Author: Kishe-Machumu, Mary Alphonce
Title: Inter-guild differences and possible causes of the recovery of cichlid species in Lake Victoria, Tanzania
Date: 2012-09-26

Inter-guild differences and possible causes of the recovery of cichlid species in Lake Victoria, Tanzania

Kishe-Machumu, Mary Alphonce

Inter-guild differences and possible causes of the recovery of cichlid species in Lake Victoria, Tanzania

Dissertation Leiden University

An electronic version of this thesis in Adobe PDF-format is available at:
https://openacces.leidenuniv.nl/dspace/

Front cover	Sunset across Nyegezi Bay, Mwanza Gulf, seen from TAFIRI (by Frans Witte)
Cover design and layout	Mary A. Kishe-Machumu & Jacco C. van Rijssel
Printed by	Mostert & Van Onderen!, Leiden
ISBN/EAN	978-94-9085811-7

Inter-guild differences and possible causes of the recovery of cichlid species in Lake Victoria, Tanzania

PROEFSCHRIFT

ter verkrijging van

de graad van Doctor aan de Universiteit Leiden,

op gezag van Rector Magnificus Prof. Mr. P.F. van der Heijden,

volgens besluit van het College voor Promoties

te verdedigen op woensdag 26 september 2012

klokke 13:45 uur

door

Mary Alphonce Kishe-Machumu

geboren te Moshi, Kilimanjaro, Tanzania

in 1970

Promotiecommissie

Promotor: Prof. Dr. Michael K. Richardson
Copromotoren: Dr. Jan H. Wanink
Dr. Frans Witte

Overige leden: Prof. Dr. Carel J. ten Cate
Prof. Dr. Petrus G. L. Klinkhamer
Dr. Leo A. J. Nagelkerke (Wageningen University)
Prof. Dr. Menno Schilthuizen
Prof. Dr. John J. Videler (Groningen University)
Dr. Jacobus Vijverberg (Netherlands Institute of Ecology)

This work was supported by the Netherlands Foundation for Scientific Research in the Tropics and Developing Countries (NWO-WOTRO, grant no. WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC) and the International Foundation for Science (IFS, Sweden). Additional financial support came from the Schure Beijerinck-Popping Fonds.

To my son Elias-Jr and my daughter Juliah

Contents

Chapter 1

General introduction and outline of the thesis

LAKE VICTORIA AND ITS HISTORY

Lake Victoria is the largest tropical lake in the world (Fryer & Iles 1972) and has a surface area of 68,800 km^2. It is located between latitudes 00^0 20'N - 03^0 00'S and longitudes 31^{0}39'E - 34^0 53'E (Fig. 1.1) and situated at an altitude of 1134 m above sea level (Hecky & Bugenyi 1992). Its waters are shared by three East African riparian states; Tanzania (51%), Uganda (43%) and Kenya (6%) (Fig. 1.1). The shape of the lake resembles a rectangular of 400 x 320 km. The lake has a shoreline of 3300 km (Greenwood 1974) and a catchment area of almost 200,000 km^2 extending to Rwanda and Burundi through the Kagera River, and lies at the head of the Nile River basin system. A great part of the lake is relatively shallow with a mean depth of 40 m and a maximum depth of about 70 m (Stager & Johnson 2008). Lake Victoria is shallow compared to other *African Great Lakes* – Malawi/Nyassa (704 m deep) and Tanganyika (1470 m deep). The lake receives nearly 80% of its water inputs from rain directly to the surface; a similar amount is lost through evaporation (Bootsma & Hecky 1993). The lake bottom is mainly covered by a thick layer of organic mud with patches of hard substrate, sand, shingle or rock (Scholz et al. 1990). The shoreline is extremely irregular with numerous bays and gulfs, and many of the bays end in dense papyrus swamps.

Lake Victoria came into existence as a result of tectonic uplifting 400,000 years ago (Johnson et al. 2000). A period of drought that occurred between 18,000 and 14,000 years ago caused a serious drop in lake water and according to the latest data, the lake dried up and started to fill up again ca. 15,000 years ago (Johnson et al. 1996), an observation disputed by Fryer (2004). It is unclear whether the lake was completely dry during this desiccation event or if some remnant waters were present (Fryer 2001; Seehausen 2002; Fryer 2004; Stager & Johnson 2008). Among the *African Great Lakes*, Lake Victoria is the youngest. Lake Tanganyika which has been estimated to be 9–12 million years old (Cohen et al. 1993) is considered to be the oldest, while Lake Malawi is the second with an estimated age of 1–2 million years (Fryer & Iles 1972).

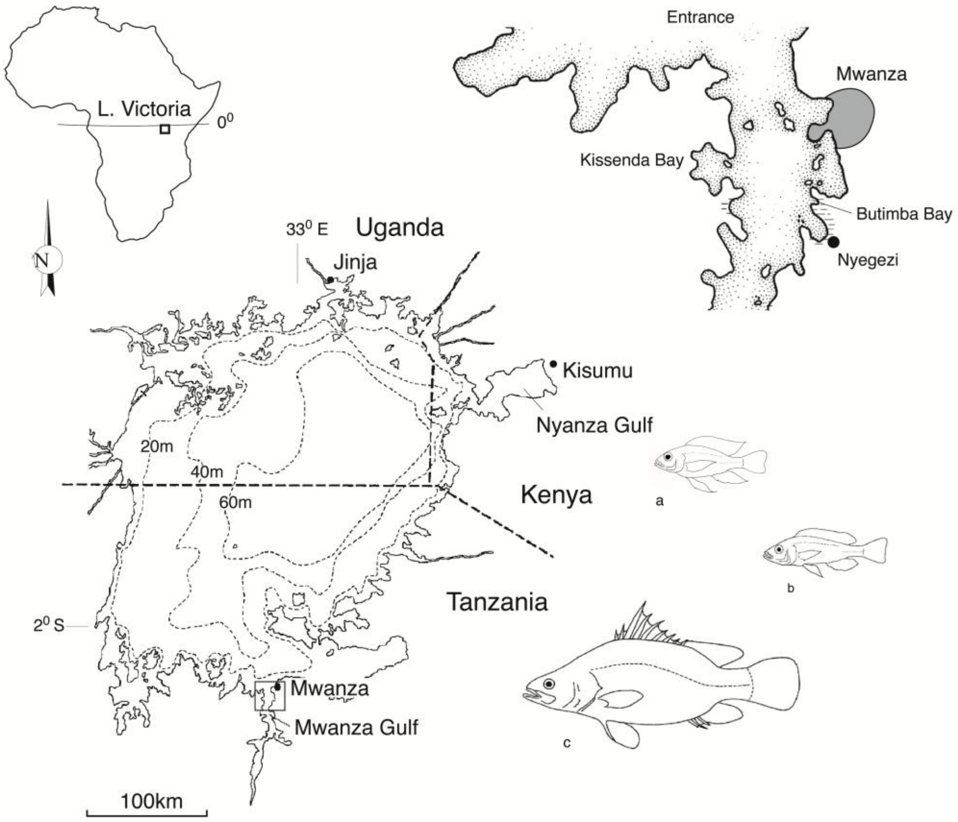

Fig. 1.1 Map of Africa showing the location of Lake Victoria and the study area in the Mwanza Gulf, with the main fish taxa featuring in this thesis: a, detritivorous haplochromine; b, zooplanktivorous haplochromine; c, Nile perch.

FISH FAUNA, FISHERIES AND FISH INTRODUCTIONS

Lake Victoria supports one of the world’s most productive inland fisheries with a total catch of about 1million tonnes per annum. It supports about 30 million lakeshore inhabitants (Ntiba et al. 2001) and the catch is valued at more than US$ 400 million which includes US$ 250 million in exports contributing 3-5% of the total Gross Domestic Product (G.D.P.) of the three riparian countries (Ogutu-Ohwayo & Balirwa 2006).

The most distinctive feature of Lake Victoria’s fish fauna was the high diversity of endemic haplochromine cichlids, of which 500+ species have been found (Kaufman et al. 1997; Witte et al. 2007a). Those fish dominated the lake during the pre-Nile perch period, but the upsurge of Nile perch in the mid 1980s had a dramatic effect on them. Their numbers were greatly reduced and many species had apparently been driven to extinction (Barel et al. 1985; Witte et al. 1992a, 2007b). The apparent destruction of the endemic haplochromine species-flock in Lake Victoria was one of the most controversial aspects of the species introductions and invasions into the ecosystem that attracted widespread criticism (Ribbink 1987; Bruton 1990).

Haplochromines have been very successful ecologically and showed an extreme level of adaptive radiation. They occupied most habitats in the lake and utilised almost all available food sources (Greenwood 1974; Witte & van Oijen 1990; Seehausen 1996). Trophic specializations encompassed by the haplochromines included among others detritivory, zooplanktivory, insectivory, molluscivory, phytophagy and piscivory in various forms. Within each of these broad trophic divisions, there were further sub-divisions of specialization. For instance, the mollusc eaters may crush their prey between hypertrophied pharyngeal bones and teeth, or between the oral jaws, or they may lever the snail’s body from its shell before ingesting the soft parts. One group of piscivores, the paedophages, had specialised in feeding on haplochromine embryos and larvae removed from the buccal cavity of brooding female fishes. The great majority of piscivores, however, were predators on free-living haplochromines. In the 1970s, at least 15 (sub)-trophic groups had been identified among the Lake Victoria haplochromines. Each trophic specialization was represented by several species and the number of species per trophic group differed considerably (Greenwood 1974; Witte & van Oijen 1990; Seehausen 1996). Before the 1980s, piscivores and insectivores were the most common groups in terms of the number of species whereas, concerning biomass, the detritivores/phytoplanktivores and zooplanktivores were most important, at least in the sub-littoral habitat (6-20 m deep) and probably also in the open waters of the lake (Witte et al. 2009a). By that time, detritivores/phytoplanktivores comprised about 13 species making up about 50% of the haplochromine biomass in the sublittoral waters followed by the zooplanktivores (12+ species) comprising about 25% (Goldschmidt et al. 1993).

The cichlids have become of particular interest to biologists as suitable fishes for evolutionary and ecological studies. However, it was not until recently that the Lake Victoria haplochromine cichlids have been extensively studied focusing on their diversity and the controlling factors (Kaufman 1992; Witte et al. 1992b, 2005, 2007a,b, 2008; Goldschmidt et al. 1993; Kaufman & Ochumba 1993; Kaufman et al. 1997; Seehausen et al. 1997a,b, 2008b; Wanink & Witte 2000a; Katunzi et al. 2003; Kishe-Machumu et al. 2008 [Chapter 3]).

Graham (1929) was the first person to report a lake-wide description of the fishery in Lake Victoria. At the beginning of the 20th century, the lake was sparsely fished with a variety of simple traditional methods (Graham 1929). The introduction of gill nets in 1905 (Graham 1929), beach seines in the early 1920's and outboard motors in 1950s, increased the fishing pressure (Garrod 1960). The main target species was *Oreochromis esculentus* (Graham). The improved technology and developments in transport systems opened inland markets and further developments in the fishing industry. Fishing accelerated in the 1950s and 1960s and a number of authors have recorded the effects of overfishing from the decline of some species to the virtual disappearance of others (Garrod 1960). The history of the fishery in Lake Victoria has been briefly reviewed by Barel et al. (1991) and Witte et al. (2009b). Increased fishing pressure in Lake Victoria resulted in decreases in catch per fishing effort, especially for the endemic tilapiine species and *Labeo victorianus* Boulenger in the 1950s (Fryer & Iles 1972; Ogutu-Ohwayo 1990a). Other species including *Barbus altianalis* Boulenger and *Mormyrus kannume* Forskåll were also becoming rare in the catches (Garrod 1960).

To improve the dwindling catches, the Nile perch, *Lates niloticus* (Linnaeus), a large centropomid piscivore, was introduced in Lake Victoria from lakes Albert and Turkana during the 1950s and 1960s (Pringle 2005). At the same period, Nile tilapia, *Oreochromis niloticus* (Linnaeus), *O. leucostictus* (Trewavas), *Tilapia zillii* (Gervais) and *T. rendalli* Boulenger were also introduced to the lake for the same purpose. After its introduction, Nile perch remained a relatively insignificant fish species in terms of the fish biomass in Lake Victoria until the late 1970s, when it started dominating the catches. The first major ecosystem shift only became noticeable in the 1980s (Reynolds & Greboval 1988) when the very diverse and complex haplochromine-based ecosystem was replaced by a system dominated by only four species; the exotic Nile perch and Nile tilapia, the native dagaa *Rastrineobola argentea* (Pellegrin) and the atyid shrimp *Caridina nilotica* Roux (Kaufman 1992; Witte et al. 1992a,b; Goudswaard et al. 2008). The haplochromine cichlids in the sub-littoral and offshore areas vanished almost completely (Barel et al. 1985; Witte et al. 1992b). It was estimated that some 200 of the endemic haplochromine species may have gone extinct (Witte et al. 1992b). However, other perturbations including: excessive fishing effort, destruction of fish breeding and nursery habitats, water pollution and eutrophication have also contributed to the declining fish diversity (Hecky et al. 1994; Seehausen et al. 1997a; Witte et al. 2005). Nile tilapia displaced the two native tilapiines, *O. variabilis* Boulenger and *O. esculentus*, mainly through competition and possibly hybridization (Ogutu-Ohwayo 1990a; Goudswaard et al. 2002). The other introduced tilapiine species, have remained at low levels and do not appear to have had major impacts on the lake. An explosion of dagaa possibly was a result of the release of competition by haplochromines (Wanink 1991).

EUTROPHICATION AND OTHER ENVIRONMENTAL CHANGES

During the 1980s, eutrophication of the lake strongly increased. However, data derived from sediment cores indicated that eutrophication had already begun in the 1920s and 1930s (Hecky 1993; Verschuren et al. 2002). Eutrophication ran parallel with human population growth, industrialization and agricultural activities in the Lake Victoria drainage-basin (Verschuren et al. 2002). The effects of eutrophication included a change in the composition of the phytoplankton with a shift from diatoms to cyanobacteria, blue-green algae, along with an increase in algal biomass (Ochumba & Kibaara 1989; Hecky 1993; Mugidde 1993). Decomposition of the increased amount of phytoplankton resulted into low oxygen concentrations near the bottom and consequently leads to occasional mass fish kills

(Hecky et al. 1994). The transparency of water was also declined due to algal biomass and silt carried in by rivers (Seehausen et al. 1997a; Witte et al. 2005). A further consequence of eutrophication was an explosion of the invasive water hyacinth, *Eichhornia crassipes* (Martias) Solms. The infestation was brought under control through biological control methods (Albright et al. 2004), whereby in 1996 South American weevils (*Neochetina eicchorniae* Warner and *N. bruchi* Hustache) were introduced into the lake and water hyacinth strongly declined. However, it is disputed whether this decline was due to the weevils alone or to the effects of El Niño in 1997/1998 as well (Williams et al. 2005, 2007).

At the same period, increases in densities of invertebrate species such as midge larvae and molluscs were observed (Kaufman 1992; Witte et al. 1995). Most striking was the enormous increase of the detritivorous shrimp, *Caridina nilotica* (Goldschmidt et al. 1993; Goudswaard et al. 2006; Budeba & Cowx 2007), which became an important prey item of the Nile perch (Ogari & Dadzie 1988; Hughes 1992; Mkumbo & Ligtvoet 1992; Katunzi et al. 2006). An increase of small-bodied predatory cyclopoid copepods and a decrease in the abundance of the large-bodied herbivorous calanoids and cladocerans was also reported (Mwebaza-Ndawula 1994; Wanink et al. 2002). According to Hecky et al. (2010), transition to the new ecosystem state "may have been triggered by a period of low wind stress and then generally warming climate since the 1970s".

THE AIM OF THE THESIS

In the course of the 1990s, after a decline in Nile perch in Lake Victoria due to intensive fishing (Pitcher & Bundy 1995; Ntiba et al. 2001), a slow resurgence of some haplochromine species was observed (Witte et al. 1995, 2000, 2007b; Seehausen et al. 1997b; Balirwa et al. 2003). However only two trophic groups, zooplanktivores and detritivores, recovered successfully and the ratio between them reversed (Witte et al. 2007a,b). Before the 1980s, detritivores/phytoplanktivores (further referred to as detritivores) made up about 75 to 85% of the total number of haplochromines in the bottom trawl catches and zooplanktivores contributed between 10 and 20% (Table 2.2 [Chapter 2]; Witte et al. 2007b). By 2005, detritivores along the research transect constituted only 26% and zooplanktivores more than 70% (Witte et al. 2007a). The majority of other specialized trophic groups have not recovered to the same extent as the detritivores and zooplanktivores (Witte et al. 2007a). The resurgent haplochromine species had changed their diet hence we further put them in double quotation marks throughout this thesis (see section *Identification of haplochromines* below).

The resurgence of some haplochromine cichlids in the Mwanza Gulf triggered questions as to why some trophic groups and species recovered successfully and others not (Witte et al. 2000, 2007a,b). The available data on the recovery of haplochromines in the Mwanza Gulf however, was mainly based on occasional samples. The lack of detailed sampling, covering long time-series in the same area, turned out to be a drawback for answering questions about differential recovery.

The main objective of this thesis is to provide an insight into the inter-guild differences in the recovery of haplochromines along the research transect across the Mwanza Gulf in Lake Victoria (Tanzania). The two key research questions are: (1) what is the recovery rate and the current level of abundance of haplochromine trophic groups and species in the lake? (2) what are the main factors determining differential resurgence? To answer these questions, the following hypotheses have been coined:

(i) Due to the shift in phytoplankton composition from a dominance of diatoms to a dominance of cyanobacteria (Mugidde 1993), digestibility and nutrient quality of detritus may have decreased. This might have an impact on the condition of “detritivorous” cichlids.

(ii) “Detritivorous” species could be more susceptible to Nile perch predation than “zooplanktivorous” species, because of a greater habitat overlap with Nile perch. “Zooplanktivorous” haplochromines lived partly pelagic (Goldschmidt et al. 1990), whereas “dertritivorous” species were predominantly bottom dwellers (Goldschmidt et al. 1993). It is assumed that Nile perch preferably hunts near the bottom (Hamblyn 1966).

(iii) Decreased oxygen concentrations near the bottom and elevated levels of heavy metals in bottom sediments and fish have been reported for various locations in Lake Victoria, including the Mwanza Gulf (Campbell et al. 2003; Kishe & Machiwa 2003). Through the dominant food pathway (Hall et al. 1997), heavy metals may have a stronger impact on “detritivores” than on “zooplanktivores”, as bioaccumulation into “zooplanktivores” is thought to be prevented by molting of zooplankton (A. Schäffer & H.T. Ratte, unpublished data). Negative synergy between hypoxia and heavy metal contamination produces stronger contamination effects (Yediler & Jacobs 1995; Vosylienà & Kazlauskienà 1999), and since “detritivores” were living closer to the bottom they might be more affected than “zooplanktivores”.

(iv) The recovering “zooplanktivores” revealed ecological and morphological adaptations to the new environmental conditions (van Oijen & Witte 1996; Wanink & Witte 2000a; Katunzi et al. 2003; Witte et al. 2008; van der Meer et al. 2012). If the potentials for adaptive responses in “detritivores” would be less than in “zooplanktivores” this might explain the difference in recovery rates.

This thesis mainly focuses on the first two of the above hypotheses. The knowledge on the status of the haplochromines in Lake Victoria and the underlying causes of differential resurgence that are gathered in this thesis are of paramount importance for sound management of biodiversity and the fishery as a whole.

THE STUDY AREA

The study area of this thesis was the research transect situated in the northern part of the Mwanza Gulf between Butimba Bay and Kissenda Bay (Fig. 1.2). The Mwanza Gulf is one of the largest gulfs at the southern end of Lake Victoria (van Densen & Witte 1995). The research transect is approximately 5 km long and six sampling stations (E, F, G, H, I and J) with depths ranging from 5.5 to 13 m were sampled. The bottom of these stations is covered with a thick deposit of organic mud (Witte 1981). Additional samples of some haplochromine species from the old ecosystem were caught in Butimba Bay at stations A and B. These stations have a sandy bottom with depth ranges of respectively 2-4 and 4-6 m.

I limited my study to the transect across the Mwanza Gulf because it is the area in which the most extensive and comprehensive researches has been undertaken in past decades. Among others, from 1977 for 25 years, the Haplochromis Ecology Survey Team (HEST) of Leiden University, in co-operation with the Tanzania Fisheries Research Institute (TAFIRI) has been studying the cichlid community, ecology and fishery biology of Nile perch and the abundant pelagic cyprinid *Rastrineobola argentea* in the Mwanza Gulf. In addition, this area is among the most affected areas in terms of overfishing and environmental degradation. In the period between 1979 and 1982, these stations used to be inhabited by more than 72 species, divided into 12 different trophic groups (Witte et al. 1992b), whereas for the period between 1987 and 1988, only few individuals of "zooplanktivorous" species (*Haplochromis laparogramma* Greenwood & Gee and *H. pyrrhocephalus* Witte & Witte-Maas, one individual of *H.* 'argens') and one individual of a "detritivorous" species (Witte et al. 1992b) could be found. Thus, it is the only area where the species composition prior to and during the environmental changes in the lake has been monitored in detail.

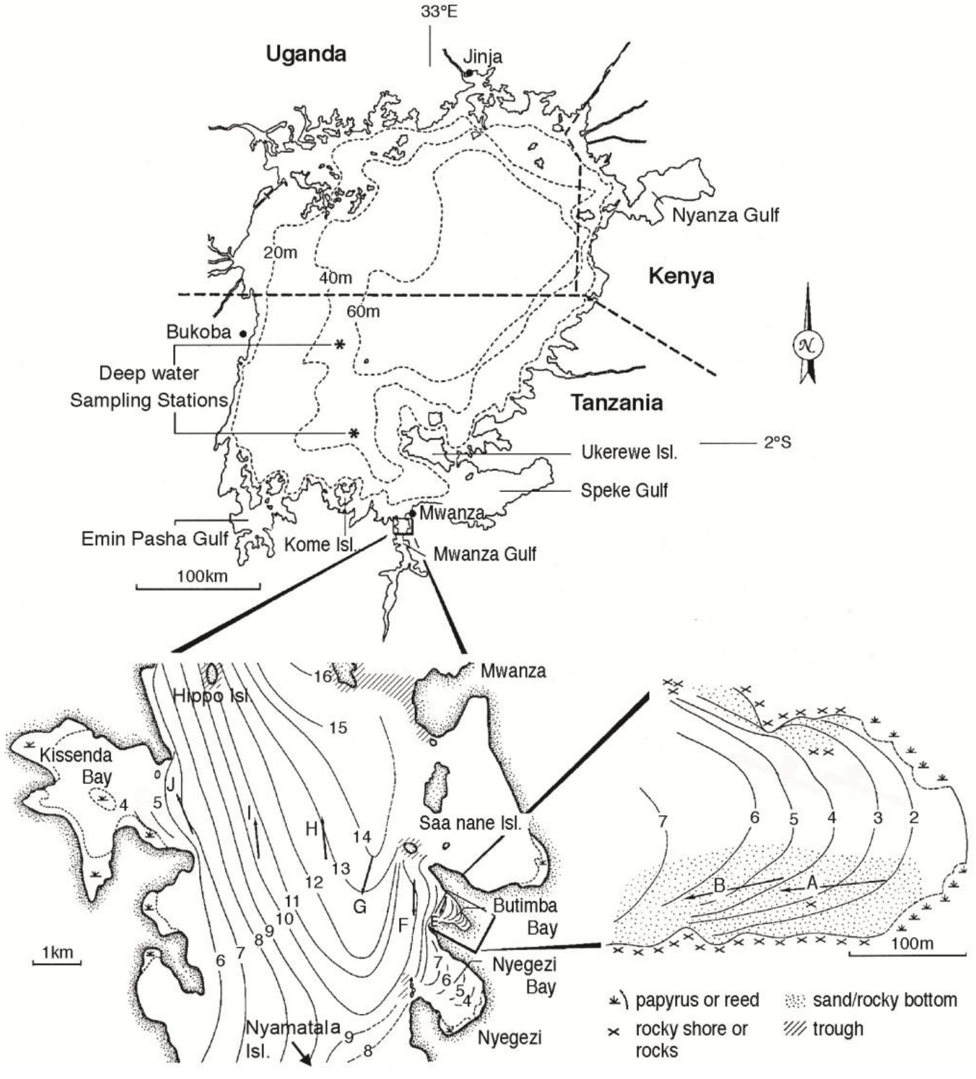

Fig. 1.2 Map of Lake Victoria showing the sampled stations in the northern part of Mwanza Gulf.

IDENTIFICATION OF HAPLOCHROMINES

Species

Intraspecific variation, including ontogenetic changes, sexual dimorphism, phenotypic plasticity and colour polymorphism, has been found in the haplochromine cichlids of Lake Victoria (Witte et al. 1997), at the same time inter-specific differences in morphology are often extremely small (Greenwood 1974; Barel et al. 1977). Male colouration appears to play an important role in mate recognition (Seehausen & van Alphen 1998), and was in most cases also used for species identification (Witte et al. 1997; Seehausen et al. 1998), however, this applies only to sexually active males.

For reference purposes, representative fish specimens of the most common species were photographed in a small perspex tank soon after being caught, to avoid discoloration. Specimens were then fixed in 5% formalin and later preserved in 70% ethanol for identity confirmation and morphometric measurements. To confirm the identification, fish specimens were compared with the preserved specimens that were collected before the ecological changes and stored in the Netherlands Centre for Biodiversity, Naturalis, Leiden.

Following Witte et al. (1992b), species that are not yet formally described were given nicknames enclosed in single (‘ ’) quotation marks.

Trophic groups

A trophic group consists of species using the same food category. Though many species feed on several food types, the dominant food category was taken as an important aspect for the trophic classification (Witte 1981; Witte & van Oijen 1990). Generally, species within a trophic group share morphological characters that are related to the uptake and processing of their dominant food (Greenwood 1974; Witte & van Oijen 1990). In some cases, subgroups can be identified based on feeding techniques, location of prey in the environment, and on the part of the prey that is eaten. For instance, within molluscivores, one can distinguish pharyngeal mollusc crushers, crushing the shell with the pharyngeal jaws and oral mollusc shellers, wrenching the snail from the shell (Greenwood 1974; Witte & van Oijen 1990). Identification of haplochromine trophic groups was made possible with the help of the keys in Witte and van Oijen (1990) and in Seehausen (1996).

The diet of most of the recovering haplochromine cichlids differed from that of the past (Katunzi et al. 2003; Kishe-Machumu et al. 2008 [Chapter 3]; Chapter 4). However, the trophic group classification used in this thesis corresponds with that based on morphological features as presented by Witte and van Oijen (1990) and by Seehausen (1996), and consequently, corresponds with the diet in the past, and not with the current diet. To indicate that the name of the trophic groups not really represent their diets in both periods we used double (“ ”) quotation marks.

THESIS OUTLINE

Chapter 2 forms the backbone of this thesis; it addresses the key research question 1. The chapter provides a general overview of the recovery of haplochromine cichlids along the transect in the Mwanza Gulf. It also gives an insight into the differential rate of resurgence and the spatial distribution of the trophic groups and their main species. **Chapters 3** to **7** address the key research question 2. They assess potential ecological factors (listed above) for the differential recovery and the shift in dominance between the two haplochromine trophic groups; “detritivores” and “zooplanktivores”. Differences in foraging adaptability between the two groups were expected to provide a contribution to their differential recovery. **Chapter 3** specifically assesses the diets of “detritivorous” haplochromine species in the modern ecosystem in comparison with those collected in the past, using gut content analysis. **Chapter 4** on the other hand assesses the diets of the recovered “zooplanktivorous” species and also compares their current diets with the past ones. The issue of diet in “detritivorous” and “zooplanktivorous” species as a potential factor for the differential resurgence of the two groups is discussed. In **chapter 5,** stable isotope analysis techniques on formalin/alcohol-preserved “detritivorous”, phytoplanktivorous and “zooplanktivorous” species are used mainly to assess the differences in stable isotope signatures between the three trophic groups (and their constituent species) in the periods before (old) and after (modern) the environmental changes.

In the 1960s and 1970s, the first two decades after the introduction of the Nile perch, haplochromine cichlids were the major prey of this predator (Hamblyn 1966; Gee 1969; Okedi 1971). When the density of haplochromines in the sub-littoral and offshore waters declined in the course of the 1980s, Nile perch switched to other food items (Ogari & Dadzie 1988; Ogutu-Ohwayo 1990b; Mkumbo &

Ligtvoet 1992; Katunzi et al. 2006). In **chapter 6**, it is examined whether the Nile perch in the Mwanza Gulf switched back to haplochromines as their major food source after the resurgence. **Chapter 7** quantifies the impact of Nile perch predation on the “detritivores” and the “zooplanktivores”. Differences in predation pressure by Nile perch on the “detritivores” and “zooplanktivores”, one of the potential factors for the differential recovery of the two groups, is verified.

In **chapter 8**, the main findings and conclusions presented in this thesis are summarized. I discuss the implications of my findings for our understanding of haplochromine resurgence and briefly indicate how these findings may guide future research, conservation and fisheries management in the Lake Victoria basin.

Chapter 2

Resurgence and distribution patterns of haplochromine cichlids in southern Lake Victoria

Mary A. Kishe-Machumu, Frans Witte, Jacco C. van Rijssel, Jan H. Wanink

ABSTRACT

Lake Victoria's fauna comprised a large endemic flock of more than 500 haplochromine cichlid species that made up more than 80% of the demersal ichthyomass. After the Nile perch boom in the 1980s, the haplochromines had almost vanished. During 1990s, after heavy exploitation of Nile perch, a resurgence of some haplochromine species was observed. Though morphologically these species could be allocated to the former trophic groups, their diets had become similar; all dominated by macro-invertebrates. To establish the status of the recovering haplochromines, we studied their resurgence rate and distribution pattern in the northern part of Mwanza Gulf.

The study revealed a strong resurgence of few "detritivorous", "zooplanktivorous" and "oral mollusc shelling" haplochromine species. In 2006, the "zooplanktivores" along the transect reached and even outnumbered their level of abundance reported at the end of 1970s. Their densities were also much higher than those of the "detritivores", whereas the reverse was observed in 2008. Before the environmental changes in the 1980s, "detritivores" were the dominant guild, followed by "zooplanktivores" which conforms to the observation in 2008. Qualitative observations in March and April 2011 confirmed the "detritivores" being dominant again. The resurging species revealed extensions of their former habitats, and in contrast to the past not only "zooplanktivores", but also the "detritivores" migrated towards the surface during the night.

Reduced Nile perch predation seems to be one of the main causes of the recovery of the haplochromines, though adaptive ecological and morphological responses of the resurging species to the environmental changes may also have contributed. Based on their current contribution to the diet of Nile perch, the resurgence of haplochromine cichlids in the lake could boost the fishery.

INTRODUCTION

Lake Victoria is among the world's well known examples of fish species rich lacustrine ecosystems. Prior to the expansions of exotic fish species, Lake Victoria supported a multispecies fishery comprising several families (Garrod 1960). More than 90% of the species in Lake Victoria belonged to a single family, the cichlids (Cichlidae, Perciformes; Snoeks 2000). This family was represented by a few tilapiine species and more than 500 endemic haplochromine species, all female mouth brooders (Greenwood 1974; Kaufman & Ochumba 1993; Seehausen 1996; Witte et al. 2007a). They made up more than 80% of the demersal ichthyomass (Kudhongania & Cordone 1974). It is of particular interest to note that almost all haplochromines in Lake Victoria are endemic and belong to either a monophyletic group or derived from just a few ancestral species (Seehausen et al. 2003; Verheyen et al. 2003).

In the 1960s, Nile perch, *Lates niloticus* (Linnaeus), was introduced into the lake to boost the fishery after the decline of indigenous fish species. In the same period, four tilapiines; *Tilapia zillii* (Gervais), *T. rendalli* Boulenger, *Oreochromis leucostictus* (Trewavas) and *O. niloticus* (Trewavas), Nile tilapia, were also introduced into the lake to support the fishery (Welcomme 1988). During the first 25 years following its introduction, Nile perch catches were insignificant. In the second half of 1980s, an explosive increase of the catches of Nile perch took place (Goudswaard et al. 2008). Concurrently, stocks of many other fish species declined in several areas of the lake (Hughes 1983; Ogutu-Ohwayo 1990a; Witte et al. 1992a,b). Most prominent was the decline of about 40% of the 500+ species of endemic haplochromine cichlids (Witte et al. 1992b). Many haplochromine species virtually disappeared from the sub-littoral (6-20 m deep) and offshore (> 20 m) waters and were thought to be extinct (Barel et al. 1985, 1991; Witte et al. 1992b). At the same period, blooms of cyanobacteria (blue-green algae) greatly increased due to eutrophication (Ochumba & Kibaara 1989; Hecky 1993; Mugidde 1993). This resulted in decreased levels of dissolved oxygen (Hecky et al. 1994; Wanink et al. 2001) and decreased water transparency (Seehausen et al. 1997a; Witte et al. 2005).

In the course of the 1990s, after a decline of Nile perch due to intensive fishing, a resurgence of some haplochromine species was observed in the sub-littoral area of the Mwanza Gulf (Seehausen & Witte 1995; Witte et al. 1995, 2000, 2007a,b; Seehausen et al. 1997b). Similar observations had been made in other areas of the lake without specifying species or trophic groups that recovered (CIFA 1990; Balirwa et al. 2003; Getabu et al. 2003).

The decline and resurgence of the haplochromines was best studied on a research transect in the northern part of the Mwanza Gulf. The transect was sampled frequently from 1979 till 2002, and it is one of the most affected areas, especially with respect to overfishing and environmental degradation. Actually, it is the only area where the species composition prior to and during the environmental changes in the lake has been monitored in detail. The data showed dramatic changes in composition of trophic groups and in composition of species within these groups (Witte et al. 1992a,b, 2000, 2007a,b). Only a restricted number of “zooplanktivorous” and “detritivorous” species recovered and, notably, the “zooplanktivores” had become the dominant group instead of the “detritivores”. To update the ongoing changes, year round sampling along the transect was repeated in 2006 and 2008. This chapter presents the results of these surveys, focusing on: (1) the differential rate of resurgence of the trophic groups and species (2) the spatial distribution of trophic groups and species.

MATERIALS AND METHODS

Study area

The offshore part of a 5-km long transect across the Mwanza Gulf (Fig. 1.2 [Chapter 1]) was used for this study. Six sampling stations (E, F, G, H, I and J) on this transect were sampled during 2006 and 2008. Depths of these sub-littoral stations with a muddy bottom ranged from 5.5-13 m.

Fish sampling

Trawling: In order to assess the abundance and horizontal distribution of haplochromine trophic groups and species in the northern part of the Mwanza Gulf, trawling was performed during day time. A small boat powered by a 20- or 25 hp outboard engine, towing a bottom trawl of 4.6 m head-rope and 5 mm cod-end mesh (Goudswaard et al. 1995) was used to sample fish from all stations. Stations were sampled monthly in 2006 (except for station F in January, due to technical problems), and every two months in 2008. Trawl shots at each station lasted 10 minutes.

Gillnetting: Day and night gillnet sampling sessions were performed at stations E (5.5-6 m deep) and G (12.5-13 m deep) once per three months in 2006 and every two months in 2008. These sessions were conducted to assess vertical migration of fish at day and night. Vertical gillnets measured 5 m in length and were as high as the water column (viz. 6 m at station E and 13 m at station G). Monofilament (knotless) webbing with a stretched mesh size of 2.5 cm was used for these nets, which were marked vertically every meter. An extensive description of vertical gillnets is given in Goudswaard et al. (1995). The nets were set for 3 hours duration each during day time and during the night. In 2006, a single gillnet was used at each station, while in 2008 two gillnets were used per station in order to increase the number of fish. In order to further increase the fish samples, in 2008, conventional nylon gillnets measuring 60 m in length, 1.5 m in height and with a stretched mesh size of 2.5 cm, were also used to sample fish at stations E and G. Three conventional gillnets of the same size were set each at the surface, in mid-water and at the bottom (Goudswaard et al. 1995) concurrently with the vertical monofilament gillnets. After each haul, fish were packed in plastic bags with labels of their respective station and depth, stored on ice and afterwards identified to species and trophic group levels. For both trawling and gillnetting, day fishing was performed between 07.00 and 13.00 hour and night fishing between 20.00 and 01.00 hour.

Fish identification

Among the Lake Victoria haplochromine fish, so far, 15 (sub)-trophic groups have been identified (Witte & van Oijen 1990). Only four of these trophic groups were frequently encountered on the research transect during the present study. The remaining fish were allocated to the category *rest* group.

Only adult fish (≥ 4.0 cm standard length [SL]) were used to identify species and/or trophic composition. Individuals belonging to “detritivores”, to “zooplanktivores”, and to “oral mollusc shellers” were identified to the species level and those individuals that could not be identified to the species level, but could be allocated to a trophic category, were recorded as *others* within the trophic group to which they belong, e.g. other “detritivores”.

The morphology of a number of haplochromine species has changed during the past decades (Witte et al. 2008; de Zeeuw et al. 2010). In case of doubt as to whether a specie~~s~~ was identical to a species known from the past, the name was followed with the word *like*. All species, of which the identity was uncertain or unknown, were included under the *rest* species.

Habitat segregation

Habitat segregation among the haplochromine species was studied by determining their spatial distribution (both horizontally and vertically) along the research transect. Catches of the small bottom trawler during the day in 2006 and 2008 were used, and data from each year were analyzed separately. Gillnet catches were used to determine the vertical distribution of fish during day and night hours. Due to small catches collected by gillnets, fish from 2006 and 2008 were combined.

Comparison with data from 1979/80

A comparison of the trophic and species distribution was made with those in 1979/80, when the research transect was sampled for the first time. During that period, the stations were sampled monthly from February 1979 to January 1980 with the same type of bottom trawl as in the present study. No samples were taken at stations H, I and J in April and November 1979 and at station I in February 1979. To enable a proper comparison we re-analysed the data in the same way as those of 2006 and 2008, with the exception that in 1979/80 all fish > 5 cm were considered adults, as both mean adult size and size at first maturity were larger at that time than in 2006 and 2008 (Witte et al. 1995). Further we focused our comparison on the trophic groups and species that were common in 2006 and 2008.

Data analysis

The catch data (numbers) at different stations were tested for normal distribution with the Kolmogorov-Smirnov test. Our data deviated from normal distributions, so the Kruskall-Wallis test (KW) was used to compare the number of fish at different stations within each year, and when significant, Dunn’s Multiple Comparisons Test (further referred to as Dunn’s test) was used to trace the differences in number of fish among the stations. To test if the catches of 2006 and 2008 differed significantly, the Mann Whitney U-test was employed. All tests were done by using the Instant statistical software, version 3.06 (GraphPad Instat 2003).

RESULTS

Abundance and spatial distribution of trophic groups prior to and after the environmental changes

Haplochromines in general

In 2006 and 2008, a total of at least 27 haplochromine species belonging to nine trophic groups were encountered on stations E-J along the research transect. In 1979/80 the number of species was more than 72 belonging to 12 trophic groups: prawn eaters, scale scrapers and parasite eaters were not present in 2006 and 2008 (Table 2.1). The strongest reduction in species number occurred in the piscivores and the paedophages, the smallest in the “zooplanktivores” and in the “oral mollusc shellers".

Table 2.1 Total number of haplochromine species per trophic group collected at stations E to J in the northern part of the Mwanza Gulf before the environmental changes (1979-1982; source: Witte et al. 1992b), and after the recovery (2006 and 2008; source: present study).

	1979-1982	**2006-2008**
“Detritivores/phytoplanktivores”	12	5+
Phytoplanktivores	3	1
Epiphytic algae grazers	2	1
Molluscivores (phar. crush.)	4+	1+
“Molluscivores” (oral shell.)	5+	4
“Zooplanktivores”	13+	8
Insectivores	7+	4+
Prawn eaters	1+	0
Piscivores	16+	2
Paedophages	6+	1
Scale eaters	1	0
Parasite eaters	1	0
Unknown	1+	0
Total	**72+**	**27+**

“Zooplanktivores”

In 1979/80 the “zooplanktivorous” haplochromines were the largest group on the transect, with an average of 159 individuals per trawl of 10 minutes duration, making up 20% of all haplochromines in the catches (Table 2.2). In 2006, they were by far the largest trophic group, with an average of 594 individuals, constituting 71% of the total number of haplochromines. In 2008, the mean number of “zooplanktivores” decreased to 270 individuals, constituting 33% of all haplochromines (Table 2.2). Due to the great variation in the catches, especially in 2006 and 2008, the differences among the three years were not significant (KW = 5.0, $P = 0.08$).

Although “zooplanktivorous” cichlids occurred at all stations, they were significantly unequally distributed (KW 1979/80 = 12.8, $P = 0.025$; KW 2006 = 19.6, $P = 0.002$; KW 2008 = 12.5, $P = 0.028$). In 1979/80, the number of “zooplanktivores” was significantly higher at station E than at station I (Dunn’s test, $P < 0.05$). In 2006, the mean number of “zooplanktivores” was significantly lower at station E than at stations F, G and H (Dunn’s test, $P < 0.05$ for E versus F and G, and $P < 0.01$ for E vs H), and in 2008 the mean number of “zooplanktivores” at station E was significantly lower than at station J (Dunn’s test, $P < 0.05$).

“Detritivores”

In 1979/80, the average number of “detritivorous” haplochromines per catch comprised 602 individuals and they made up 75% of all haplochromines. With an average of 175 individuals per catch, “detritivorous” haplochromines were the second most abundant group at the transect in 2006, comprising 21% of the total catch (Table 2.2). In 2008, “detritivorous” haplochromines were the dominant group again, whereby they increased to an average of 422 individuals per catch, making up 52% of the catch (Table 2.2). The differences in densities of “detritivores” among the years were significant (KW = 56.0, $P < 0.001$). Dunn’s test showed that significant differences were only present between 1979/80 and each of the two recent years ($P < 0.001$ in each case) and not between 2006 and 2008 ($P > 0.05$).

There was no significant difference in mean number of “detritivores” among the sampling stations in 1979/80 (KW 9.0, $P = 0.108$), but significant differences were present in 2006 (KW 2006 = 14.0, $P = 0.016$); the mean number was significantly lower at station G than at station J (Dunn’s test, $P < 0.05$). In 2008, the Kruskall-Wallis test also indicated differences among the sampling stations (KW = 12.6, $P = 0.028$). However, the Dunn’s test revealed no significant differences among any pair of individual stations ($P > 0.05$).

“Oral mollusc shellers”

On average, only 1.1 individual of “oral mollusc shellers” per haul was caught along the transect in 1979/1980, which was 0.1% of the total catch (Table 2.2). The average number of “oral mollusc shellers” in 2006 was 27 individuals, constituting 3% of the number of haplochromines in the catch (Table 2.2). In 2008, the average number increased to 49 individuals per haul making up 6% of the catch (Table 2.2). The difference in mean number of “oral mollusc shellers” among the years was significant (KW = 18.9, $P < 0.001$). Both in 2006 and 2008, the catches of “oral mollusc shellers” were higher than in 1979/80 (Dunn’s test, $P < 0.001$ in each case), but no significant difference was present among 2006 and 2008 (Dunn’s test, $P > 0.05$). The differences in mean numbers of “oral mollusc shellers” among the sampling stations were significant (KW 1979/80 = 18.4, $P = 0.002$; KW 2006 = 20.7, $P < 0.001$; KW 2008 = 24.5, $P < 0.001$). In 1979/80, the mean number of “oral mollusc shellers” was significantly higher at station F than at station H (Dunn’s test, $P < 0.05$); in 2006, the mean numbers were significantly higher at stations E and J than at stations G and H (Dunn’s test, $P < 0.05$ in each case), and in 2008 the mean number was significantly higher at stations E and J than at stations F and H (Dunn’s test, $P < 0.05$ for E vs F, E vs H and J vs F, and $P < 0.01$ for J vs H).

Piscivores

On average, five piscivorous individuals were caught per haul in 1979/80, 1.5 and 2.2 in 2006 and 2008 respectively. In each year they made up < 1% of the trawl catch (Table 2.2). The difference in mean number of piscivores among the years was significant (KW = 24.9, $P < 0.001$), but only for 1979/80 and each of the two recent years (Dunn's test, $P < 0.001$ in each case) and not for 2006 and 2008 (Dunn's test, $P > 0.05$). In 1979/80, the mean number of piscivores did not differ significantly among the sampling stations (KW = 6.3, $P = 0.259$), but in 2006 the difference was significant (KW = 11.1, $P = 0.049$). The mean number was significantly lower at station G than at station E (Dunn's test, $P < 0.05$, Table 2.2). In contrast, the mean numbers of piscivores in 2008 were not significantly different among the sampling stations (KW = 7.0, $P = 0.223$).

Rest group

The mean numbers of individuals in the rest group were 37, 43 and 67 per trawl catch, constituting 5%, 5% and 8% of all haplochromine cichlids in 1979/80, 2006 and 2008 respectively (Table 2.2). This group mainly comprised unknown fishes and further some unidentified insectivores and pharyngeal crushers. The difference in mean numbers of the rest group among years was significant (KW = 32.6, $P < 0.001$), with significantly lower numbers in 1979/80 than in 2006 and 2008 (Dunn's test, $P < 0.001$ in each case) and not for 2006 and 2008 (Dunn's test, $P > 0.05$).

The difference in mean numbers of the rest group among the sampling stations was not significant in 1979/80 (KW = 8.8, $P = 0.076$), but in 2006 and 2008 the differences were significant (KW 2006 = 30.8, $P < 0.001$; KW 2008 = 24.5, $P < 0.001$). In 2006, the mean numbers were significantly higher at station E than at stations F, G and H (Dunn's test, $P < 0.05$ for E vs F and $P < 0.001$ for E vs G and H). In 2008, the mean number of the rest group was significantly higher at station E than stations F, G and I (Dunn's test, $P < 0.05$ for E vs F and G, $P < 0.01$ for E vs I) and at station I the number was significantly lower than at station J ($P < 0.05$).

Table 2.2 Number (mean ± standard deviation) and percentages of haplochromines per species and per trophic groups in bottom trawls of 10 minutes duration per station at research transect in 1979/80, 2006 and 2008. Rest group comprised unidentified insectivores, pharyngeal crushers and unknown haplochromines, n represents number of catches.

Trophic group	Year	E	F	G	H	I	J	Transect
	1979/80	n =12	n =12	n =12	n =10	n =9	n =10	n =65
	2006	n =12	n =11	n =12	n =12	n =12	n =12	n =71
	2008	n = 6	n = 6	n = 6	n = 6	n = 6	n = 6	n = 36
Total haplochromines	1979/80	973 ± 654	672 ± 673	1097 ± 977	874 ±764	599 ± 483	521 ± 457	804 ± 707
	2006	412 ±375	1146 ±1885	692 ± 965	1573 ± 2687	563 ± 859	679 ± 612	840 ±1465
	2008	340 ± 215	1518 ± 3289	227 ± 195	139 ±64	822 ±1227	1809 ±1606	809 ± 1604
Zooplanktivores	1979/80	210 ± 127	235 ±417	170 ± 336	123 ± 189	66 ± 77	113 ± 138	159 ± 253
		22%	35%	15%	14%	11%	22%	20%
	2006	50 ± 85	899 ± 1638	629 ± 973	1410 ± 2325	333 ± 644	269 ± 242	594 ± 1291
		12%	78%	91%	90%	59%	40%	71%
	2008	17 ± 27	938 ± 2237	151 ± 206	90 ± 58	197 ± 226	226 ±158	270 ± 911
		5.1%	62%	67%	64%	24%	12%	33%
Detritivores	1979/80	698 ± 534	411 ± 328	867 ± 849	699 ± 549	508 ± 404	384 ± 315	602 ± 548
		72%	61%	79%	80%	85%	74%	75%
	2006	114 ± 198	225 ± 267	58 ± 64	157 ± 386	180 ± 219	321 ± 296	175 ± 262
		28%	20%	8.4%	10%	32%	47%	21%
	2008	88 ± 84	573 ± 1053	72 ± 53	47 ± 29	576 ± 925	1175 ± 1101	422 ± 790
		26%	38%	31.8%	34%	70%	65%	52%
Oral mollusc shellers	1979/80	2.0 ± 3.7	1.7 ± 1.8	0.5 ± 1.7	0	0.8 ± 2.5	1.1 ± 1.2	1.1 ± 2.2
		0.2%	0.2%	0.1%		0.1%	0.2%	0.1%
	2006	68 ± 75	11 ± 16	4.2 ± 9.7	4.7 ± 12	19 ± 25	52 ± 61	27 ± 47
		16%	0.9%	0.6%	0.3%	3.3%	7.7%	3.2%
	2008	60 ± 48	0.7 ± 1.2	2.5 ± 4.0	0.2 ± 0.4	47 ± 87	181 ± 278	49 ± 129
		18%	0.04%	1.1%	0.1%	5.7%	10%	5.9%

Table 2.2 Continued

Piscivores	1979/80	13 ± 21	2.2 ± 2.4	2.8 ± 7.1	4.0 ± 7.1	5.3 ± 4.2	1.8 ± 1.9	5.0 ± 10
		1.3%	0.3%	0.3%	0.5%	0.9%	0.3%	0.6%
	2006	4.2 ± 8.3	4.3 ± 9.9	0	0.1 ± 0.3	0.7 ± 2.3	0.3 ± 0.6	1.5 ± 5.4
		1.0%	0.4%		0.01%	0.1%	0.04%	0.2%
	2008	0.2 ± 0.4	3.0 ± 6.4	0	0.2 ± 0.4	1.3 ± 3.3	8.7 ± 12	2.2 ± 6.2
		0.1%	0.2%		0.1%	0.2%	0.5%	0.3%
Rest group	1979/80	50 ± 62	22 ± 34	57 ± 39	48 ± 45	19 ± 16	21 ± 19	37 ± 42
		5.2%	3.3%	5.2%	5.5%	3.2%	4.0%	4.6%
	2006	176 ± 184	8.0 ± 12	0.4 ± 1.2	1.5 ± 4.6	31 ± 70	37 ± 101	43 ± 108
		43%	0.7%	0.1%	0.1%	5.5%	5.4%	5.1%
	2008	175 ± 147	2.8 ± 6.5	1.3 ± 2.4	2.5 ± 3.3	0.7 ± 1.6	219 ± 508	67 ± 221
		51%	0.04%	0.6%	1.8%	0.1%	12%	8.3%

Abundance and spatial distribution of the main recovering species

"Zooplanktivorous" species

Of the "zooplanktivorous" species that were abundant in 2006 and 2008, only *Haplochromis (Yssichromis) pyrrhocephalus* Witte & Witte Maas was common at the sub-littoral part of the transect in 1979/80. The mean number per haul of *H. pyrrhocephalus* in 1979/80 was 27 and those of *H. tanaos* van Oijen & Witte and *H. (Yssichromis) laparogramma* Greenwood & Gee were 0.1 each (Table 2.3). In 2006, the densities of the three species had increased strongly; *H. pyrrhocephalus* constituted by far the most abundant species, with a mean number of 551 individuals per trawl catch (Table 2.3). It was followed by *H. tanaos* (mean 29 individuals) and *H. laparogramma* (mean 17 individuals). Apart from these three species, occasionally, an individual of *H.* 'argens' or an unidentified "zooplanktivorous" species was caught. In 2008, the densities of *H. pyrrhocephalus* and *H. laparogramma* seemed lower than in 2006. However, though Kruskall-Wallis tests revealed significant differences among the three years for each of the three species (KW ranging from 33.0-52.9, $P < 0.001$), differences were only significant among 1979/80 and each of the two recent years (Dunn's test, $P < 0.001$) and not among 2006 and 2008 (Dunn's test, $P > 0.05$).

The mean number of *H. pyrrhocephalus* was significantly different among the sampling stations (KW 1979/80 = 38.2, $P < 0.001$; KW 2006 = 25.3, $P < 0.001$; KW 2008 = 14.4, $P = 0.013$). In 1979/80 the mean number of *H. pyrrhocephalus* was significantly lower at stations E, F and J than at stations G (Dunn's test, $P < 0.001$) and also significantly lower at station E than at station H (Dunn's test, $P < 0.05$). In 2006, the mean number of *H. pyrrhocephalus* was significantly lower at station E than at stations F, G and H (Dunn's test, $P < 0.05$ for E vs F and $P < 0.01$ for E vs G and H) as well as lower at station I than at station H ($P < 0.05$). In 2008 the mean number of *H. pyrrhocephalus* was significantly lower at station E than at station I (Dunn's test, P < 0.05).

The distribution of *H. tanaos* was not significantly different among stations in 1979/80 (KW 1979/80 = 9.0, *P* = 0.112) but it was in 2006 and 2008 (KW 2006 = 18.8, *P* = 0.002; KW 2008 = 19.9, *P* = 0.001). In 2006, the mean number was significantly lower at station G than at stations I and J (Dunn's test, *P* < 0.05 for G vs I and *P* < 0.01 for G vs J) and in 2008 the mean number was significantly lower at stations F, G and H than at station J (Dunn's test, *P* < 0.05 for J vs F and G, *P* < 0.01 for J vs H). There were no significant differences in the mean numbers for *H. laparogramma* among the sampling stations (KW 1979/80 = 3.2, *P* = 0.666; KW 2006 = 10.8, *P* = 0.055 and KW 2008 = 5.6, *P* = 0.350).

"Detritivorous" species

With average, catches of 102 and 105 individuals in 2006 and 2008 respectively, *H. (Enterochromis)* 'paropius-like' was the dominant "detritivorous" species and the second most abundant species of all haplochromine cichlids on the transect (Table 2.3). In 1979/80, this species was caught only twice (two individuals per haul) at station J (Table 2.3). Densities among the three years were significant for *H.* 'paropius-like' (KW = 98.7, *P* < 0.001), but differences were only significant among 1979/80 and each of the two recent years (Dunn's test, *P* < 0.001) and not among 2006 and 2008 (Dunn's test, *P* > 0.05).

In 1979/80, the difference in mean numbers of *H*. 'paropius-like' among the stations was just significant (KW = 11.2, *P* = 0.048). However, the Dunn's test revealed no significant differences among any pair of individual stations (*P* > 0.05). In both 2006 and 2008, the differences in mean numbers of *H*. 'paropius-like' among the sampling stations were not significant (KW 2006 = 7.9, *P* = 0.163; KW 2008 = 8.0, *P* = 0.159).

Apart from *H*. 'paropius-like', many other unidentifiable "detritivorous" species were found in 2006 and 2008, including individuals that resembled *H. (Enterochromis) antleter* Mietes & Witte and *H. (E.) cinctus* Greenwood & Gee and some individuals resembling *H. (E) katunzii* Ter Huurne & Witte and *H. (E) coprologus* Niemantsverdriet & Witte.

"Oral mollusc shelling" species

Among the "oral mollusc shellers", *Platytaeniodus degeni* Boulenger and *Haplochromis (Ptyochromis) xenognathus* Greenwood were abundant in 2006 and 2008 (Table 2.3). However, in 1979/870 they were absent or extremely rare at the studied stations. In 2006 and 2008, *P. degeni* was the most abundant "oral sheller" along the transect, with average numbers of 18 and 43 individuals per haul respectively (Table 2.3). *Haplochromis xenognathus* was only common at station E both in 2006 and 2008. A few individuals were caught in 2006 at stations F and J (Table 2.3) and on average, 7 and 4 individuals of *H. xenognathus* were caught per haul in 2006 and 2008 respectively. Densities among the years differed significantly for both *P. degeni* (KW = 20.7, $P < 0.001$) and for *H. xenognathus* (KW = 8.6, $P = 0.014$). However, for *P. degeni* differences were only significant among 1979/80 and each of the two recent years (Dunn's test, $P < 0.001$) and not among 2006 and 2008 (Dunn's test, $P > 0.05$). For *H. xenognathus* differences were only significant among 1979/80 and 2006 (Dunn's test, $P < 0.05$) and not among 2008 and 1979/80 and 2008 and 2006 (Dunn's tests, $P > 0.05$).

The mean numbers of *P. degeni* were significantly different among the sampling stations (KW 1979/80 = 18.8, $P = 0.002$; KW 2006 = 15.1, $P = 0.010$; KW 2008 = 21.1, $P < 0.001$). In 1979/80, the mean number per haul was significantly lower at station G than at station F (Dunn's test, $P < 0.01$). In 2006, the mean number was significantly lower at station H than at station J (Dunn's test, $P < 0.05$) and in 2008 mean numbers were significantly lower at stations F, G and H than at station J (Dunn's test, $P < 0.05$ for stations J vs F and G; $P < 0.01$ for H vs J).

The differences in mean numbers of *H. xenognathus* were significant among sampling stations in 2006 and 2008 (KW 2006 = 32.8, $P < 0.001$; KW 2008 = 21.8, $P < 0.001$). In both years, the mean numbers were significantly higher at station E than at the other five stations (Dunn's test, $P < 0.01$ for E vs F and $P < 0.001$ for E vs G, H, I and J for 2006; $P < 0.01$, in all cases for 2008).

Apart from *P. degeni* and *H. xenognathus* occasionally a few individuals of *H. (Ptyochromis) fischeri* Seegers and *H. (Paralabidochromis) plagiodon* Regan & Trewavas were caught in 2006 and 2008 at station E.

Table 2.3 Number (mean ± standard deviation) of adult haplochromines per species in bottom trawls of 10 minutes duration at stations E to J in 1979/80 and in 2006 and 2008, n-values are the same as in table 2.2.

Species	Year	E	F	G	H	I	J	Transect
H. pyrrhocephalus	1979/80	0	1.7 ± 3.6	112 ± 251	27 ± 53	7.3 ± 12	6.0 ± 19	27 ± 113
	2006	36 ± 76	859 ± 1571	631± 951	1358 ± 2319	275 ± 614	175 ± 207	551 ± 1271
	2008	1.7 ± 3.2	937 ± 2238	136 ± 173	78 ± 45	147 ± 148	78 ± 137	230 ± 912
H. laparogramma	1979/80	0	0	0.5 ± 1.8	0.2 ± 0.6	0	0.1 ± 0.3	0.1 ± 0.8
	2006	0.6 ± 1.4	30 ± 61	15 ± 25	43 ± 74	9.8 ± 17	2.2 ± 4.6	17 ± 42
	2008	0.7 ± 1.6	0.7 ± 1.6	14 ± 34	12 ± 23	2.3 ± 4.4	0.2 ± 0.4	5 ± 17
H. tanaos	1979/80	0.7 ± 1.9	0	0	0	0	0	0.1 ± 0.8
	2006	12 ± 22	9.7 ± 13	2.4 ± 5.5	9.1 ± 18	48 ± 56	90 ± 108	29 ± 59
	2008	15 ± 27	1.2 ± 2.4	0.8 ± 1.6	0.2 ± 0.4	47 ± 89	148 ± 144	35 ± 84
H. ‘paropius-like’	1979/80	0	0	0	0	0	0.4 ± 0.8	0.1 ± 0.3
	2006	72 ± 165	191 ± 213	32 ± 43	106 ± 290	74 ± 88	145 ± 194	102 ± 184
	2008	40 ± 74	408 ± 717	50 ± 46	24 ± 7.4	74 ± 91	33 ± 49	105 ± 308
P. degeni	1979/80	1.8 ± 3.8	1.7 ± 1.8	0	0	0.8 ± 2.5	1.0 ± 1.1	0.9 ± 2.1
	2006	20 ± 21	9.6 ± 15	4.2 ± 9.7	4.7 ± 12	19 ± 25	52 ± 61	18 ± 33
	2008	27 ± 24	0.7 ± 1.2	2.5 ± 4.0	0.2 ± 0.4	47 ± 87	181 ± 278	43 ±128
H. xenognathus	1979/80	0	0	0	0	0	0	0
	2006	41 ± 71	0.9 ± 3.0	0	0	0	0	7 ± 32
	2008	26 ± 44	0	0	0	0	0	4 ± 19

Diel vertical distribution in vertical and conventional gillnets

“Zooplanktivores”

Among the zooplanktivorous species, only *H. pyrrhocephalus* and *H. laparogramma* were caught with gillnets. Gillnet catches of each of these closely related species were too low to analyse them separately. However, as in the past both of them migrated towards the surface at night (Goldschmidt et al. 1990), we analysed them together. During day time, a few individuals of *H. pyrrhocephalus* and *H. laparogramma* were caught in mid-water only at station E (Fig. 2.1). At night they dominated in the surface part of water column at both stations E and G.

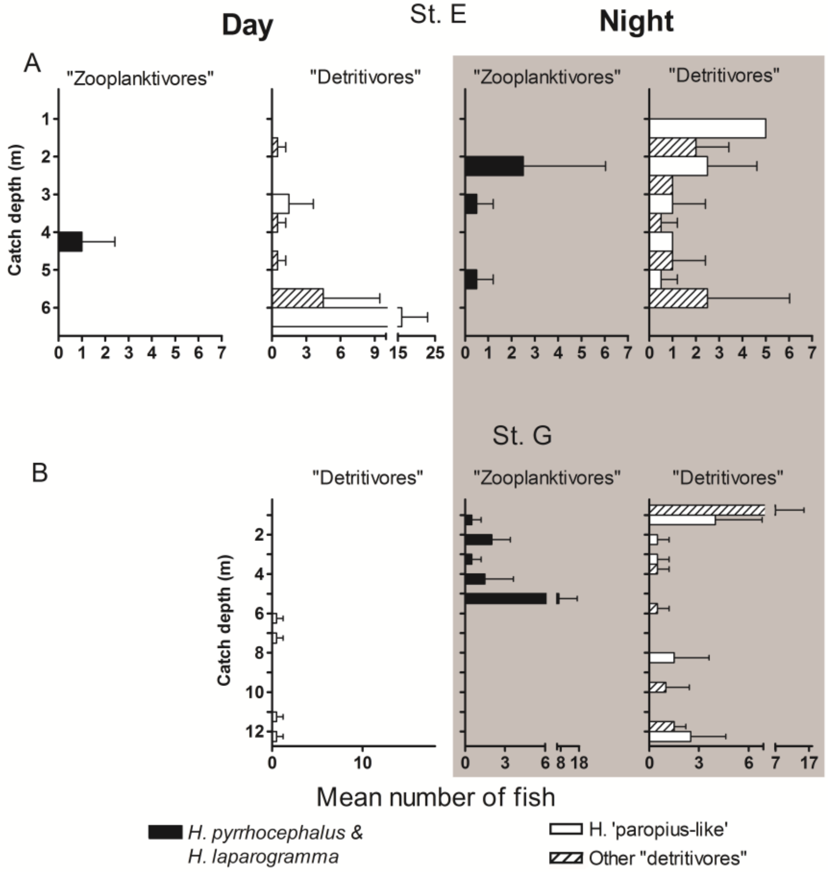

Fig. 2.1 Vertical distribution in mean number (and standard deviation) of “detritivorous” and “zooplanktivorous” haplochromine species caught with vertical gillnets during the day and night at stations E and G in 2006 and 2008. Number of catches at station E = 10; at station G = 10

In total, only five individuals of *H. pyrrhocephalus* were caught with conventional gillnets; all were caught during the day, in the bottom net at station G (not shown in Fig. 2.2).

"Detritivores"

During the day, *H.* 'paropius-like' was caught at both stations mainly near the bottom and in mid-water in both vertical and conventional gillnets (Figs 2.1, 2.2). During day time, other "detritivorous" species were caught at station E near the bottom and a few higher in the column (Figs 2.1, 2.2), but they were absent in the catches of both net types at station G. At night, both *H.* 'paropius-like' and other "detritivorous" species were caught at stations E and G all over the water column with relatively high numbers near the surface (Figs 2.1, 2.2).

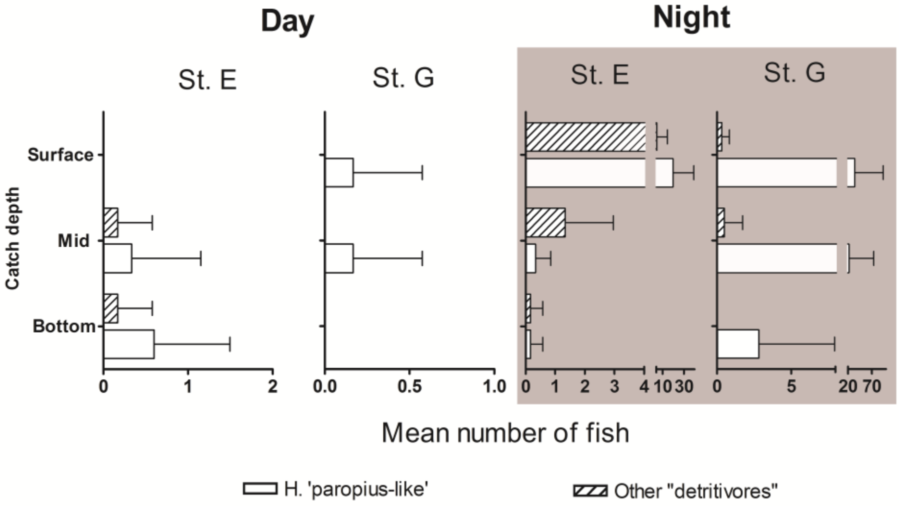

Fig. 2.2 Vertical distribution in mean number (and standard deviation) of "detritivorous" haplochromine species from surface-, mid- and bottom-set gillnets. Conventional nets were set at stations E and G during day and night in 2008. Number of catches at station E = 6; at station G = 6

DISCUSSION

During field work to collect live fish in March and April 2011, bottom trawl catches along the transect were made by JCVR and FW. Observations made during these catches are used to confirm some of the results described above.

Haplochromine recovery in other areas of the lake

The resurgence of haplochromine cichlids in the northern part of the Mwanza Gulf was not unique. Since the 1990s, reappearance of haplochromine species has been reported in various areas of Lake Victoria (CIFA 1990; Witte et al. 1995, 2000; Seehausen et al. 1997b; Balirwa et al. 2003; Getabu et al. 2003). Data on fish landings along the Speke Gulf, at Nyamikoma, Kalemera and Igombe at the end of 1990s, showed a strong resurgence of haplochromines (Witte et al. 2000). Consequently, a corresponding expansion in the haplochromine fishery has already been noted in several parts of the lake especially in Tanzania (M. A. Kishe-Machumu pers. obs.). In Ugandan waters, haplochromines were the second most abundant fish after Nile perch in the trawl catches, with a significant increase from 6% to 22% between 2005 and 2006 (NaFIRRI report 2007).

Abundance of trophic groups prior to and after the environmental changes

During the period of the study, there was a distinct difference in the composition of the main haplochromine trophic groups. At the end of the 1970s, before the environmental changes in the Mwanza Gulf, the mean number of “detritivores” along the transect (stations E-J combined) was more than three times as high as that of the “zooplanktivores” (Table 2.1; Witte 1981). In contrast, in 2006, the abundance of “zooplanktivores” was more than three times as high as that of the “detritivores”, whereas in 2008, the abundance of “detritivores” was almost twice higher than that of the “zooplanktivores” (Table 2.2). Based on the present data and those from Witte et al. (2007a,b), a review of the composition of “detritivorous” and “zooplanktivorous” haplochromines over the past three decades has been made (Fig. 2.3). It should be noted that only stations G to J were included in this figure, as stations E and F were not sampled throughout the whole period. Figure 2.3 shows that the originally dominant “detritivores” declined faster than the “zooplanktivores” and that in 1986 just before the complete collapse of the haplochromines, “zooplanktivores” were the most common group. From the start of the resurgence of haplochromines on the transect in the early 1990s until 2006, “zooplanktivores” remained the dominant group and their densities became even higher than at the end of the 1970s. Only in 2008, a sudden reverse in the composition was observed, back to a dominance of “detritivores” (Table 2.2; Fig.

2.3). As for both “zooplanktivores” and “detritivores”, differences in abundance among 2006 and 2008 were not significant; this reverse may just be a matter of chance. However, the bottom trawl catches in March and April 2011 confirmed that the shift to a dominance of “detritivores” was not just temporarily. In most catches, “detritivores” (especially *H.* ‘paropius-like’) dominated, mainly at the deeper stations G, H and I. However, the “detritivores” dominated the shallower stations E and J as well. A sample from two catches at station J on 3 March 2011 contained 73% “detritivores”, 16% “zooplanktivores”, and 11% “oral shellers” (n = 113). The relative densities of “zooplanktivores” and “detritivores” in 2011 were very similar to those in 1979/80 and in 2008, and seem to support the suggestion of Witte et al. (2000), that the dominance of “zooplanktivores” in the first years of this millennium was only an intermediate stage in the process of resurgence of haplochromine cichlids.

The abundance of “mollusc shelling” individuals at the transect was higher in 2006 and 2008 than at the end of 1970s, which was mainly caused by the increased densities of *P. degeni* (see below). This increase was still present in 2011. In the past, “mollusc shelling” species mainly occurred in relatively shallow water over sand (Witte 1981; Witte et al. 1992b) while in 2006 and 2008 they were common at mud stations (see below). The number of piscivorous individuals decreased significantly between 1979/80 and 2006/08. As far as we could identify them, they represented only two species (*H.* ‘big teeth’ and *H.* ‘green dentex’) in the recent period, whereas in 1979-1982, a total of 16 species was caught at stations E –J of the transect (Witte et al. 1992b). The same two species were observed in the catches made in 2011.

The rest group, though higher in number in 2006 and 2008 than in 1979/80, the higher number of individuals especially at station E like in 2011, was mainly due to the high number of individuals that could not be accommodated in one of the species or trophic groups known from the past. This partly may have been caused by hybridization due to the environmental changes (De Zeeuw et al. 2010).

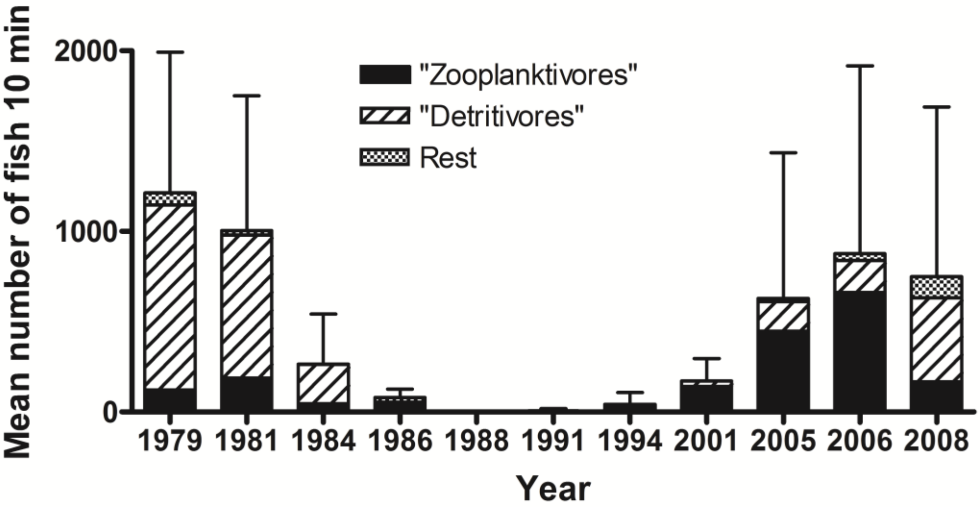

Fig. 2.3 Mean number of haplochromine cichlids (and standard deviation) in catches of 10 minutes duration with the small bottom trawler at stations G-J in the Mwanza Gulf in 1979-2008. Sources: Witte et al. 2007a (1979-2005) and present study (2006 and 2008). Note that the numbers in this figure differ from those in Table 2.2; this figure shows the mean number of fish at stations G-J whereas Table 2.2 shows the mean number of fish at station G-J.

Spatial distribution of trophic groups and main recovering species over the stations

In 1979/80, depth related distribution patterns of trophic groups at stations E to J seemed hardly present, except for the "oral mollusc shellers", which were more common at shallow stations close to the shore (Table 2.2; Witte 1981; Witte et al. 1992b). Though the numbers of "oral mollusc shellers" had strongly increased in 2006 and 2008 compared to the late 1970s, the same distribution pattern was observed. For the rest group, in 2006, 2008 and 2011, relatively high numbers were also found at stations E and J, which was mainly due to a high number of unknown haplochromines at these shallow stations.

Though the abundance of "zooplanktivores" was significantly higher at deeper stations than shallow stations, they were not showing consistent patterns related to depth over the years 1979/80, 2006 and 2008. For "detritivores", almost no significant depth related differences in densities could be found whereas for the "oral mollusc shellers", the same distribution pattern related to depth was observed over the three periods of the study.

Depth related distribution patterns at haplochromine species level used to be more distinct than at trophic group level. Within each trophic group, the distribution per species seemed to be determined by bottom type and water depth, which suggested that species were (partly) excluding each other (e.g. Witte 1981; Goldschmidt et al. 1990; Witte et al. 1992b). In 1979/80, *H. pyrrhocephalus* mainly occupied the deeper stations of the transect especially station G (Table 2.3; Goldschmidt et al. 1990). At shallower stations it was displaced by *H. (Astatotilapia) piceatus* Greenwood & Gee, whereas *H. (Yssichromis) heusinkveldi* Witte & Witte-Maas, a species closely related to *H. pyrrhocephalus* (Witte & Witte-Maas 1987), dominated at station H (Goldschmidt et al. 1990). *Haplochromis laparogramma* another close relative of *H. pyrrhocephalus* (Witte & Witte-Maas 1987) mainly occurred outside the Mwanza Gulf, at depths > 20 m (Goldschmidt et al. 1990). After its resurgence, *H. pyrrhocephalus* was still more common at the deeper stations (e.g. station H) than at the shallower stations (e.g station E; Table 2.3). However, the densities increased and it also occupied station E that in the past was dominated by *H. piceatus* (Goldschmidt et al. 1990; Witte et al. 1992b).

No significant differences were found for *H. laparogramma* among stations in 2006 and 2008, though in 2011 most *H. laparogramma* were caught at station I, and its densities were much lower than those of *H. pyrrhocephalus*. However, it also increased in numbers after resurgence and showed a similar trend in depth distribution as *H. pyrrhocephalus*. Densities of both *H. pyrrhocephalus* and *H. laparogramma* seemed lower in 2008 than in 2006, but as these differences were not significant they are not conclusive. In 2011, *H. pyrrhocephalus* was mainly caught at station F and it has been suggested that it is currently flourishing, in spite of low light intensities and low DO levels compared to those in past, because of its eyes that were already suitable for low light conditions (van der Meer et al. 1995, 2012) and the strong increase (64%) in size of its gill surface (Witte et al. 2008).

Before the environmental changes, *H. tanaos* mainly occurred at the shallow sand stations in Butimba Bay (see *H.* ‘double stripe’ in Witte et al. 1992b; van Oijen & Witte 1996), but after its resurgence it became common at the shallow mud stations, especially those on the western side of the transect (stations I and J; Table 2.3; van Oijen & Witte 1996; Seehausen et al. 1997b). In 2011, *H. tanaos* was more common at station J. After the resurgence, *H. pyrrhocephalus* and *H. tanaos* had approximately complementary distribution patterns along the transect, the latter partly having the same distribution pattern as *H. piceatus* before the environmental changes. The retina structure of *H. tanaos* seems to have become adapted to the relatively low light conditions over mud and in deeper water (Witte et al. 2005; van der Meer et al. 2012).

The “detritivorous” *H.* ‘paropius like’ was only caught twice at station J in 1979/80, whereas in 2006 and 2008 it was abundant at all stations, without a clear distribution pattern within the studied area. In 2011, the species dominated especially at the deeper stations G, H, I.

Of the five oral “mollusc shellers” species that were caught on the transect in 1979-1982, three (*H. (Ptyochromis) granti* Boulenger, *H. fischeri*, *Macropleurodus bicolor* Boulenger) were predominantly sand dwellers occurring in shallow water (2-4 m), and each of them was only caught once at station E (Witte 1981; Witte et al. 1992b). *Haplochromis xenognathus* was also a typical sand dweller, however, in 2006, 2008 and 2011 it was common at station E and occasionally caught at station F, which both have a mud bottom. In contrast, *P. degeni*, in 1979-1982 was caught over both sand and mud at stations up to 10 m depth (Table 2.3; Witte et al. 1992b). In 2006, 2008 and 2011, the number of *P. degeni* had increased strongly and they were caught at all stations, but their densities tended to be higher at the shallow stations E, I and J, and especially at the latter station.

It has been suggested that relatively high light intensities are important for successful oral shelling, hence their occurrence in shallow sandy habitats (Witte et al. 2005). However, it should be noted that the diet of *P. degeni* in the Mwanza Gulf only comprised a small amount of snails (ca. 10%) and a relatively large amount of detritus (ca 40%; Katunzi 1980). In 2005/06 the amount of snails in its diet had not changed, but detritus decreased and insects and other macro-invertebrates increased (E. van Reenen, unpublished data). Thus, *P. degeni* was not really dependent on oral shelling which may have facilitated its extension into deeper water. We have no information on the diet of *H. xenognathus* before and after the environmental changes.

Vertical distribution

Active fish have a greater chance being caught by gillnets than passive fish, while the reverse is true for trawl nets (Goudswaard et al. 2004). During day time, gillnets had relatively low catch rates compared to the same nets at night, which may be due to the nets being better visible during day time. Nevertheless, the gillnet catches suggest that “zooplanktivorous” species are at least active in the upper half of the water column during the night. *Haplochromis tanaos* was never caught in gillnets during the present study, which could be caused by its slender body providing opportunity to pass through the nets.

In the past, upward migration of “detritivorous” species during the night was restricted to a few meters only, and they were mainly caught in the lower half of the water column (Goldschmidt et al. 1993; Goudswaard et al. 2004). However, in 2006 and 2008 a major part of *H.* ‘paropius-like’ and the other “detritivores” migrated up to the surface, where they were even more abundant than the “zooplanktivores”. In spite of this, they were also caught at the other depths, so that at night the “detritivores” covered the whole column, in contrast to the “zooplanktivores”. It should be noted here that due to their relatively shallow body depth, the catch efficiency of “zooplanktivores” in gillnets was probably lower than that of “detritivores”, especially in 2006 and 2008, when the size of adult haplochromines was reduced compared to that at the end of the 1970s (Witte et al. 1995, 2007b).

Diel migration of “zooplanktivorous” and “detritivorous” haplochromines could be driven by factors related to feeding, to predation or to diel variation in abiotic factors (Goudswaard et al. 2004). According to Goudswaard et al. (2004), the distinct upward migration of “zooplanktivorous” haplochromines during the night was likely due to the upward migration of their main prey items (zooplankton and *Chaoborus* larvae) at night. The fact that the “detritivorous” species, which before the environmental changes mainly fed on bottom debris, did show little vertical migration seemed to support food as a causal factor. In 2006/08 the former “detritivorous” species changed their diet mainly to midge larvae (chaoborids and chironomids), zooplankton, insects and shrimps (Kishe-Machumu et al. 2008 [Chapter 3]). In the Mwanza Gulf, all these prey types seemed to migrate upward during the night (Goldschmidt et al. 1990, 1993; Goudswaard et al. 2004). So, the shift in diet of the “detritivorous” haplochromines after the environmental changes might explain their upward migration during the night. Though the resurging “zooplanktivores” also showed a shift in diet, they still took a considerable amount of their old prey types (zooplankton and midge larvae) and, apart from molluscs, most of the prey items they added to their diet probably also moved upward by night.

In addition, an upward migration could be an adaptive response to the changed environmental conditions, i.e. lower light conditions and lower dissolved oxygen concentrations. Moreover, it may reduce habitat overlap with Nile perch, which generally stay closer to the bottom (Goudswaard et al. 2004).

Potential causes of (differential) resurgence of haplochromine trophic groups and species

Impacts of Nile perch predation: From the trophic relationship that exists between the Nile perch and cichlids, it seems likely that the former is responsible for the loss of the cichlid diversity through excessive predation pressure. The catches of the Nile perch started rising sharply in the 1980s and concomitantly the haplochromines declined; resurgence of the latter started in the beginning of 1990s when the former declined (Witte et al. 2007b). Indeed, Nile perch predation could be among the major factors as the continuing decline of the Nile perch stock since the turn of the century coincided with a further resurgence of the haplochromines (Fig. 2.3).

At the beginning of its disruption, Nile perch was predicted to have less impact on the "zooplanktivores", which were partly pelagic, than on the bottom-dwelling "detritivorous" haplochromines. The latter would be more susceptible to predation by the bottom dwelling Nile perch due to habitat overlap (Witte & Goudswaard 1985). The "zooplanktivores" were indeed the last haplochromines surviving in sub-littoral areas, but in 1987 they also had almost vanished (Witte et al. 1992a). It is interesting to note that most of resurging "detritivorous" species are no longer fulltime bottom dwellers, but also partly pelagic-dwelling haplochromines.

In Lake Nabugabo, where Nile perch had been introduced as well (Pringle 2005), the haplochromines also declined strongly with increasing Nile perch densities (Ogutu-Ohwayo 1993; Chapman et al. 1996) and haplochromine resurgence coincided with a decline of Nile perch (Chapman et al. 2003; Paterson & Chapman 2009). Hence, the resurgence of some species on the transect across the Mwanza Gulf as a potential response to a decline of Nile perch is not a unique phenomenon.

Further, in satellite lakes around Lake Victoria and Kyoga, where Nile perch was absent, haplochromines generally remained abundant (Ogutu-Ohwayo 1993; Mwanja et al. 2001; Mbabazi et al. 2004; Katunzi et al. 2010). These observations suggest that reduction in predation pressure may play a major role in resurgence of the haplochromines.

Adaptive responses: Concomitant to the explosive population of the introduced Nile perch and disappearance of the dominating haplochromine cichlids in the ecosystem of Lake Victoria in the 1980s, eutrophication and algal blooms increased (Ochumba & Kibaara 1989; Hecky 1993; Muggide 1993). The survival and extinction of haplochromines may also depend on how the species respond to these environmental changes.

Ecological and morphological changes were indeed observed in some of the resurging haplochromine species in Lake Victoria. Ecological changes comprised increased fecundity (Wanink & Witte 2000a), changes in diet (van Oijen & Witte 1996; Katunzi et al. 2003; Kishe-Machumu et al. 2008 [Chapter 3]; Chapters 4, 5) and habitat extension (Table 2.3). It is striking that habitat extension also occurred in the direction from shallow sand bottoms towards deeper mud bottoms, which normally have lower light conditions and DO levels. Both, habitat extension (this Chapter) and changes in diet (Kishe-Machumu et al. 2008 [Chapter 3]; Chapters 4, 5) might be the result of competitive release. Morphological changes included: changes in body shape which might enhance escaping Nile perch predation (Chapman et al. 2008; van Rijssel & Witte 2012); in jaw structures facilitating eating of tougher prey (Witte et al. 2008); an increase gill surface, which is beneficial to low DO levels (Witte et al. 2008); and a change in retina structure, facilitating vision in murky water (van der Meer et al. 2012). These morphological changes may be the result of phenotypic plasticity, natural selection or a combination of both (Witte et al. 2008; van der Meer et al. 2012).

CONCLUSION AND RECOMMENDATIONS

This study reveals a strong resurgence of haplochromines which reflects a lake wide phenomenon. The study further concludes that a decline in Nile perch densities may have played a role in resurgence, but only those species that could cope with the changed environmental conditions e.g. low water transparency and low oxygen concentration recovered.

As mentioned in this chapter, Lake Victoria currently contains some haplochromine species which were hard to identify. A thorough study still has to be done as these species seem to represent a range of intermediate forms that could well represent the hybrids. Thus, for management of the lake and for evolutionary studies, trophic and species composition of the recovering haplochromine species should be monitored in the future years.

Management strategies should also put in place to control sub-littoral areas from destructive fishing gears e.g beach seines, as they seem to accommodate some of resurging haplochromine species as well as other fishes. The resurgence of haplochromine cichlids in the lake could boost the fishery based on their current contribution on the diet of the Nile perch (Kishe-Machumu et al. 2012 [Chapter 6]). Moreover, measures against aspects leading to eutrophication and other pollution related activities of the lake should also put in place as they could play an important role both for the maintenance and restoration of haplochromine diversity and the fishery at large.

ACKNOWLEDGEMENTS

The present study and earlier studies of Haplochromis Ecology Survey Team (HEST) were financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) grants W87-129, W87-161, W87-189, W84-282, W84-488, WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC), the International Foundation for Science (IFS), the Schure Beijerinck-Popping Fonds, the van Tienhoven Stichting, and Yellow Springs Instruments. The administration of the Tanzania Fisheries Research Institute in Mwanza (TAFIRI) provided logistical support and research facilities. We thank Dr. Martien van Oijen of Naturalis, Leiden for taking care of the fish samples from Tanzania, as well as for his help with identification of the piscivorous haplochromines. Thanks also go to Maaike Nieveen for her assistance on sample preparation. We wish to acknowledge the crew members of the small bottom trawler; Messrs Mhoja Kayeba, Mohamed Haruna and Rajabu Machage for their hard work and patience during the field surveys.

Chapter 3

Dietary shift in “detritivorous” cichlids after the ecological changes in Lake Victoria

Mary A. Kishe-Machumu, Frans Witte, Jan H. Wanink

Original version published in *Journal of Animal Biology* 58**:** 401-417 (2008)

ABSTRACT

Cichlid fishes of Lake Victoria are well known for their trophic specializations. In our study area, the sub-littoral waters of the Mwanza Gulf (Tanzania), at least 12 trophic groups coexisted in the 1970s. After the Nile perch upsurge and eutrophication in the 1980s, most cichlids disappeared from the area. During the 1990s, heavy exploitation of Nile perch reduced the abundance of this predator. Subsequently, some cichlid species, mainly "zooplanktivores" and "detritivores", recovered. To establish their ecological role in the changed environment, among other factors we studied their diet.

Stomach contents of fish caught before and after the ecological changes were compared. The "detritivores" shifted from a diet dominated by detritus and phytoplankton, supplemented with small quantities of midge larvae and zooplankton, to a diet of invertebrate preys of larger sizes. Currently, the diet includes zooplankton, midge larvae, shrimps and molluscs, and a very small amount of detritus and phytoplankton.

Apparently, the recovering "detritivores" have a more carnivorous than a herbivorous diet. Concomitantly, the ratio of intestine length to standard length of the "detritivores" decreased with 30% and the average stomach fullness decreased as well. The observed dietary shifts may be due to (1) the changed availability of food types and a decline of the nutritious quality of detritus and phytoplankton due to the strong increase of cyanobacteria in the lake, (2) the decline of the former trophic specialists, and (3) the reduced water clarity. The diet of the former "detritivores" is currently very similar to that of the "zooplanktivores". Consequently, if diet plays a role in the relatively slow recovery of the "detritivores" compared to the "zooplanktivores", this would only hold if they are relatively poorly adapted to their new diet.

INTRODUCTION

Until the 1980s, Lake Victoria, the second largest lake in the world, had an extremely rich fish fauna that was dominated by more than 500 species of haplochromine cichlids (Greenwood 1981; Witte et al. 1992b; Kaufman & Ochumba 1993; Seehausen 1996; Witte et al. 2007a). At the middle of the last century, the commercial fishery in Lake Victoria, which started after the introduction of gill nets in 1905, resulted in overfishing of some target species, especially the tilapiine cichlids (Ogutu-Ohwayo 1990a). To improve the fishery, exotic fish species were introduced into the lake in the 1950s. Those included the Nile perch, *Lates niloticus* (Linnaeus), a large-growing predator, and the phytoplanktivorous/detritivorous Nile tilapia, *Oreochromis niloticus* (Linnaeus) (Welcomme 1988).

At the beginning of the 1980s, the Nile perch population suddenly increased. Simultaneously, about 200 haplochromine cichlid species in the sub-littoral and off-shore areas vanished (Barel et al. 1985; Witte et al. 1992b). The contribution of haplochromine cichlids to the demersal ichthyomass in the Mwanza Gulf decreased from more than 80% in 1969-1970 (Kudhongania & Cordone 1974) to less than 1% in 1987 (Witte et al. 2000). A similar situation was observed in all other parts of the lake that have been studied like Napoleon Gulf, Nyanza Gulf, Speke Gulf, Emin Pasha Gulf and several off-shore areas (e.g. Okemwa 1981; Ogutu-Ohwayo 1990a; Okaranon 1994; Goudswaard et al. 2008). Simultaneously with the decline of haplochromines, many other ecological changes occurred in the lake. Among them were the increase of algal blooms (Ochumba & Kibaara 1989; Hecky 1993; Mugidde 1993), decreased levels of dissolved oxygen (Hecky et al. 1994; Wanink et al. 2001), decreased water transparency (Seehausen et al. 1997a; Witte et al. 2005), and the increase of the cyprinid *Rastrineobola argentea* (Pellegrin) (Wanink 1991, 1999; Wanink et al. 1999) and of the shrimp *Caridina nilotica* (Roux) (Goudswaard et al. 2004; Budeba & Cowx 2007).

In the 1990s and 2000s, after a decline of the Nile perch population due to heavy fishing (Pitcher & Bundy 1995; Ntiba et al. 2001; Kayanda et al. 2009), a resurgence of some haplochromine species was observed (Witte et al. 1995; Seehausen et al. 1997b; Witte et al. 2000; Balirwa et al. 2003; Witte et al. 2007b; Witte et al. 2007a). Of more than 71 species originally found at six stations along a research transect in the Mwanza Gulf, about 27 species recovered (Table 2.1

[Chapter 2]; Witte et al. 1992b; Witte et al. 2007b). Originally, the “detritivores”, formed the most important trophic group in the sub-littoral waters of the Mwanza Gulf, with more than 12 species and making up ca. 75% to 85% of the number of haplochromines in the bottom trawl catches (Table 2.2 [Chapter 2]; Goldschmidt et al. 1993; Witte et al. 2007b). They were followed by more than 13 “zooplanktivorous” species, contributing between 10% and 20% to the total number of individuals (Table 2.2 [Chapter 2]; Goldschmidt et al. 1993; Witte et al. 2007b). However, the decline of the “detritivores” went faster, and their recovery much slower than that of the “zooplanktivores” (Fig. 2.3 [Chapter 2]). From the 1990s till 2006 “zooplanktivores” dominated the catches and the total number of “zooplanktivorous” individuals became even higher than in the 1970s (Table 2.2 [Chapter 2]; Witte et al. 2000; 2007a,b). Only in 2008, the “detritivores” became dominant by numbers again (52% versus 21% “zooplanktivores”); almost reaching their former densities.

The Nile perch upsurge, the dramatic decline of the haplochromine cichlids, and other ecological changes in Lake Victoria, triggered many studies and debates on the extent of these changes and their causes (Barel et al. 1985; Acere 1988; Ogutu-Ohwayo 1990a; Kaufman 1992; Witte et al. 1992b; Hecky et al. 1994; Seehausen et al. 1997a,b; Verschuren et al. 2002; Goudswaard et al. 2008). It was noted that a careful study of the differential decline and recovery of haplochromine trophic groups and species may help unravelling the causes (Witte et al. 2007b; Witte et al. 2007a). Among other ecological factors, changes in food availability may have played a role. It might have contributed to both the disappearance and recovery of some haplochromine species. Before the ecological changes, several studies (Greenwood 1974; van Oijen 1982; Hoogerhoud et al. 1983; Goldschmidt et al. 1990; Goldschmidt et al. 1993) on the diet of haplochromine species concluded that they could be classified into rather distinct trophic groups. However, studies on the diet of two recovering “zooplanktivorous” species, revealed a shift from a diet dominated by zooplankton to a diet including large-sized food items like shrimps, insect larvae and bivalves (van Oijen & Witte 1996; Katunzi et al. 2003). Shifts in diet after the ecological changes in Lake Victoria were also observed in other fish species, e.g. the tilapiine cichlid *Oreochromis niloticus* (Gophen et al. 1995; Balirwa 1998; Njiru et al. 2004; Bwanika et al. 2006), the cyprinid *R. argentea* (Wanink 1998), the catfishes *Bagrus docmak*

(Forskåll) and *Schilbe intermedius* (Linnaeus) (Olowo & Chapman 1999) and the characid *Brycinus sadleri* (Boulenger) (Wanink & Joordens 2007). In this paper, we compare the feeding habits of the “detritivorous” haplochromines from the Mwanza Gulf in the modern ecosystem with those in the past, and we explore whether changes in diet may account for the relatively slow recovery of this trophic group.

MATERIALS AND METHODS

Samples of “detritivorous” species were collected by bottom trawling during the day at six sampling stations (E, F, G, H, I and J) in the Mwanza Gulf (Fig. 1.2 [Chapter 1]) in both 1977-1982 (old ecosystem) and 2005-2006 (modern ecosystem). In both study periods, the structural aspects of the habitats at the sampling stations were the same, though during the latter period water clarity was lower and longer periods of hypoxia were prevalent. During the latter study period, the abundances of several macro-invertebrates were generally higher. Sampling stations had depths between 6-14 m in the past (Witte 1981; Goldschmidt et al. 1993), but were 5.5-13 m deep in 2005-2006 due to the low water level in the lake (M. A. Kishe-Machumu, unpublished data). In the latter period and a part of the former (1979-1980), sampling was conducted once every month at each station. In both periods a small trawler, powered by a 20-30 hp outboard engine, was used for bottom trawling (trawl head-rope 4.6 m, cod-end mesh 5 mm). Trawl shots at each station lasted 10 minutes. For the period 1977-1982 also some fish were included that were caught near the research transect (hatched area in Fig. 1.2 [Chapter 1]).

Catches were stored on ice and in the laboratory sorted by trophic group and, where possible, by species. After identification, fishes were labelled and preserved in a formaldehyde (5%) solution. Before further analyses, fish samples were transferred in steps (30%, 60%, and 70%) to alcohol. Only adult fish (> 4 cm standard length) were used for identification and diet analysis.

Before the Nile perch upsurge, the “detritivores” at the research transect used to comprise some taxonomically complicated species, of which particularly the females were hard to identify. For that reason, in earlier ecological studies, several species were pooled as the curved head group (e.g. Goldschmidt et al. 1993). Though after the recovery, based on general morphological features fish could still be identified as belonging to the same group, identification to the species level became even more difficult due to morphological changes that may have resulted from phenotypic plasticity, natural selection and/or hybridization (Seehausen et al. 1997b). Similar morphological changes were observed in species from other trophic groups (Chapman et al. 2008; Witte et al. 2008). Therefore, we pooled the "detritivores" in this study, with the exception of *Haplochromis (Enterochromis)* 'paropius-like'. This species, with its distinct mid lateral band in both males and females, used to be rare at the research transect before the Nile perch upsurge (Witte et al. 1992b), but is currently one of the most common species. The species has been referred to as *H.* 'broken bar' by Seehausen et al. (1997b) and is possibly the same as *H. paropius* Greenwood & Gee from the northern part of the lake. However, until this has been confirmed by a proper taxonomic study we prefer using the cheironym *H.* 'paropius-like' that was used by Witte et al. (1992b). The pooled "detritivores" comprised fish that showed features of *H. (E.) cinctus* Greenwood & Gee, *H. (E.) antleter* Mietes & Witte, *H. (E.) coprologus* Niemantsverdriet & Witte, *H. (E.)* 'purple head' and *H. (E.) katunzii* Ter Huurne & Witte. We studied 50 pooled "detritivores" collected in 2005 and 2006 (the modern ecosystem) and 26 "detritivores" from the same area collected in the period 1977-1982 (the old ecosystem), comprising eight *H. antleter,* six *H. katunzii,* four *H. cinctus,* four *H.* 'purple head' and four *H. coprologus*. Of *H.* 'paropius-like', 14 specimens from the old and 26 specimens from the modern ecosystem were investigated. Specimens collected in the period 1977-1982 had been stored in the Natural History Museum, Naturalis, Leiden. Of all studied specimens, the standard length (SL) and length of the intestine (IL) were measured. Dissection microscopes (maximum magnifications 50x and 63x) were used for diet analysis. Intestines were divided into four equal parts, each of which was studied separately, thus keeping the amount of food that had to be sorted manageable. The results of the four parts were finally combined for each fish. Food items were classified in the following ways: (1) as pooled groups or taxa: viz. detritus, phytoplankton (mainly containing diatoms and cyanobacteria), zooplankton (mainly copepods and cladocerans), ostracods, midge larvae (chaoborids and chironomids), insects (parts of unidentifiable species), leeches, molluscs (bivalves and snails), shrimps and fish; (2) according to the size of the smallest diameter of individual items (following Katunzi et al. 2003): small (< 0.5 mm), intermediate (c. 0.5-1 mm), intermediate-large (c. 1-2 mm), large (> 2 mm); (3) according to plant and animal material.

Frequency of occurrence and the volume percentages were used in assessing the contribution of a particular prey item to the diets of the pooled “detritivores” and *H.* ‘paropius-like’. The frequency of occurrence of food items in the total gut (stomach plus intestine) was scored for individuals from a period and expressed as percentage of the total number of investigated fishes containing food in that period. Volume per food type was estimated as a percentage of the total volume of ingested food per stomach or intestine part. This was done by estimating the percentage of surface covered by each food type in a petri dish. Stomach and intestine fullness were also estimated by eye, and classified as 25, 50, 75 or 100% full. In the beginning, estimates of fullness and food volumes were performed independently by two persons on the same fish to check the reliability of the estimates. Corrections on volumes per food type were made for the percentage of fullness. Empty stomachs and intestines, and those estimated to be less than 25% full were discarded.

The Kolmogorov-Smirnov test was used to test data for normal distribution. To test for differences in standard length of the studied fish from the old and modern ecosystem we used the t-test. Ratios between intestine length and standard length were also tested with the t-test. Differences in percentages of frequency of occurrence per prey item between the two periods were tested with the Fisher’s Exact Probability test. Volume percentages of food items in fishes were not normally distributed, therefore, the nonparametric Mann Whitney U-test was used to test for differences between the modern and old ecosystem. In case of multiple comparisons, sequential Bonferroni corrections were performed. All tests were done in SPSS 15.0 for Windows.

RESULTS

Fish size

The standard lengths of the investigated pooled “detritivores” ranged from 47-70 mm (61.4 ± 5.9 mm, n = 26) and 48-71 mm (57.5 ± 6.2 mm, n = 49) in respectively the old and modern ecosystem. The sizes of *H.* ‘paropius-like’ from the old and modern ecosystem were 54-68 mm (60.5 ± 4.0 mm, n = 14) and 45-71 mm (58.3 ± 8.5 mm, n = 19) respectively. Though the fish of the latter period seemed slightly smaller, the difference was not significant (pooled “detritivores” t-test, *P* = 0.085; *H.* ‘paropius-like’ t-test, *P* = 0.335).

Ratio between intestine length and standard length

For the two groups of investigated fish, the ratios of intestine length and standard length were significantly higher in specimens collected in the old ecosystem than in those from the modern ecosystem. The pooled "detritivorous" species had ratios ranging from 1.2-4.0 (2.3 ± 0.6, n = 26) and 0.7-2.1 (1.5 ± 0.3, n = 49) in the old and modern ecosystem, respectively (t-test, $P < 0.001$). The ratios for *H.* 'paropius-like' ranged from 1.4-2.1 (1.8 ± 0.2, n = 14) in the old ecosystem and 0.8-1.6 (1.0 ± 0.3, n = 19) in the modern ecosystem (t-test, $P < 0.001$).

Stomach fullness

The average stomach fullness in the pooled "detritivores" was significantly lower in the modern than in the old ecosystem (69 ± 21% modern vs 98 ± 7% old, Mann Whitney U-test, $P < 0.001$). The same held for the intestine fullness (78 ± 20% modern vs 90 ± 20% old, Mann Whitney U-test, $P < 0.001$). A similar trend was present in *H.* 'paropius-like', where stomach fullness decreased from 82 ± 23% in the old to 62 ± 25% in the modern ecosystem (Mann Whitney U-test, $P = 0.026$) and intestine fullness from 83 ± 15% to 77 ± 21% (Mann Whitney U-test, $P = 0.545$), but after Bonferroni corrections both differences in *H.* 'paropius-like' were not significant.

Frequency of occurrence of prey items

Pooled "detritivores": The diet of the pooled "detritivores" in the modern ecosystem differed considerably from that in the old ecosystem (Table 3.1). The frequency of occurrence of phytoplankton and detritus was significantly lower. On the other hand, the pooled "detritivores" were found to feed more frequently on midge larvae (chironomids and chaoborids), insects, molluscs and shrimps in the modern ecosystem. Molluscs, shrimps and leeches were new prey items for the pooled "detritivorous" species, but the increase in frequency of occurrence of leeches was not significant; it occurred in only one fish (Table 3.1).

H. ‘paropius-like’: Similar diet changes were found for H. ‘paropius-like’; phytoplankton, detritus and ostracods were less often present in the modern ecosystem (Table 3.1). However, the decrease for detritus was not significant after Bonferroni correction. The same held for the increase in frequency of occurrence of molluscs, which were new prey items for *H.* ‘paropius-like’ (Table 3.1).

Table 3.1 Frequency of occurrence (Foo, in percentages) of food items in the diet of “detritivorous” species in the old and modern ecosystems and P-values of two-tailed Fisher’s exact tests (significant values after sequential Bonferroni corrections are in bold).

	Pooled “detritivores”			*H.* ‘paropius-like’		
Prey	Old (n = 26)	Modern (n = 49)	*P*	Old (n = 14)	Modern (n = 19)	*P*
Detritus	100	38	< **0.001**	93	42	= 0.009
Phytoplankton	100	2	< **0.001**	100	0	< **0.001**
Zooplankton	80	92	= 0.259	79	95	= 0.283
Ostracods	24	27	= 1.000	64	11	**= 0.002**
Midge larvae	60	98	< **0.001**	79	95	= 0.283
Insects	8	44	**= 0.002**	36	21	= 0.704
Leeches	0	2	= 1.000	0	0	
Molluscs	0	48	< **0.001**	0	32	= 0.031
Shrimps	0	48	< **0.001**	7	32	= 0.198
Fish	0	0		14	0	= 0.162

Volume percentages of prey items

Changes in the diet of the pooled “detritivores” and *H.* ‘paropius-like’ were also observed when using the volume percentage method.

Pooled “detritivores” (Fig. 3.1): The stomachs and intestines of pooled “detritivores”, in the modern ecosystem contained significantly less detritus (stomachs: 36 ± 12% old, 4 ± 10% modern; intestines: 33 ± 16% old, 4 ± 8% modern) and phytoplankton (stomachs: 49 ± 13% old, 0% modern; intestines: 46 ± 20% old, 0.01 ± 0.1% modern) than in the old ecosystem (Mann Whitney U-tests in all cases $P < 0.001$). In contrast, significantly higher percentages were found for midge larvae (stomachs: 5 ± 10% old, 31 ± 27% modern; intestines: 3 ± 6% old, 34 ± 22% modern), shrimps (stomachs: 0% old, 10 ± 18% modern; intestines: 0% old, 10 ± 15% modern) and remains of unidentified insects (stomachs: 0% old, 5 ± 16% modern; intestines: 0.1 ± 0.5% old, 3 ± 7% modern) (Mann Whitney U-tests for midge larvae and shrimps $P < 0.001$, for insect remains $P = 0.009$ for stomachs, and $P = 0.017$ for intestines). Zooplankton and molluscs were significantly more abundant in the intestines only, in the modern ecosystem (zooplankton: 8 ± 14% old, 16 ± 17% modern; molluscs 0% old, 9 ± 16% modern; Mann Whitney U-test, $P = 0.010$ and $P < 0.001$ respectively). Ostracods were eaten in low quantities in both periods. The occurrence of leeches in the stomach of one fish in the modern ecosystem did not change the diet significantly.

H. ‘paropius-like’ (Fig. 3.2): The results for *H.* ‘paropius-like’ resemble those for the pooled “detritivores”. Detritus comprised 24 ± 17% and 29 ± 16% of the stomach and intestine volumes in the old ecosystem and 4 ± 6% and 8 ± 12% respectively in the modern ecosystem (Mann Whitney U-test, $P < 0.001$ in both cases), while phytoplankton dropped from 38 ± 17% in stomachs and 31 ± 21% in intestines to 0% (Mann Whitney U-test, $P < 0.001$, in both cases). Midge larvae in the diet of *H.* ‘paropius-like’ increased from 11 ± 11% to 36 ± 24% and from 13 ± 15% to 42 ± 19% in stomachs and intestines respectively (Mann Whitney U-test, $P = 0.005$ and $P < 0.001$). Zooplankton only increased significantly in the intestines (4 ± 4% old, 15 ± 13% modern; Mann Whitney U-test, $P = 0.007$). Other prey items including ostracods, remains of unidentified insects, shrimps and fish were eaten in low percentages in one or both periods (Fig. 3.2). Molluscs, a new food item of which the frequency of occurrence was significantly higher in *H.* ‘paropius-like’ from the modern ecosystem (Table 3.1), on average only comprised 2 ± 5%

and 2 ± 8% of the volume in stomachs and intestines respectively. In contrast to the frequency of occurrence, the differences in volume between old and modern ecosystem were not significant.

Prey type diversity

Both the pooled “detritivores” and *H.* ‘paropius-like’ included new prey types in their diet (Table 3.1; Figs 3.1, 3.2). The number of prey types per individual of the pooled “detritivorous” species ranged from two to six (mean 3.7) in the old, and from two to seven (mean 4.4) in the modern ecosystem; the increase in the mean number of prey types was significant (t-test, $P = 0.025$). For *H.* ‘paropius-like’, the number of prey types per individual in the old and modern ecosystem ranged from three to six (mean 5) and from two to six (mean 3.6) respectively. In this case the mean number of prey types decreased significantly (t-test, $P < 0.001$).

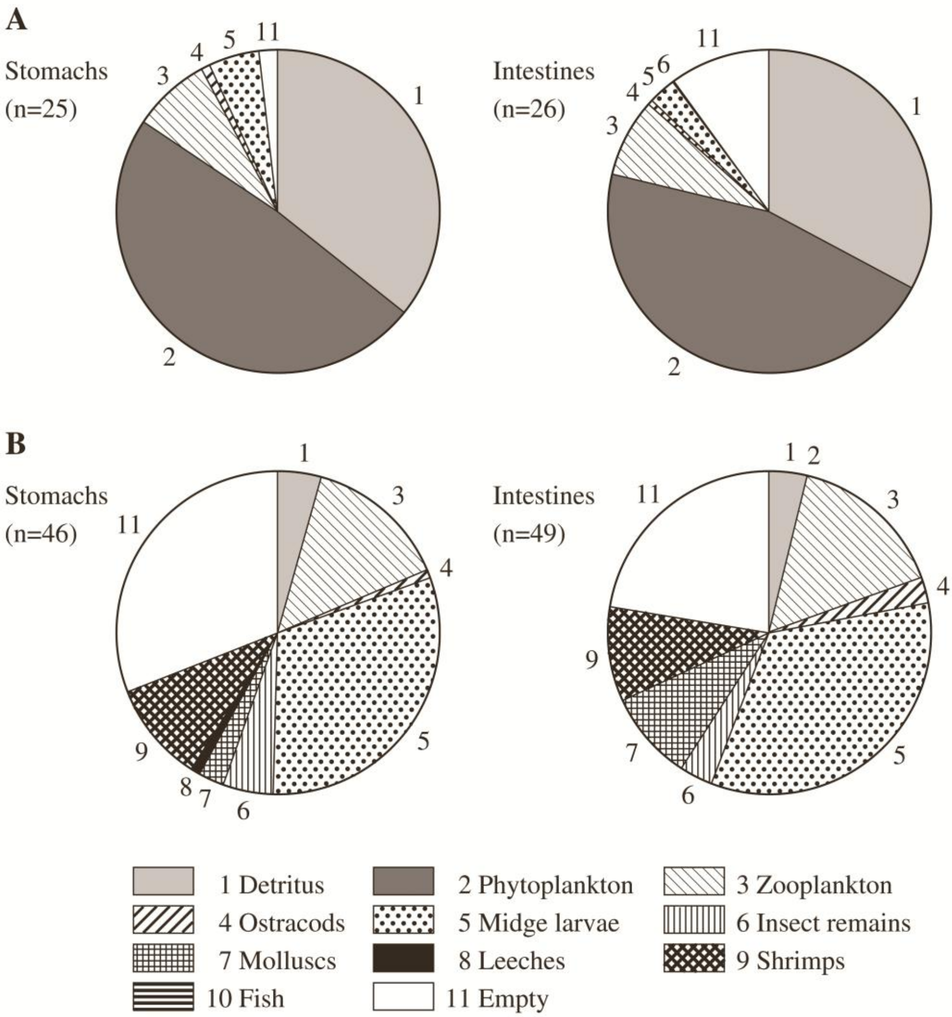

Fig. 3.1 Diet composition (mean volume percentages) by day in stomachs of the pooled “detritivores” in the Mwanza Gulf (a) in the old ecosystem (1977-1982; *H. cinctus*, *H. antleter*, *H. coprologus*, *H.* ‘purple head’) (b) in the modern ecosystem (2005-2006).

Prey size

In stomachs of the pooled “detritivores”, the volume percentage of small-sized preys decreased from 93% to 19%, whereas intermediate-sized preys increased from 5% to 31%. Intermediate-large and large prey items that did not occur in the diet in the old ecosystem also increased significantly in volume percentage. For the intestines, the results were similar (Table 3.2).

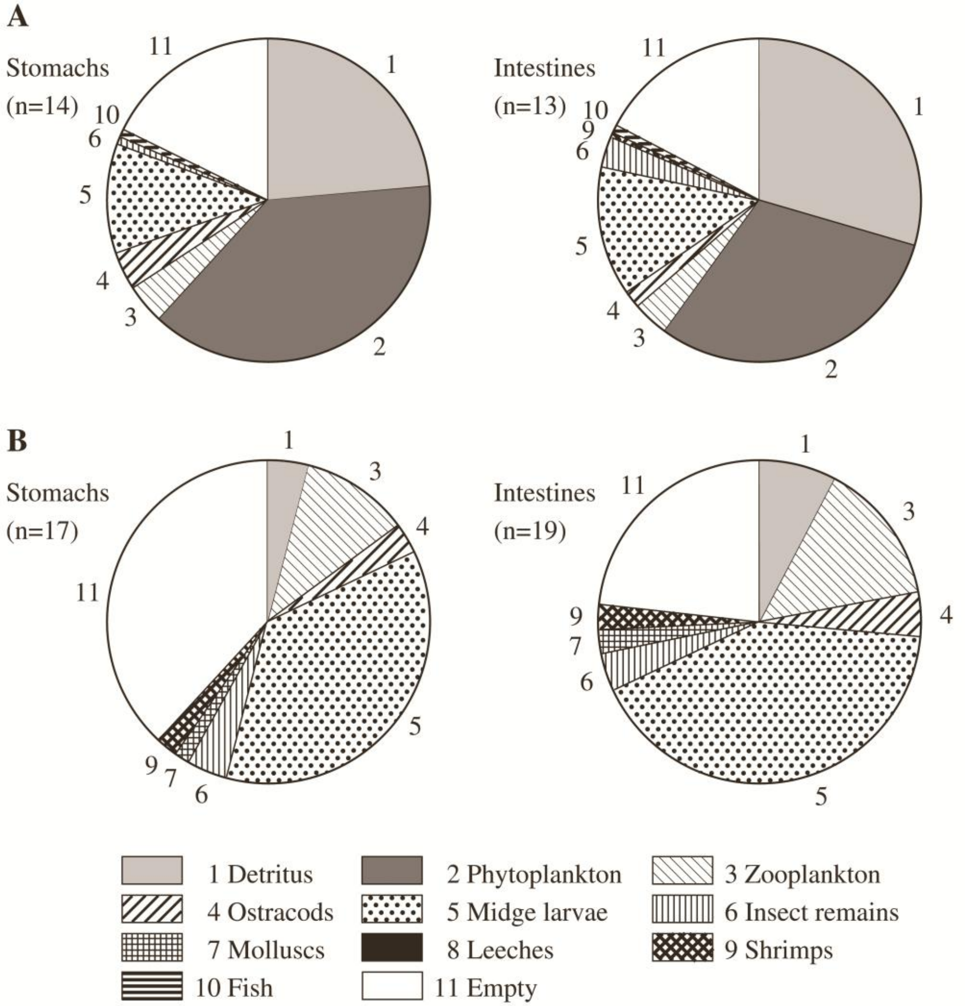

Fig. 3.2 Diet composition (mean volume percentages) in stomachs and intestines of *H.* ‘paropius-like’ by day in the Mwanza Gulf (a) in the old ecosystem (1977-1982); (b) in the modern ecosystem (2005-2006).

For *H.* ‘paropius-like’ small-sized prey items in stomachs decreased from 70% to 18% and intermediate preys increased from 11% to 36%. There were no significant differences between the two periods for intermediate-large and large prey items (Table 3.2). Similar results were obtained for the intestines of *H.* ‘paropius-like’ (Table 3.2).

Table 3.2 Abundance of prey sizes (mean volume percentages ± standard deviation) of pooled "detritivorous" species and *H.* 'paropius-like' in the old and modern ecosystems and P-values of Mann Whitney U-test (significant values after sequential Bonferroni corrections are in bold).

		Pooled "detritivores"			*H.* 'paropius-like'		
Prey size	Part	% Old	% Modern	*P*	% Old	% Modern	*P*
Small	Stomach	93 ± 11	19 ± 18	< **0.001**	70 ± 19	18 ± 16	< **0.001**
	Intestine	87 ± 22	22 ± 18	< **0.001**	65 ± 23	26 ± 21	< **0.001**
Intermediate	Stomach	5 ± 10	31 ± 27	< **0.001**	11 ± 11	36 ± 24	**= 0.005**
	Intestine	3 ± 6	34 ± 21	< **0.001**	13 ± 14	42 ± 19	< **0.001**
Intermediate-	Stomach	0	6 ± 18	**= 0.009**	1 ± 3	4 ± 16	= 0.984
large	Intestine	0.1 ± 0.5	3 ± 7	**= 0.017**	3 ± 6	4 ± 12	= 0.762
Large	Stomach	0	13 ± 20	< **0.001**	1± 3	4 ± 6	= 0.200
	Intestine	0	18 ± 21	< **0.001**	1 ± 3	5 ± 11	= 0.343

Plant and animal prey types

Pooling of prey items into plant and animal prey types, revealed a shift from a diet in which plant material dominated (detritus excluded) to a mainly carnivorous diet. In the pooled "detritivores" volume percentages of plant material, in stomachs and intestines, decreased from 49% to 0% and from 46% to 0% respectively (Table 3.3). In contrast, animal materials increased from 14% to 65% and from 11% to 74% in stomachs and intestines respectively (Table 3.3). *H.* 'paropius-like' showed similar changes (Table 3.3).

Table 3.3 Abundance of plant and animal preys (mean volume percentage ± standard deviations) of pooled "detritivorous" species in the old and modern ecosystems and P-values of Mann Whitney U-test (significant values after sequential Bonferroni corrections are in bold).

		Pooled "detritivores"			*H.* 'paropius-like'		
Prey material	Part	% Old	% Modern	*P*	% Old	% Modern	*P*
Plant	Stomach	49 ± 13	0	< **0.001**	38 ± 17	0	< **0.001**
	Intestine	46 ± 20	0.1± 0.1	< **0.001**	31 ± 21	0	< **0.001**
Animal	Stomach	14 ± 15	65 ± 23	< **0.001**	20 ± 18	58 ± 25	< **0.001**
	Intestine	11 ± 18	74 ± 21	< **0.001**	23 ± 17	69 ± 21	< **0.001**

DISCUSSION

The diet composition in the old ecosystem (1977-1982) found in the present study for the pooled "detritivores" (*H. cinctus*, *H. katunzii*, *H. antleter*, *H. coprologus* and *H.* 'purple head') showed similarities to that reported by Goldschmidt et al. (1993) for *H. coprologus* and the curved head group (mainly *H. cinctus* and *H. katunzii*) at station G during 1981-1982. Note that in contrast to Goldschmidt et al. (1993), we included the category "empty", in the pie charts. This slightly reduced our food volume percentages compared to those in Goldschmidt et al. (1993). Nevertheless, in both cases detritus and phytoplankton together, made up more than 75% of the diet, whereas the remaining food consisted mainly of zooplankton and midge larvae. The only difference was that in the study of Goldschmidt et al. (1993) the diet during daytime comprised more detritus (about 75% of the volume) than phytoplankton (about 10%), whereas we found 36 and 33% detritus and 49 and 46% phytoplankton in stomach and intestine respectively. The difference may be due to the fact that a wider range of species, years and stations were included in our study of the old system than in that of Goldschmidt et al. (1993). The difficulty to discriminate between phytoplankton and detritus could also be a source of the observed difference. Greenwood & Gee (1969) reported on the gut content of one *H. cinctus* specimen that was collected in the northern part of the lake; the stomach and intestine were "filled with colonial blue green algae (cyanobacteria), diatoms and other algaceous material". For *H. paropius* they investigated 20 individuals, which all contained "large quantities of blue-green algae and diatoms, and smaller amounts of other plant material". Eight of these guts contained in addition, "fragmentary remains of larval Diptera (probably chironomids)" (Greenwood & Gee 1969).

Obviously, all studies, including ours, show that in the past the "detritivores" in the sub-littoral and off-shore areas were mainly feeding on bottom debris and phytoplankton, whereas currently they feed mainly on invertebrates such as zooplankton, midge larvae, molluscs and shrimps.

Shifts in diet after the ecological changes in the lake were observed in several fish taxa. (1) "zooplanktivorous" haplochromines, which formerly fed mainly on zooplankton (copepods), currently are including shrimps, fish, molluscs, midge larvae and insects in their diet (van Oijen & Witte 1996; Katunzi et al. 2003; Chapter 4). (2) Wanink (1998) observed a similar shift from a diet dominated by zooplankton to one including larger prey (like midge larvae, shrimps and small fish) in the cyprinid *R. argentea* (3) The introduced tilapiine cichlid *O. niloticus*, originally had a predominantly phytoplanktivorous/detritivorous diet (Welcomme 1967) and currently includes considerable amounts of macro-invertebrates in its diet (Gophen et al. 1995; Balirwa 1998; Njiru et al. 2004; Bwanika et al. 2006). (4) Of two investigated catfish species, *Bagrus docmak* exhibited a shift from a primarily piscivorous diet dominated by haplochromine cichlids to a broader diet including a significant proportion of invertebrates and the cyprinid *R. argentea*, while *Schilbe intermedius* showed a shift from a piscivorous diet dominated by haplochromines to an insectivorous diet (Olowo & Chapman 1999) (5) A dietary shift was recorded for the characid *Brycinus sadleri*, which originally mainly fed on plant material during daytime and surface insects at night. After the ecological changes midge larvae and pupae, shrimps, odonata nymphs and fish were included in the diet (Wanink & Joordens 2007).

In all cases the shifts comprised an increase in macro-invertebrates. There are several possible explanations for these shifts in diet *(1) Availability of suitable food types:* Although, with the increased algae blooms after the ecological changes (Ochumba & Kibaara 1989; Hecky 1993; Mugidde 1993), bottom debris and phytoplankton are unlikely to have decreased in abundance or to be limiting resources in the lake, a shift in algae composition may have reduced the nutritional quality of these food types. Diatoms were the dominant taxa of phytoplankton (Hecky 1993; Mugidde 1993) and the main phytoplankton taken by the “detritivores” in the past (Goldschmidt et al. 1993) and contributed most to the bottom debris in the lake (Verschuren et al. 2002). Currently, they are replaced by cyanobacteria (Verschuren et al. 2002), which are notorious for being difficult to digest (Bowen 1988). The current dominance of cyanobacteria in the lake may have lowered the quality of phytoplankton and detritus and made them less suitable for fish, though Moriarty et al. (1973) showed that both *O. niloticus* and *H. (E.) nigripinnis* Regan from Lake George are able to digest cyanobacteria. A switch to more profitable prey, when these become abundant, is a common ecological phenomenon (Krebs & Davies 1978). Densities of shrimps, molluscs, insects and midge larvae in the lake increased after the ecological changes (Kaufman 1992; Goldschmidt et al. 1993; Witte et al. 1995; Goudswaard et al. 2006; Budeba & Cowx 2007). As these potential prey all have high energy content per item in comparison to phytoplankton and detritus, they could all be profitable to the “detritivores” if the handling times are not too long. Molluscs will probably be less profitable than midge larvae and shrimps because of a relatively low ratio of energy and handling time and the disadvantage of swallowing large amounts of relatively heavy indigestible material (Hoogerhoud 1987; Slootweg et al. 1994).

(2) Decline of the trophic specialists: In addition to the increase of certain prey types, the formerly common insectivorous, molluscivorous and piscivorous haplochromines are currently rare (Seehausen et al. 1997b; Witte et al. 2000; Witte et al. 2007b; Witte et al. 2007a). Thus, the increase of profitable prey items in the lake and the absence of efficient competitors may have resulted in a competitive release, which possibly gave the former “detritivores” an opportunity to include new prey types in their diet. *(3) Decrease in water clarity:* For successful prey selection, a visual predator is dependent on the optical characteristics of the water and the conspicuousness of the prey (Seehausen et al. 2003). Seehausen et al. (2003) argued that, due to reduced water clarity in the modern ecosystem, fish might become less choosy, as their encounter rate with preferred prey types decreases. In that case one would expect an increase in prey type diversity, because the fish will include less preferable prey in their diet. However, though we found a small increase in mean prey type diversity in the pooled “detritivores”, this appeared to decrease in *H.* ‘paropius-like’. Alternatively, it has been found that

cichlids that grew up under low light conditions increased their light sensitivity by giving up some of their visual resolution (van der Meer 1993), making it difficult to spot small-sized prey items. Research on retina structures of the old and modern populations should be carried out to check if the resolution in the latter decreased. So far, we have no indication which of the above potential explanations is the most likely; possibly more than one is involved.

In the past, the diet of the “detritivores” and “zooplanktivores” in the sub-littoral area of the Mwanza Gulf differed considerably. During daytime 70-90% of the stomach contents of the “zooplanktivores” (with exception of the bottom dwelling *H.* ‘reginus’) consisted of zooplankton (mainly copepods), while some midge larvae where generally also present (Goldschmidt et al. 1990). In contrast, in the “detritivores” similar percentages were made up by detritus and phytoplankton (Figs. 3.1a, 3.2a; Goldschmidt et al. 1993). Due to the dietary shifts of the recovering “detritivores” and “zooplanktivores”, their diets presently show a considerable overlap, both groups including zooplankton, midge larvae, insects, molluscs and shrimps in their diet (Figs. 3.1b, 3.2b; van Oijen & Witte 1996; Katunzi et al. 2003; Chapter 4). In the past, morphological differences in Lake Victoria haplochromines used to correlate with differences in their natural diet (Greenwood 1974; Barel et al. 1977; Witte & van Oijen 1990). However, laboratory and field studies on functional morphology and ecology provided evidence that many cichlids could potentially feed more broadly on available resources than their specialised feeding apparatus did suggest (Liem 1980; Barel 1983; Mckaye & Marsh 1983; Ribbink 1990). This may hold particularly for the “detritivores” with their rather generalized morphology. Moreover, recent studies on the “zooplanktivorous” *Haplochromis (Yssichromis) pyrrhocephalus* Witte and Witte-Maas and the cyprinid *R. argentea* before and after the ecological changes revealed some morphological changes that are probably related to the larger prey types they currently consume (Wanink & Witte 2000b; Witte et al. 2008). Detailed morphological comparisons between the feeding apparatuses of the “detritivores” of past and present still have to be made. However, relative intestine length has been included in this study. In both, the pooled “detritivores” and *H.* ‘paropius-like’ the average relative intestine length in 2006 was approximately 33% shorter than before the ecological changes. The current average IL/SL ratios of respectively 1.5 and 1.2 fall within the range of 1.1-1.7 that was most common in “zooplanktivores” before the ecological changes (Witte & van Oijen 1990). It is not clear whether these changes are the result of natural selection or of phenotypic responses. The lower stomach fullness observed in the modern ecosystem also agrees with the current carnivorous diet of the “detritivorous” species.

If diet indeed would contribute to the relatively slow recovery of the “detritivores”, this would only hold if they are relatively poorly adapted to their new diet in comparison to the “zooplanktivores”, which currently use the same food sources. A follow up study should focus on this.

Acknowledgements

We thank our colleagues from the Haplochromis Ecology Survey Team (HEST), the Tanzania Fisheries Research Institute (TAFIRI) and the Freshwater Fisheries Training Institute at Nyegezi for support and co-operation during the fieldwork. We wish to thank Mhoja Kayeba and other the crewmembers of the trawlers for their skilful labour. We are indebted to John Videler and two anonymous referees for comments on an earlier draft of the paper and to Martin Brittijn for making the figures. The research of HEST was financially supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO; grants W87-129, W87-161, W87-189, W84-282, W84-488, WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC), the International Foundation for Science (IFS), the Schure Beijerinck-Popping Fonds, the van Tienhoven Stichting, and Yellow Springs Instruments.

Chapter 4

Changes in the diet of the “zooplanktivorous” cichlids in Lake Victoria

Mary A. Kishe-Machumu, Frans Witte, Jan H. Wanink

ABSTRACT

Until some decades ago, haplochromine cichlids in Lake Victoria comprised over 500 species, which occupied virtually all trophic levels. As a result of Nile perch introduction and other ecological changes, populations of haplochromine species declined and many of them became rare.

In the 1990s, some "zooplanktivorous" species reappeared. In this study gut contents of the "zooplanktivores" *H. pyrrhocephalus* and *H. tanaos* caught prior to and after the ecological changes are compared. In the old ecosystem zooplankton, midge larvae and remains of unidentified insects dominated the diet of both species. In the modern ecosystem, the contribution of zooplankton declined and the diet became more diverse due to the addition of new prey items, viz. ostracods, molluscs and shrimps. In general there was a shift towards larger prey items, even including small fish. The two species still segregate to some extent because *H. tanaos* includes more benthic prey than *H. pyrrhocephalus*. Shifts in diet in the modern ecosystem towards macro-invertebrates were also found for former "detritivorous" species and for several other fish taxa. This indicates that currently there is more overlap of food items among different fish species than in the past. The factors that caused these changes in diet are discussed.

INTRODUCTION

Prior to the Nile perch introduction, the fish fauna of Lake Victoria comprised a presumably monophyletic flock of more than 500 endemic haplochromine cichlid species (Meyer et al. 1990; Seehausen 1996; Witte et al. 2007a). This species flock showed an extreme level of adaptive radiation; virtually all habitats and food types were exploited (Witte & van Oijen 1990).

During the 1980s, the haplochromines from the sub-littoral and offshore areas (estimated at more than 200 species) vanished almost completely (Witte et al. 1992b; Witte et al. 2007b). Commercial trawl fishery, the upsurge of the introduced Nile perch, *Lates niloticus* (Linnaeus) (Ogutu-Ohwayo 1990a; Goudswaard et al. 2008) and an increase of eutrophication (Hecky 1993) were possible causes of this decline. The rate at which the trophic groups declined differed; the relatively large piscivores, insectivores and molluscivores were the first to disappear from the catches. The small-sized group; “detritivores” and “zooplanktivores”, declined at lower rates (Witte et al. 2007b). During the 1970s, “detritivorous” species formed the most important guild with at least 12 species making up ca. 75% to 85% of the number of haplochromines in the catches. They were followed by more than 13 species of “zooplanktivores”, comprising 10-20% of the number of individuals (Witte 1981; Witte et al. 2007b).

From the beginning of the 1990s, a resurgence of some “detritivorous” and “zooplanktivorous” species was observed (Seehausen et al. 1997b; Witte et al. 2000; Getabu et al. 2003; Witte et al. 2007a,b), but during the first years the relative abundance of the two groups reversed. Up to 2006 the “zooplanktivorous” haplochromines were even far more abundant than previously and made up more than 70% of the number of haplochromines, whereas the former dominant “detritivores” generally constituted less than 25% (Witte et al. 2007a,b). However, in 2008, the “detritivores” became dominant by numbers again (52% versus 21% “zooplanktivores”; Table 2.2 [Chapter 2]).

Among other factors, feeding habits might play a role in differential recovery. Gut contents of recovering “detritivores” from the years 2005 and 2006 have been studied by Kishe-Machumu et al. (2008) and revealed a shift in diet from detritus and phytoplankton towards macro-invertebrates. In the present paper we investigate the diets of the resurging “zooplanktivores” *H. (Yssichromis) pyrrhocephalus* Witte & Witte-Maas and *H. tanaos* van Oijen & Witte, which are now common species in the lake (Witte et al. 2007a) and are major prey items in the diet of Nile perch (Chapter 7). Preliminary studies on diets of resurging *H. tanaos* and *H. pyrrhocephalus* were made by van Oijen & Witte (1996) and by Katunzi et al. (2003) respectively. However, these studies were not comparable to that of the "detritivores", because the methods and the time spans over which the diets were studied differed. Of *H. tanaos* combined stomach and intestine contents (expressed as volume percentages) of only ten specimens collected in 1993 were compared with diets of fish from the pre-Nile perch era. The diet of *H. pyrrhocephalus* has only been studied by comparing the frequency of occurrence of prey items in pre-Nile perch specimens with those in specimens collected between 1991 and 2001 (Katunzi et al. 2003).

In the present study we use both frequency of occurrence and volume percentages to assess the diets of the two recovered "zooplanktivorous" species and we compare diets in 2005 and 2006 with those from the past. The issue of diet as a potential factor for the differential resurgence of "zooplanktivores" and "detritivores" is discussed.

MATERIALS AND METHODS

All samples were collected during day time using bottom trawls in the northern part of the Mwanza Gulf, between Nyamatala Island and Hippo Island (Fig. 1.2 [Chapter 1]). Sampling was conducted in the periods 1977-1981 and 2005-2006, and the collected material is referred to as samples from the old and modern ecosystem respectively.

Samples of *H. pyrrhocephalus* and *H. tanaos* from the modern ecosystem were collected at sub-littoral stations (E to J, Fig. 1.2 [Chapter 1]) with mud bottoms on a research transect across the Mwanza Gulf. Due to fluctuations in water level, depths ranged from 5.5 to13 m in the period 2005-2006 and from 6 to14 m in the period 1977-1981. As we had no sufficient *H. pyrrhocephalus* from the transect in the old ecosystem, we added specimens that were collected in catches over mud bottoms near the transect at similar depths (hatched area in Fig. 1.2 [Chapter 1]).

In the old ecosystem, *H. tanaos* was only caught in Butimba Bay at stations A and B (Fig. 1.2 [Chapter 1]). These stations have a sand bottom with depth ranges of respectively 2 to 4 and 4 to 6 m. They form the eastern end of the research transect and were not sampled in the modern ecosystem.

During sampling, immediately after hauling, catches were stored on ice and in the laboratory they were sorted by trophic groups and by species. Only adult fishes (> 4 cm standard length) were used for identification and diet analysis. After identification, the visceral cavity was opened by a cut from the anus to the shoulder girdle and the specimens were preserved in a 5% formaldehyde solution. Before diet analysis, fish samples were transferred in steps (30%, 60%) to 70% alcohol. Of *H. pyrrhocephalus*, 31 specimens from the old and 63 specimens from the modern ecosystem were analyzed and of *H. tanaos* 32 and 25 specimens from the old and modern ecosystem respectively. Samples from the old ecosystem had been stored in the National Museum of Natural History (Naturalis) in Leiden.

Standard length (SL) of the specimens was measured to the nearest 0.1 mm and length of the intestine (IL) to the nearest mm. Dissection microscopes (maximum magnifications 50x and 63x) were used for diet analysis. The stomach was separated from the intestine and its content was examined. Each intestine was divided into four equal parts, which were checked separately. Results of the four intestine parts for each fish were finally combined. Food items were classified as follows: (1) as pooled groups or taxa: viz. detritus, phytoplankton (mainly containing diatoms and cyanobacteria), zooplankton (mainly copepods and cladocerans), ostracods, midge larvae (mainly chaoborids and chironomids), insects (parts of un-identifiable species of insects), leeches, molluscs (bivalves and snails), shrimps, fish and others (mainly oligochaeta and un-identified materials); (2) by size/diameter of individual food items following Katunzi et al. (2003): small (<0.5 mm), intermediate (c. 0.5–1 mm), intermediate-large (c. 1-2 mm), large (> 2 mm).

Frequency of occurrence and the volume percentages were used in assessing the contribution of a particular prey item to the diets of *H. pyrrhocephalus* and *H. tanaos*. The frequency of occurrence of food items in the total gut (stomach plus intestine) was scored for individuals from a period and expressed as percentage of the total number of investigated fishes containing food in that period. Volume per food item was estimated as a percentage of the total volume of ingested food per stomach or intestine. This was done by estimating the percentage of surface covered by each food type in a petri dish. Stomach and intestine fullness were also estimated visually and classified as 25%, 50%, 75% or 100% full. To establish the average diet of a species, corrections on volumes per food type were made for the percentages of fullness of each fish. Empty stomachs and intestines and those estimated to be less than 25% full were discarded.

The Kolmogorov-Smirnov (KS) test was used to test data for normal distribution. The t-test was used for testing the differences in standard length of the investigated fish from the old and modern ecosystems. Differences in percentages of frequency of occurrence per prey item between the two periods were tested with the Fisher’s Exact Probability test. Volume percentages of food items in fishes were not normally distributed; therefore, the non-parametric Mann Whitney U-test was used to test for differences between the modern and old ecosystems. In case of multiple comparisons, sequential Bonferroni corrections were performed. The Mann Whitney U-test was also used to test for differences in fullness of stomachs and intestines between the modern and old ecosystem. All tests were performed by SPSS 15.0 for Windows.

RESULTS

Fish size

The standard lengths of *H. pyrrhocephalus* selected for diet analysis ranged from 50.3-82.1 mm (64.7 ± 6.2, n = 31) in the old ecosystem and from 46.0–69.3 mm (56.8 ± 5.1, n = 65) in the modern ecosystem. The difference in standard lengths between the two periods was significant (t-test, $P < 0.001$). The sizes of *H. tanaos* ranged from 48.1–70 mm (62.4 ± 5.8, n = 25) and from 52–77 mm (61.6 ± 6.6, n = 38) in the old and modern ecosystem respectively and were not different (t-test, $P = 0.609$).

Ratio between intestine length and standard length

The mean ratio of intestine to standard length of *H. pyrrhocephalus* was 1.3 ± 0.2 both in the old and modern ecosystem. Similarly, the ratio of intestine to standard length for *H. tanaos* collected in the old ecosystem was not different from that in the modern ecosystem (1.2 ± 0.2 old, 1.2 ± 0.3 modern).

Stomach and intestines fullness

There was no significant difference for the average fullness of *H. pyrrhocephalus* between the two periods for the stomachs (71.7 ± 22.8% old; 73.5 ± 21.3% modern; Mann Whitney U-test, $P = 0.842$) and intestines (67.9 ± 23.3% old; 66.4 ± 20.4% modern; Mann Whitney U-test, $P = 0.727$)

Similarly, in *H. tanaos,* there was no difference in stomach fullness (71.7 ± 28.1% old; 71.9 ± 26.0% modern; Mann Whitney U-test, $P = 0.962$) between the old and modern population. This also held for the intestines, whereby the average fullness was 79.4 ± 20.0% in the old ecosystem and 77.9 ± 13.7% in the modern ecosystem (Mann Whitney U-test, $P = 0.478$).

Frequency of occurrence

H. pyrrhocephalus

The frequency of occurrence of detritus, ostracods and shrimps increased in modern *H. pyrrhocephalus* (Table 4.1). However, after Bonferroni correction, the difference for ostracods was not significant. Ostracods and shrimps were not encountered in the old population of *H. pyrrhocephalus*. Leeches and molluscs were also new prey items in the modern population, but their increases were not significant. Zooplankton, midge larvae (*Chaoborus* and chironomids) and unidentified insects, which were present in most old *H. pyrrhocephalus*, did not change in frequency of occurrence in the modern population (Table 4.1).

The mean number of prey items per individual for *H. pyrrhocephalus* increased significantly from 2.7 ± 1.0 in the old to 3.7 ± 1.3 in the modern population (t-test, $P < 0.001$).

H. tanaos

The frequency of occurrence of zooplankton, the main prey item of old *H. tanaos*, was significantly lower in the modern population (Table 4.1). Phytoplankton, which was consumed by 16% of the old population, was not encountered in modern *H. tanaos*; however, its decrease was not significant after the Bonferroni correction. Modern *H. tanaos* were found to feed more frequently on ostracods, shrimps and fish. Only the differences for the two new prey items; ostracods and shrimps were significant after the Bonferroni correction. Though molluscs were also a new prey item in the modern ecosystem, their increase was not significant. The mean number of prey items per individual increased significantly from 3.0 ± 1.0 in the old ecosystem to 3.9 ± 1.4 in the modern ecosystem (t-test, $P < 0.001$).

Table 4.1 Frequency of occurrence (Foo, in percentages) of food items in the diet of "zooplanktivorous" species in the old and modern ecosystems and P-values of two-tailed Fisher's exact tests (significant values after sequential Bonferroni corrections are in bold).

	H. pyrrhocephalus			*H. tanaos*		
Prey	Old (n = 31)	Modern (n = 63)	*P*	Old (n = 25)	Modern (n = 32)	*P*
Detritus	10	49	**<0.001**	44	69	= 0.104
Phytoplankton	23	19	= 0.786	16	0	= 0.032
Zooplankton	97	86	= 0.157	100	56	**<0.001**
Ostracods	0	19	= 0.007	0	44	**<0.001**
Midge larvae	74	71	= 1.000	56	78	= 0.092
Insects	52	41	= 0.383	72	66	= 0.775
Leeches	0	3	= 1.000	0	0	
Molluscs	0	13	= 0.049	0	9	= 0.248
Shrimps	0	22	**= 0.004**	0	34	**= 0.001**
Fish	13	32	= 0.077	4	28	= 0.032
Others	7	13	= 0.488	12	6	= 0.645

Volume percentages of prey items

H. pyrrhocephalus

Zooplankton, which formed the most important prey item for old *H. pyrrhocephalus* significantly decreased in the modern population. The decrease also held for the intestines, but was not significant after Bonferroni correction (Table 4.2).

Shrimps (a new prey type) and detritus were more common in modern *H. pyrrhocephalus*, however after Bonferroni corrections, the differences were only significant for the intestines. Increases in volume percentages of the new food items ostracods, leeches and molluscs, were not significant after Bonferroni corrections (Table 4.2).

In 15 stomachs and 19 intestines *H. pyrrhocephalus* from the old ecosystem and 49 stomachs and 50 intestines from the modern ecosystem, zooplankton was subdivided into copepods and cladocerans. In the stomachs of old *H. pyrrhocephalus*, cladocerans made up 2% of the food and copepods 47%; in the intestines, it was 1% for cladocerans and 38% for copepods. In the modern population, the fractions of cladocerans and copepods in the stomachs were 3% and 26% respectively, and in the intestines they were 3% and 27%.

From the same sub-samples, midge larvae were subdivided into C*haoborus* and chironomids. In old *H. pyrrhocephalus*, *Chaoborus* comprised 1% of the food in stomachs, whereas chironomids were absent; the intestines contained 8% *Chaoborus* and 4% chironomids. In the modern population, the food comprised 6% *Chaoborus* and 4% chironomids in the stomachs, and 9% *Chaoborus* and 4% chironomids in the intestines.

When prey items were categorized by size it was found that in the stomachs of *H. pyrrhocephalus* the volume percentage of small sized prey items decreased significantly from 62% to 32% (Table 4.2). However, in the intestines the decrease was not significant. Intermediate and intermediate-large sized preys did not change significantly between the two periods, but for the large sized prey items, a significant increase was found both in stomachs (3% to 26%) and intestines (0.1% to 15%; Table 4.2).

H. tanaos

The contribution of phytoplankton in the diet of *H. tanaos* dropped from 5% in the stomachs and 2% in the intestines in the old to 0% both in stomachs and intestines in the modern population, however, after Bonferroni correction, the differences were not significant (Table 4.3). The volume percentages of zooplankton, the main prey item of *H. tanaos* in the old ecosystem, decreased significantly in the modern ecosystem, both in the stomachs (41% to 5%) and intestines (45% to 7%; Table 4.3). The volume percentages of midge larvae were higher in the modern than in the old population, but after Bonferroni correction the increase was only significant for the intestines (6% to 24%; Table 4.3). Ostracods and shrimps, new prey items in the diet of *H. tanaos* in the modern ecosystem, only increased significantly in the intestines (from 0% to 7% for ostracods and 0% to 12% for shrimps; Table 4.3).

Like in *H. pyrrhocephalus*, zooplankton in the diet of *H. tanaos* was subdivided into cladocerans and copepods (in this case all specimens could be used). In contrast to *H. pyrrhocephalus*, in the old ecosystem, cladocerans formed a larger proportion in the diet of *H. tanaos* than copepods, both in stomachs (cladocerans 30%, copepods 11%) and intestines (cladocerans 35%, copepods 11%). In the modern ecosystem, the fractions did not differ; cladocerans and copepods in the stomachs were 2% and 4% respectively, and in the intestines they were 4% for both groups.

A subdivision of midge larvae into *Chaoborus* and chironomids revealed that in the old ecosystem both groups contributed low and similar percentages to the diet of *H. tanaos* (stomachs: 2% *Chaoborus*, 3% chironomids; intestines: 2% *Chaoborus*, 4% chironomids). In the modern ecosystem, *Chaoborus* contributed only 0.1% to the food in the stomachs and 1% to that in the intestines, whereas chironomids contributed 19% and 23% in the stomachs and intestines respectively.

Small sized prey items, which formed the main prey size group for *H. tanaos* in the old ecosystem decreased significantly from 54% to 8% and from 50% to 18% in stomachs and intestines respectively (Table 4.3). The volume percentages of intermediate sized prey items increased, but after Bonferroni correction the increase was only significant for intestines (6% to 24%). No significant difference was found for intermediate-large sized prey items between the two periods, but large prey items increased significantly in both stomachs (0% to 33%) and intestines (1% to 18%; Table 4.3).

Table 4.2 Volume percentages (mean ± standard deviation) of the food items in the diet of *H. pyrrhocephalus* in the old and modern ecosystems in Mwanza Gulf of Lake Victoria (significant values after sequential Bonferroni corrections are in bold).

Prey category	STOMACHS Old (n = 23)	STOMACHS Modern (n = 49)	STOMACHS *P*	INTESTINES Old (n = 30)	INTESTINES Modern (n = 50)	INTESTINES *P*
Detritus	0.4 ± 1	2 ± 4	= 0.133	0.04 ± 0.2	3 ± 6	< **0.001**
Phytoplankton	6 ± 13	1 ± 7	= 0.143	2 ± 8	0.5 ± 1.5	= 0.553
Zooplankton	55 ± 25	29 ± 29	< **0.001**	42 ± 21	31 ± 26	= 0.025
Ostracods	0	0.5 ± 4	= 0.329	0	1.3 ± 4.3	= 0.033
Midge larvae	3 ± 8	10 ± 20	= 0.237	17 ± 19	13 ± 19	= 0.232
Insects	5 ± 20	5 ± 15	= 0.975	7 ± 9	4 ± 7	= 0.041
Leeches	0	0.4 ± 2	= 0.329	0	0	
Molluscs	0	0.1 ± 0.7	= 0.493	0	0.4 ± 2	= 0.114
Shrimps	0	4 ± 12	= 0.021	0	3 ± 9	**= 0.004**
Fish	3 ± 7	22 ± 36	= 0.059	0.04 ± 0.3	9 ± 19	= 0.033
Others	0	0.1 ± 7	= 0.493	0.04 ± 0.2	2 ± 8	= 0.572
Prey size						
Small	62 ± 23	32 ± 28	< **0.001**	44 ± 23	36 ± 25	= 0.114
Intermediate	3 ± 8	10 ± 20	= 0.237	17 ± 18	13 ± 19	= 0.232
Intermediate-large	5 ± 19	5 ± 15	= 0.678	7 ± 8	4 ± 7	= 0.041
Large	3 ± 7	26 ± 36	**= 0.001**	0.1±0.4	15 ± 20	< **0.001**

Table 4.3 Volume percentages (mean ± standard deviation) of the food items in the diet of *H. tanaos* in the old and modern ecosystems in Mwanza Gulf of Lake Victoria (significant values after sequential Bonferroni corrections are in bold).

	STOMACHS			INTESTINES		
Prey category	Old (n = 15)	Modern (n = 32)	*P*	Old (n = 25)	Modern (n = 32)	*P*
Detritus	8 ± 19	2 ± 4	= 0.728	3 ± 6	3 ± 4	= 0.077
Phytoplankton	5 ± 12	0	= 0.010	2 ± 8	0	= 0.018
Zooplankton	41 ± 35	5 ± 12	< **0.001**	45 ± 35	7 ± 13	< **0.001**
Ostracods	0	1 ± 2	= 0.157	0	7 ± 12	< **0.001**
Midge larvae	5 ± 11.2	19 ± 26	= 0.030	6 ± 13	24 ± 25	**= 0.001**
Insects	13 ± 25.8	12 ± 28	= 0.577	22 ± 23	19 ± 26	= 0.333
Leeches	0	0		0	0	
Molluscs	0	1 ± 3	= 0.494	0	0.3 ± 1.2	= 0.127
Shrimps	0	12 ± 28	= 0.053	0	11 ± 21	**= 0.005**
Fish	0	17 ± 33	= 0.037	1 ± 2	7 ± 16	= 0.059
Others	0	4 ± 33	= 0.328	1 ± 3	0	= 0.042
Prey size						
Small	54 ± 30	8 ± 13	< **0.001**	50 ± 32	18 ± 19	< **0.001**
Intermediate	5 ± 11	19 ± 26	= 0.030	6 ± 13	24 ± 25	**= 0.001**
Intermediate-large	13 ± 26	12 ± 28	= 0.577	22 ± 23	19 ± 26	= 0.333
Large	0	33 ± 39	**= 0.001**	0.5 ± 2	18 ± 25	**= 0.004**

Comparison of the diets of *H. pyrrhocephalus* and *H. tanaos*

In the old ecosystem, where *H. pyrrhocephalus* was mainly caught in sublittoral waters (6-20 m deep) over mud bottoms and *H. tanaos* occurred over littoral (1-6 m) sand bottoms, there were some significant differences in diet (Table 4.2, 4.3). Though present in low quantities, detritus was more common in the intestines of *H. tanaos* than in those of *H. pyrrhocephalus* (3% vs 0.04%, Mann Whitney U-test, $P = 0.001$) and the reverse held for midge larvae (6% vs 17%, Mann Whitney U-test, $P = 0.002$). Further, the composition of zooplankton was different; *H. tanaos* had significantly more cladocerans in its diet than *H. pyrrhocephalus* (stomachs, 30% vs 1%; intestines, 35% vs 1%; Mann Whitney U-tests, $P \leq 0.001$), whereas copepods were more important in *H. pyrrhocephalus* than in *H. tanaos* (stomachs, 47% vs 11%; intestines, 38% vs 10%).

Comparison of the diets of *H. pyrrhocephalus* and *H. tanaos* in the modern ecosystem, where habitat overlap was considerable, revealed the following significant differences in volume percentages. Zooplankton was more common in *H. pyrrhocephalus* than in *H. tanaos* (Table 4.2, 4.3; stomachs 29% vs 5% and intestines 31% vs 7%; Mann Whitney U-test, $P < 0.001$ in both cases). Ostracods and insect remains were more common in the intestines of *H. tanaos* than in those of *H. pyrrhocephalus* (Table 4.2, 4.3; ostracods 7% vs 1.3% Mann Whitney U-test, $P = 0.002$; insects 19% vs 4% Mann Whitney U-test, $P = 0.001$). *Chaoborus* larvae were more common in the intestines of *H. pyrrhocephalus* than in those of *H. tanaos* (6% vs 0.1% in stomachs, Mann Whitney U-test, $P = 0.089$; 9% vs 1% in intestines, Mann Whitney U-test, $P = 0.001$). The reverse was true for chironomids; they were less common in *H. pyrrhocephalus* than in *H. tanaos* (4% vs 19% in stomachs; 4% vs 23% in intestines, both Mann Whitney U-tests, $P \leq 0.001$).

DISCUSSION

Comparison of *H. pyrrhocephalus* populations

Comparison of the diets of old and modern *H. pyrrhocephalus,* revealed a distinct change in prey composition. Diet of the old population of *H. pyrrhocephalus* showed similarities to that reported by Goldschmidt et al. (1990) for volume percentages, and by Katunzi et al. (2003) for frequency of occurrence. Zooplankton was the most abundant prey type, followed by midge larvae and other insects. In contrast to both other studies, we found phytoplankton (23% frequency of occurrence, 6% of stomach volume) contributing to the diet of the old *H. pyrrhocephalus*. However, it should be noted that it is not easy to discriminate between phytoplankton and detritus, and the latter was found in a greater quantity by Goldschmidt et al. (1990) than in the present study. Other differences are the absence of leeches and ostracods in post-Nile perch *H. pyrrhocephalus* studied by Katunzi et al. (2003). This may be partly related to sampling period; Katunzi et al. (2003) used fish collected between 1991 and 1999 to represent the modern ecosystem, while we used fish from 2005 and 2006. Between 1999 and 2005 changes in the ecosystem have been observed, among others including an increase of haplochromine densities at the research transect (Witte et al. 2007a,b). In spite of these differences, both Katunzi et al. (2003) and our study reveal that modern *H. pyrrhocephalus* ate larger prey items (comprising shrimps, fish and molluscs) than the old population, while the amount of zooplankton was reduced. The increase in prey size cannot be explained by a larger size of the investigated fishes, as their average size was even smaller than in the past.

Comparison of *H. tanaos* populations

Like in *H. pyrrhocephalus,* the diet of *H. tanaos* changed after its resurgence in the 1990s. In old *H. tanaos*, zooplankton was making up more than 50% of the diet, followed by insects and midge larvae, whereas in the modern population midge larvae, insects, shrimps and fish were about equally dominant and zooplankton contributed less than 10%. The diet shift from zooplankton to larger invertebrates and fish agrees with that observed by van Oijen & Witte (1996), who studied 10 fish collected between October and December 1993 in Kissenda Bay. However, in the diet of 1993, insects made up more than 50% followed by midge larvae, fish, ostracods and zooplankton (van Oijen & Witte 1996), whereas in our study insects contributed less than 25%. Shrimps and molluscs that were contributing to the diet in 2005 and 2006 were not present in 1993, but ostracods were found in both periods.

The differences in diet between 1993 and 2005/6 may be explained by the difference in sampling years, though the relatively low number of fish that were collected in 1993 from a smaller area and during shorter time period than in 2005/6 may also have contributed. Nevertheless, like for *H. pyrrhocephalus*, both studies on *H. tanaos* revealed a shift from a diet dominated by zooplankton to one dominated by macro-invertebrates. In contrast to the case of *H. pyrrhocephalus*, however, the shift in diet of *H. tanaos* went together with a habitat shift from littoral sand bottoms of 2 to 6 m deep to sub-littoral mud bottoms with depths of 6 to 12 m (van Oijen & Witte 1996; Seehausen et al. 1997b; Chapter 2). Consequently, this habitat shift could play a major role in the diet shift.

Comparison of the diets of *H. pyrrhocephalus* and *H. tanaos*

The original segregation of *H. pyrrhocephalus* and *H. tanaos* by habitat might explain the differences in zooplankton composition in their diets in the past, *viz*. cladocerans dominating in *H. tanaos* and copepods in *H. pyrrhocephalus*. However, in the modern ecosystem, there is a considerable overlap in habitat and in this case the differences in diet may tell something about food preferences or microhabitat segregation. The relatively low contributions of *Chaoborus* and zooplankton and the high contributions of chironomids and ostracods to the diet of *H. tanaos* compared to that of *H. pyrrhocephalus* suggest that *H. tanaos* is feeding closer to the bottom than *H. pyrrhocephalus*. Chironomid larvae and ostracods are mainly bottom dwellers, whereas zooplankton and, by night, *Chaoborus* larvae as well, are more pelagic.

In the past, *Chaoborus* larvae were major food items for *H. pyrrhocephalus* at night, when zooplankton, *Chaoborus* larvae and fish migrated to the surface (Goldschmidt et al. 1990; Goudswaard et al. 2004). Migration towards the surface of *H. pyrrhocephalus* has also been observed in the modern ecosystem (Chapter 2). Since *H. tanaos* were only caught with bottom trawls both during day and night (Chapter 2), they apparently are bottom dwellers rather than pelagic or vertical migrant species and consequently there is habitat segregation between the two species.

Dietary shifts in other fish species after the ecological changes

Shifts in the diet following the ecological changes in the lake were observed in several fish species. A shift from a diet dominated by zooplankton to large invertebrates such as midge larvae and shrimps was also observed in the cyprinid *Rastrineobola argentea* (Pellegrin) (Wanink 1998; Wanink & Witte 2000a,b). The "detritivorous" haplochromines in Lake Victoria shifted from a diet dominated by detritus and phytoplankton, supplemented with small quantities of midge larvae and zooplankton, to a diet of invertebrate preys including zooplankton, midge larvae, shrimps and molluscs and very small amounts of detritus and phytoplankton (Kishe-Machumu et al. 2008 [Chapter 3]). *Oreochromis niloticus* (Linnaeus), an introduced tilapiine cichlid, originally had a diet dominated by phytoplankton/detritus (Welcomme 1967), but currently includes considerable amounts of macro-invertebrates in its diet (Balirwa 1998; Njiru 2003). A dietary shift was also reported for *Brycinus sadleri* (Boulenger), which originally fed mainly on plant material during day time and insects on the surface water column at night. After the ecological changes they included midge larvae and pupae, shrimps, Odonata nymphs and fish in their diet (Wanink & Joordens 2007). *Bagrus docmak* (Forsskåll) and *Schilbe intermedius* (Linnaeus) exhibited shifts from predominantly piscivorous diets, dominated by haplochromine species, to broader diets; *B. docmak* included significant proportions of invertebrates and the cyprinid *R. argentea* in its diet, whereas *S. intermedius* became mainly insectivorous (Olowo & Chapman 1999).

All these diet shifts in the modern ecosystem concern increases of macro-invertebrates. As discussed by Kishe-Machumu et al. (2008), potential factors for these shifts could be: (1) the increased availability of profitable food items; (2) the loss of competitors and (3) the increased water turbidity in the modern ecosystem. It is possible that more than one of these factors is responsible for the observed changes.

In the old ecosystem, diets of the former "detritivores" comprised mainly detritus and phytoplankton (Goldschmidt et al. 1993; Kishe-Machumu et al. 2008 [Chapter 3]), whereas in the "zooplanktivores", zooplankton and midge larvae dominated (Goldschmidt et al. 1990; this chapter). As a consequence, both groups were well separated by diet. Currently, the former "detritivores" do not take plant material anymore, and a higher proportion of macro-invertebrates than in the past is found in both “zooplanktivores” and “detritivores” (Kishe-Machumu et al. 2008 [Chapter 3]). As a consequence there is a greater overlap of food items between the “zooplanktivores” and the former “detritivores”. An increase in overlap was also found for the average ratios in intestine lengths and standard lengths between the two groups; in the “zooplanktivores” they were 1.2 (*H. tanaos*) and 1.3 (*H. pyrrhocephalus*) in both the old and modern ecosystem and in the former “detritivores” they were 1.8 (*H.* ‘paropius-like’) and 2.3 (pooled “detritivores”) in the old ecosystem and 1.0 and 1.5 respectively in the modern ecosystem (Kishe-Machumu et al. 2008 [Chapter 3]). These observations, suggest, that unless the former “detritivores” are less well adapted to their new diet than the “zooplanktivores”, diet is not likely to explain the relatively slow recovery of “detritivores” compared to that of “zooplanktivores”. Therefore, other possible causes for these differences, like differential predation pressure by Nile perch or differential impacts of environmental changes should be considered in further studies.

ACKNOWLEDGEMENTS

The authors would like to thank their colleagues from the Haplochromis Ecology Survey Team (HEST) and the Tanzania Fisheries Research Institute (TAFIRI) for their co-operation and logistical support during the fieldwork. We wish to thank Messrs Mhoja Kayeba, Mohamed Haruna and Rajabu Machage for their assistance in the field operations. We are indebted to John Videler and two anonymous referees for their thoughtful comments on an earlier draft of the chapter. The HEST and doctoral researches were financially supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO; grants W87-129, W87-161, W87-189, W84-282, W84-488, and WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC), the International Foundation for Science (IFS), the Schure Beijerinck-Popping Fonds, the van Tienhoven Stichting, and Yellow Springs Instruments.

Chapter 5

Stable isotope evidence for the dietary shift and diet overlap amongst haplochromine cichlids in Lake Victoria

Mary A. Kishe-Machumu, Jacco C. van Rijssel, Amanda Poste, Robert E. Hecky, Frans Witte

ABSTRACT

Lake Victoria once hosted a diverse fish community dominated by a large species flock of haplochromine cichlids. After the Nile perch upsurge and eutrophication in the 1980s, most haplochromines became either extinct or extremely rare. During the 1990s, some haplochromines reappeared with new diets and overlap of food items among species. However, the information on dietary changes and trophic relationships mostly relied on traditional gut content analysis. In this study, stable carbon and nitrogen isotope analyses were used to investigate how these stable isotopes differ among "detritivorous" and "zooplanktivorous" species before and after the environmental changes.

The study revealed a significant distinction along the $\delta^{13}C$ and $\delta^{15}N$ signatures among all species collected from the old ecosystem. In contrast, there was a remarkable similarity in $\delta^{13}C$ and $\delta^{15}N$ signatures among species in the modern ecosystem. The above mentioned results can be explained by the different diets among the species of the old ecosystem whereas in the modern ecosystem they shared a similar diet. Two out of three modern species showed higher $\delta^{15}N$ signatures than the same species in the former ecosystem which concurred with a diet shift towards fish and invertebrates. Moreover, based on gut content analysis, we found evidence of one "zooplanktivorous" species which partly shifted its diet back to zooplankton and this was reflected in the $\delta^{13}C$ signature as well. This study revealed that significant differences in $\delta^{13}C$ and $\delta^{15}N$ values exist among haplochromine trophic groups *and* among species. This is one of the first studies that successfully applied a stable isotope analysis on formalin preserved cichlids and it confirmed that preserved museum material still can provide useful stable isotope data.

INTRODUCTION

During the past three decades, Lake Victoria has been subject of many ecological studies as its ever changing limnology provides a unique opportunity to study the effects of environmental changes on fish species. The population boom of the introduced predatory Nile perch in the 1980s (Ogutu-Ohwayo 1990a; Pringle 2005; Goudswaard et al. 2008) together with the increased eutrophication of the lake (Ochumba & Kibaara 1989; Hecky 1993; Verschuren et al. 2002) resulted in increased phytoplankton blooms, particularly cyanobacteria which caused low water transparency and low dissolved oxygen (DO) levels (Mugidde 1993; Hecky et al. 1994; Seehausen et al. 1997a; Witte et al. 2005). Concurrent with higher phytoplankton productivity and a rapid increase in Nile perch abundance, a higher abundance of shrimps, molluscs, insects and small cyprinid fish (dagaa) were observed (Hecky 1993; Witte et al. 1995, Wanink & Witte 2000a; Goudswaard et al. 2006) while there was a dramatic decline in the density of haplochromines and their diversity in the late 1980s (Ogutu-Ohwayo 1990a; Kaufman 1992; Witte et al. 1992a; Seehausen et al. 1997a).

During the 1990s, some haplochromines recovered (Witte et al. 2000). However, the recovering “detritivorous” and “zooplanktivorous” cichlids species had shifted their diet from detritus/phytoplankton and zooplankton to larger sized and more robust prey such as insects, shrimps, molluscs and small fish (van Oijen & Witte 1996; Katunzi et al. 2003; Kishe-Machumu et al. 2008 [Chapter 3]; Chapter 4). In addition, it was found that there is currently more overlap of food items among haplochromine species and among the trophic groups than in the past (Kishe-Machumu et al. 2008 [Chapter 3]; Chapter 4). These studies were based on dietary gut content analyses. Though such analyses are the only means of establishing details of the types and amounts of prey taken, they do not show from where the diets originate (Gearing 1991). If dietary studies are complemented by analyses of stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes, they can provide a clearer understanding of diets because stable isotopes reflect the actual assimilation of organic matter into consumer tissue rather than merely its consumption. Furthermore, they provide an average of the diet over periods of weeks to months (Gearing 1991). Therefore, $\delta^{13}C$ and $\delta^{15}N$ values can estimate long-term dietary patterns of fish species.

Stable isotope analysis has been successfully applied to analyse the diets, feeding patterns, food web structure and energy flow in fish species of the Lake Victoria basin (Campbell et al. 2003). Fish were studied from the Napoleon Gulf (Uganda; Campbell et al. 2003) and the Winam Gulf (Kenya; Campbell et al. 2003; Ojwang et al. 2004, 2010) of Lake Victoria. Other studies have focused on Lake Kyoga and some of the satellite lakes of Lake Victoria (Mbabazi et al. 2004; Schwartz et al. 2006), as well as on some smaller Ugandan lakes M̃buro and Kachera (M̃babazi 2004) and on riverine fish from the Lake Victoria watershed (Ojwang et al. 2007). All studies were done on material collected after the mid 1990s and covered relatively short time scales. Nothing is known, however, about the degree to which stable isotope signatures (δ^{13}C and δ^{15}N) differ among the haplochromine trophic groups and species before and after the environmental changes that occurred during the 1980s in Lake Victoria. Moreover, as far as we know, no attempts have been made to apply stable isotope techniques on preserved museum specimens of haplochromines from Lake Victoria. This study uses formalin/alcohol-preserved haplochromine tissue from the Mwanza Gulf (Tanzania) to answer the following questions: 1) is there an impact of formalin/alcohol preservation on tissue δ^{13}C and δ^{15}N signatures 2) are there significant differences in stable isotope signatures between “detritivorous” and “zooplanktivorous” trophic groups and species of haplochromines within the old and within the modern ecosystem 3) are there significant differences in stable isotope signatures between trophic groups (and species) collected in the old and those collected in the modern system.

Concerning questions two and three, we expect that differences in stable isotopes between and within species will reflect differences (changes) in diet. Over the time period sampled in this study, there were substantial changes in the productivity, abundance and composition of phytoplankton, especially in the inshore regions of Lake Victoria in Uganda (Mugidde 1992; Hecky 1993; Kling et al. 2001; Hecky et al. 2010). Phytoplankton biomass increased five to six-fold and shifted to cyanobacterial dominance by filamentous N fixers such as *Anabaena* and to colonial *Microcystis*. There was also a profound species shift in the diatoms from heavily silicified *Aulacoseira* to thinly silicified *Nitzschia* as dissolved Si concentrations plummeted. These changes were accompanied by an increase by as much as 2‰ in the δ^{13}C (Suess corrected) recorded in the organic matter deposited in inshore areas of the lake. In contrast, there was little change in δ^{15}N in sediments. The increase in $\delta^{13}C$ would be expected as the increased phytoplankton biomass raised the demand for CO_2 and reduced isotopic fractionation (Hecky & Hesslein 1995).

If similar changes in basal signature occurred in the Mwanza Gulf, which also experienced increased phytoplankton biomass, then we would expect that consumers in this area would reflect this change at the base of the food web and shift to heavier $\delta^{13}C$ signatures. In contrast, sedimentary $\delta^{15}N$ did not change substantially (R.E. Hecky, unpublished data), and so any shift of $\delta^{15}N$ in consumers is most likely reflecting a change in the diet.

MATERIALS AND METHODS

Study area and periods

Haplochromines were caught in the northern part of the Mwanza Gulf between Nyamatala Island and Hippo Island (Fig. 1.2 [Chapter 1]; Appendix 1) in 1977-1982 (old ecosystem) and 1993-2007 (modern ecosystem). The division in old and modern ecosystem is based on the following observations in the Mwanza Gulf: 1) a strong decline of haplochromines in the period between 1983 and 1988 and a slow recovery since 1990 (Witte et al. 2007b); 2) phytoplankton blooms that were first observed in 1986 (Witte et al. 1992a); 3) low DO concentrations and low Secchi values observed in 1987/88 (Wanink et al. 2001; Witte et al. 2005).

Most samples were collected at seven stations (B, E, F, G, H, I, J) on a transect crossing the Mwanza Gulf from Butimba to Kissenda Bay (Fig. 1.2 [Chapter 1]). Additional samples were collected in the sublittoral area (6-18 m deep), north and south of the transect (Appendix 1). Except for the littoral station B (4-6 m deep), which has a sand bottom, all other stations have a soft muddy bottom.

Fish sampling

Haplochromine species were collected by trawling (bottom and surface) and gillnetting. After each haul, the specimens were stored on ice, species and trophic groups were identified in the laboratory. Specimens collected between 1977 and 2001 were stored in the Netherlands Centre for Biodiversity, Naturalis, Leiden. They had been preserved in formaldehyde (5% solution) and were afterwards transferred to 70% alcohol. The time that the fish were kept in formaldehyde depended on the moment of shipment to the Netherlands (where they were stored in alcohol) and varied from several weeks to several years. The standard length (SL) of each specimen was measured. A part of the epaxial muscle (dorsal to the lateral line) was dissected and the skin was removed from the sample. Individuals >5 cm SL collected in 2005 and 2007 were dissected in the same way, however, smaller individuals (4-5 cm TL) were filleted and a part of the hypaxial musculature was included.

For the samples collected in 2005 and 2007, only muscle tissue from one side was preserved in formaldehyde and later transferred to alcohol 70%. This preservation treatment was similar to the preservation procedures that have been applied to museum specimens. In this way, materials collected in 2005 and 2007 became comparable with the museum material in terms of preservation treatment, though the duration of preservation in formaldehyde and alcohol was shorter (several weeks to a year). The muscles from the other side of the fish collected in 2007 were oven-dried at 60^0C for 24-48 hours and stored in vials before being transported to Canada for analysis. All samples were analyzed in the Environmental Isotope Laboratory (University of Waterloo, Canada).

Species studied

Three “zooplanktivorous” species, three “detritivorous” species and one true phytoplanktivorous species were studied. The three “zooplanktivores” were *Haplochromis (Yssichromis) pyrrhocephalus* Witte & Witte-Maas, *H. (Y.) laparogramma* Greenwood & Gee and *H. tanaos* van Oijen & Witte, which were relatively easy to identify, both before and after the environmental changes in the lake. The “detritivores” comprised *H. (Enterochromis) cinctus* Greenwood & Gee, *H. (E.) coprologus* Niemantsverdriet & Witte, and *H. (E.)* ‘paropius-like’ of which it is uncertain whether it is conspecific with *H. (E.) paropius* Greenwood & Gee. The phytoplanktivorous species was *H. bwathondii* Niemantsverdriet & Witte.

Before the environmental changes, the “detritivorous” trophic group in the northern part of the Mwanza Gulf used to comprise several morphologically and ecologically similar species (mainly differing in depth distribution) with a curved dorsal head profile, of which sexually active males could be easily identified, but females and non-active males were hard to identify (de Zeeuw et al. 2010). For that reason, in earlier ecological studies, these species were pooled as the 'curved head' group (Goldschmidt et al. 1993). The three most common species of this group were *H. cinctus, H. (E.) antleter* Mietes & Witte and *H. (E.) katunzii* Ter Huurne & Witte. After the recovery, based on general morphological features, specimens could still be identified as belonging to the ‘curved head’ group. However, specific identification (even of sexually active males) in the modern ecosystem became more difficult due to changes in breeding colour and morphology that may have resulted from hybridization (Seehausen et al. 1997; de Zeeuw et al. 2010). Therefore, we treated them as the ‘curved head’ group, just like Goldschmidt et al. (1993). This modern ‘curved head’ group comprised individuals that showed features of the three above mentioned species, but we cannot exclude introgression of *H. coprologus* in this group. Only two modern individuals could be identified as *H. cinctus* with some certainty.

We compared the stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of “detritivorous” and “zooplanktivorous” species collected in the modern ecosystem with those collected in the old ecosystem. In the case of *H. pyrrhocephalus*, the fish from the modern ecosystem comprised a relatively large sample (n = 16) over a long period (1993-2007). Therefore, we divided the modern group into two subgroups referred to as *H. pyrrhocephalus* 1990s (1993, 1999 and 2001, n = 7) and *H. pyrrhocephalus* 2000s (2005 and 2007, n = 9).

Stable isotope analysis

Small sub-samples of fish tissue were freeze-dried and ground into fine powder for $\delta^{15}N$ and $\delta^{13}C$ analyses using a Micromass VG-Isochrom Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS) at the Environmental Isotope Laboratory, University of Waterloo. The ratios of the stable isotopes were then measured against the reference standards PeeDee belemnite for $\delta^{13}C$ and the nitrogen gas in ambient air for $\delta^{15}N$ (see equation). The delta notation (δ), the difference (‰, or parts per thousand) between the isotopic ratio of the sample and the standard, was calculated as:

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

where $R = {}^{13}CO_2 / {}^{12}CO_2$ for $\delta^{13}C$ or $R = {}^{15}N_2 / {}^{14}N_2$ for $\delta^{15}N$

Working standards used to determine inter- and intra-run variation and accuracy of the results included the International Atomic Energy Agency (IAEA) standards CH6 ($\delta^{13}C$ = –10.4‰), N1 ($\delta^{15}N$ = 0.36‰) and N2 ($\delta^{15}N$ = 20.3‰), and the in-house standards: EIL-70 (powdered lipid-extracted Lake Ontario walleye; $\delta^{13}C$ = –19.34‰, $\delta^{15}N$ = 16.45‰) and EIL-72 (powdered Whatman cellulose fiber; $\delta^{13}C$ = –25.4‰). The food web structure was graphically represented by plotting $\delta^{15}N$ against $\delta^{13}C$ for all fish.

The standard lengths, sampling stations and year of sampling of specimens used in analysis are given in Appendix 1. Over the past 30 years, due to deforestation and fossil fuel burning, CO_2 levels containing the low natural concentrations of $\delta^{13}C$ in the atmosphere have risen over 20% (Francey et al. 1999). This change of carbon isotopes due to anthropogenic effects is also known as the Suess effect (Keeling 1979) and has been most dramatic as the present day is approached (Verburg 2007). As atmospheric and aquatic CO_2 equilibrate, it was necessary to apply a Suess correction for the $\delta^{13}C$ according to the following formula:

$$7.7738118 * 10^{-16} * Y^{6} - 1.2222044 * 10^{-11} * Y^{5} + 7.1612441 * 10^{-8} * Y^{4} - 2.1017147 * 10^{-4} * Y^{3} + 3.3316112 * 10^{-1} * Y^{2} - 273.715025 * Y + 91703:261,$$

with Y as year since 1700, as recommended by Verburg (2007), to compare fish specimens collected as much as 30 years apart.

Data analysis

All fish species (*H.* 'paropius-like', *H. cinctus, H. pyrrhocephalus, H. tanaos, H. laparogramma*) collected in 2007 were included in a test for the overall differences in stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ between preserved and dried samples from the same individuals. The $\delta^{13}C$ values of the dried and preserved muscles were not normally distributed (Shapiro-Wilk-test), therefore, a paired Wilcoxon test was employed whereas for the $\delta^{15}N$, values were normally distributed (Shapiro-Wilk-test), thus, a paired student t-test was used.

A linear regression was performed on stable isotopes which had a significant Pearson correlation with SL. The grouped residuals of this regression were used to test for normality with the Shapiro-Wilk test. Residuals of non-correlated stable isotopes were calculated by subtraction of the average stable isotope values from the raw data. We used the residuals of the linear regression and the residuals which were calculated manually for further analysis. In this way, stable isotopes which had significant correlation with SL were corrected for the SL. A One-way ANOVA was performed on both residuals to test for inter-specific differences in the same period and for intra-specific differences among periods. A Bonferroni correction was used for the *P*-values. Although the two modern specimens of *H. laparogramma* were shown in the figures, they were not included in the statistical analysis due to their small number. Also two specimens of the 'curved head' were not included in the analysis because their stable isotopes strongly deviated from other specimens of the same sample and species identification was uncertain. All statistical tests were performed with SPSS 16.0 for Windows.

RESULTS

Effects of preservation

The dried and the formalin/ethanol preserved samples of the same individual showed small though significant differences in their stable isotope values (Appendix 2). This is illustrated by the preserved and dried samples of *H.* 'paropius-like', which show small differences and generally into the same direction (Fig. 5.1). The preserved samples of all species combined had significantly lower $\delta^{13}C$ values than the dried samples (preserved -18.88‰ ± 2.71, dried -18.22‰ ± 2.78; $Z = -2.975$, $P = 0.003$), and significantly higher $\delta^{15}N$ values than the dried samples (preserved 9.07‰ ± 1.59, dried 8.73‰ ± 1.52; $t = -2.307$, $P = 0.028$). Although the differences were significant, the magnitudes are small relative to the changes observed among species and over time in the same/similar species (see below).

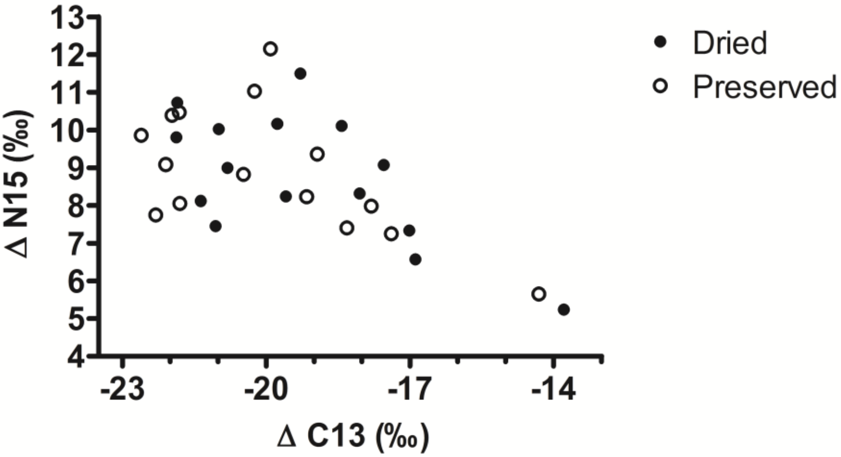

Fig. 5.1 Isotopic composition of dried and preserved samples of *H.* 'paropius-like'.

Effects of fish size

Old (1977-1982) and 1990s *H. pyrrhocephalus* had a significant negative Pearson correlation between δ^{13}C and SL ($P < 0.05$; Table 5.1). A significant positive Pearson correlation with SL for δ^{15}N was found for old *H. pyrrhocephalus* specimens as well as for modern *H.* 'paropius-like' specimens ($P < 0.05$; Table 5.1). All residuals of the sequential linear regression were normally distributed (Shapiro-Wilk test, $P > 0.05$).

Table 5.1 Pearson correlations per species and period between δ^{13}C, δ^{15}N and SL. Significant values are depicted in bold.

		δ^{13}C		δ^{15}N	
Old	**n**	***R***	***P***	***R***	***P***
H. bwathondii	10	0.265	0.46	0.291	0.415
H. cinctus	10	0.301	0.399	-0.366	0.299
H. coprologus	10	-0.11	0.976	0.371	0.291
H. pyrrhocephalus	10	**-0.741**	**0.014**	**0.705**	**0.023**
H. tanaos	5	0.324	0.595	0.4	0.505
Modern					
H. 'curved head'	12	0.045	0.879	-0.229	0.43
H. 'paropius-like'	15	-0.303	0.273	**0.611**	**0.015**
H. pyrrhocephalus '90s	7	**-0.766**	**0.045**	0.220	0.636
H. pyrrhocephalus '00s	9	0.395	0.292	-0.340	0.370
H. tanaos	6	0.417	0.411	-0.143	0.787

Old populations

The stable isotope analysis of the old species resulted in a distinct clustering by species (Figs 5.2A, B). Significant differences between δ^{13}C and between δ^{15}N values of old species were found ($P < 0.001$). A strong distinction was found along the δ^{13}C axis with all species differing significantly from each other ($P < 0.01$) except for the "detritivore" *H. coprologus* and the "zooplanktivore" *H. tanaos* ($P = 1.000$). The δ^{13}C and δ^{15}N values of the "detritivore" *H. cinctus* were significantly lower than those of the other four species ($P < 0.001$). Of these four species, the phytoplanktivore *H. bwathondii* had significantly higher δ^{13}C values, and lower δ^{15}N values compared to the other three species ($P < 0.01$). Of the two "zooplanktivorous" species, *H. pyrrhocephalus* showed significantly higher δ^{13}C values compared to *H. tanaos* ($P = 0.002$). The δ^{15}N values of the "detritivore" *H. coprologus* and the "zooplanktivores" *H. pyrrhocephalus* and *H. tanaos* were the highest and did not differ significantly from each other.

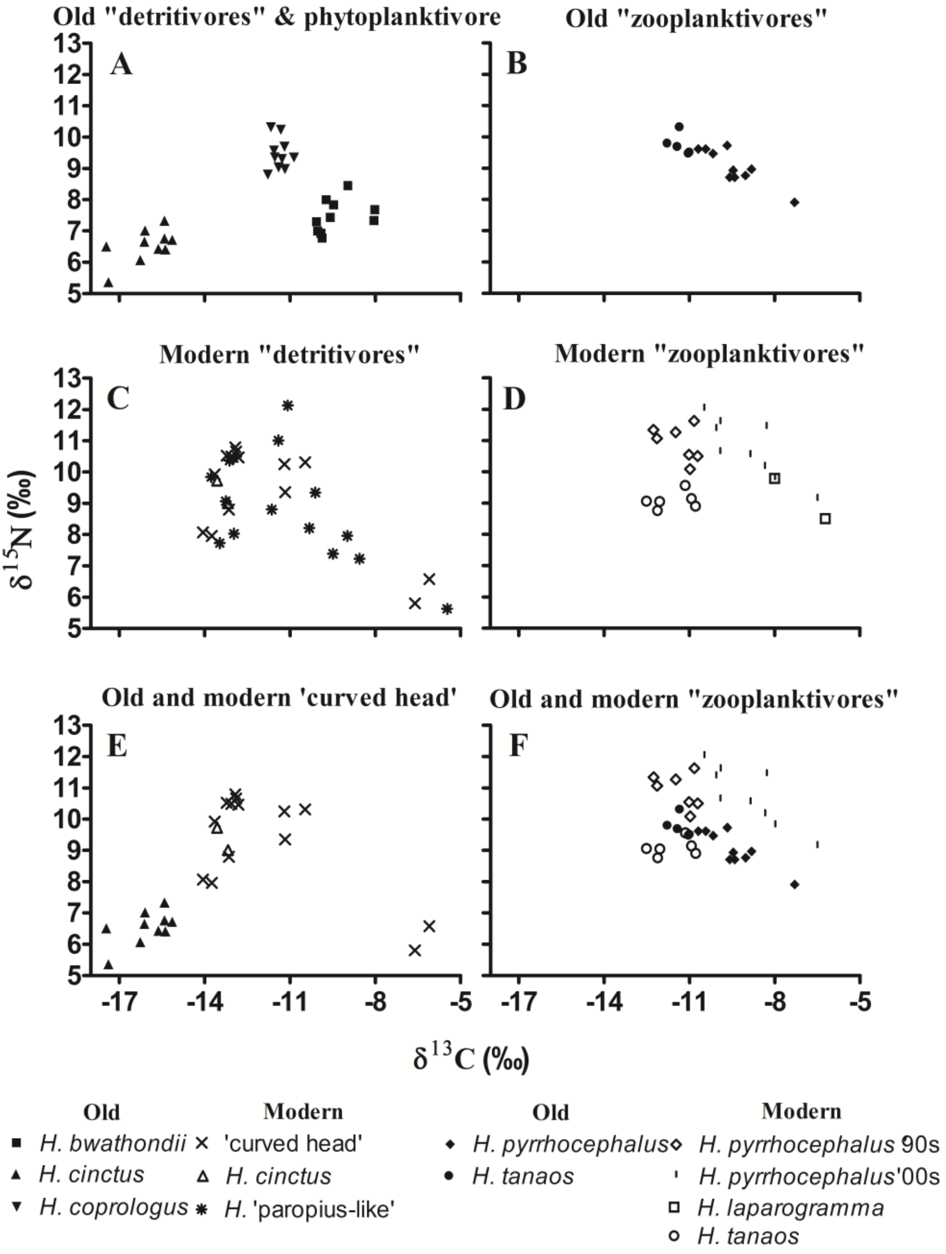

Fig. 5.2 Isotopic composition of different species of different trophic groups. Filled symbols represent old species, unfilled symbols represent modern species. A. old “detritivores” and a phytoplanktivore; B. old “zooplanktivores”; C. “modern detritivores”; D. modern “zooplanktivores”; E. old and modern ‘curved head’ group; F. old and modern “zooplanktivores”. No statistics were performed on modern specimens of *H. laparogramma* and are shown for illustration only. Two aberrant ‘curved head’ specimens with low δ15N values were excluded from the analysis.

Modern populations

The analysis of the modern populations showed a clustering per species as well (Figs 5.2C, D), but it was less clear than in the old populations. Both, the $\delta^{13}C$ and the $\delta^{15}N$ values differed significantly among species ($P < 0.001$; $P = 0.010$ respectively). Pair wise comparison of $\delta^{13}C$ values between species showed higher values for *H. pyrrhocephalus* 2000s compared to the other species ($P < 0.05$). *Haplochromis pyrrhocephalus* 1990s had significantly higher $\delta^{15}N$ values than *H. tanaos* ($P = 0.038$), but did not differ from the *H. pyrrhocephalus* 2000s, the “detritivorous” ‘curved head’ group and *H.* ‘paropius-like’ ($P = 1.000$, $P = 0.239$, $P = 1.000$ respectively). The $\delta^{13}C$ and the $\delta^{15}N$ values of the “zooplanktivorous” *H. laparogramma* showed overlap with those of the *H. pyrrhocephalus* 2000s population.

Old and modern populations

Modern ‘curved head’ populations had significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than the old *H. cinctus* ($P < 0.001$; Fig. 5.2E). The population of *H. pyrrhocephalus* 1990s showed significantly lower $\delta^{13}C$ and higher $\delta^{15}N$ values than the old population (respectively $P = 0.002$; $P = 0.003$; Fig. 5.2F). The *H. pyrrhocephalus* 2000s population did not differ from the old population in $\delta^{13}C$ values ($P = 0.868$), but had significantly higher $\delta^{15}N$ values ($P = 0.006$). The two modern populations did not differ in $\delta^{15}N$ values ($P = 1.000$), but the population of *H. pyrrhocephalus* 2000s did have significantly higher $\delta^{13}C$ values than *H. pyrrhocephalus* 1990s ($P = 0.003$). Old and modern *H. tanaos* populations did not show significant differences. As mentioned above, the $\delta^{13}C$ values of the old populations of *H. pyrrhocephalus* and *H. tanaos* did differ significantly from each other, while there was no difference in $\delta^{15}N$ values. The $\delta^{13}C$ of both modern populations did not differ significantly, while $\delta^{15}N$ values of modern *H. pyrrhocephalus* ('90s and '00s) were significantly higher compared to those of modern *H. tanaos* ($P = 0.001$; $P = 0.001$ respectively).

DISCUSSION

Problems with species identification and the effects of outliers

Since it was difficult to identify the "detritivorous" species after the environmental changes, we grouped them as the 'curved head' group as in Goldschmidt et al. (1993). According to the latter authors, the 'curved head' group was mainly made up of *H. cinctus* and *H. katunzii*. In our case, this group may have also contained hybrids of these two species and of *H. antleter*. Two modern 'curved head' specimens were so similar to *H. cinctus* that we allocated them to that species. As expected, their $\delta^{13}C$ and the $\delta^{15}N$ values fell in the range of the other 'curved head' specimens.

Two outliers of the modern 'curved head' group were excluded from our dataset. The effect of outlier exclusion was explored by comparison of statistical outputs of the two datasets (with and without outliers). The inclusion of the outliers resulted in a non-normal distribution of the modern 'curved head' group. To avoid discrepancy between statistical analyses, we assumed a normal distribution for this group (with outliers). Results of the dataset with outliers deviated slightly from the dataset without outliers. Although *P*-values differed, relative differences between species remained the same. So, although there are some slight interspecific differences between datasets, the exclusion of the two outliers did not affect differences in time between "detritivorous" populations and our major conclusions (see below).

Preserved and dried samples

The observed depletion of $\delta^{13}C$ in formalin/alcohol-preserved samples was small (3.5%) and may have occurred due to hydrolysis of proteins by formalin (Arrington & Winemiller 2002 and Sarakinos et al. 2002, and references therein). The depletion could be also due to uptake of formalin and alcohol into the tissues as both preservatives are carbon-based chemicals with characteristic $\delta^{13}C$ signatures. Once preserved samples are immersed, their signatures may shift toward that of the preservative (Arrington & Winemiller 2002 and Sarakinos et al. 2002, and references therein). Our findings indicated that formalin/alcohol preservation leads to a small increase in $\delta^{15}N$ (3.7%). The specific mechanism that leads to the observed increase in $\delta^{15}N$ is unknown, however, nitrogen enrichment has been also observed by many other studies of preservation effects, e.g. Arrington & Winemiller (2002) and Sarakinos et al. (2002).

Nevertheless, when we look at the order of magnitude, the differences found between periods are much larger than the differences found between dried and preserved samples. For instance, the differences in $\delta^{13}C$ (Suess corrected) and $\delta^{15}N$ values between old *H. pyrrhocephalus* and *H. pyrrhocephalus* 1990s are 19% and 17% respectively which is much higher compared to the above mentioned differences between dried and preserved specimens (Figs 5.1, 5.2; Appendices 1, 2). Moreover, the samples used in this study have all been preserved the same way in order to avoid discrepancies in the dataset due to different preservation treatments.

Old populations

Though the specimens from the old populations were collected in different years and, for *H. pyrrhocephalus*, at different locations in the northern part of the Mwanza Gulf (Appendix 1), they revealed distinct and well separated conspecific clusters. Moreover, as expected, the two “zooplanktivorous” species had higher $\delta^{15}N$ values than two of the three “detritivorous” species. These observations suggest that this formalin/alcohol-preserved museum material still provides ecologically meaningful stable isotope data, or at minimum that preservation did not impose a common signal arising from the formalin/ethanol preservative (Table 5.2).

Table 5.2 Range and mean values of $\delta^{13}C$ (uncorrected and corrected) for preserved fish species in the old and modern ecosystems on the transect of Mwanza Gulf. n is the number of samples from each fish species.

Period	Trophic group	Species	Year	n	Uncorrected $\delta^{13}C$			Suess Corrected $\delta^{13}C$		
					Min	Max	**Mean**	Min	Max	**Mean**
Old	Phytoplanktivores	*H. bwathondii*	1981-1982	10	-17.5	-15.5	**-16.8**	-10.0	-8.0	**-9.4**
	"Detritivores"	*H. cinctus*	1981-1982	10	-25.0	-22.6	**-23.5**	-17.5	-15.1	**-16**
		H. coprologus	1981-1982	10	-19.3	-18.4	**-18.9**	-11.8	-10.9	**-11.4**
	"Zooplanktivores"	*H. pyrrhocephalus*	1977-1978	10	-18.1	-14.7	**-16.8**	-10.7	-7.3	**-9.5**
		H. tanaos	1979	5	-19.2	-18.4	**-18.7**	-11.8	-11.0	**-11.3**
Modern	"Detritivores"	'Curved head'	2005 & 2007	16	-22.4	-14.4	**-20.3**	-14.1	-6.1	**-12.0**
		H. 'paropius-like'	2007	15	-22.1	-13.8	**-19.4**	-13.8	-5.5	**-10.0**
	"Zooplanktivores"	*H. laparogramma*	2007	2	-16.3	-14.5	**-15.4**	-8.0	-6.2	**-7.1**
		H. pyrrhocephalus	1993-2001	7	-20.3	-18.8	**-19.3**	-12.3	-10.7	**-11.3**
		H. pyrrhocephalus	2005 & 2007	9	-18.8	-14.8	**-17.2**	-10.5	-6.5	**-8.9**
		H. tanaos	2005 & 2007	6	-20.8	-19.0	**-19.8**	-12.1	-8.0	**-10.8**

The distinction along the $\delta^{13}C$ and $\delta^{15}N$ axes can partly be explained by the different diets of the species. The bottom dwelling detritivore *H. cinctus,* which mainly fed on detritus and phytoplankton and included some copepods and midge larvae, had the lightest $\delta^{13}C$ and $\delta^{15}N$ values. Unexpectedly, the other detritivore, *H. coprologus*, had the heaviest $\delta^{15}N$ values. *Haplochromis coprologus* fed mainly on detritus and phytoplankton during the day, but also included some copepods in its diet. Apart from detritus, *H. coprologus* also fed on the diatom *Aulacoseira*, especially at night, when it occurred a little higher in the water column (Goldschmidt et al. 1993), but this does not explain the relatively high $\delta^{15}N$ values. The overlap of $\delta^{13}C$ and $\delta^{15}N$ values between *H. coprologus* and *H. tanaos* may be due to habitat overlap between these two species during a part of the life cycle of *H. coprologus*. Juveniles of *H. coprologus* occurred in the same sheltered bays (e.g. Butimba Bay), and fed mainly on zooplankton (F. Witte, pers. obs.) like *H. tanaos*, which in the old ecosystem used to occur in this habitat throughout its life (Goldschmidt et al. 1993; van Oijen & Witte 1996). The “zooplanktivorous” diet of *H. coprologus* juveniles might have contributed to their heavy $\delta^{15}N$ values.

The pelagic phytoplanktivore, *H. bwathondii,* had relatively heavy $\delta^{15}N$ values compared to *H. cinctus*, while $\delta^{13}C$ values were the heaviest of all species; the latter may be due to its phytoplanktivorous habits. *Haplochromis bwathondii* fed mainly on Cyanophyta (*Microcystis* and *Anabaena*) and diatoms such as *Aulacoseira* and occasionally *Nitzschia*. Larger phytoplankton such as colonial or filamentous species, like the ones that contribute to diet of *H. bwathondii*, are subject to boundary layer effects which might explain why the larger phytoplankton species have heavier ^{13}C values compared to the smaller species (France 1995; Hecky & Hesslein 1995). At night, *H. bwathondii* also consumed considerable amounts of adult insects and *Chaoborus* larvae and pupae as well as some copepods (Goldschmidt et al. 1993). The uptake of insects and zooplankton seems to have resulted in relatively heavier $\delta^{15}N$ values compared to *H. cinctus*, however, $\delta^{15}N$ values were much lighter than those of *H. coprologus*.

The high $\delta^{15}N$ values of the “zooplanktivores” *H. pyrrhocephalus* and *H. tanaos* is consistent with their diet, mainly cyclopoid/calanoid copepods and cladocerans respectively (Goldschmidt 1989; van Oijen & Witte 1996). The higher $\delta^{13}C$ values of *H. pyrrhocephalus* compared to those in *H. tanaos* might be the result of a difference in habitat of both species. *Haplochromis pyrrhocephalus* occurred in open water while *H. tanaos* was mainly caught in bays. This habitat difference might have resulted in different plant food for the zooplankton, which could result in different δ^{13}C values.

Modern populations

The clustering of the stable isotopes of the modern populations showed less species distinction than the clustering of the old populations. This stable isotope overlap confirms the findings of earlier diet studies of these species; reporting a dietary shift to a more carnivorous diet, with overlap between the former “detritivores” and “zooplanktivores” (Kishe-Machumu et al. 2008 [Chapter 3]; Chapter 4). After their resurgence, both trophic groups included zooplankton, midge larvae, insects, molluscs and shrimps in their diet (van Oijen & Witte 1996; Katunzi et al. 2003; Kishe-Machumu et al. 2008 [Chapter 3]; Chapter 4). The δ^{15}N values of the ‘curved head’ group and *H.* ‘paropius-like’ had a very broad range. The broad range of the latter species might be explained by the large variation in SL (Appendix 1), as smaller fish might have a different diet than larger fish. Diet analysis revealed that in the modern ‘curved head’ group, prey diversity was higher than in the pooled old “detritivores” (four ‘curved head’ species and *H. coprologus* Kishe-Machumu et al. 2008 [Chapter 3]). However, it should be noted that prey diversity does not necessarily reflect the range of δ^{15}N, as some prey types have similar values and others may differ greatly. The ‘curved head’ group did not differ from *H. pyrrhocephalus* 1990s in stable isotope composition, which agrees with a shift of the diet of this group in the modern ecosystem towards insects, zooplankton, shrimps and molluscs instead of detritus and phytoplankton (Kishe-Machumu et al. 2008 [Chapter 3]). As expected, the two modern *H. laparogramma* specimens, collected in 2007, fell in the range of the closely related *H. pyrrhocephalus* 2000s population (Fig. 5.1D). Their relatively high δ^{13}C and low δ^{15}N can probably be explained by the relatively small size of the two *H. laparogramma* individuals (Appendix 1). Analyses of *H. laparogramma* collected in 1998 by Campbell et al. (2003) revealed means of -19.9 and 7.9 for δ^{13}C and δ^{15}N respectively in the Napoleon Gulf and values of -26.7 and -24.7 for δ^{13}C and 10.1 and 10.5 for δ^{15}N in the Winam Gulf. Ojwang et al. (2004) found mean values of -21.4 and 11.9 respectively for δ^{13}C and δ^{15}N in *H. laparogramma* collected in 2002 in the Winam Gulf. The δ^{13}C values of modern *H. laparogramma* and closely related *H. pyrrhocephalus* 2000s in the Mwanza Gulf were much heavier (*H. laparogramma* δ^{13}C = -6.2 and -8.0; *H. pyrrhocephalus* mean δ^{13}C = -8.9.) than those of *H. laparogramma* from the Napoleon and Winam Gulf. This can mainly be attributed to the Suess correction that was not applied by Campbell et al. (2003) and Ojwang et al. (2004). Our uncorrected values of both species in the 2000s ranged from -18.8 to -14.5 (Table 5.2). In addition, the δ^{13}C values of *H. pyrrhocephalus* 1990s, a sampling period similar to those in Campbell et al. (2003) and Ojwang et al. (2004), were again closer to the results reported for *H. laparogramma* in these studies (Table 5.2). The δ^{15}N values (8.5 and 9.8) of our modern *H. laparogramma* were in-between those found in the Napoleon Gulf and Winam Gulf. The δ^{15}N values of the modern *H. pyrrhocephalus* were close to those of *H. laparogramma* from the Winam Gulf. It should be noted that no information on size (correction) is given for *H. laparogramma* in the papers of Campbell et al. (2003) and Ojwang et al. (2004).

Old and modern species

The higher δ^{15}N values of the modern ‘curved head’ group compared to the old population were in agreement with the diet change towards more insects, zooplankton, shrimps and molluscs (Kishe-Machumu et al. 2008 [Chapter 3]). The higher δ^{13}C values in the modern ‘curved head’ group agrees with the hypothetical changes at the base of the food web, leading to a shift to heavier δ^{13}C signatures, as described in the introduction. However, the lower δ^{13}C values of *H. pyrrhocephalus* in the 1990s do not agree with this hypothesis and suggest an impact of the changed diet. The higher δ^{15}N values of *H. pyrrhocephalus* 1990s (compared to the old population) may have been caused by the higher intake of insects and midge larvae in their diet during the 1990s (Katunzi et al. 2003; Chapter 4). The *H. pyrrhocephalus* 2000s population retained high δ^{15}N values, however, δ^{13}C values increased again to the level of the old population. In 2005 and 2006 the diet of *H. pyrrhocephalus* contained again relatively more zooplankton than in the 1990s, though still less than in the 1970s (Table 5.3), which may explain the reversal to heavier δ^{13}C values of the 2000s if C in zooplankton is based on a different phytoplankton source than in insects and midge larvae. Stable isotopes of modern *H. tanaos* did, surprisingly, not differ from the old population, whereas they *did* shift their diet towards more insects, and midge larvae in the 2000s (Table 5.3). Comparison with the above described shifts in *H. pyrrhocephalus* is hampered, as currently no data on stable isotopes of *H. tanaos* from the 1990s are available. Future stable isotope analysis on specimens from 1993 used in the study of van Oijen & Witte (1996) may give definitive conclusions on this matter.

Table 5.3 Mean volume percentages (± standard deviations) of stomach and gut contents of *H. pyrrhocephalus* and *H. tanaos* throughout time.

	H. pyrrhocephalus			*H. tanaos*		
	n = 32 **1977-82**[1]	n = 13 **1999-2001**[2]	n = 48 **2005-06**[3]	n = 47 **1977-81**[4]	n = 10 **1993**[5]	n = 31 **2005-06**[6]
Detritus	4.2 ± 17.8	12.6 ± 16.8	4.6 ± 7.9	2.9 ± 7.2	0.8 ± 2.6	4.9 ± 6.4
Phytoplankton	3.6 ± 9.4	4.8 ± 11.6	1.1 ± 2.7	1.4 ± 7.1	0	0
Zooplankton*	63.9 ± 30.8	29.9 ± 27.3	46.9 ± 33.6	57.1 ± 39.3	5.7 ± 8.9	10.7 ± 21.1
Ostracods	0	0.8 ± 1.7	1.7 ± 5	0	6.1 ± 15.2	7.1 ± 12.1
Chironomids	2.1± 5.9	16.5 ± 29	5.3± 14.4	7.7± 22.8	13.4 ± 29.1	30.5 ± 33
Chaoborus	15.6± 20.7	12.3 ± 25.9	10.9± 18.4	4.6± 14.8	0	1.3 ± 5.4
Insects	6.8 ± 9.8	8.5 ± 17.8	4.8 ± 8.7	24.3 ± 30.1	64.6 ± 37.8	20.4 ± 30
Molluscs	0	11.4 ± 21	0.6 ± 2.7	0	0	0.5± 1.4
Shrimps	0	1.5 ± 5.3	6.4 ± 15	0	0	13.6± 25.4
Fish	0.4 ± 1.4	0.6 ± 1.2	15 ± 16	0	8.9 ± 19.3	10.8 ± 22.7
Others	3.5 ± 9.4	1.1± 2.3	2.7 ± 12	2.2 ± 8.7	0.5 ± 1.6	0.1 ± 0.7

* *H. pyrrhocephalus* mainly fed on copepods, *H. tanaos* mainly fed on cladocerans. Data derived from: [1] Katunzi et al. 2003, Chapter 4; [2] Katunzi et al. 2003; [3] Chapter 4; [4] van Oijen & Witte 1996, Chapter 4; [5] van Oijen & Witte 1996; [6] Chapter 4

CONCLUSION

The findings under this study suggest that preserved specimens may be used for stable isotope analysis as preservation only affected $\delta^{13}C$ and $\delta^{15}N$ values by three to four percent while the magnitude of changes over time and among species were much larger. This confirms the conclusions of Campbell et al. (2003) explaining that stable isotope analyses are a robust tool to study trophic positions and dietary sources in Lake Victoria. Many museums have substantial historical archives of preserved fish specimens. Therefore, this study supports the possibility of using archived collections to characterize food-web structures of aquatic ecosystems at scales of tens to hundreds of years.

This study revealed that significant differences both in $\delta^{13}C$ and $\delta^{15}N$ values exist among haplochromine trophic groups as well as among species in agreement with their diets. Stable isotope changes in time were observed for several species which were likely the result of diet changes towards prey of higher trophic levels and different C sources and a partly reversal of diet change in *H. pyrrhocephalus*. However, further studies on the reverting to former diets for some resurgent species are recommended.

ACKNOWLEDGEMENTS

This project was financially supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO) grants W87-129, W87-161, W87-189, W84-282, W84-488, WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC), the International Foundation for Science (IFS), the Schure Beijerinck-Popping Fonds. We are grateful to all institutions mentioned above for their support. We also extend our thanks to the crew members; Mhoja Kayeba, Mohammed Haruna, Rajabu Machage and the late Aloys Peter for their assistance during field work. We are indebted to Tom de Jong who provided us with statistical advice.

Appendix 1 Fish species used in stable isotope analysis

Period	Trophic group	Species	SL (cm)	Station	Year of sampling	Un-corrected $\delta^{13}C$	Suess corrected $\delta^{13}C$	$\delta^{15}N$
Old	Phytoplanktivores	*H. bwathondii*	6.5	G	1982	-17.4	-9.9	6.8
		H. bwathondii	6.9	G	1982	-17.1	-9.6	7.4
		H. bwathondii	7.2	G	1982	-17.2	-9.7	8.0
		H. bwathondii	7.1	G	1981	-16.9	-9.4	7.8
		H. bwathondii	6.8	G	1981	-15.5	-8.0	7.3
		H. bwathondii	7.2	G	1982	-15.5	-8.0	7.7
		H. bwathondii	6.7	G	1981	-16.4	-8.9	8.4
		H. bwathondii	6.5	G	1982	-17.5	-10.0	7.0
		H. bwathondii	6.5	G	1982	-17.5	-10.0	7.3
		H. bwathondii	7.3	G	1982	-17.4	-9.9	6.9
		Mean	**6.9**			**-16.8**	**-9.4**	**7.5**
		St. dev	**0.3**			**0.8**	**0.8**	**0.5**
	“Detritivores”	*H. cinctus*	6.2	G	1981	-22.9	-15.4	6.8
		H. cinctus	6.1	G	1981	-24.9	-17.4	5.4
		H. cinctus	5.7	G	1982	-23.6	-16.1	7.0
		H. cinctus	6	G	1981	-22.6	-15.1	6.7
		H. cinctus	5.8	G	1982	-25.0	-17.5	6.5
		H. cinctus	6.2	G	1981	-22.8	-15.4	6.4
		H. cinctus	6.1	G	1982	-22.9	-15.4	7.3
		H. cinctus	6.1	G	1981	-23.1	-15.6	6.4
		H. cinctus	5.9	G	1982	-23.6	-16.1	6.7
		H. cinctus	6.4	G	1981	-23.7	-16.3	6.1
		Mean	**6.1**			**-23.5**	**-16.0**	**6.5**
		St. dev	**0.2**			**0.8**	**0.8**	**0.5**
		H. coprologus	6.1	G	1982	-19.3	-11.8	8.8
		H. coprologus	5.9	G	1982	-18.4	-10.9	9.4
		H. coprologus	5.2	G	1981	-19.0	-11.5	9.4
		H. coprologus	5.8	G	1982	-18.7	-11.2	9.7
		H. coprologus	6.3	G	1982	-18.8	-11.3	10.2
		H. coprologus	5.5	G	1981	-18.7	-11.2	9.0
		H. coprologus	5.8	G	1982	-18.8	-11.3	9.3
		H. coprologus	5.4	G	1981	-18.9	-11.4	9.0
		H. coprologus	5.8	G	1982	-19.2	-11.7	10.3
		H. coprologus	5.7	G	1982	-19.1	-11.6	9.6
		Mean	**5.8**			**-18.9**	**-11.4**	**9.5**
		St. dev	**0.3**			**0.3**	**0.3**	**0.5**
	“Zooplanktivores”	*H. pyrrhocephalus*	6.6	Mz G[a]	1978	-17.0	-9.6	8.7
		H. pyrrhocephalus	6.3	Mz G[a]	1978	-16.4	-9.0	8.8
		H. pyrrhocephalus	6.8	Mz G[a]	1977	-16.8	-9.4	8.7
		H. pyrrhocephalus	6.5	Mz G[a]	1978	-16.2	-8.8	9.0
		H. pyrrhocephalus	7.3	Mz G[a]	1977	-17.5	-10.2	9.5
		H. pyrrhocephalus	6.2	Mz G[a]	1978	-14.7	-7.3	7.9

Appendix 1 continued

		H. pyrrhocephalus	6.9	Mz G[a]	1977	-17.8	-10.4	9.6
		H. pyrrhocephalus	6.8	Mz G[a]	1978	-17.1	-9.7	9.7
		H. pyrrhocephalus	6.7	Mz G[a]	1978	-16.9	-9.5	8.9
		H. pyrrhocephalus	6.7	Mz G[a]	1977	-18.1	-10.7	9.6
		Mean	**6.7**			**-16.8**	**-9.5**	**9.0**
		St. Dev	**0.3**			**1.0**	**1.0**	**0.6**
		H. tanaos	6.2	B	1979	-19.2	-11.8	9.8
		H. tanaos	7	B	1979	-18.8	-11.3	10.3
		H. tanaos	6.7	B	1979	-18.8	-11.4	9.7
		H. tanaos	6.9	B	1979	-18.5	-11.0	9.5
		H. tanaos	6.3	B	1979	-18.4	-11.0	9.5
		Mean	**6.6**			**-18.7**	**-11.3**	**9.7**
		St. Dev	**0.4**			**0.3**	**0.3**	**0.3**
Modern	“Detritivores”	‘Curved head’	5.7	E	2005	-19.4	-11.2	9.4
		‘Curved head’	6.1	F	2005	-21.3	-13.1	10.5
		‘Curved head’	5.5	H	2005	-21.0	-12.8	10.5
		‘Curved head’	5.5	G	2005	-21.5	-13.2	10.5
		‘Curved head’	6.1	F	2005	-21.1	-12.9	10.7
		‘Curved head’	6	H	2005	-21.2	-12.9	10.8
		‘Curved head’	5.3	I	2005	-19.4	-11.2	10.3
		‘Curved head’	6.6	G	2007	-22.0	-13.6	9.9
		‘Curved head’	6.5	G	2007	-22.1	-13.7	8.0
		‘Curved head’	7.5	G	2007	-21.5	-13.1	8.8
		‘Curved head’	7.1	G	2007	-18.8	-10.5	10.3
		‘Curved head’	6	G	2007	-22.4	-14.1	8.1
		‘Curved head’ (*cinctus*)	6.8	G	2007	-21.5	-13.2	9.0
		‘Curved head’ (*cinctus*)	6.6	G	2007	-21.9	-13.6	9.7
		‘Curved head’[b]	6.7	J	2007	-14.4	-6.1	6.6
		‘Curved head’[b]	5.9	J	2007	-14.9	-6.6	5.8
		Mean	**6.2**			**-20.3**	**-12.8**	**9.3**
		St. dev.	**0.6**			**2.4**	**1.1**	**1.5**
		H. ‘paropius-like’	5.8	E	2007	-21.6	-13.3	9.1
		H. ‘paropius-like’	4.7	E	2007	-20.0	-11.6	8.8
		H. ‘paropius-like’	5	E	2007	-13.8	-5.5	5.6
		H. ‘paropius-like’	6.2	E	2007	-19.7	-11.4	11.0
		H. ‘paropius-like’	6	E	2007	-21.3	-13.0	10.5
		H. ‘paropius-like’	5.8	E	2007	-19.4	-11.1	12.1
		H. ‘paropius-like’	5.2	G	2007	-18.6	-10.3	8.2
		H. ‘paropius-like’	4.8	G	2007	-17.8	-9.5	7.4
		H. ‘paropius-like’	5.7	J	2007	-18.4	-10.1	9.3
		H. ‘paropius-like’	4.7	J	2007	-21.3	-13.0	8.0
		H. ‘paropius-like’	4.6	J	2007	-21.8	-13.5	7.7
		H. ‘paropius-like’	8	G	2007	-21.4	-13.1	10.4
		H. ‘paropius-like’	5.1	G	2007	-22.1	-13.8	9.8
		H. ‘paropius-like’	4.5	G	2007	-17.3	-9.0	8.0

Appendix 1 continued

	H. ‘paropius-like’	5.1	G	2007	-16.9	8.6	7.2
	Mean	**5.4**			**-19.4**	**-11.1**	**8.9**
	St. dev.	**0.9**			**2.3**	**2.3**	**1.7**
“Zooplanktivores”	*H. laparogramma*[b]	4.4	J	2007	-14.5	-6.2	8.5
	H. laparogramma[b]	4.3	J	2007	-16.3	-8.0	9.8
	Mean	**4.4**			**-15.4**	**-7.1**	**9.2**
	H. pyrrhocephalus	6.9	T	1999	-20.2	-12.1	11.1
	H. pyrrhocephalus	5.6	G	2001	-18.8	-10.7	10.5
	H. pyrrhocephalus	6.8	T	1999	-19.5	-11.5	11.3
	H. pyrrhocephalus	5.6	I	1993	-18.8	-11.0	10.5
	H. pyrrhocephalus	6.6	T	1999	-19.0	-11.0	10.1
	H. pyrrhocephalus	6.6	T	1999	-20.3	-12.3	11.3
	H. pyrrhocephalus	5.9	G	2001	-18.9	-10.8	11.6
	Mean	**6.3**			**-19.3**	**-11.3**	**10.9**
	St. dev.	**0.6**			**0.6**	**0.6**	**0.6**
	H. pyrrhocephalus	5.5	F	2005	-18.1	-9.9	11.6
	H. pyrrhocephalus	5.2	F	2005	-18.1	-9.9	10.6
	H. pyrrhocephalus	5.1	F	2005	-18.3	-10.0	11.3
	H. pyrrhocephalus	4.3	E	2007	-18.8	-10.5	12.0
	H. pyrrhocephalus	5.8	E	2007	-14.8	-6.5	9.1
	H. pyrrhocephalus	4.7	J	2007	-16.7	-8.3	9.41
	H. pyrrhocephalus	4.4	J	2007	-16.7	-8.3	10.1
	H. pyrrhocephalus	5.1	J	2007	-17.2	-8.9	10.5
	H. pyrrhocephalus	4.9	J	2007	-16.6	-8.3	11.4
	Mean	**5.0**			**-17.3**	**-9.0**	**10.7**
	St. dev.	**0.5**			**1.2**	**1.3**	**1.00**
	H. tanaos	6.5	G & H	2005	-19.4	-8.0	9.6
	H. tanaos	6.5	G & H	2005	-20.3	-11.1	8.8
	H. tanaos	6.1	G	2005	-19.1	-12.1	9.1
	H. tanaos	6.3	G & H	2005	-20.3	-10.9	9.0
	H. tanaos	6.7	G & H	2005	-19.0	-12.0	8.9
	H. tanaos	6.1	J	2007	-20.8	-10.8	9.1
	Mean	**6.4**			**-19.8**	**-10.8**	**9.1**
	St. dev.	**0.2**			**0.7**	**0.7**	**0.3**

[a] Northern part of the Mwanza Gulf between Nyamatala Island and Hippo Island.

[b] Specimens were not included in analysis.

T = Transect

Mz G = Mwanza Gulf

Appendix 2 The values of $\delta^{13}C$ and $\delta^{15}N$ in formalin/alcohol-preserved and dried fish muscle tissues.

Trophic group	Species	$\delta^{13}C$		$\delta^{15}N$	
		Formalin/alcohol	Dried	Formalin/alcohol	Dried
"Detritivores"	*H.* 'paropius-like'	-21.58	-17.91	9.07	10.09
		-19.96	-19.07	8.80	8.22
		-13.79	-13.27	5.63	5.22
		-19.73	-19.25	11.01	10.15
		-21.30	-20.47	10.45	10.00
		-19.39	-18.77	12.13	11.48
		-18.64	-20.85	8.21	8.10
		-17.80	-21.34	7.39	10.71
		-18.42	-17.03	9.34	9.05
		-21.29	-20.54	8.03	7.43
		-21.79	-17.53	7.73	8.30
		-21.45	-21.36	10.37	9.79
		-22.09	-20.29	9.84	8.98
		-17.29	-16.50	7.96	7.32
		-16.87	-16.37	7.23	6.55
	H. cinctus	-21.50	-21.11	9.01	8.79
		-21.96	-21.42	9.92	9.50
		-22.06	-21.40	7.96	7.70
		-21.88	-21.50	9.73	9.52
		-21.46	-21.05	8.80	8.62
		-18.79	-21.30	10.32	8.69
		-22.38	-21.72	8.07	7.72
		-14.41	-13.97	6.58	6.30
		-14.92	-14.26	5.80	5.56
"Zooplanktivores"	*H. pyrrhocephalus*	-18.78	-17.93	11.99	11.04
		-14.81	-17.81	9.11	10.01
		-16.65	-15.97	9.41	8.77
		-16.65	-15.83	10.13	9.35
		-17.17	-16.55	10.51	9.80
		-16.59	-15.98	11.41	10.81
	H. tanaos	-20.80	-13.80	9.05	8.01
	H. laparogramma	-14.51	-13.58	8.49	7.42
		-16.31	-15.49	9.78	9.17
	Mean	**-18.88**	**-18.22**	**9.07**	**8.73**
	St. dev.	**2.71**	**2.78**	**1.59**	**1.52**

Chapter 6

The diet of Nile perch, *Lates niloticus* (L.) after resurgence of haplochromine cichlids in the Mwanza Gulf of Lake Victoria

Mary A. Kishe-Machumu, Frans Witte, Jan H. Wanink, Egid F.B. Katunzi

Original version published in *Hydrobiologia* 682**:** 111-119 (2012)

ABSTRACT

Haplochromine cichlids used to be the main prey of the introduced Nile perch, *Lates niloticus,* in Lake Victoria. After depletion of the haplochromine stocks at the end of the 1980s, Nile perch shifted to the shrimp *Caridina nilotica* and to a lesser degree to its own young and the cyprinid *Rastrineobola argentea*. In the present study we investigated the Nile perch diet in the northern Mwanza Gulf after resurgence of some of the haplochromine species and compare it with data collected in the same area in 1988/89. It became clear that haplochromines are again the major prey of Nile perch. The dietary shift from invertebrate feeding (shrimps) to feeding on fish (haplochromine cichlids) occurs at a smaller size than it did when Nile perch were taking primarily dagaa and juvenile Nile perch as their fish prey. The apparent preference for haplochromines as prey has reduced the degree of cannibalism considerably, which may have a positive impact on Nile perch recruitment.

INTRODUCTION

Nile perch, *Lates niloticus* (Linnaeus), was introduced into Lake Victoria in the 1950s and early 1960s from lakes Turkana (Kenya) and Albert (Uganda) where it is native (Pringle 2005). A dramatic increase of the Nile perch in the 1980s (Ogutu-Ohwayo 1990a; Goudswaard et al. 2008) coincided with the disappearance of about 40% of the 500+ endemic haplochromine cichlid species (Witte et al. 1992b). Concomitant with the disappearance of haplochromine species, increases of the cyprinid *Rastrineobola argentea* (Pellegrin), locally called dagaa, and of the shrimp *Caridina nilotica* (Roux) were noted (Wanink 1999; Goudswaard et al. 2006). About a decade later, Nile perch yields declined due to intense fishing and resurgence of some haplochromine species was observed in the lake (Seehausen et al. 1997b; Balirwa et al. 2003; Getabu et al. 2003; Witte et al. 2007a).

During the period of the 1970s, when haplochromine cichlids were the dominant fish in the lake (Kudhongania & Cordone 1974), they were the major prey of the Nile perch (Hamblyn 1966; Gee 1969). In the course of the 1980s, when the density of haplochromines in the sub-littoral and off-shore waters declined to almost zero (Ogutu-Ohwayo 1990a; Witte et al. 1992b), Nile perch switched to shrimps, dagaa and to its own young (Ogari & Dadzie 1988; Ogutu-Ohwayo 1990b; Mkumbo & Ligtvoet 1992; Katunzi et al. 2006). A similar shift in diet was noted in Lake Kyoga, where Nile perch had been introduced as well (Ogutu-Ohwayo 1990b). In the Mwanza Gulf (Fig. 1.2 [Chapter 1]) the switch from haplochromines to shrimps, juvenile Nile perch and dagaa, was rather abrupt, and occurred between September 1986 and June 1987 (Mkumbo & Ligtvoet 1992). In absence of haplochromine cichlids, shrimps seemed to be the preferred prey of Nile perch up to 30 cm TL in the sub-littoral areas of the Mwanza Gulf in 1988/89. Even when juvenile Nile perch and dagaa were abundant, shrimps were eaten almost exclusively by this size class (Katunzi et al. 2006). However, it has been suggested that, with their recovery, haplochromines would take over the role as key prey again (Katunzi et al. 2006).

During the past 15 years, the abundance of some haplochromine species in the sub-littoral waters of the Mwanza Gulf has increased again and currently the total number of individuals of haplochromines is about the same as in the 1970s (Witte et al. 2007a; Chapter 2). Studies by Budeba & Cowx (2007) and by Ngupula & Mlaponi (2010) showed that after their resurgence in the Tanzanian waters of the lake, haplochromines became important prey of Nile perch again. However, these studies were mainly aimed at the role of the shrimp *C. nilotica* in the Nile perch diet and did not make comparisons with Nile perch diets in the past from the same areas of the lake. To examine explicitly whether Nile perch from sub-littoral waters in the Mwanza Gulf switch back to haplochromines as their major food source after the resurgence of some of some species, we first quantified the diet of Nile perch on a research transect in the Mwanza Gulf between Butimba Bay and Kissenda Bay (Fig. 1.2 [Chapter 1]). We then compared these data to a subset of data that were collected in 1988-1998 by Katunzi et al. (2006) from an area that partially overlapped with the transect. To enable comparisons with earlier studies, we used both the frequency of occurrence method and the volumetric percentage method to characterize the Nile perch diet.

MATERIALS AND METHODS

Study area

The Nile perch samples were collected in the sub-littoral (6-20 m) waters on a research transect across the Mwanza Gulf, between Butimba Bay and Kissenda Bay (Fig. 1.2 [Chapter 1]). The research transect is approximately 5 km long and six sampling stations (E, F, G, H, I & J) with depths ranging from 5.5 to 13 m were sampled.

Sampling techniques

A small trawler, used for sampling haplochromine cichlids, was powered by a 25 hp outboard engine and towed a bottom trawl net with a 4.6 m head-rope and a 5 mm cod-end mesh. It only caught small-sized Nile perch (up to ca 30 cm TL). Therefore, large trawlers (165-215 hp) using nets with a head rope of 22-27 m and a wider stretched cod-end mesh (50-100 mm) were used to catch large-sized Nile perch. Trawl shots lasted for 10 minutes and 30 minutes with the small and large trawlers respectively. Sampling in 2006 and 2008 was mostly conducted in the morning hours between 08.00 and 12.00. The only exception was 7 March 2008, when 25 Nile perch with food in their stomachs were collected with a large trawler between 14.50 and 18.00 hours.

With the small trawler, a trawl-shot was made at each station once per month in 2006 and once per two months in 2008. The large trawlers were used in January, March, May and December 2006 and in March, August, October and December 2008. In each month three to four hauls were made on one day, and each trawl shot covered 2-3 stations on the transect. For data analysis the Nile perch samples from the small and large trawlers were combined.

Biotic data and stomach examination

Total length (TL) of Nile perch was measured to the nearest cm (digits ending at ≥ 0.5 were rounded to the nearest cm above). Depending on the size of the catch, stomach contents of all Nile perch ≤ 20 cm TL, or of a sub-sample, were analysed, while all fish > 20 cm TL were all analysed. When using a large trawler identification of stomach contents was performed on board, immediately after each haul. In case of the small trawler, fish were kept on ice and analysis was performed in the laboratory on the same day. The entire stomach of each fish was removed. Before opening the stomach, its fullness was estimated at five levels; 0, 25, 50 75 and 100%. The prey items were identified to the lowest possible taxonomic level. Small prey items like zooplankton and midge larvae that could only be observed with the aid of a microscope were discarded in this study, as we were mainly interested in the contribution of haplochromines and other large prey items to the diet. Moreover, Katunzi et al. (2006) showed that they were relatively unimportant prey types for Nile perch at the research transect (their station 3). Zooplankton was only eaten by fish < 5 cm TL (frequency of occurrence < 15%), and midge larvae mainly by fish < 10 cm (frequency of occurrence < 30%).

The frequency of occurrence of each food item was expressed as the percentage of fish containing that food item out of the total number of fish containing food. Volume per food type was estimated for each fish separately as a percentage of the total volume of food it had ingested and then a correction on volume per food type was made for the percentage of fullness of the stomach. This implied that the sum of the volume percentages of all food types, together with the empty part added up to 100%.

For calculating frequencies of occurrence and volume percentages of prey items, fish with empty stomachs were discarded and those filled less than 25% were discarded for calculating volume percentages. In total, 1073 fish (2.5-114 cm TL) from 2006 and 2008 with food in their stomachs were used for calculating frequencies of occurrence of prey items, whereas 1070 were used for volume percentages. Fish were grouped into size classes of 5 cm. The minimum number of individuals per length class was 11 (46-50 cm TL) and maximum number was 242 (11-15 cm TL).

Comparison with data collected in 1988/89

For a comparison of Nile perch diets in 2006/2008 with those in 1988/89, we used fish up to 30 cm TL, as this was the size range studied by Katunzi et al. (2006). From the latter study we only used Nile perch containing food (n = 1392) that were collected at station 3 (12-16 m deep), whereas from the present study we used Nile perch containing food (n = 639) from the deeper stations of the transect (F, G, H and I; 9.5-13 m), as these stations roughly overlapped with station 3 in Katunzi et al. (2006). Data collected by Katunzi et al. (2006) for 1 cm classes of Nile perch were lumped as 5 cm classes to make them comparable with those in the present study.

Data analysis

A Pearson correlation coefficient was calculated between the percentages of empty stomachs and fish size classes (5 cm) for all stations combined. The Jonckheere-Terpstra test was used to test for trends of prey items among size classes. A Chi-Square test was used for testing if differences in frequencies of occurrence of food items between 1988/89 and 2006/2008 were significant. Sequential Bonferroni corrections were applied in case of repeated tests. Statistical tests were performed with SPSS 17.0 for Windows.

RESULTS

Frequency of occurrence of prey items

On average, 28.4 ± 11.5% of all studied stomachs were empty. The average percentage of empty stomachs was positively correlated with Nile perch length class (Pearson correlation coefficient, $R = 0.868$; $P = 0.001$; n = 11). The average percentage of empty stomachs in Nile perch from 1 to 30 cm was 21.1 ± 8.7%.

The shrimp *C. nilotica* and haplochromine cichlids were the most common prey types in Nile perch (Table 6.1). With increasing size of Nile perch, the frequency of occurrence of shrimps decreased significantly (98-0%; Jonckheere-Terpstra test, $P \leq 0.001$; n = 1073), whereas that of haplochromines increased significantly (0-60%; Jonckheere-Terpstra test, $P \leq 0.001$; n = 1073). Dagaa was eaten by a relatively small proportion of all size-classes of Nile perch. Juveniles of its own species were found in low proportions of Nile perch ≥ 11 cm TL. For dagaa and juvenile Nile perch the frequency of occurrence increased significantly with Nile perch size (Jonckheere-Terpstra test, $P \leq 0.001$; n = 1073 for both prey types), especially for the size classes ≥ 26 cm TL, reaching maxima of about 20% in fish > 50 cm (Table 6.1). Other fish taxa were rather rare in the Nile perch diet and mainly comprised juvenile *Oreochromis niloticus* (Linnaeus) and *Barbus* spp. A relatively large percentage of Nile perch contained fish remains that could not be further identified as they were too far digested (Table 6.1). The frequencies of unidentifiable fish also increased significantly with Nile perch size (Jonckheere-Terpstra test, $P = 0.011$; n =1073). The highest frequencies (10-11%) of dragonfly nymphs (Odonata) and molluscs were occurring in the intermediate size classes (Table 6.1). Two large fish (one of 46-50 cm and one ≥ 51 cm) contained crab and plant remains in their stomachs, listed as *other prey*.

Table 6.1 Frequency of occurrence (percentages) of prey types in Nile perch per 5 cm length class in the Mwanza Gulf in 2006 & 2008 (n = number of fish with food).

Size class (cm, TL)	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51+
n	44	205	242	201	110	81	65	46	26	11	42
Odonata	0	1	4	10	11	7	11	4	4	0	2
Molluscs	0	0	3	2	5	10	11	7	0	0	0
Shrimps	98	80	71	62	32	25	26	11	0	0	0
Dagaa	2	1	1	2	4	5	9	4	15	9	21
Nile perch	0	0	1	1	2	2	6	11	4	18	19
Haplochromines	0	12	19	25	51	57	57	85	73	64	60
Other fish	0	0	0	1	2	0	0	0	0	9	5
Unidentified fish	0	10	14	13	26	36	35	20	27	27	45
Other prey	0	0	0	0	0	0	0	0	0	9	2

Volume percentages of food items

With the volume percentage method, similar results as with the frequency of occurrence were obtained (Table 6.2). Shrimps dominated the diet (40-86%) in Nile perch up to 20 cm TL, whereas haplochromines dominated (33-46%) in Nile perch from 21 cm onwards. The contribution of juvenile Nile perch to the diet increased slowly with predator length, but was never more than 9%; the unidentifiable fish species reached a maximum of 12% in size class 46-50 cm TL.

Insects, molluscs, dagaa and other fish taxa never contributed more than 9% to the diet of each size class. The volume percentages of *other prey* were negligible.

Table 6.2 Nile perch diet composition (mean volume percentages) per 5 cm length class in the Mwanza Gulf in 2006 and 2008 (n = number of fish of which the stomach fullness was > 25%).

Size class (cm, TL)	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51+
n	44	205	242	200	109	81	64	46	26	11	42
Odonata	0	0	2	5	3	1	1	1	0	0	0
Molluscs	0	0	1	1	1	2	1	1	0	0	0
Shrimps	86	64	48	40	15	7	6	1	0	0	0
Dagaa	2	1	1	1	2	2	3	0	3	1	2
Haplochromines	0	8	15	18	33	37	34	46	43	34	34
Nile perch	0	0	0	1	1	1	2	4	6	9	7
Other fish	0	0	0	0	1	0	0	0	0	9	2
Unidentified fish	0	9	6	5	12	11	6	4	9	11	12
Other prey	0	0	0	0	0	0	0	0	0	1	0
Empty	11	18	27	30	33	38	47	44	39	34	42

Comparison of data collected in 1988/89 and 2006/2008

The proportion of Odonata in the diet of Nile perch was independent of time period for all size classes, except for Nile perch of 11-15 cm, where the proportion was higher in 2006/2008 (Fig. 6.1; Chi-Square, P = 0.009). For the other size classes the difference in the frequency of occurrence of Odonata was not significant (Chi-Square, P ranging from 0.102 to 0.777). However, all other food items showed striking differences amongst both periods. In 2006/2008, Nile perch up to 20 cm TL ate shrimps more frequently than in 1988/89 (Chi-Square, $P \leq$ 0.009), whereas the reverse was true for Nile perch of 21-30 cm TL (Chi-Square, $P \leq$ 0.004; Fig. 6.1). After Bonferroni corrections the frequencies of occurrence of dagaa in Nile perch from 16-30 cm TL were strikingly lower in 2006/2008 than in 1988/89 (Chi-Square, P = 0.032-0.191 for size range 1-15 cm and $P \leq$ 0.006 for size range 16-30 cm; Fig. 6.1). Moreover, for Nile perch ranging from 1–30 cm TL, in1988/89, the frequency of occurrence of dagaa increased significantly with Nile perch size (Jonckheere-Terpstra test, $P \leq$ 0.001; n = 1392), but this was not the case in 2006/2008 (Jonckheere-Terpstra test, P = 0.373; n = 639). In 1988/89 juvenile Nile perch were present in 25-30% of the stomachs of their conspecifics larger than 6 cm, whereas in 2006/2008 this had declined to less than 3% (Fig. 6.1; Chi-Square, $P \leq$ 0.001 for all Nile perch classes between 6 and 30 cm).

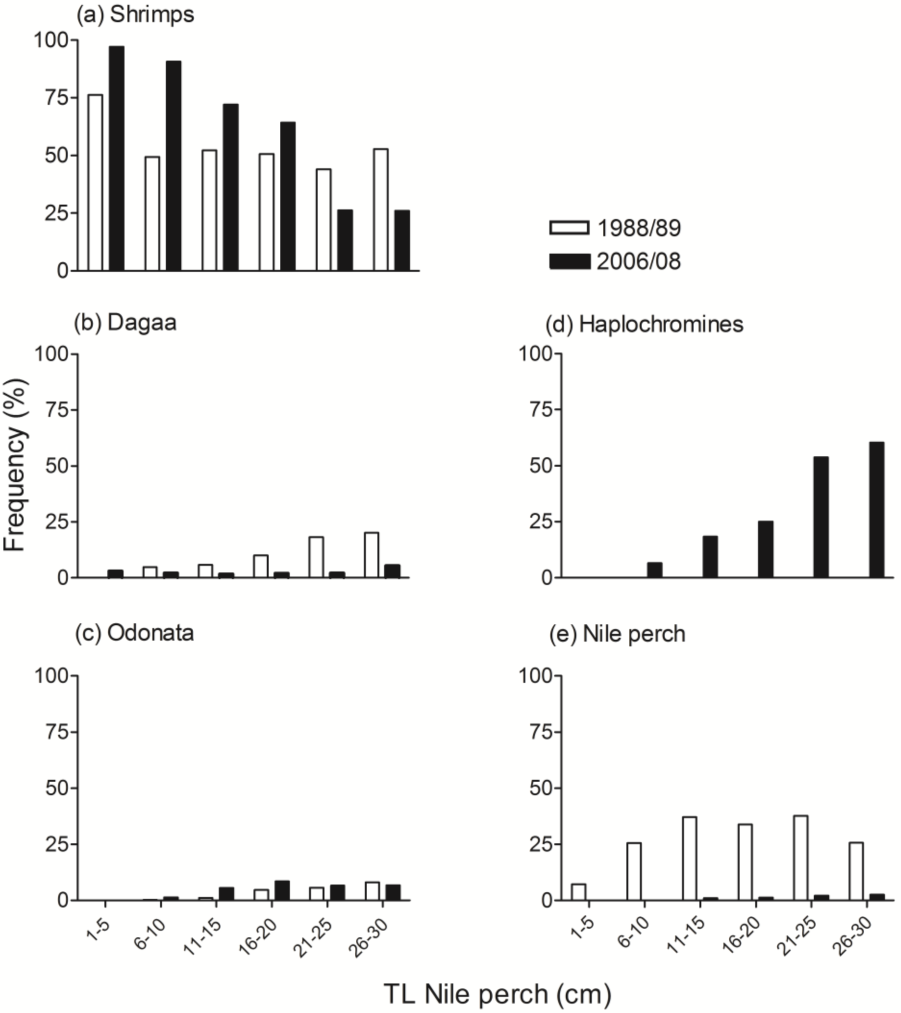

Fig. 6.1 Frequency of occurrence of the main prey types of Nile perch up to 30 cm TL (per 5-cm size class) in 1988/89 (n = 1392) and 2006/2008 (n = 639): (a) shrimps, (b) dagaa, (c) Odonata nymphs, (d) haplochromines, (e) Nile perch. For 2006/2008 only Nile perch were used collected at stations F, G, H and I, which approximately cover station 3 sampled by Katunzi et al. (2006) in 1988/1989.

In 1988/89 haplochromines were virtually absent in sub-littoral waters in the northern part of the Mwanza Gulf and consequently also absent in Nile perch stomachs. Molluscs were not encountered in the diet of Nile perch from 1988/89. The average percentage of empty stomachs in Nile perch from 1 to 30 cm in 2006-2008 (21.1 ± 8.7%) was similar to that found during the non-haplochromine diet regime (viz. 21.2 ± 5.6%) in 1988/89 by Katunzi et al. (2006).

DISCUSSION

Obviously, shrimps and haplochromines were the key preys of Nile perch in the northern part of the Mwanza Gulf in 2006/2008. In Nile perch up to 20 cm the dominant prey items were shrimps and in the larger size classes they were haplochromines. Though unidentified fishes also contributed significantly to the frequency of occurrence of prey types, their contribution to the volume percentages was much smaller (Tables 6.1, 6.2). Moreover, it should be noted that most likely a major part of the unidentified fishes were haplochromines that were too far digested to be identified. During a survey in the entire Tanzanian sector of the lake in November 2006, it was found that shrimps dominated in the diet of Nile perch < 50 cm TL by contributing 54% by volume, whereas haplochromines made up 41% of the diet of Nile perch > 50 cm TL (Ngupula & Mlaponi 2010). Our data indicate that in the northern part of the Mwanza Gulf the switch from shrimps to haplochromines as dominant prey occurred already at the size of about 20 cm TL. Similar results were found in 1999-2002 by Budeba & Cowx (2007) for their zone A, which included the Speke Gulf, the Mwanza Gulf and the offshore area between Kome Island and Ukerewe Island. In the other two zones (zone B near Musoma and zone C covering the south-western part of the Tanzanian waters) haplochromines only became the dominant prey in Nile perch > 50-60 cm TL. As there is no information on haplochromine and shrimp densities in these areas, the cause of this delayed switch is not clear.

In September 1986, when haplochromine catches in the Mwanza Gulf had decreased to ca 60 kg h^{-1} (from ca 1500 kg h^{-1} in the 1970s), haplochromines still were the most frequently occurring prey (> 60%) in Nile perch of 15–40 cm TL (Mkumbo & Ligtvoet 1992). Between June 1987 and August 1988, when haplochromines had virtually vanished from the trawl catches (Goudswaard et al. 2008), the frequency of occurrence of haplochromines in Nile perch of 15–40 cm

TL had decreased to less than 5% (Mkumbo & Ligtvoet 1992). Finally, in the period of September 1988 to September 1989, no haplochromines at all were found in Nile perch up to 30 cm TL (Fig. 6.1; Katunzi et al. 2006). The shift from haplochromines to shrimps as the main prey between 1986 and 1989 in the Mwanza Gulf was clearly due to the decline of the haplochromines (Witte et al. 1992b; Goudswaard et al. 2008) and the concomitant increase of shrimps (Goudswaard et al. 2006).

Katunzi et al. (2006) found that in 1988/89 at station 3 in the Mwanza Gulf, Nile perch up to 30 cm TL, in addition to shrimps (the most common prey), fed on juvenile Nile perch (≤ 5 cm TL), and with lower frequency on dagaa. However, it appeared that in seasons with high abundance of shrimps, juvenile Nile perch and dagaa were neglected, even if their abundance was high. Though the biomass of dagaa increased in the lake during the past decade (Tumwebaze et al. 2007; Witte et al. 2009b), their contribution to the Nile perch diet in 2006/2008 was much lower than in 1988/89 and never exceeded 3% by volume percentage (Table 6.2). Our current observations suggest that Nile perch > 20 cm TL prefer haplochromines over shrimps. From 40 cm TL onwards, no shrimps at all were present in the diet, whereas during the second half of the 1980s, when haplochromines were absent, shrimps were eaten by Nile perch up to 60 cm TL (Ogutu-Ohwayo 1990b; Mkumbo & Ligtvoet 1992) and in the Nyanza Gulf (Kenya) even by fish of more than one metre (Hughes 1986; Ogari & Dadzie 1988). Concordantly, the frequency of occurrence of shrimps in the diet of Nile perch up to 30 cm TL did not show a trend across size classes in 1988/89 when haplochromines were absent, but a significant negative trend was found after the recovery of the haplochromines in 2006/2008 (Fig. 6.1).

In Lake Kyoga, where the upsurge and decline of the Nile perch occurred about a decade earlier than in Lake Victoria (Ogutu-Ohwayo 1990a, 2004), a similar pattern was observed as in the Mwanza Gulf; shrimps were more important than haplochromines in the diet of Nile perch < 20 cm and of 20-59 cm TL in 1978-1980. However, in 1991-1993, haplochromines dominated in the diet of Nile perch of these two size classes, as well as in the size class of 60-100 cm TL (Ogutu-Ohwayo 2004).

In Lake Nabugabo, where shrimps appeared to be absent, dagaa and juvenile Nile perch were the main prey types before the mid-1990s, when haplochromines were extremely rare in the lake (Ogutu-Ohwayo 1993; Schofield & Chapman 1999). After the mid-1990s, when haplochromines were resurging in Lake Nabugabo, the diet of the Nile perch changed and in 2000 and 2007 it was dominated by haplochromine cichlids (Paterson & Chapman 2009). Notably, the shift from invertebrates to fish occurred at a smaller size (between 10 and 15 cm TL) in case of haplochromines than in case of dagaa and juvenile Nile perch (between 30 and 35 cm TL; Paterson & Chapman 2009). This agrees with our observations in the Mwanza Gulf, where in 1988/89 shrimps were eaten more frequently than fish by Nile perch up to at least 30 cm TL, while in 2006/2008 haplochromines became the most frequently eaten prey from 21 cm onwards. In conclusion it seems that haplochromines are the preferred prey of Nile perch that are large enough to feed on them.

Between 1987 and 1989, when haplochromines had virtually vanished from the Mwanza Gulf (Witte et al. 1992b; 2007a), cannibalism became important in Nile perch ≥ 5 cm TL (Mkumbo & Ligtvoet 1992; Katunzi et al. 2006), whereas it strongly decreased after resurgence of the haplochromines. Also in other parts of Lake Victoria and in Lake Kyoga, Nile perch began feeding on their young only when haplochromine species were depleted (Ogutu-Ohwayo 1993). Hopson (1972) stated that cannibalism in Lake Chad may have resulted partly from the scarcity of preferable prey items. During the past years there has been some worry that the resurging haplochromines may do harm to the Nile perch stocks by feeding on Nile perch eggs and larvae (Kolding et al. 2008). Though this may be the case (Goudswaard et al. 2008), the data of our study indicate that the preference of Nile perch for haplochromines instead of for their own young, reduces cannibalism. This may counterbalance the loss of eggs and larvae or even enhance rates of recruitment of Nile perch, which is of great importance for a sound fishery.

CONCLUSION

Based on a modelling study by Kaufman & Schwarz (2002), indicating that Nile perch prefer and grow fastest on a haplochromine prey base, it has been suggested that conservation of biodiversity and fishery sustainability may not have to be antitheses in the management of Lake Victoria (Balirwa et al. 2003). The observed reduction of cannibalism by Nile perch when haplochromines are available seems to support this suggestion.

Since haplochromines are now taken as a by-catch in the dagaa fishery, management measures in dagaa fishery should take haplochromines into account. If the recovery of the haplochromine cichlids will continue, high dependence of the Nile perch on haplochromines and low rates of cannibalism, may contribute to another round of the Nile perch success in Lake Victoria.

ACKNOWLEDGEMENTS

We would like to thank the following organisations that funded this study: the Netherlands Foundation for the Advancement of Tropical Research (WOTRO; grants W 87-189, W 84-488, WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC), the International Foundation for Sciences (IFS), the Schure Beijerinck-Popping Fonds and the section DPO of the Netherlands Ministry of Foreign Affairs. We are also grateful to the crew members of the small trawler; Mhoja Kayeba, Mohamed Haruna and Rajabu Machage, the master fishermen; Raphael Mamelela and Gabriel Mbaya of the larger trawlers (R.V. Lake Victoria Explorer and M.V. Mdiria) and all other crew members for making sampling successful.

Chapter 7

Can differential resurgence of haplochromine trophic groups be explained by selective Nile perch predation?

Mary A. Kishe-Machumu, Tanja Voogd, Jan H. Wanink, Frans Witte

ABSTRACT

The introduced Nile perch in Lake Victoria is considered to have been a major contributor to the decline in species and trophic diversity of haplochromines in Lake Victoria. In the second half of the 1990s, the abundance of Nile perch declined due to heavy over-fishing and some haplochromines, mainly “detritivores” and “zooplanktivores”, started to recover. However, the resurgence of “detritivores” was much slower than that of “zooplanktivores”. Some studies suggested differential Nile perch predation is the primary cause for the differential recovery of these two dominant groups. To confirm this, the frequency of occurrence (FOO) of the “detritivores” and “zooplanktivores” in the stomachs of the Nile perch and their FOO in the lake were compared. Further, we investigated the potential impacts of the differences in body shape between “detritivorous” and “zooplanktivorous” haplochromines on their vulnerability to predation. In the Nile perch stomach 13.7% “detritivores” and 86.3% “zooplanktivores” occurred, whereas in trawl catches the FOOs were 24.3% and 75.7% respectively. The FOO of “detritivores” in the Nile perch diet was significantly lower than in the environment. The same holds for the FOO of juvenile haplochromines (13% in the diet and 45% in the environment). There was no significant difference between average lengths of “detritivores” and “zooplanktivores” retrieved from Nile perch stomachs. In contrast, body depth of “detritivores” in the diet of the studied Nile perches was significantly larger than that of the “zooplanktivores”, but based on their mouth gape size only Nile perches smaller than 13 cm TL would not be able to swallow the largest “detritivores”. Even if this would have a significant impact on prey selection it would imply that “detritivores” would be less vulnerable to predation. Thus, relatively slow resurgence of “detritivores” cannot be explained by selective predation on this trophic group by Nile perch.

INTRODUCTION

In the late 1950s and early 1960s, the predatory Nile perch, *Lates niloticus* (Linnaeus), was introduced into the Lake Victoria basin (Pringle 2005) to improve the declining fishery (Ogutu-Ohwayo 1990a). A lake-wide survey in 1969-1970 revealed that 80% of the demersal fish mass consisted of haplochromine cichlids (Kudhongania & Cordone 1974). In the 1980s, the Nile perch suddenly increased in Lake Victoria and, concomitantly, the haplochromines in the sub-littoral and off-shore areas vanished almost completely (Barel et al. 1985, 1991; Ogutu-Ohwayo 1990a; Witte et al., 1992b). The dramatic decline of haplochromines cichlids in Lake Victoria triggered many studies and debates about the possible causes and consequences of their decline (e.g. Barel et al. 1985; Acere 1988; Witte et al. 1992a,b; Goldschmidt et al. 1993; Hecky 1993; Seehausen et al. 1997a,b). Although environmental changes and local overfishing played a role in the decline of the haplochromines (Hecky 1993; Hecky et al. 1994, 2010; Seehausen 1997a; Balirwa et al. 2003), Nile perch is thought to have been a major cause of the faunal collapse in Lake Victoria (Witte et al. 1992b).

Since the 1990s, the Nile perch population in the lake has declined due to over-exploitation (Pitcher & Bundy 1995; Ntiba et al. 2001) and a concomitant resurgence of some haplochromine species was observed (Seehausen et al. 1997b; Witte et al. 2000, 2007b; Balirwa et al. 2003; Getabu et al. 2003). However, the rate at which the trophic groups recovered differed. “Detritivores” and “zooplanktivores” that previously dominated the ichthyomass were more successful in recovering than other trophic groups in the Mwanza Gulf (Witte et al. 2007b; Chapter 2). Prior to the Nile perch upsurge, “detritivores” in this area made up ca. 75% to 85% of the total number of haplochromines in the bottom trawl catches and “zooplanktivores” contributed between 10% and 20% (Table 2.2 [Chapter 2]; Goldschmidt et al. 1993; Witte et al. 2007b). Between 1990 and 2006, “zooplanktivore” numbers increased faster than those of “detritivores” (Witte et al. 2007b; Chapter 2). In 2006, “detritivores” comprised about 21% of the number of haplochromines and “zooplanktivores” made up about 71%, but since 2008, the former is the dominant group again (Chapter 2).

Some papers discussed the possible factors of the differential recovery and shift in dominance between these two groups (Witte et al. 2007b; Kishe-Machumu et al. 2008 [Chapter 3]). Kishe-Machumu et al. (2008) showed that the slower recovery of “detritivores” is unlikely to be a result of their diet as they switched to one that was similar to that of the “zooplanktivores” (Kishe-Machumu et al. 2008 [Chapter 3]; Chapters 4, 5). In recent years, the density of Nile perch has further decreased (Matsuishi et al. 2006; Kayanda et al. 2009), but it is still more abundant than in the 1970s (Goudswaard et al. 2008) and haplochromines once again became a considerable part of its diet after their resurgence (Kishe-Machumu et al. 2012 [Chapter 6]). Differential predation by Nile perch might cause differences in resurgence rate between haplochromine trophic groups. Based on the slower recovery of “detritivores”, we hypothesized that the impact of predation by Nile perch was higher on “detritivores” than on “zooplanktivores”. To test this hypothesis, we compared the ratio of both trophic groups in the environment to their ratio in stomach contents of Nile perch. Further, we investigated the potential impacts of the differences in body shape and length between “detritivorous” and “zooplanktivorous” haplochromines on their vulnerability to predation.

MATERIALS AND METHODS

Study area and fish sampling

Fish samples were collected at the research transect between Butimba and Kissenda Bay in the Mwanza Gulf (Fig. 1.2 [Chapter 1]) from January to December in 2006. The water depths of the transect ranged from 5.5 to 13 m and the bottom consisted of soft organic mud (Witte 1981).

A small bottom trawler powered by a 25 hp outboard engine towing a bottom trawl net with a 4.6 m head-rope and a 5 mm cod-end mesh was used for sampling at six sampling stations (E, F, G, H, I and J) along the research transect. As this trawler caught only small-sized Nile perch (up to ca. 30 cm TL), larger individuals were collected from the same area with a large trawl net (24 m head-rope, cod-end mesh 50 mm), mounted on the R.V. Lake Victoria Explorer (250 hp). Haplochromines were only collected with the small trawler because they were too small to be caught in the wider cod-end meshes of the large trawl net.

After each haul, haplochromines were sorted into trophic groups and species. The total length (TL, to the nearest cm) of each Nile perch was recorded, the gut was opened and the gut contents were visually identified.

All haplochromine prey from the Nile perch stomachs were sorted and preserved in a 5% formaldehyde solution and later transferred to 70% alcohol for identification. With the small trawler, a trawl-shot was made at each station once per month, whereas the large trawler was used in January, March, May and December.

Identification of "zooplanktivorous" and "detritivorous" haplochromines

Intact "detritivores" and "zooplanktivores" from the Nile perch stomachs were classified according to their morphological differences. Of these two groups, "zooplanktivores" are generally more slender-bodied than "detritivores" (Witte & van Oijen 1990), so we used depth/length ratios to distinguish the two groups. The body depth/standard length (BD/SL) ratio in "zooplanktivores" is < 33% but > 33% in "detritivores" (Witte & van Oijen 1990). Since haplochromine individuals from Nile perch stomachs were often partly digested with part of the head or the tail missing, it was not always possible to measure SL or BD. Therefore, alternative morphometric ratios were established and used to discriminate between the two groups. The alternative ratios had to meet two main criteria: (1) they should be significantly different in "detritivores" and "zooplanktivores", and (2) they should be applicable to most haplochromines obtained from Nile perch stomachs.

From a so called 'control group' of 57 individuals of which 30 were "zooplanktivores" and 27 "detritivores" (Table 7.1), BD/SL and 17 alternative depth/length (D/L) ratios fulfilling the above two criteria were selected as reference measures for trophic group identification of haplochromines from Nile perch stomachs (Table 7.2).

Table 7.1 The number of *Haplochromis* species in the 'control group'.

"Zooplanktivores"	Number	"Detritivores"	Number
H. pyrrhocephalus	13	*H.* 'paropius-like'	10
H. tanaos	12	*H.* 'straight head dusky'	10
H. laparogramma	5	*H.* 'cinctus-like'	4
		H. antleter	3
Total	**30**	**Total**	**27**

It should be noted that the definitions of BD and head length (HL) (Fig. 7.1) differed from those given in Barel et al. (1977), because it was not always possible to find the exact landmarks used by them in fish taken from Nile perch stomachs.

The haplochromines from the Nile perch stomachs were placed on graph paper with a ruler as reference measure next to it. Seven landmarks that were least affected by Nile perch digestion (Fig. 7.1) were put on the left side of the fish with a permanent marker pen. Digital photographs were taken with a Nikon Coolpix E990 camera and distances between landmarks were measured with ImageJ. The D/L ratios (Table 7.2) were used to determine to which of the two trophic groups the individuals belonged.

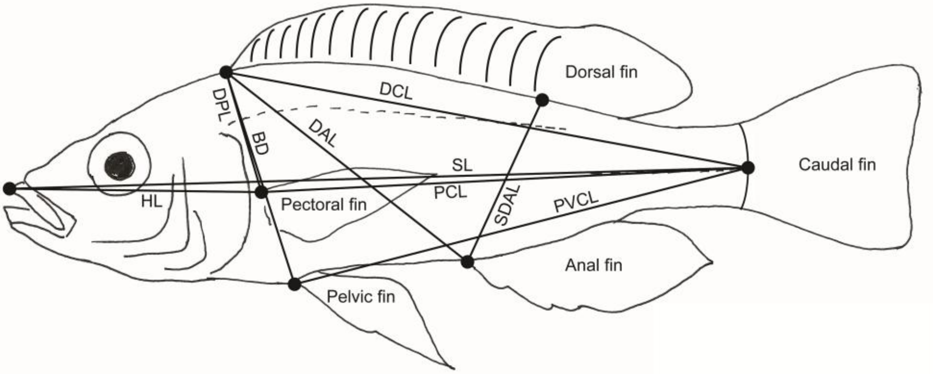

Fig. 7.1 Positions of landmarks used to measure the lengths of each haplochromine. Abbreviations are as follows: SL = standard length (snout to origin of caudal fin), HL = head length (snout to base of pectoral fin), DPL = rostral insertion of dorsal fin to dorsal insertion of pectoral fin, BD = body depth (rostral insertion of dorsal fin to rostral insertion of pelvic fin), DAL = rostral insertion of dorsal fin to rostral insertion of anal fin, DCL = rostral insertion dorsal fin to origin of caudal fin, SDAL = base of last spinous dorsal fin ray to rostral insertion of anal fin, PVCL = rostral insertion of pelvic fin to origin of caudal fin and PCL = dorsal insertion pectoral fin to origin of caudal fin.

Nile perch and prey size

To test if the whole size range of Nile perch analysed in the present study was able to swallow the available “zooplanktivores” and “detritivores”, the maximum body depth (BD) of these two groups (from the Nile perch stomachs) was compared to the mouth gape (MG) of the Nile perch. The mouth gape of Nile perch was related to its total length by MG = 0.112 * TL + 0.43 (both MG and TL in cm; Ligtvoet & Mkumbo 1990). In addition, we compared the maximum TL of “detritivores” and “zooplanktivores” with the TL of the studied Nile perch. Nile perch can feed on prey up to 25-30% of its own length in Lake Victoria (Hamblyn 1966; Gee 1969; Oguto-Ohwayo 1985), although Hopson (1972) suggested that in Lake Chad, “Nile perch of all lengths are capable of eating fish up to approximately half their own length”. In this study, the TL of many haplochromines from Nile perch stomachs could not be measured because the caudal fin was damaged. However, for those specimens of which SL could be measured, TL could be determined since TL = SL * 5/4, as the caudal fin length is generally 25% of the SL in both trophic groups (Witte & Witte-Maas 1987; de Zeeuw et al. 2010). Both haplochromine groups mature at about 4 cm SL (Witte et al. 2007b), so the percentage of haplochromine prey smaller than 4 cm SL was calculated to establish the frequency of juveniles in the diet.

Prey selectivity

Prey selectivity of Nile perch was determined by comparing the frequency of occurrence (FOO) of haplochromines in the environment with their frequency of occurrence in the stomachs of Nile perch. The FOO of haplochromine trophic groups in the environment was calculated from every small trawl catch of 10 minutes at the research transect from which the Nile perch were used and the haplochromines could be identified in their stomachs. For those Nile perch which were collected with the large trawl, all catches at all six stations made with the small trawl on that particular month were used. This is because we did not make representative haplochromines catches with the large trawler and the large trawl catches covered all stations. Except for seven individuals from three night catches (between 09.30 and 11.30 pm) with the small trawler, all Nile perch were collected at day hours.

Data analysis

Depth/Length ratios of “detritivores” and “zooplanktivores” in the ‘control group’ were not normally distributed (Shapiro Wilk test); therefore, the non-parametric Mann-Whitney U-test was used to test for differences between the D/L ratios of “detritivores” and “zooplanktivores”.

A discriminant analysis was used to determine to which trophic group each haplochromine obtained from the Nile perch stomachs belonged. Ungrouped fish from Nile perch stomachs (out-group) were compared to the grouping variable, the trophic groups (“detritivores” and “zooplanktivores”) defined in the ‘control group’. It was rarely possible to obtain all 18 ratios for each individual haplochromine and because a discriminant analysis cannot analyse cells with missing values, it was not possible to run the analysis for all individuals together. Therefore, individuals having the same kind of ratios were analysed together.

Univariate general linear models (GLM) with haplochromine trophic group (“detritivores” versus “zooplanktivores”) as factor and Nile perch length (TL) as covariant were used to test for differences in BD and TL of the “detritivores” and “zooplanktivores” eaten by Nile perch.

A Chi-square test was performed to test if the frequencies of occurrence of “detritivorous” and “zooplanktivorous” haplochromines in Nile perch stomachs were significantly different from the frequencies that were found in the trawl catches. The statistical packages SPSS 15.0 and 16.0 for Windows were used for all tests.

RESULTS

Control group

In the ‘control group’, there were 18 D/L ratios that were significantly different between “detritivores” and “zooplanktivores” (Mann Whitney U-test, $P < 0.001$ in all cases). The ranges of ten ratios however, overlapped in which the minimum value(s) for “detritivores” were lower than the maximum value(s) for “zooplanktivores” (Table 7.2).

Table 7.2 Mean (± standard deviation) and range of morphometric ratios in “detritivores” and “zooplanktivores”. Abbreviations are defined in Fig. 7.1.

Measurements ratios	“Detritivores” (n = 27)		“Zooplanktivores” (n = 30)	
	Mean	Range (min.-max.)	Mean	Range (min.-max.)
BD/SL*	0.35 ± 0.015	(0.32 - 0.37)	0.28 ± 0.021	(0.24 - 0.32)
BD/PCL*	0.53 ± 0.025	(0.48 - 0.58)	0.42 ± 0.033	(0.36 - 0.48)
BD/DCL*	0.49 ± 0.021	(0.46 - 0.53)	0.40 ± 0.025	(0.36 - 0.45)
BD/PVCL	0.54 ± 0.028	(0.50 - 0.60)	0.44 ± 0.036	(0.37 - 0.51)
DAL/SL	0.46 ± 0.015	(0.42 - 0.48)	0.41 ± 0.018	(0.36 - 0.45)
DAL/PCL	0.70 ± 0.027	(0.63 - 0.74)	0.61 ± 0.028	(0.54 - 0.67)
SDAL/SL	0.27 ± 0.015	(0.24 - 0.30)	0.22 ± 0.013	(0.19 - 0.25)
SDAL/PCL	0.41 ± 0.025	(0.37 - 0.46)	0.33 ± 0.019	(0.28 - 0.37)
SDAL/PVCL	0.43 ± 0.027	(0.38 - 0.48)	0.34 ± 0.022	(0.28 - 0.39)
SDAL/DCL*	0.39 ± 0.021	(0.35 - 0.43)	0.31 ± 0.014	(0.28 - 0.34)
DPL/SL*	0.22 ± 0.009	(0.21 - 0.25)	0.17 ± 0.015	(0.14 - 0.20)
DPL/PCL*	0.34 ± 0.014	(0.31 - 0.37)	0.26 ± 0.023	(0.22 - 0.31)
DPL/PVCL*	0.35 ± 0.017	(0.32 - 0.39)	0.27 ± 0.024	(0.23 - 0.32)
BD/HL	1.00 ± 0.048	(0.92 - 1.09)	0.82 ± 0.069	(0.69 - 0.97)
SDAL/HL	0.79 ± 0.046	(0.70 - 0.88)	0.65 ± 0.043	(0.56 - 0.73)
DAL/PVCL	0.72 ± 0.032	(0.66 - 0.77)	0.64 ± 0.031	(0.56 - 0.71)
DAL/DCL	0.65 ± 0.021	(0.61 - 0.68)	0.59 ± 0.017	(0.56 - 0.62)
DPL/DCL*	0.32 ± 0.012	(0.30 - 0.35)	0.25 ± 0.018	(0.21 - 0.28)

* Indicates ratios that do not overlap in the two groups.

Frequency of haplochromine trophic groups in Nile perch stomachs

A total of 344 identifiable haplochromines was collected from the Nile perch stomachs of which 105 (31%) were intact enough to be measured. Of 95 (28%) of these haplochromines, the trophic group could be identified with a probability ≥ 90% in which 82 specimens were identified as “zooplanktivores” and 13 as “detritivores” (Table 7.3). The remaining 10 individuals, eight of them were identified as “zooplanktivores” and two “detritivores”, but the probability of correct identification was < 90%, so they were not included in the ratio of "detritivores" and "zooplanktivores" in the Nile perch stomachs. The identifiable haplochromines were obtained from 60 Nile perch arranging in size range from 13.6-43.2 cm TL.

Nile perch size and haplochromine body depth

The body depth of "detritivores" from the Nile perch stomachs ranged from 0.8-1.9 cm (n = 11) and those of "zooplanktivores" from 0.6-1.7 cm (n = 50). The GLM for BD of the "zooplanktivores" and "detritivores" in Nile perch stomachs, showed that there was a slight increase in prey BD with increasing Nile perch size (BD = 1.296 + 0.009 TL for "detritivores" and BD = 0.97 + 0.009 TL for "zooplanktivores"; $P = 0.042$). Body depth of the "detritivores" in the stomachs was significantly larger than that of the "zooplanktivores" (estimated marginal means: 1.53 ± 0.08 versus 1.23 ± 0.04 respectively; $P = 0.001$). The smallest Nile perch in the present study (TL 13.6 cm, MG 2.0 cm) swallowed a detritivore of 1.3 cm BD (Fig. 7.2a). The "detritivore" with the largest body depth (1.9 cm) had been eaten by a relatively small Nile perch of 20.2 cm TL, with a MG of 2.7 cm.

Nile perch size and haplochromine length

The size of the "detritivores" eaten by Nile perch ranged from 5.3-7.2 cm TL (4.2-5.8 cm SL, n = 5) while "zooplanktivores" ranged from 3.4-7.7 cm TL (2.7-6.1 cm SL, n = 18; Fig. 7.2b). The GLM for total length of the "detritivores" and "zooplanktivores" in the Nile perch diet revealed no significant increase in length of "detritivores" and "zooplanktivores" in relation to Nile perch size. There was also no significant difference in total length between the two groups. None of the "detritivores" and only three of the "zooplanktivores" had a SL < 4 cm, which implies that the number of juvenile haplochromines eaten was only 13% of all the juveniles collected in the samples. The longest haplochromine (7.7 cm TL) in the stomach contents was a "zooplanktivore" eaten by the largest Nile perch (43.2 cm TL). The smallest Nile perch that had eaten a haplochromine in the present study had a TL of 6.8 cm, but the trophic group and size of this prey could not be identified. The TL of the two relatively largest prey in the present study were 37.8% and 35.6% of the Nile perch length that swallowed them; a "zooplanktivore" of 5.6 cm in a Nile perch of 14.8 cm and a "detritivore" of 7.2 cm in a Nile perch of 20.2 cm respectively (Fig. 7.2b).

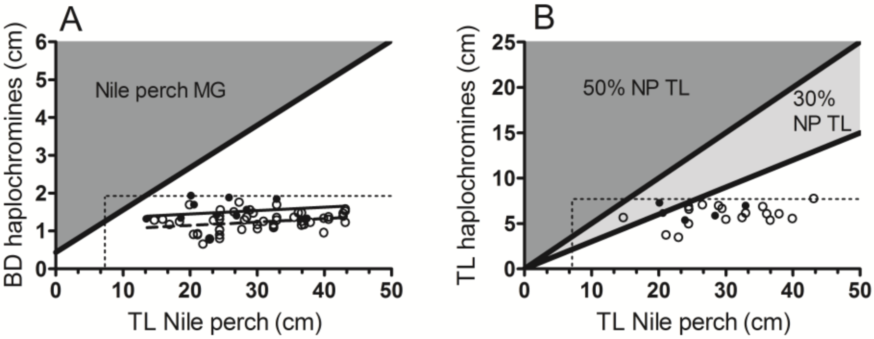

Fig. 7.2 Relationships between Nile perch size and its prey size: (a) Body depth (BD) of haplochromines against total length (TL) of Nile perch (b) TL of haplochromines against TL of Nile perch. Filled circles represent detritivores and open circles zooplanktivores. In case of a significant effect of the TL of Nile perch, regression lines as estimated by the general linear model are depicted. Shaded areas represent Nile perch features that restrict prey sizes: (a) haplochromine BD > Nile perch mouth gape (MG); (b) haplochromine TL > 30 - 50% Nile perch TL. Vertical dotted lines indicate smallest Nile perch that had eaten a haplochromine; horizontal dotted lines indicate measure of largest prey in this study. The corner of the dark shaded area enclosed by the dotted lines indicates the Nile perch size range that (theoretically) cannot eat the maximum prey size of haplochromines (for further explanation see text).

Prey selectivity

The total numbers of “detritivores” and “zooplanktivores” in 36 bottom trawl catches of 10 minutes in 2006 (from the same days and stations as the Nile perches with identifiable haplochromine prey), were 7,108 and 22,148 respectively. By comparison, “detritivores” accounted for 24.3% of haplochromines in the catches and “zooplanktivores” 75.7% and in the Nile perch stomachs 13.7% and 86.3% respectively (Table 7.3). There was a significant difference between the FOO of “detritivores” and “zooplanktivores” in the environment (indicated in their proportion in trawl catches) and in the Nile perch stomachs; the “detritivore”: “zooplanktivore” ratio was about two times lower in Nile perch stomachs than in the environment. This suggests that “detritivores” occurred less frequently than expected in the diet of Nile perch while “zooplanktivores” were more frequent.

Table 7.3 Frequency of occurrence (total numbers and percentages) and ratios of “detritivorous” and “zooplanktivorous” haplochromines in Nile perch stomachs and in trawl catches of 10 minutes duration.

	“Detritivores”	“Zooplanktivores”	Ratio D:Z
Nile perch stomachs (n = 60)	13 (13.7%)	82 (86.3%)	1: 6.3
Trawl catches (n = 36)	7108 (24.3%)	22,148 (75.7%)	1: 3.1
X^2 5.8, df 1, *P* < 0.025			

The total number of adult “detritivorous” and “zooplanktivorous” individuals in the trawl catches was 29,256 and they made up 95.1% of the total number adult haplochromines (30,758). The total number of juvenile haplochromines in the same catches was 23,757. Assuming that for juveniles, the percentage of “zooplanktivores” and “detritivores” was about the same as for adults, this would result in 0.95 x 23,757 = 22,569 juvenile “zooplanktivores” and “detritivores”. Thus, in the environment the percentage of juveniles (< 4 cm SL) was about 45% (Table 7.4). The FOO of juvenile haplochromines in the Nile perch stomachs (13%) was significantly lower than in the trawl catches (Table 7.4).

Table 7.4 Frequency of occurrence (total numbers and percentages) and ratios of juvenile and adult “detritivorous” + “zooplanktivorous” haplochromines in Nile perch stomachs and in trawl catches of 10 minutes duration.

	Juveniles	Adults	Ratio J:A
Nile perch stomachs (n = 60)	3 (13.0%)	20 (87.0%)	1: 6.7
Trawl catches (n = 36)	22,569 (45.0%)	29,256 (55.2)	1: 1.3
X^2 = 8.7, df 1, *P* < 0.005			

DISCUSSION

The hypothesis that the slow recovery of “detritivores” was a result of Nile perch predation appears to have been refuted as the data suggest the Nile perch selectively preyed upon “zooplanktivores”. Some possible factors which could have affected the outcome of our study are discussed below.

Problems with trophic group identification

Although there were several morphological differences between “detritivorous” and “zooplanktivorous” haplochromines especially in D/L ratios, separating these trophic groups in Nile perch stomachs was a complex matter. In many cases fish were too far digested to enable the measurements necessary for their identification to be made. Only 28% (95) of the haplochromines from the Nile perch stomachs were intact enough to establish their trophic group with a certainty of 90%. Nevertheless, since the rate of digestion of “detritivores” and “zooplanktivores” is unlikely to differ, this sample probably gave a reasonable impression of the ratio of the two trophic groups in the Nile perch diet.

Vulnerability of “detritivores” and “zooplanktivores” to Nile perch predation

Body shape differences

As the body depth of “detritivorous” haplochromines was significantly greater than that of “zooplanktivores” of the same size (Table 7.2; Witte & van Oijen 1990), they were to be less vulnerable to predation by relatively small Nile perch. The greater body depth of “detritivores” did not seem to determine predation by Nile perch in the studied size range, since their mouth gape was always large enough to allow them to ingest these haplochromines. There was an increase in body depth with increasing Nile perch size, but it should be stressed that the increase was extremely small, and only just significant. This may be an artefact caused by the small size of the sample. Nile perch < 13 cm TL could find it more difficult to ingest “detritivores” than “zooplanktivores” owing to their deeper bodies. However, as only a relatively small fraction of Nile perch < 13 cm included haplochromines in their diet (Table 6.1, Kishe-Machumu et al. 2012 [Chapter 6]), the effect of differential predation by these small Nile perch may not be large.

Moreover, if there is any relationship between body depth and prey selectivity then predation pressure on the deeper bodied “detritivorous” haplochromines would be expected to be lower than on the “zooplanktivores”.

In this study, the maximum length of prey was 38% of the Nile perch total length (a Nile perch of 14.8 cm TL). This is between the values of 25-30% reported for Lake Victoria (Hamblyn 1966; Gee 1969; Ogutu-Ohwayo 1985) and the maximum of 50% in Lake Chad by Hopson (1972), but since haplochromines do not grow as large as Nile perch, their relative size decreases in the stomachs of larger fish (Fig. 7.2b). If Nile perch in Lake Victoria could eat haplochromines with a length up to 50% of their own total length, the Nile perch in the size range of 6.8 cm TL (the smallest that had eaten a haplochromine; Kishe-Machumu et al. 2012 [Chapter 6]) and 15.4 cm TL (the longest haplochromine was 7.7 cm TL) would not be able to swallow all haplochromines. For a prey to predator ratio of 30%, a Nile perch should be even 25.6 cm to swallow a haplochromine of 7.7 cm (Fig. 7.2b). However, as the mean lengths of “detritivores” and “zooplanktivores” did not differ, it is unlikely that prey length will cause a differential predation effect by Nile perch smaller than those in the present study.

Body shape of “zooplanktivores” might be better adapted to burst swimming because of a relatively low ratio between head surface area and caudal peduncle area. This would facilitate predator escape as is described by Langerhans et al. (2004) for guppies. In both resurgent groups; “detritivorous” and “zooplanktivorous” haplochromines of Lake Victoria, it has been found that the ratio between head surface area and caudal peduncle area decreased compared to that before the Nile perch boom (van Rijssel & Witte 2012). Nevertheless, “detritivores” had and still have a higher head surface/caudal peduncle area ratio than “zooplanktivores”, which theoretically might make them more vulnerable to Nile perch predation. But, in spite of this, “detritivores” were under-represented in the Nile perch diet. It is unlikely therefore that difference in size or body shape between the two trophic groups has had a major impact on their vulnerability to predation by Nile perch.

Habitat differences

It was suggested that "detritivores" which live closer to the bottom than "zooplanktivores", had a larger habitat overlap with Nile perch and may therefore have been more susceptible to Nile perch predation than "zooplanktivores" (Witte & Goudswaard 1985; Goudswaard et al. 2004; Witte et al. 2007b; Witte et al. 2012). In the past, "detritivores" were mainly caught in the lowest three metres of the water column (Goldschmidt et al. 1993; Goudswaard et al. 2004; Witte et al. 2012), but in 2006 and 2008, a major part of the "detritivorous" population migrated to the surface along with "zooplanktivores" (Figs 2.1, 2.2). In addition, the diet of both trophic groups overlapped to a greater extent than before their reduction in numbers. It seems unlikely that differences in habitat between the two trophic groups can explain why in 2006 the contribution of "detritivores" to the Nile perch diet was lower than expected from their frequency in the environment.

The similarity in size and distribution of the resurgent "zooplanktivores" and "detritivores", seems to provide little reason for selective feeding on one of the two groups. Thus, the question of why the "detritivores", which were more numerous than zooplanktivores in the pre-Nile perch era, have not recovered as rapidly as the "zooplanktivores" has not been answered. Since selective predation is evidently not the cause, some other factors must be responsible for it but these have yet to be determined (See chapter 8).

ACKNOWLEDGEMENTS

This study was financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO; grant WB84-587), the Netherlands Organization for International Cooperation in Higher Education (NUFFIC) and the International Foundation for Sciences (IFS). Tanzania Fisheries Research Institute provided logistical support and research facilities. The administration of the Nyegezi freshwater Fisheries Training Institute is acknowledged for their cooperation. Special thanks to Dr. Martien van Oijen of the Naturalis, Leiden for receiving fish samples sent from Tanzania. We are also grateful to Prof. Brian Marshall for his comments on earlier drafts of this chapter. We wish to acknowledge all crew members of the small and larger trawlers (R.V. Lake Victoria Explorer and M.V. Mdiria) for their skilful fishing.

Chapter 8

Synthesis

Previous studies on the occurrence of haplochromines have mentioned the resurgence of haplochromines in various areas of Lake Victoria (CIFA 1990; Witte et al. 1995, 2000, 2007a,b; Seehausen et al. 1997b; Balirwa et al. 2003; Getabu et al. 2003). However, most of these studies were based on occasional samples (Witte et al. 1995, 2000) or short sampling periods only (Seehausen et al. 1997b), and catches at different stations were combined. Lack of sufficiently detailed sampling programs and inconsistency in sampling procedures were thought to be among factors which hamper discussion and conclusion about the status of resurgent species. This thesis contributes this important information and provides a detailed overview of the status of the haplochromine trophic groups and species in the northern part of the Mwanza Gulf of Lake Victoria. To understand the resurgence rate and differences in resurgence among the groups and species, I sampled *all sub-littoral stations* along the long-term HEST/TAFIRI research transect (Witte 1981) and treated them *separately*. Moreover, I sampled near the bottom and in the column, thus giving a more complete picture of the resurging species and their *distribution* patterns. This thesis goes further into investigating the possible causes for the differential recovery and reverse in abundance dominance between the “detritivorous” and “zooplanktivorous” groups.

Resurgence and distribution patterns of haplochromine cichlids in the Mwanza Gulf, Lake Victoria

The major goal of the study is to provide an insight into the inter-guild differences in the recovery of cichlid species which should allow for testing of four hypotheses that may explain the differential resurgence. In **chapter 2**, inter-guild differences in recovery of cichlids were assessed along the transect located in the northern part of the Mwanza Gulf sampled in two years; 2006 and 2008, a period after the ecological changes. The chapter further deals with the spatial distribution of haplochromine species and vertical migration of fish during day and night.

The chapter shows that in 2006 and 2008 the abundance of haplochromines had increased to the levels of the 1970s again. However, the number of species is lower than in the period of the 1970s, and the trophic composition has changed. Until 2006, “zooplanktivores” remained the dominant group. Their densities even surpassed those from the past. However, in 2008, a reverse in abundance of trophic groups was observed in which the “detritivores” dominated again, like in the 1970s. The study revealed a strong resurgence of the former “detritivorous”, “zooplanktivorous” and “oral mollusc shelling” species. Other trophic groups including phytoplanktivores, insectivores, piscivores, pharyngeal mollusc crushers, epiphytic algae grazers and paedophages, are currently rare along the transect. Trophic groups that used to be rare before the ecological changes (prawn eaters, scale scrapers and parasite feeders) have not (yet) recovered. **Chapter 2** suggests that the strong resurgence of haplochromines, as observed along the transect in the Mwanza Gulf, reflects a lake-wide phenomenon.

It was further shown that spatial distribution patterns have changed. Some species were recovered in habitats where they were formerly absent or less common. For instance, *Haplochromis pyrrhocephalus,* which was still common at the deeper stations, as it was in the past, additionally occupied shallower stations than in the past. This was also the case for *H. laparogramma*. Before the environmental changes, *Haplochromis tanaos* mainly occurred at the shallow (2-6 m) sandy stations (Witte et al. 1992b; van Oijen & Witte 1996). After the resurgence, however, the species became common at muddy stations of 6-10 m and was even caught at 13 m depth. The resurgent “detritivorous” species were abundant at all stations without showing a clear distribution pattern along the studied area. Before the ecological changes, most “oral mollusc shellers” were typical sand dwellers, but after the resurgence they were also common at mud-bottom stations, and at greater depths than in the past.

Chapter 2 showed that after the resurgence, the “detritivores”, which were strictly demersal in the past, joined the “zooplanktivores” in their nocturnal migration to the water surface. This observation could be related to changes in the feeding habits of the two groups (**Chapters 3** and **4**) as well as to adaptive responses to the changed environmental conditions.

During the past decades, the fish species diversity in Lake Victoria has declined dramatically due to human induced perturbations in the ecosystem. Since the ecosystem is still in a flux, with unpredictable changes to fish stocks and environmental conditions, the sustainability of the fish stocks in the lake has been questioned (Balirwa 2007). In recent years, some authors observed that many of the recovering haplochromine species show remarkable changes in ecological (van Oijen & Witte, 1996; Wanink & Witte 2000a; Katunzi et al. 2003; Kishe-Machumu et al. 2008 [Chapter 3]; Chapter 4) and morphological features (Chapman et al. 2008; Witte et al. 2008; van der Meer et al. 2012; van Rijssel & Witte 2012). These changes seem to be adaptive responses to the changed environment. However, the adaptive responses to human induced environmental stress seem to be restricted and species dependent (Witte et al. 2008). Measures to reduce environmental stress in Lake Victoria are an urgent issue to protect native fish species and the ecosystem at large.

Changes in the diet of the “detritivorous” and “zooplanktivorous” cichlids in Lake Victoria

According to the first hypothesis (see page 14) the shift in phytoplankton composition from a dominance of diatoms to a dominance of cyanobacteria, could have decreased the digestibility and nutrient quality of detritus. Consequently, this may have had an impact on the condition of “detritivorous” cichlids. To confirm this, the dietary differences between the “detritivorous” and “zooplanktivorous” cichlids were assessed. **Chapters 3** and **4** respectively evaluated the diets of resurgent “detritivorous” and “zooplanktivorous” haplochromine species, and compared these with those in the past using gut content analysis. In contrast to the expectations, both “detritivorous” and “zooplanktivorous” species shifted from diets dominated by detritus and zooplankton respectively, to diets dominated by the larger sized and tougher prey such as insects, shrimps, molluscs, midge larvae and small fish. In addition, in 2006 and 2008 the diet of the former “detritivores” was very similar to that of the “zooplanktivores”. Consequently, it is unlikely that the relatively slow recovery of the “detritivores” in the modern ecosystem was caused by a decrease in quality of their originally main food sources; detritus and phytoplankton, as was hypothesized. If the current resurgence rate of “detritivorous” and “zooplanktivorous” cichlids will continue, their greater interspecific diet overlap may lead to increased competition followed by another round of decline or feeding specializations.

Stable isotope evidence for the dietary shift and diet overlap amongst haplochromine cichlids

As it has been explained in **chapters 3** and **4**, recovering “detritivores” and “zooplanktivores” returned with a new diet, and with more overlap of food items among the two trophic groups and their respective species than in the past. However, these findings were based on gut content analysis which gives only the momentary types and amounts of prey taken. In **chapter 5,** long-term dietary patterns of fish species were assessed by analysing the stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes of preserved “detritivorous” and “zooplanktivorous” species collected in the old and those collected in the modern ecosystem. Phytoplanktivores from the old ecosystem were also included in the analysis. In this chapter, the effects of formalin/alcohol preservation on tissue $\delta^{13}C$ and $\delta^{15}N$ signatures were assessed.

Our findings indicated that formalin/alcohol preservation had little effect on $\delta^{13}C$ and $\delta^{15}N$ signatures, thus confirming the possibility of using the formalin/alcohol-preserved collections to characterize food-web structures of aquatic ecosystems. The chapter further revealed that “detritivorous”, phytoplanktivorous and “zooplanktivorous” species, which were collected from the old ecosystem, showed a strong distinction along the $\delta^{13}C$ axis. Almost all species differed from each other significantly. Similarly, the species were rather well separated along the $\delta^{15}N$ axis. Values of $\delta^{13}C$ for phytoplanktivorous *H. bwathondii,* were higher than those of “detritivorous” species. This supports the phytoplanktivorous habits of *H. bwathondii* in the past, which fed mainly on cyanophyta (*Microcystis* and *Anabaena*) and diatoms such as *Aulacoseira* and, occasionally, *Nitzschia*. France (1995) and Hecky & Hesselein (1995) suggested that larger phytoplankton, such as colonial or filamentous species — like the ones that contribute to diet of *H. bwathondii* — are subject to boundary layer effects. This might explain the higher ^{13}C values in the larger phytoplankton species as compared with the smaller species.

Values of $\delta^{13}C$ for "detritivores" extended over a broader range and were lower than those of "zooplanktivores". This could be explained by differences of plant materials at the base of the food chain consumed by the two groups, which passed up in the food chain (Campbell et al. 2003). Apparently, the plant material on which the former group feeds, comes from different plant material than that eaten by herbivorous zooplankton; the main prey item of "zooplanktivorous" haplochromines. Values of $\delta^{15}N$ for the "detritivore" *H. cinctus* and the phytoplanktivore *H. bwathondii* were lower than those for the zooplanktivores, which corresponds with their lower position in the food chain. The value of $\delta^{15}N$ for the "detritivore" *H. coprologus* fell in the range of that of the zooplanktivores, which might be due to the zooplanktivorous feeding behaviour of its juveniles.

In contrast, the clustering of the stable isotopes of the modern "detritivorous" and "zooplanktivorous" haplochromines showed less distinction between trophic groups and their constituent species than those of the old haplochromines. Both "detritivores" and "zooplanktivores" moved higher into the food chain. They also seem to have a greater overlap in diet in the modern system**,** thus rejecting the possibility that differences in diet can explain the differences in rate of resurgence. These results concur with the outcome of gut content analyses, which showed that both groups had switched from a more restricted diet in the old system to a diverse, but similar diet after their resurgence **(Chapters 3** and **4)**. Furthermore, this chapter shows how stable isotope techniques can be used to characterize the food-web changes at time scales of decades by using museum material. This study is among the first few that successfully apply stable isotope techniques on formalin/alcohol-preserved specimens.

The current diet of Nile perch, *Lates niloticus* (L.) following haplochromine resurgence

The second hypothesis postulates that "detritivorous" species could be more susceptible to Nile perch predation than "zooplanktivorous" species, because of a greater habitat overlap with Nile perch. “Zooplanktivorous” haplochromines lived partly pelagic (Goldschmidt et al. 1990), whereas “detritivorous” species were predominantly bottom dwellers (Goldschmidt et al. 1993). It is assumed that Nile perch preferably hunts near the bottom (Hamblyn 1966). Consequently this was assumed to lead to the slow recovery of the “detritivores”. During the period of the 1970s, when haplochromine cichlids were the dominant fish in the lake, they were the major prey of the Nile perch. In the 1980s, the density of haplochromines in the sub-littoral and offshore waters crashed. At this time, Nile perch switched to other food items including the shrimp *Caridina nilotica*, its own young ones and the cyprinid *Rastrineobola argentea* (dagaa). Thus, the second hypothesis only could be examined after assessing the post-cichlid resurgence diet of Nile perch, and prove that they feed on haplochromines again. In **chapter 6,** the diet of Nile perch was assessed to see whether the predator switched back to haplochromines as its main food source following the resurgence of the latter. It shows that in 2006 and 2008, haplochromines were again the major prey of Nile perch. The results further imply that the switch in frequency of occurrence from shrimps to fish in the diet occurs at a smaller Nile perch size for haplochromines than for other fish (i.e. juvenile Nile perch and dagaa). This suggests that haplochromines are the most preferable prey. If this is true, it could reduce the degree of cannibalism. Considerably, it could have a positive impact on Nile perch recruitment.

Can differential resurgence of haplochromine trophic groups be explained by selective Nile perch, *L. niloticus* predation?

The results of **chapter 6** allowed for testing the second hypothesis, which assumes that “detritivorous” species could be more susceptible to Nile perch predation than “zooplanktivorous” species, because of a greater habitat overlap with Nile perch, though it should be noted, that the difference in vertical distribution between the two trophic groups decreased after their resurgence (**Chapter 2**). Thus, in **chapter 7,** Nile perch predation on these two groups was assessed by comparing their ratios in the stomachs of Nile perch with those in the environment. In contrast to what was expected, “detritivores” were significantly less frequently occurring in Nile perch stomachs than in the environment. To assess if differences in body shape among the “detritivores” and “zooplanktivores” could make one of them more vulnerable to Nile perch predation than the other, the mouth gape of Nile perch was compared with the body depth of the two groups. As expected, the “detritivores” in the stomach of checked Nile perch had a larger body depth than the “zooplanktivores”. However, on the basis of their mouth gape, only the smallest piscivorous Nile perch (7-13 cm TL) would not be able to feed on the largest “detritivores”. Thus, mouth gape is no serious restriction to feed on “detritivores”. In addition, the study revealed that there was no differential predation effect by Nile perch based on the length of “detritivores” and “zooplanktivores”. Thus, this chapter concludes that there seems to be little evidence for selective predation by the Nile perch on ”detritivores”. Consequently, selective predation by Nile perch cannot explain the relatively slow resurgence of this trophic group.

Implications for future research and fisheries management

As mentioned in **chapter 1**, this thesis focuses mainly on the first two hypotheses. The following are recommendations for future studies on the other two hypotheses and for follow-up related studies.

The third hypothesis

It has been hypothesized that since “detritivores” were living closer to the bottom they might be more affected by heavy metals than “zooplanktivores”. Yediler & Jacobs (1995) and Vosylienà & Kazlauskienà (1999) stated that negative synergy between hypoxia and heavy metal contamination produces stronger contamination effects. In addition, through the dominant food pathway (Hall et al. 1997), heavy metals may have a stronger impact on “detritivores” than on “zooplanktivores”, as bioaccumulation into “zooplanktivores” is thought to be prevented by molting of zooplankton (A. Schäffer & H.T. Ratte unpublished data). This mechanism seemed to make sense because a distinct difference in diet between “zooplanktivores” and “detritivores” existed before the ecological changes. After the resurgence, this was not the case anymore. Both “zooplanktivores” and “detritivores” shifted their diet to prey such as insects, shrimps, molluscs, midge larvae, and small fish (**Chapters 3** and **4**).

It was found that in 2006/2008, “detritivores” at night migrated higher into the water column than in the past. In 2006 and 2008, the concentration of dissolved oxygen near the bottom at most sampling stations was low (< 3 mgl^{-1}), particularly during the rainy periods. The oxycline was situated higher in the water column (M.

A. Kishe-Machumu unpublished data) than during the late 1970s. The situation in the Mwanza Gulf for 1987-1988 (Wanink et al. 2001) did not differ much from that of 2006 and 2008.

Preliminary results from the study on heavy metals in haplochromines from the Mwanza Gulf show that metal concentrations in muscles were significantly higher in *H. pyrrhocephalus*, a “zooplanktivore” than in *H.* ‘paropius-like’, a “detritivore”. This is opposite to our expectation that “detritivores” would be relatively heavily contaminated, as they were more bound to the bottom layer than the “zooplanktivores”. However, the small sample size of fish analysed thus far, does not allow for sound conclusions. There is a need to work on more individuals representing both the abundant and the rare species within the two groups, including species that are true bottom dwellers. The results of these analyses should be correlated with hypoxia data. This may give an answer to the question if heavy metals have any impact on the slow recovery of “detritivorous” haplochromines in Lake Victoria.

The fourth hypothesis

The recovering “zooplanktivores” revealed morphological adaptations to the new environmental conditions. These include changes in body shape that facilitate a faster escape to predators, adaptations in the feeding apparatus to larger and tougher prey, an increase in gill area to cope with deteriorated oxygen conditions, and adaptations in the retina to improve light sensitivity in murky environments (Chapman et al. 2008; Witte et al. 2008; van der Meer et al. 2012; van Rijssel & Witte 2012). In the present study, only one morphological aspect was investigated, viz. the relative intestine length of “zooplanktivores” and “detritivores”. In the latter group, the relative length of the intestine decreased significantly, which seemed to be a response to the more carnivorous diet. Other morphological features of the "detritivores", such as mentioned above for the “zooplanktivores”, have still to be investigated. A detailed morphological study is of great importance. The study is currently performed in a separate PhD project (titled: *Contemporary morphological changes in Lake Victoria cichlids*) funded by the Netherlands Organization for scientific Research (NWO). Some of the fish that were collected under the present study are used in that project. If there are more morphological constraints in “detritivores” than in “zooplanktivores”, the potentials to adapt to the new environmental conditions could be smaller in “detritivores” than in “zooplanktivores”, and this might explain their slower recovery.

Other related studies

As was shown in this thesis, some of the haplochromine species that currently occur in Lake Victoria are hard to identify. At the same time, little effort is made to train taxonomists in the region. Yet, a thorough study is needed, as some of these species seem to include a range of intermediate forms that could well represent hybrids.

Currently, the largest taxonomic collections of Lake Victoria haplochromines from before the environmental changes are stored at the British Museum of Natural History in London and at the Netherlands Centre for Biodiversity in Leiden. Identification of resurging haplochromines will be hard without comparing them with the preserved specimens in these collections. Since Lake Victoria is still an unstable ecosystem, it is strongly recommended to establish an institutional or national museum for fish and other aquatic animals for future scientific research.

While the findings presented in this thesis can be used as baseline data for management of the lake and for evolutionary studies, trophic and species composition of the recovering haplochromine species should be monitored regularly in the future. The differential resurgence that was found for haplochromine communities, trophic groups and species, indicates that it is not always recommended to consider the haplochromine cichlids as a homogeneous unit. Systematic studies of haplochromine cichlids are crucial for the management of both the biodiversity and the fish production, as well as for fisheries management of Lake Victoria at large.

The findings of the present study reflect a proper picture of the Mwanza Gulf. However, future research should also include other areas of the lake, encompassing much deeper areas, as well as the satellite lakes. A clear knowledge of the composition and ecology of the recovering species of haplochromines in different areas of the lake and existing haplochromine population in the satellite lakes is crucial for managing Lake Victoria.

Fisheries management

Lake Victoria's target commercial fish species, including Nile perch, Nile tilapia and *R. argentea,* receive the vast attention of the fisheries management. Very little attention is focused on issues and strategies for management of many other fishes which are of less commercial importance, including the haplochromines. Management strategies should be directed to all fish species as they are critical to the structuring of aquatic biotic communities and are associated with trophic interactions and food webs. Therefore, I recommend strongly that all plans for conservation and management strategies for fisheries should incorporate haplochromine populations as a component to be protected and to maintain the aquatic ecosystem integrity in the lake. It has been postulated that sustainability in the Nile perch fishery could be maintained by ensuring an abundance of haplochromines, the preferred prey of Nile perch (Balirwa et al. 2003; Kishe-Machumu et al. 2012 [**Chapter 6**]). Resurgence of haplochromine cichlids in the lake could boost the Nile perch production rates (Kishe-Machumu et al. 2012 [**Chapter 6]**). Hence, management strategies should therefore include conservation plans. Setting up reserve areas and prohibition of further habitat degradation in such reserves may provide refugia for haplochromine species. Satellite lakes harbour more than 20 haplochromine species (Mwanja et al. 2001; Katunzi & Kishe 2004; Mbabazi et al. 2004; Katunzi et al. 2010). Such reserves and satellite lakes could function as sources of haplochromine seeds for the main lake.

Conclusions

The present study does not give a positive answer for the cause of the difference in rate of resurgence among "detritivores" and "zooplanktivores". Some of the possibilities have been tested and it appeared that it is not likely that they played an important role. Nevertheless, the study has given evidence for a strong resurgence of some haplochromine species in the Mwanza Gulf that seems to be a lake-wide phenomenon. Moreover, it gives hope that more species might recover as they adapt to the new environmental conditions.

References

REFERENCES

Acere TO (1988) Recent trends in the fisheries of Lake Victoria (Uganda, northern part). In: *FAO Fish. Rep.* 338: 72-85.

Albright TP, Moorhouse TG & McNabb J (2004) The rise and fall of water hyacinth in Lake Victoria and the Kagera River Basin, 1989-2001. *Journal of Aquatic Plant Management* 42: 73-84.

Arrington DA & Winemiller KO (2002) Preservation effects on stable isotope analysis of fish muscle. *Transactions of the American Fisheries Society* 131: 337-342.

Balirwa JS (1998) Lake Victoria wetlands and the ecology of the Nile tilapia, *Oreochromis niloticus* Linné. PhD Thesis, Wageningen: Wageningen University.

Balirwa JS, Chapman CA, Chapman LJ, Cowx IG, Geheb K, Kaufman L, Lowe-McConnell RH, Seehausen O, Wanink JH, Welcomme RL & Witte F (2003) Biodiversity and fishery sustainability in the Lake Victoria Basin: An unexpected marriage? *Bioscience* 53: 703-715.

Balirwa JS (2007) Ecological, environmental and socioeconomic aspects of the Lake Victoria's introduced Nile perch fishery in relation to the native fisheries and the species culture potential: lessons to learn. *African Journal of Ecology* 45: 120-129.

Barel CDN, van Oijen MJP, Witte F & Wittemaas ELM (1977) Introduction to taxonomy and morphology of haplochromine cichlidae from Lake Victoria - Manual to Greenwoods revision papers. *Netherlands Journal of Zoology* 27: 333-389.

Barel CDN (1983) Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Netherlands Journal of Zoology* 33: 357-424.

Barel CDN, Dorit R, Greenwood PH, Fryer G, Hughes N, Jackson PBN, Kawanabe H, Lowemcconnell RH, Nagoshi M, Ribbink AJ, Trewavas E, Witte F & Yamaoka K (1985) Destruction of Fisheries in Africas Lakes. *Nature* 315: 19-20.

Barel CDN, Ligtvoet W, Goldschmidt T, Witte F & Goudswaard PC (1991) The haplochromine cichlids in Lake Victoria: an assessment of biological and fisheries interests. In: MHA Keenleyside (ed), *Cichlid fishes. Behaviour, ecology and evolution*. Chapman & Hall, London, pp. 258-279.

Bootsma HA & Hecky RE (1993) Conservation of the African Great Lakes - a limnological perspective. *Conservation Biology* 7: 644-656.

Bowen SH (1988) Detritivory and Herbivory. In: C Lévêque, MN Bruton & GW Ssentongo (ed), *Biologie et Écologie des Poissons d'Eau douce Africains*. ORSTOM, Paris, pp. 243-247.

Bruton MN (1990) The conservation of the fishes of Lake Victoria, Africa - an ecological perspective. *Environmental Biology of Fishes* 27: 161-175.

Budeba YL & Cowx IG (2007) The role of the freshwater shrimp *Caridina nilotica* (Roux) in the diet of the major commercial fish species in Lake Victoria, Tanzania. *Aquatic Ecosystem Health & Management* 10: 368-380.

Bwanika GN, Chapman LJ, Kizito Y & Balirwa J (2006) Cascading effects of introduced Nile perch (*Lates niloticus*) on the foraging ecology of Nile tilapia (*Oreochromis niloticus*). *Ecology of Freshwater Fish* 15: 470-481.

Campbell LM, Hecky RE & Wandera SB (2003) Stable isotope analyses of food web structure and fish diet in Napoleon and Winam Gulfs, Lake Victoria, east Africa. *Journal of Great Lakes Research* 29: 243-257.

Chapman LJ, Chapman CA, OgutuOhwayo R, Chandler M, Kaufman L & Keiter AE (1996) Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conservation Biology* 10: 554-561.

Chapman LJ, Chapman CA, Schofield PJ, Olowo JP, Kaufman L, Seehausen O & Ogutu-Ohwayo R (2003) Fish Faunal Resurgence in Lake Nabugabo, East Africa. *Conservation Biology* 17: 500-511.

Chapman LJ, Chapman CA, Kaufman LS, Witte F & Balirwa J (2008) Biodiversity conservation in African inland waters: Lessons of the Lake Victoria region. *Verhandlungen der Internationalen Verein Limnologie* 30: 16-34.

CIFA (1990) Report of the 5th session of the sub-committee for the development and management of the fisheries in Lake Victoria. In: *FAO Fish. Rep.* vol. 430 Mwanza, Tanzania, 12-14 September 1989, pp. 1-97.

Cohen AS, Bills R, Cocquyt CZ & Caljon AG (1993) The Impact of Sediment Pollution on Biodiversity in Lake Tanganyika. *Conservation Biology* 7: 667-677.

de Zeeuw MP, Mietes M, Niemantsverdriet P, ter Huurne S & Witte F (2010) Seven new species of detritivorous and phytoplanktivorous haplochromines from Lake Victoria. *Zoologische Mededelingen (Leiden)* 84: 201-250.

France RL (1995) C-13 Enrichment in Benthic Compared to Planktonic Algae - Foodweb Implications. *Marine Ecology-Progress Series* 124: 307-312.

Francey RJ, Allison CE, Etheridge DM, Trudinger CM, Enting IG, Leuenberger M, Langenfelds RL, Michel E & Steele LP (1999) A 1000-year high precision record of delta(13)C in atmospheric CO(2). *Tellus Series B-Chemical and Physical Meteorology* 51: 170-193.

Fryer G & Iles TD (1972) The cichlid fishes of the great lakes of Africa: their biology and evolution. Oliver and Boyd, Edinburgh, pp. 641.

Fryer G (2001) On the age and origin of the species flock of haplochromine cichlid fishes of Lake Victoria. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 1147-1152.

Fryer G (2004) Speciation rates in lakes and the enigma of Lake Victoria. *Hydrobiologia* 519: 167-183.

Garrod DJ (1960) The fisheries of Lake Victoria, 1954-1959. *East African agricultural and forestry journal* 26: 42-48.

Gearing JN (1991) The study of diet and trophic relationships through natural abundance ^{13}C. In: DC Coleman & B Fry (ed), *Carbon isotope techniques*. Academic Press, San Diego, pp. 201-218.

Gee JM (1969) A comparison of certain aspects of the biology of *Lates niloticus* (Linneaus) in some East African lakes. *Revue de Zoologie et Botanique Africaines* 80: 244-262.

Getabu A, Tumwebaze R & MacLennan DN (2003) Spatial distribution and temporal changes in the fish populations of Lake Victoria. *Aquatic Living Resources* 16: 159-165.

Goldschmidt T (1989) Reproductive strategies, subtrophic niche differentiation and the role of competition for food in haplochromine cichlids (Pisces) from Lake Victoria, Tanzania. *Annales du Museé Royal de l'Afrique Centrale, Sciences Zoologiques* 257: 199-132.

Goldschmidt T, Witte F & De Visser J (1990) Ecological segregation in zooplanktivorous haplochromine species (Pisces, Cichlidae) from Lake Victoria. *Oikos* 58: 343-355.

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

Gophen M, Ochumba PBO & Kaufman LS (1995) Some aspects of perturbation in the structure and biodiversity of the ecosystem of Lake Victoria (East-Africa). *Aquatic Living Resources* 8: 27-41.

Goudswaard KPC, Wanink JH, Witte F, Katunzi EFB, Berger MR & Postma DJ (2004) Diel vertical migration of major fish-species in Lake Victoria, East Africa. *Hydrobiologia* 513: 141-152.

Goudswaard KPC, Witte F & Wanink JH (2006) The shrimp *Caridina nilotica* in Lake Victoria (East africa), before and after the Nile perch increase. *Hydrobiologia* 563: 31-44.

Goudswaard KPC, Witte F & Katunzi EFB (2008) The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. *Environmental Biology of Fishes* 81: 127-139.

Goudswaard PC, Mous PJ, Ligtvoet W & van Densen WLT (1995) Gears and boats. In: F Witte & WLT van Densen (ed), *Fish stocks and fisheries of Lake Victoria. A handbook for field observations*. Samara Publishing, Cardigan, Dyfed, U.K, pp. 83-117.

Goudswaard PC, Witte F & Katunzi EFB (2002) The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. *Journal of Fish Biology* 60: 838-856.

Graham M (1929) The Victoria Nyanza and its fisheries. In: *A report on the fishing survey of Lake Victoria 1927-1928*. Crown Agents, London, pp. 255.

GraphPad InStat (2003) GraphPad InStat software Inc. 3.06.

Greenwood PH & Gee JM (1969) A revision of the Lake Victoria Haplochromis species (Pisces: Cichlidae) Part 7. *Bulletin of the British Museum (Natural History) Zoology* 18: 1-65.

Greenwood PH (1974) The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bulletin of the British Museum (Natural History) Zoology, Supplement* 6: 1-134.

Greenwood PH (1981) The haplochromine fishes of the East African lakes: collected papers on their taxonomy, biology and evolution. Kraus International Publications, Munich.

Hall BD, Bodaly RA, Fudge RJP, Rudd JWM & Rosenberg DM (1997) Food as the dominant pathway of methylmercury uptake by fish. *Water Air and Soil Pollution* 100: 13-24.

Hamblyn EL (1966) The food and feeding habits of Nile perch: *Lates niloticus* (Linné) (Pisces: Centropomidae). *Revue de Zoologie et Botanique Africaines* 74: 1-28.

Hecky RE & Bugenyi FWB (1992) Hydrology and chemistry of the African Great Lakes and water quality issues: problems and solutions. *Mitteilung Internationale Vereinigung fuer Theoretische und Amgewandte Limnologie* 23: 45-54.

Hecky RE (1993) The eutrophication of Lake Victoria. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 25: 39-48.

Hecky RE, Bugenyi FWB, Ochumba P, Talling JF, Mugidde R, Gophen M & Kaufman L (1994) Deoxygenation of the Deep-Water of Lake Victoria, East-Africa. *Limnology and Oceanography* 39: 1476-1481.

Hecky RE & Hesslein RH (1995) Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* 14: 631-653.

Hecky RE, Mugidde R, Ramlal PS, Talbot MR & Kling GW (2010) Multiple stressors cause rapid ecosystem change in Lake Victoria. *Freshwater Biology* 55: 19-42.

Hoogerhoud RJC, Witte F & Barel CDN (1983) The ecological differentiation of 2 closely resembling haplochromis species from Lake Victoria (*Haplochromis iris* and *Haplochromis hiatus* Pisces, Cichlidae). *Netherlands Journal of Zoology* 33: 283-305.

Hoogerhoud RJC (1987) The adverse-effects of shell ingestion for molluscivorous cichlids, a constructional morphological approach. *Netherlands Journal of Zoology* 37: 277-300.

Hopson AJ (1972) A study of Nile perch (*Lates niloticus* L., Pisces: Centropomidae) in Lake Chad. Overseas Research Publications, London.

Hughes NF (1983) A study of the Nile perch, an introduced predator in the Kavirondo Gulf, Lake Victoria. Oxford University, Oxford, pp. 75.

Hughes NF (1986) Changes in the feeding biology of the Nile perch, *Lates niloticus* (L) (Pisces, Centropomidae), in Lake-Victoria, East-Africa since its introduction in 1960, and its impact on the native fish community of the Nyanza-Gulf. *Journal of Fish Biology* 29: 541-548.

Hughes NF (1992) Nile Perch, *Lates niloticus*, predation on the fresh-water prawn, *Caridina nilotica*, in the Nyanza Gulf, Lake Victoria, East-Africa. *Environmental Biology of Fishes* 33: 307-309.

Johnson TC, Scholz CA, Talbot MR, Kelts K, Ricketts RD, Ngobi G, Beuning K, Ssemmanda I & McGill JW (1996) Late pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273: 1091-1093.

Johnson TC, Kelts K & Odada E (2000) The holocene history of Lake Victoria. *Ambio* 29: 2-11.

Katunzi EFB (1980) Food preferences of four haplochromine cichlids from Mwanza Gulf in Lake Victoria, MSc Thesis. Dar Es Salaam, Tanzania: University of Dar Es Salaam.

Katunzi EFB, Zoutendijk J, Goldschmidt T, Wanink JH & Witte F (2003) Lost zooplanktivorous cichlid from Lake Victoria reappears with a new trade. *Ecology of Freshwater Fish* 12: 237-240.

Katunzi EFB & Kishe MA (2004) Changes in population structures of the major fish species in selected satellite lakes around Lake Victoria following changes in fishing effort. *Tanzania Journal of Science* 30: 53-64.

Katunzi EFB, van Densen WLT, Wanink JH & Witte F (2006) Spatial and seasonal patterns in the feeding habits of juvenile *Lates niloticus* (L.), in the Mwanza Gulf of Lake Victoria. *Hydrobiologia* 568: 121-133.

Katunzi EFB, Mbonde A, Waya R & Mrosso HDJ (2010) Minor water bodies around southern Lake Victoria-a replica of lost biodiversity. *Aquatic Ecosystem Health & Management* 13: 277-283.

Kaufman L (1992) Catastrophic change in species rich freshwater ecosystems. *Bioscience* 42: 846-858.

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

Kaufman L & Schwarz J (2002) Nile perch population dynamics in Lake Victoria: implications for management and conservation. In: M Ruth & J Lindholm (ed), *Dynamic modelling for marine conservation*. Springer, New York, pp. 257-313.

Kaufman LS, Chapman LJ & Chapman CA (1997) Evolution in fast forward: Haplochromine fishes of the Lake Victoria region. *Endeavour* 21: 23-30.

Kayanda R, Taabu MA, Tumwebaze R, Muhoozi L, Jembe T, Mlaponi E & Nzungi P (2009) Status of the major commercial fish stocks and proposed species-specific management plans for Lake Victoria. *African Journal of Tropical Hydrobiology and Fisheries* 12: 15-21.

Keeling CD (1979) The Suess Effect: ^{13}Carbon-^{14}Carbon Interrelations. *Environment International* 2: 229-300.

Kishe-Machumu M, Witte F & Wanink JH (2008) Dietary shift in benthivorous cichlids after the ecological changes in Lake Victoria. *Animal Biology* 58: 401-417.

Kishe-Machumu MA, Witte F, Wanink JH & Katunzi EFB (2012) The diet of Nile perch, *Lates niloticus* (L.) after resurgence of haplochromine cichlids in the Mwanza Gulf of Lake Victoria. *Hydrobiologia* 682: 111-119.

Kishe MA & Machiwa JF (2003) Distribution of heavy metals in sediments of Mwanza Gulf of Lake Victoria, Tanzania. *Environment International* 28: 619-625.

Kling HJ, Mugidde R & Hecky RE (2001) Recent changes in the phytoplankton community of Lake Victoria in response to eutrophication. In: M Munawar & RE Hecky (ed), *The great lakes of the world (GLOW) - Food-web, fealth and integrity*. Backhuys Publishers, Leiden, pp. 47-65.

Kolding JP, van Zwieten P, Mkumbo OC, Silsbe G & Hecky RE (2008) Are the Lake Victoria fisheries threatened by exploitation or eutrophication? Towards an ecosystem based approach to management. In: G Bianchi & HR Skjodal (ed), *The ecosystem approach to fisheries*. Cab International, 309-354.

Krebs JR & Davies NB (1978) Behavioural Ecology, an Evolutionary Approach. Blackwell Scientific Publications,Oxford.

Kudhongania AW & Cordone AJ (1974) Batho-spatial distribution patterns and biomass estimates of the major demersal fishes in Lake Victoria. *The African Journal of Tropical Hydrobiology and Fisheries* 3: 15-31.

Langerhans RB, Layman CA, Shokrollahi AM & DeWitt TJ (2004) Predator-driven phenotypic diversification in Gambusia affinis. *Evolution* 58: 2305-2318.

Liem KF (1980) Adaptive significance of intraspecific and interspecific differences in the feeding repertoires of cichlid fishes. *American Zoologist* 20: 295-314.

Ligtvoet W & Mkumbo OC (1990) Synopsis of ecological and fishery research on Nile perch (*Lates Niloticus*) in Lake Victoria, conducted by HEST/TAFIRI. In: *CIFA, Report of the fifth session of the sub-committee for the development and management of Lake Victoria, 12-14 September 1989* vol. 430. FAO Fisheries Report Mwanza, pp. 35-74.

Matsuishi T, Muhoozi L, Mkumbo O, Budeba Y, Njiru M, Asila A, Othina A & Cowx IG (2006) Are the exploitation pressures on the Nile perch fisheries resources of Lake Victoria a cause for concern? *Fisheries Management and Ecology* 13: 53-71.

Mbabazi D (2004) Trophic characterisation of the dominant fishes in the Victoria and Kyoga Lake basins, PhD-Thesis. Kampala, Uganda: Makerere University.

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

Mckaye KR & Marsh A (1983) Food switching by 2 specialized algae-scraping cichlid fishes in Lake Malawi, Africa. *Oecologia* 56: 245-248.

Meyer A, Kocher TD, Basasibwaki P & Wilson AC (1990) Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial-DNA sequences. *Nature* 347: 550-553.

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

Moriarty DJ, Darlingt.Jp, Dunn IG, Moriarty CM & Tevlin MP (1973) Feeding and grazing in Lake-George, Uganda. *Proceedings of the Royal Society of London Series B-Biological Sciences* 184: 299-319.

Mugidde R (1992) Changes in phytoplankton productivity and biomass in Lake Victoria (Uganda), MSc-Thesis. Waterloo: University of Waterloo.

Mugidde R (1993) The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 25: 4.

Mwanja WW, Armoudlian AS, Wandera SB, Kaufman L, Wu LZ, Booton GC & Fuerst PA (2001) The bounty of minor lakes: the role of small satellite water bodies in evolution and conservation of fishes in the Lake Victoria Region, East Africa. *Hydrobiologia* 458: 55-62.

Mwebaza-Ndawula L (1994) Changes in relative abundance of zooplankton in northern Lake Victoria, East Africa. *Hydrobiologia* 272: 259-264.

NaFFIRRI (2007) Implementation of a Fisheries Management Plan (IFMP) for Lake Victoria. In: *A report of the bottom trawls monitoring survey of Lake Victoria, Uganda* Uganda, pp. 72.

Ngupula GW & Mlaponi E (2010) Changes in abundance of Nile shrimp, *Caridina nilotica* (Roux) following the decline of Nile perch and recovery of native haplochromine fishes, Lake Victoria, Tanzanian waters. *Aquatic Ecosystem Health & Management* 13: 196-202.

Njiru M (2003) Population characteristics and feeding ecology of Nile tilapia, *Oreochromis niloticus* (L.) in Lake Victoria, Kenya, PhD-Thesis. Kenya: University of Moi.

Njiru M, Okeyo-Owuor JB, Muchiri M & Cowx IG (2004) Shifts in the food of Nile tilapia, *Oreochromis niloticus* (L.) in Lake Victoria, Kenya. *African Journal of Ecology* 42: 163-170.

Ntiba MJ, Kudoja WM & Mukasa CT (2001) Management issues in the Lake Victoria watershed. *Lakes & Reservoirs: Research & Management* 6: 211-216.

Ochumba PBO & Kibaara DI (1989) Observations on blue-green-algal blooms in the open waters of Lake Victoria, Kenya. *African Journal of Ecology* 27: 23-34.

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

Oguto-Ohwayo R (1985) The effects of predation by Nile perch introduced in Lake Kyoga in relation to the fisheries of Lake Kyoga and Victoria. In: Series, *CIFA, Report of the third session of the sub-committee for the development* *and management of Lake Victoria, 4-5 October 1984* vol. 335. FAO Fisheries Report Jinja, pp. 18-41.

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

Ogutu-Ohwayo R (1990b) Changes in the prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). *Journal of Fish Biology* 37: 55-63.

Ogutu-Ohwayo R (1993) The effects of predation by Nile perch, *Lates niloticus* L, on the fish of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. *Conservation Biology* 7: 701-711.

Ogutu-Ohwayo R (2004) Management of the Nile perch, *Lates niloticus* fishery in Lake Victoria in light of the changes in its life history characteristics. *African Journal of Ecology* 42: 306-314.

Ogutu-Ohwayo R & Balirwa JS (2006) Management challenges of freshwater fisheries in Africa. *Lakes & Reservoirs: Research & Management* 11: 215-226.

Ojwang WO, Kaufman L, Asila AA, Agembe S & Michener B (2004) Isotopic evidence of functional overlap amongst the resilient pelagic fishes of Lake Victoria, Kenya. *Hydrobiologia* 529: 27-35.

Ojwang WO, Kaufman L, Soule E & Asila AA (2007) Evidence of stenotopy and anthropogenic influence on carbon source for two major riverine fishes of the Lake Victoria watershed. *Journal of Fish Biology* 70: 1430-1446.

Ojwang WO, Ojuok JE, Mbabazi D & Kaufman L (2010) Ubiquitous omnivory, functional redundancy and the resiliency of Lake Victoria fish community. *Aquatic Ecosystem Health & Management* 13: 269-276.

Okaranon JO (1994) Current composition, distribution and relative abundance of the fish stocks of Lake Victoria, Uganda. *African Journal of Tropical Hydrobiology Fisheries* 5: 89-100.

Okedi J (1971) Further observations on the ecology of the Nile perch (*Lates niloticus* Linneaus) in Lake Victoria and Lake Kyoga. In: *EAFFRO Annual Report (1970)* pp 42-55.

Okemwa EN (1981) Changes in the fish species composition of Nyanza Gulf of Lake Victoria. In: *Proceedings of the workshop of the Kenya Marine and Fisheries Research Institution on Aquatic Resources of Kenya, Mombasa, 13-19 July 1981, pp. 138-156*. Kenya Marine and Fisheries Research Institute and Kenya National Academy for the Advancement of Arts and Sciences, Nairobi.

Olowo JP & Chapman LJ (1999) Trophic shifts in predatory catfishes following the introduction of Nile perch into Lake Victoria. *African Journal of Ecology* 37: 457-470.

Paterson JA & Chapman LJ (2009) Fishing down and fishing hard: ecological change in the Nile perch of Lake Nabugabo, Uganda. *Ecology of Freshwater Fish* 18: 380-394.

Pitcher TJ & Bundy A (1995) Assessment of the Nile perch fishery in Lake Victoria. In: TJ Pitcher & PJB Hart (ed), *The impact of species changes in African Lakes*. Chapman & Hall, London, pp. 163-180.

Pringle RM (2005) The origins of the Nile perch in Lake Victoria. *Bioscience* 55: 780-787.

Reynolds E & Greboval DF (1988) Socio-economic effects of the evolution of Nile perch fisheries in Lake Victoria: A review. In: *Food and Agricultural Organization of the United Nations*Rome, Italy.

Ribbink AJ (1987) African lakes and their fishes - conservation scenarios and suggestions. *Environmental Biology of Fishes* 19: 3-26.

Ribbink AJ (1990) Alternative life-history styles of some African cichlid fishes. *Environmental Biology of Fishes* 28: 87-100.

Sarakinos HC, Johnson ML & van der Zanden MJ (2002) A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80: 381-387.

Schofield PJ & Chapman LJ (1999) Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. *Environmental Biology of Fishes* 55: 343-358.

Scholz CA, Rosendahl BR, Versfelt JW & Rach N (1990) Results of high-resolution echo-sounding of Lake Victoria. *Journal of African Earth Sciences* 11: 25-32.

Schwartz JDM, Pallin MJ, Michener RH, Mbabazi D & Kaufman L (2006) Effects of Nile perch, *Lates niloticus*, on functional and specific fish diversity in Uganda's Lake Kyoga system. *African Journal of Ecology* 44: 145-156.

Seehausen O & Witte F (1995) Extinction of many and survival of some: the current situation of the endemic cichlids in southern Lake Victoria. *Tropical Fish Hobbyist* 43: 96-105.

Seehausen O (1996) Lake Victoria rock cichlids: taxonomy, ecology, and distribution. Verduyn cichlids. Zevenhuizen, The Netherlands.

Seehausen O, van Alphen JJM & Witte F (1997a) Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808-1811.

Seehausen O, Witte F, Katunzi EF, Smits J & Bouton N (1997b) Patterns of the remnant cichlid fauna in southern Lake Victoria. *Conservation Biology* 11: 890-904.

Seehausen O & van Alphen JJM (1998) The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (Haplochromis nyererei complex). *Behavioral Ecology and Sociobiology* 42: 1-8.

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

Seehausen O (2002) Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14 600 year history for its cichlid species flock. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 491-497.

Seehausen O, van Alphen JJM & Witte F (2003) Implications of eutrophication for fish vision, behavioral ecology and species coexistence. In: TL Crisman, LJ Chapman, CA Chapman & LS Kaufman (ed), *Conservation, Ecology, and Management of African Freshwaters*. University Press of Florida, Florida, pp. 268-287.

Seehausen O, Terai Y, Magalhaes IS, Carleton KL, Mrosso HDJ, Miyagi R, van der Sluijs I, Schneider MV, Maan ME, Tachida H, Imai H & Okada N (2008) Speciation through sensory drive in cichlid fish. *Nature* 455: 620-626.

Slootweg R, Malek EA & Mccullough FS (1994) The biological control of snail intermediate hosts of schistosomiasis by fish. *Reviews in Fish Biology and Fisheries* 4: 67-90.

Snoeks J (2000) How well known is the ichthyodiversity of the large East African lakes? *Advances in Ecological Research* 31: 17-38.

Stager JC & Johnson TC (2008) The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. *Hydrobiologia* 596: 5-16.

Tumwebaze R, Cowx I, Ridgway S, Getabu A & MacLennan DN (2007) Spatial and temporal changes in the distribution of *Rastrineobola argentea* in Lake Victoria. *Aquatic Ecosystem Health & Management* 10: 398-406.

van Densen WLT & Witte F (1995) Introduction. In: F Witte & WLT van Densen (ed), *Fish stocks and fisheries of Lake Victoria. A handbook for field observations*. Samara Publishing, Cardigan, Dyfed, U.K., pp. 1-10.

van der Meer HJ (1993) Light-induced modulation of retinal development in the cichlid fish *Haplochromis sauvagei* (Pfeffer, 1896). *Zoological Journal of the Linnean Society* 108: 271-285.

van der Meer HJ, Anker GC & Barel CDN (1995) Ecomorphology of retinal structures in zooplanktivorous haplochromine cichlids (Pisces) from Lake-Victoria. *Environmental Biology of Fishes* 44: 115-132.

van der Meer HJ, van Rijssel JC, De Wagenaar LC & Witte F (2012) Photopic adaptations to a changing environment in two Lake Victoria cichlids. *Biological Journal of the Linnean Society* 106: 328-341.

van Oijen MJP (1982) Ecological differentiation among the piscivorous haplochromine cichlids of Lake Victoria (East-Africa). *Netherlands Journal of Zoology* 32: 336-363.

van Oijen MJP & Witte F (1996) Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria. *Zool. Verh. Leiden* 302: 1-56.

van Rijssel JC & Witte F (2012) Adaptive responses in resurgent Lake Victoria cichlids over the past 30 years. *Evolutionary Ecology* DOI:10.1007/s10682-012-9596-9.

Verburg P (2007) The need to correct for the Suess effect in the application of delta C-13 in sediment of autotrophic Lake Tanganyika, as a productivity proxy in the Anthropocene. *Journal of Paleolimnology* 37: 591-602.

Verheyen E, Salzburger W, Snoeks J & Meyer A (2003) Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* 300: 325-329.

Verschuren D, Johnson TC, Kling HJ, Edgington DN, Leavitt PR, Brown ET, Talbot MR & Hecky RE (2002) History and timing of human impact on Lake Victoria, East Africa. *Proceedings of the Royal Society Biological Sciences Series B* 269: 289-294.

Vosylienà MZ & Kazlauskienà N (1999) Alterations in fish health state parameters after exposure to different stressors. *Acta Zoologica Lituanica, Hydrobiologia* 9: 83-94.

Wanink JH (1991) Survival in a perturbed environment: the effects of Nile perch introduction on the zooplanktivorous fish community of Lake Victoria. In: O Ravera (ed), *Terrestrial and Aquatic Ecosystems: Perturbation and Recovery*. Ellis Horwood Ltd, Chichester, UK, pp. 269-275.

Wanink JH (1998) The pelagic cyprinid *Rastrineobola argentea* as a crucial link in the disrupted ecosystem of Lake Victoria. In: *Dwarfs and Giants-African Adventures,* PhD-Thesis. Leiden University, Leiden.

Wanink JH (1999) Prospects for the fishery on the small pelagic Rastrineobola argentea in Lake Victoria. *Hydrobiologia* 407: 183-189.

Wanink JH, Goudswaard PC & Berger MR (1999) *Rastrineobola argentea,* a Major Resource in the Ecosystem of Lake Victoria. In: WLT van Densen & MJ Morris (ed), *Fish and Fisheries of Lakes and Reservoirs in Southern Asia and Africa*. Westbury Publishing, Otley, UK, pp. 295-309.

Wanink JH & Witte F (2000a) The use of perturbation as a natural experiment: Effects of predator introduction on the community structure of zooplanktivorous fish in Lake Victoria. *Advances in Ecological Research* 31: 553-570.

Wanink JH & Witte F (2000b) Rapid morphological changes following niche shift in the zooplanktivorous cyprinid Rastrineobola argentea from Lake Victoria. *Netherlands Journal of Zoology* 50: 365-372.

Wanink JH, Kashindye JJ, Goudswaard PCK & Witte F (2001) Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*? *Freshwater Biology* 46: 75-85.

Wanink JH, Katunzi EFB, Goudswaard KPC, Witte F & van Densen WLT (2002) The shift to smaller zooplankton in Lake Victoria cannot be attributed to the 'sardine' *Rastrineobola argentea* (Cyprinidae). *Aquatic Living Resources* 15: 37-43.

Wanink JH & Joordens JCA (2007) Dietary shifts in *Brycinus sadleri* (Pisces : Characidae) from southern Lake Victoria. *Aquatic Ecosystem Health & Management* 10: 392-397.

Welcomme RL (1967) Observations on the biology of the introduced species of *Tilapia* in Lake Victoria. *Revue de Zoologie et Botanique Africaines* 76: 249-279.

Welcomme RL (1988) International introduction of inland aquatic species. In: *FAO Fish. Techn. Pap.* 294: 1-318.

Williams AE, Duthie HC & Hecky RE (2005) Water hyacinth in Lake Victoria: Why did it vanish so quickly and will it return? *Aquatic Botany* 81: 300-314.

Williams AE, Hecky RE & Duthie HC (2007) Water hyacinth decline across Lake Victoria - Was it caused by climatic perturbation or biological control? A reply. *Aquatic Botany* 87: 94-96.

Witte F (1981) Initial results of the ecological survey of the haplochromine cichlid fishes from the Mwanza Gulf of Lake Victoria (Tanzania) - breeding patterns, trophic and species distribution - with recommendations for commercial trawl-fishery. *Netherlands Journal of Zoology* 31: 175-202.

Witte F & Goudswaard PC (1985) Aspects of the haplochromine fishery in southern Lake Victoria. In: *FAO Fishery Report* 335: 81-88.

Witte F & Witte-Maas ELM (1987) Implications for taxonomy and functional morphology of intraspecific variation in haplochromine cichlids of Lake Victoria. In: *From form to fishery*, PhD-Thesis. Leiden: Leiden University.

Witte F & van Oijen MJP (1990) Taxonomy, ecology and fishery of haplochromine trophic groups. *Zoologische Verhandelingen Leiden* 262: 1-47.

Witte F, Goldschmidt T, Goudswaard PC, Ligtvoet W, van Oijen MJP & Wanink JH (1992a) Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology* 42: 214-232.

Witte F, Goldschmidt T, Wanink J, van Oijen M, Goudswaard K, Wittemaas E & Bouton N (1992b) The destruction of an endemic species flock - quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* 34: 1-28.

Witte F, Goldschmidt T & Wanink JH (1995) Dynamics of the haplochromine cichlid fauna and other ecological changes in the Mwanza Gulf of Lake Victoria. In: TJ Pitcher & PJB Hart (ed), *The Impact of Species Changes in African Lakes*. Chapman & Hall, London, pp. 83-110.

Witte F, Barel KDN & van Oijen MJP (1997) Intraspecific variation of haplochromine cichlids from Lake Victoria and its taxonomic implications. *South African Journal of Science* 93: 585-594.

Witte F, Msuku BS, Wanink JH, Seehausen O, Katunzi EFB, Goudswaard PC & Goldschmidt T (2000) Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. *Reviews in Fish Biology and Fisheries* 10: 233-241.

Witte F, Wanink JH, Rutjes HA, van der Meer HJ & van den Thillart GEEJM (2005) Eutrophication and its influence on the the fish fauna of Lake Victoria. In: MV Reddy (ed), *Restoration and management of tropical eutrophic lakes*. Science Publishers, Inc., Enfield (NH), pp. 301-338.

Witte F, Wanink JH & Kishe MA (2007a) Species distinction and the biodiversity crisis in Lake Victoria. *Transactions of the American Fisheries Society* 136: 1146-1159.

Witte F, Wanink JH, Kishe-Machumu M, Mkumbo OC, Goudswaard PC & Seehausen O (2007b) Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria. *Aquatic Ecosystem Health & Management* 10: 416-433.

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

Witte F, Oijen MJP & Sibbing FA (2009a) Fish Fauna of the Nile In: HJ Dumont (ed) The Nile, vol. 89. Springer Netherlands, pp 647-675.

Witte F, Graaf M, Mkumbo OC, El-Moghraby AI & Sibbing FA (2009b) Fisheries in the Nile System. In: HJ Dumont (ed), The Nile vol. 89. Springer Netherlands, pp 723-747.

Witte F, Silsbe GM, Hecky RE, Goudswaard PC, Guildford SJ, Kishe-Machumu MA & Wanink JH (2012) Did the loss of phytoplanktivorous fish contribute to algal blooms in the Mwanza Gulf of Lake Victoria? *Hydrobiologia* 679: 283-296.

Yediler A & Jacobs J (1995) Synergistic effects of temperature - oxygen and water-flow on the accumulation and tissue distribution of mercury in carp (*Cyprinus carpio* L). *Chemosphere* 31: 4437-4453.

Nederlandse samenvatting

Introductie (hoofdstuk 1)

De cichlide-vissen in de Oost-Afrikaanse meren zijn een schoolvoorbeeld van snelle evolutie en extreme adaptieve radiatie. In het Victoriameer evolueerden meer dan 500 haplochromine cichlidensoorten die 80% van de vismassa uitmaakten en die domineerden in de meeste habitats. De verschillende soorten hebben zich gespecialiseerd in verschillende voedseltypen en in totaal werden 15 (sub-)trofische groepen onderscheiden.

In de afgelopen decennia hebben grote ecologische veranderingen in het Victoriameer plaatsgevonden. De Nijlbaars, een roofvis, die in 1954 in het Victoriameer werd geïntroduceerd, nam in de jaren 80 van de vorige eeuw explosief toe. In dezelfde periode verdwenen de cichliden uit de vangsten, nam de algenbloei toe, namen zuurstofconcentraties en helderheid van het water af, en veranderde het voedselnetwerk in het meer.

Door intensieve bevissing nam de Nijlbaarspopulatie in de jaren 90 weer af en herstelden zich enkele cichlidensoorten. Dit betrof vooral twee trofische groepen, de zoöplanktoneters en detrituseters. De verhouding van deze twee groepen was echter omgekeerd vergeleken met die in het verleden. In de vangsten van bodemtreilers in de Mwanzagolf behoorden, voor de ecologische veranderingen, 75% tot 80% van het aantal haplochrominen tot de detritivoren en 10% tot 20% tot de zoöplanktivoren. In een beperkt aantal monsters uit 2005 en enkele jaren daarvoor, maakten de detritivoren slechts 26% en de zoöplanktivoren meer dan 70% van de vangst uit.

De twee belangrijkste doelstellingen van dit proefschrift zijn: 1) een nauwkeurige bepaling van het huidige niveau van de haplochromine trofische groepen en soorten in het meer, en 2) de vraag wat de belangrijkste verklaringen zijn voor de verschillen in de terugkeer van de haplochrominen. Hiertoe werden de volgende hypothesen opgesteld:

i) Door de verschuiving in de fytoplanktonsamenstelling van een dominantie van diatomeeën naar een dominantie van blauwalgen (cyanobacteriën) is de verteerbaarheid en de voedingswaarde van detritus (bodemafval) verminderd. Dit zou een negatief effect kunnen hebben op de conditie van de detritivore cichliden.

ii) Detritivore soorten zouden gevoeliger kunnen zijn voor predatie door Nijlbaars dan zoöplanktivore soorten door een grotere habitatoverlap met de Nijlbaars. Zoöplanktivoren leven deels pelagisch, terwijl detritivore soorten vooral bodembewoners zijn. Er wordt verondersteld dat de Nijlbaars het liefst dicht bij de bodem jaagt.

iii) Afgenomen zuurstofconcentraties bij de bodem en de toename van zware metalen in bodemsedimenten en vissen zijn waargenomen op diverse plekken in het Victoriameer, met inbegrip van de Mwanzagolf. Via de dominante voedselketen, zouden zware metalen een grotere invloed kunnen hebben op detritivoren dan op zoöplanktivoren omdat bioaccumulatie bij zoöplanktivoren mogelijk wordt voorkomen door het vervellen van het zoöplankton. Negatieve synergie tussen hypoxie (lage zuurstofconcentraties) en zware metalen veroorzaakt sterkere contaminatie-effecten. Omdat detritivoren dichter bij de bodem leven, zouden zij ook daardoor meer nadelige gevolgen kunnen ondervinden dan zoöplanktivoren.

iv) De teruggekeerde zoöplanktivoren vertoonden ecologische en morfologische aanpassingen aan de nieuwe omstandigheden in de omgeving. Als de potenties voor adaptieve respons bij detritivoren geringer zouden zijn dan bij de zoöplanktivoren zou dit ook een verklaring kunnen bieden voor de verschillen in herstel tussen deze trofische groepen.

Dit proefschrift richt zich vooral op de eerste twee van de bovengenoemde hypothesen. Bemonsteringen werden uitgevoerd met een kleine treiler in 2006 (maandelijks) en in 2008 (tweemaandelijks) op zes stations van een onderzoek-transect in het noordelijke deel van de Mwanzagolf. Deze stations werden in 1979/80 maandelijks op dezelfde manier bemonsterd, waardoor een goede vergelijking mogelijk is. Daarnaast werden in 2006 en 2008 bemonsteringen met kieuwnetten in de waterkolom uitgevoerd op twee stations, net zoals in de perioden 1981/82 en 1983/84. De aantallen per vangst van haplochromine soorten en trofische groepen werden bepaald, en hun dieet werd onderzocht. Ook werd het dieet van de Nijlbaars in hetzelfde gebied bestudeerd.

Terugkeer en verspreidingspatronen van haplochromine cichliden in de Mwanzagolf, Victoriameer (hoofdstuk 2)

De vangsten in 2006 bevestigden de terugkeer van een aantal detritivore en zoöplanktivore haplochromine soorten, maar ook die van enkele slakkenwrikkende soorten. Andere trofische groepen die vroeger voorkwamen, waren zeldzaam of helemaal afwezig. Het totale aantal individuen van haplochrominen in de vangsten was ongeveer gelijk aan dat in de vangsten uit het eind van de jaren 70 van de vorige eeuw; het aantal zoöplanktoneters was zelfs groter. Er werden meer zoöplanktivoren gevangen (71%) dan detritivoren (21%), maar in 2008 domineerden de detritivoren weer (52%). Het aantal soorten dat zich heeft hersteld (27+) is echter veel kleiner dan het oorspronkelijke aantal soorten dat op het transect werd gevangen (72+).

De verspreiding van de teruggekeerde soorten is veranderd. Sommige soorten hebben hun habitat uitgebreid naar ondiepere gebieden, terwijl andere nu dieper voorkomen dan vroeger. De zoöplanktivoor *Haplochromis tanaos*, die vroeger alleen op ondiepe (2-6 m) zandstations werd gevangen, komt nu vooral voor boven modderbodems met diepten van 6 tot 10 m. De verticale verspreiding van de detritivoren in de waterkolom veranderde ook. Zij vergezellen nu de zoöplanktivoren tijdens hun nachtelijke migratie naar de oppervlakte. Dit houdt mogelijk verband met de veranderde eetgewoonten van beide groepen (**hoofdstukken 3 en 4**) en met veranderingen in de omgeving.

Veranderingen in het dieet van de detritivore en zoöplanktivore cichliden in het Victoriameer (hoofdstukken 3 en 4)

Volgens de eerste hypothese zou de verandering in samenstelling van het fytoplankton de verteerbaarheid en de voedingswaarde van het detritus aangetast kunnen hebben. Dit zou een negatief effect kunnen hebben op de conditie van de detritivoren, waardoor ze minder snel konden terugkeren. Uit het onderzoek bleek echter dat het dieet van zowel de detrituseters als van de zoöplanktoneters veranderd was. In plaats van een dominantie van respectievelijk detritus en zoöplankton, werd in 2006 en 2008 het dieet van beide groepen gedomineerd door grotere prooien, zoals insecten, garnalen, schelpdieren, muggenlarven en kleine visjes.

In tegenstelling tot vroeger vertoonde het dieet van beide groepen in 2006 en 2008 een grote mate van overlap. Daarom is het niet aannemelijk dat het langzame herstel van de detritivoren het gevolg is van een afname in de kwaliteit van hun oorspronkelijke voedsel.

Bewijs voor de dieetveranderingen en dieetoverlap bij haplochromine cichliden met behulp van stabiele isotopen (hoofdstuk 5)

Voedingspatronen over langere perioden kunnen worden afgelezen uit analyses van stabiele isotopen. Daarbij zegt de $\delta^{13}C$ iets over de oorspronkelijke koolstofbron (planten) van het voedsel, en $\delta^{15}N$ iets over het niveau in de voedselketen. De resultaten van het huidige onderzoek geven aan dat conservering met formaline en alcohol weinig effect heeft op de signaturen van $\delta^{13}C$ en $\delta^{15}N$. Hierdoor is het mogelijk om stabiele isotopen uit museummateriaal te vergelijken met recentere monsters (die overigens op dezelfde manier geconserveerd werden als het oude materiaal). De stabiele isotopen uit de periode van voor de ecologische veranderingen vertoonden duidelijke verschillen tussen de vijf onderzochte soorten (een fytoplanktivoor, twee detritivoren en twee zoöplanktivoren). De $\delta^{13}C$-waarden van de detritivoren hadden een bredere range en lagere waarden dan die van de zoöplanktivoren. Dit kan verklaard worden door verschillen in het plantenmateriaal aan de basis van de voedselketen van deze twee groepen. De fytoplanktivoor en een van de twee detritivoren hadden lagere $\delta^{15}N$-waarden dan de zoöplanktivoren wat overeenstemt met hun lagere positie in de voedselketen. De $\delta^{15}N$-waarde van tweede detritivoor viel in de range van de zooplanktivoren, een mogelijke verklaring hiervoor is dat de jongen van deze soort zoöplankton eten. Clustering van de stabiele isotopen per soort en trofische groep bij de moderne detritivoren en zoöplanktivoren was minder duidelijk dan in het verleden. Zowel detritivoren als zoöplanktivoren hadden hogere $\delta^{15}N$-waarden dan vroeger, wat wijst op een hogere positie in de voedselketen. Verder lijkt de overlap in stabiele isotopen signatuur groter te zijn dan vroeger. Deze resultaten komen overeen met de resultaten van de in de hoofdstukken 3 en 4 beschreven dieetanalyses.

Het dieet van de Nijlbaars na de terugkeer van de haplochrominen (hoofdstuk 6)

In de jaren 70 van de vorige eeuw toen haplochrominen de vismassa in het Victoriameer domineerden, waren zij de belangrijkste prooi van de Nijlbaars. Na de ineenstorting van de haplochrominen in de jaren 80 ging de Nijlbaars over op andere prooien; voornamelijk garnalen, *Rastrineobola argentea* (een karperachtig visje) en zijn eigen jongen. Het onderzoek van de maaginhouden van de Nijlbaars in 2006 en 2008 liet zien dat de haplochrominen weer de belangrijkste voedselbron werden na hun terugkeer. De omschakeling door Nijlbaars van garnalen naar vis, gebeurt als het haplochrominen betreft bij een kleinere Nijlbaarslengte dan bij andere visprooien. Dit suggereert dat haplochrominen de meest geprefereerde prooien zijn. Als dit klopt, zou de aanwezigheid van haplochrominen de mate van kannibalisme door de Nijlbaars kunnen verminderen. Dat zou een positieve invloed hebben op de rekrutering van Nijlbaars.

Kunnen de verschillen in de terugkeer van de haplochromine trofische groepen verklaard worden door selectieve predatie door de Nijlbaars, *L. niloticus*? (hoofdstuk 7)

Aangezien haplochrominen na hun terugkeer weer domineerden in het dieet van de Nijlbaars, kon getoetst worden of, vanwege een grotere habitatoverlap met de Nijlbaars, detritivoren gevoeliger zijn voor predatie dan zoöplanktivoren. Hierbij moet wel worden opgemerkt dat het verschil in verticale verspreiding tussen de twee trofische groepen na hun terugkeer is afgenomen.

In tegenstelling tot de verwachting, kwamen detritivoren verhoudingsgewijs minder vaak voor in het dieet van de Nijlbaars dan in de omgeving. Om te bepalen of de grotere lichaamsdiepte van de detritivoren kan verklaren waarom ze relatief minder vaak in het dieet voorkomen, werd de lichaamsdiepte vergeleken met de diameter van de geopende bek van de Nijlbaars. Op basis hiervan bleek dat alleen de kleinste (7–13 cm totale lengte) visetende Nijlbaarzen niet in staat zouden zijn de grootste detritivoren te eten. Ook is geen verschil gevonden in predatie van Nijlbaars op detritivoren en zoöplanktivoren op grond van hun lengte.

De conclusie is daarom, dat er geen bewijs is voor selectieve predatie van Nijlbaars op detritivoren. De tweede hypothese biedt dus geen verklaring voor het relatief langzame herstel van deze trofische groep.

Implicaties voor verder onderzoek en visserijbeheer (hoofdstuk 8)

Slechts twee van vier hypothesen voor het relatief trage herstel van de detritivore cichliden konden getoetst worden in dit proefschrift. Beide bleken geen rol van betekenis te spelen. Wat betreft de derde hypothese heeft een pilotstudy uitgewezen dat de concentratie zware metalen in het spierweefsel van de zoöplanktivoor *H. pyrrhocephalus* significant hoger was dan in het spierweefel van de detritivoor *H.* 'paropius-like'. Dit is tegenovergesteld aan de verwachting dat detritivoren sterker verontreinigd zouden zijn dan de zoöplanktivoren. Maar de monsters die tot nu toe werden onderzocht zijn nog te klein voor een duidelijke conclusie en verder onderzoek is nodig.

Toetsing van de vierde hypothese, dat potenties voor morfologische aanpassingen aan de veranderde omgeving van belang zijn voor het herstel van soorten en trofische groepen, vormt onderdeel van een promotieonderzoek dat momenteel wordt uitgevoerd door Jacco van Rijssel. In het onderzoek dat wordt beschreven in het huidige proefschrift is maar één morfologische parameter onderzocht, namelijk de darmlengte. Bij de moderne detritivoren was deze lengte significant afgenomen, wat een reactie lijkt op het meer carnivore dieet.

Het differentiële herstel dat gevonden werd voor haplochromine gemeenschappen, trofische groepen en soorten geeft aan dat het niet aan te bevelen is om de haplochromine cichliden als een homogene eenheid te beschouwen. Een goede kennis van de samenstelling en ecologie van de terugkerende soorten haplochrominen in verschillende delen van het meer en van de bestaande populaties in de satellietmeren, is cruciaal voor het beheer van het Victoriameer. Zoals aangetoond in dit proefschrift, is een aantal van de haplochromine soorten die op het moment in het Victoriameer voorkomen moeilijk te determineren. De grootste taxonomische collecties van haplochromine cichliden van voor de ecologische veranderingen, zijn opgeslagen in het British Museum of Natural History in Londen en het Netherlands Centre for Biodiversity in Leiden. Het determineren van de terugkerende soorten zonder deze te vergelijken met het materiaal in deze collecties is moeilijk. Omdat het Victoriameer nog steeds een onstabiel ecosysteem is, wordt aanbevolen een institutioneel of nationaal museum op te richten voor vissen en andere aquatische dieren uit dit meer.

In het Victoriameer krijgt het beheer van de commerciële vissoorten (Nijlbaars, Nijltilapia en de karperachtige *R. argentea*) de grootste aandacht.

Beheerstrategieën zouden geïntegreerd moeten worden, met aandacht voor alle vissoorten omdat vele ervan kritisch zijn voor het structureren van aquatisch biotische gemeenschappen en deel uitmaken van trofische interacties en voedselnetwerken. Daarom pleit ik ervoor dat alle plannen voor natuurbehoud en strategieën voor het beheer van de visserij, haplochromine populaties incorporeren als component die beschermd moet worden om de integriteit van het ecosysteem in het meer te behouden. De terugkeer van de haplochrominen kan de Nijlbaarsproductie vergroten (**hoofdstuk 6**). De beheerstrategieën moeten daarom ook zorgen voor bescherming van de haplochrominen. Het instellen van reservaten en het tegengaan van verdere degradatie van habitats in deze reservaten zou kunnen zorgen voor refugia die dienen als bronnen voor herbevolking van het meer.

Curriculum vitae and publications

CURRICULUM VITAE

Mary Alphonce Kishe-Machumu was born on the 3rd of January 1970 in Moshi, Kilimanjaro, Tanzania. She followed secondary education at Lombeta Secondary School from 1985 to 1988 (ordinary level) and at Loleza Girls' Secondary School from 1989 to 1991 (advanced level). In 1992, Mary joined the University of Dar es Salaam (Tanzania) for her Bachelor of Science degree course in Marine Biology and Applied Microbiology and she graduated in 1995. During this course, she did a field training practical course on fish community along Zanzibar Channel. It was here that she experienced the pleasures and troubles of being a Marine biologist for the first time.

From 1995 to 1996, she joined the FRONTIER TANZANIA on *Marine Survey and Monitoring Techniques Course*, which included scuba diving. In 1996, she was employed with the Tanzania Fisheries Research Institute (TAFIRI) as a research scientist and she was based at TAFIRI Mwanza Research Centre. In 1998, Mary started a Master's degree course at the University of Dar Es Salaam in Environmental Sciences. During her Master's degree, she got to conduct her field work on Lake Victoria.

As a marine scientist, Mary was involved in various research activities including the studies on fish diversity, biology, ecology and biodiversity conservation in national and regional research projects on Lake Victoria basin. In addition, she attended courses and workshops in which she presented scientific papers and reports. In 2005, she was transferred to Dar Es Salaam research centre and in the same year, she started her PhD program at Leiden University, the Netherlands where she got to work again on Lake Victoria. In course of her PhD project, she interrupted the study two times during her maternity leaves. She presented her PhD research findings at three International Symposia: (1) Changing Great Lakes of the World (GLOW IV; Bagamoyo, Tanzania, 2006) (2) 14th Benelux Congress of Zoology (Amsterdam, the Netherlands, 2007) and (3) "Asia-Africa Evolution Meeting" (Chiba, Japan, 2007). Mary is a member of professional associations including Western Indian Ocean Marine Science Association (WIOMSA), British Sub-Aqua Club (BSAq.), African Women in Agricultural Research and Development (AWARD), East African Austria Water Association (EAAWA) and Sustainable Aquaculture Research Networks in Sub Saharan Africa (SARNISSA).

LIST OF PUBLICATIONS

Kishe-Machumu MA, Witte F, Wanink JH & Katunzi, EFB (2012) The diet of Nile perch, Lates niloticus (L.) after resurgence of haplochromine cichlids in the Mwanza Gulf of Lake Victoria. Hydrobiologia 682: 111-119.

Ngatunga BP, Lugendo BR & **Kishe-Machumu MA** (2012) Checklist of Tanzanian fishes. In: Gideon H, Nyinondi P & Oyema G: Checklist of Tanzanian species. *Tanzania Commission for Science and Technology* 1: 143-194.

Witte F, Seehausen O, Wanink JH, **Kishe-Machumu MA**, Rensing M & Goldschmidt T (2012) Cichlid species diversity in naturally and anthropogenically turbid habitats of Lake Victoria, East Africa. *Aquatic Sciences* DOI: 10.1007/s00027-012-0265-4.

Witte F, Silsbe GM, Hecky RE, Goudswaard PC, Guildford SJ, **Kishe-Machumu MA** & Wanink JH (2012) Did the loss of phytoplanktivorous fish contribute to algal blooms in the Mwanza Gulf of Lake Victoria? *Hydrobiologia* 679: 283-296.

Witte F, van Oijen MJP, **Kishe-Machumu MA**, & Wanink JH (2008) Trettio års forskning om ciklider från Viktoriasjön – Ett ekologisk skådespel som erbjuder nya vetenskapliga möjligheter. *Ciklidbladet* 41 (4): 28-29.

Kishe-Machumu MA, Witte F & Wanink JH (2008) Dietary shift in benthivorous cichlids after the ecological changes in Lake Victoria. *Animal Biology* 58: 401-417.

Witte F, van Oijen M, **Kishe-Machumu MA** & Wanink JH (2007) Thirty years research on Lake Victoria cichlids; an ecological drama provide new scientific opportunities. *SILnews* 51: 12-13.

Witte F, Wanink JH & **Kishe-Machumu MA** (2007) Species Distinction and the Biodiversity Crisis in Lake Victoria. *Transactions of the American Fisheries Society* 136: 1146-1159.

Witte F, Wanink JH, **Kishe-Machumu MA**, Mkumbo OC, Goudswaard PC & Seehausen O (2007) Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria. *Aquatic Ecosystem Health and Management* 10: 416-433.

Katunzi EFB & **Kishe MA** (2004) Changes in population structure of major fish species in selected satellite lakes around Lake Victoria following changes in fishing effort. *Tanzania Journal of Science* 30 (2): 53-64.

Kishe MA (2004) Physical and chemical characteristics of water in selected locations in Lake Victoria, Tanzania. *Tanzania Journal of Science* 30 (2): 65-72.

Kishe MA & Machiwa JF (2001) Distribution of heavy metals in sediment of Mwanza Gulf of Lake Victoria, Tanzania. *Environmental International* 28 (7): 619 – 625.

In press

Witte F, **Kishe-Machumu MA**, Mkumbo OC, Wanink JH, Goudswaard PC, van Rijssel JC & van Oijen MJP. The fish fauna of Lake Victoria during a century of human induced perturbations. *Journal of Afrotropical Zoology*.