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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 (δ¹⁵N) and carbon (δ¹³C) 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 δ¹³C and δ¹⁵N signatures were assessed.

Our findings indicated that formalin/alcohol preservation had little effect on δ¹³C and δ¹⁵N 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 δ¹³C axis. Almost all species differed from each other significantly. Similarly, the species were rather well separated along the δ¹⁵N axis. Values of δ¹³C 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 $^{13}\text{C}$ values in the larger phytoplankton species as compared with the smaller species.

Values of $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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.

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.