactic Skills Training **12 ECTS**

Supervising theses

"Variability in the diet of Nile perch *(Lates niloticus)* in the Mwanza Gulf of Lake Victoria: Long-term, spatial and seasonal diet shifts and prey selectivity." MSc. thesis 2010, Andreas van den Beld

"Spatial distribution and diet overlap of Dagaa *(Rastrineobola argentea)*, zooplanktivorous haplochromine cichlids and juvenile Nile perch *(Lates niloticus)* in Mwanza Gulf, Lake Victoria." MSc. thesis 2011, Quincy de Bruijn

"Selective feeding and distribution of the cyprinid *Rastrineobola argentea* along an eutrophication gradient in Mwanza Gulf (Lake Victoria), Tanzania." Minor thesis 2011, Papius Tibihika

"Effect of eutrophication on phytoplankton in the Mwanza Gulf (Lake Victoria, Tanzania) – a mesocosm and modeling study." MSc. thesis 2011, Christian Hazenoot

“Seasonal and spatial fluctuations of Nile perch abundance and biomass in Mwanza Gulf, Lake Victoria.” MSc. thesis 2011, Benedicto Kashindye

"The influence of morphology on the diet of haplochromine cichlids in the Mwanza Gulf, Lake Victoria." MSc. thesis 2012, Jeroen Demmer

Education and Training Total **44 ECTS**

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

Colophon

This work is part of the integrated project "Exploitation or eutrophication as threats for fisheries? Disentangling social and ecological drivers of ecosystem changes in Lake Victoria (SEDEC)", supported by the Netherlands Organisation for Scientific Research (NWO/WOTRO) grant number W01.65.304.00.

Cover design by Studio Lakmoes

Printed by CPI Koninklijke Wöhrmann

Propositions

1. Despite spatial and seasonal heterogeneity in water quality and food-web structure, the distribution of Nile perch is driven by the same factors at small and large spatial scales (this thesis).
2. Food-web metrics derived from stable isotopes are not only useful for identifying large differences between ecosystems, but also for monitoring small-scale changes in the food web (this thesis).
3. Culturing genetically modified crops may help to mitigate climate change.
4. Introduction of exotic species is the greatest threat to biodiversity, although it can be a success for local economy.
5. The eventual benefits for pharmaceutical companies of distributing high-cost medicines for affordable prices in developing countries will outweigh initial financial losses.
6. Poverty enslaves people.
7. This PhD took as long as for Nile perch to grow 109 cm.

Propositions belonging to the thesis

“Eutrophication, Nile perch and food-web interactions in south-east Lake Victoria”

Ilse Jelke Maria Cornelissen

Wageningen, 9 November, 2015