Author: Kishe-Machumu, Mary Alphonce
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Chapter 3

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

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

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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, $P < 0.001$).

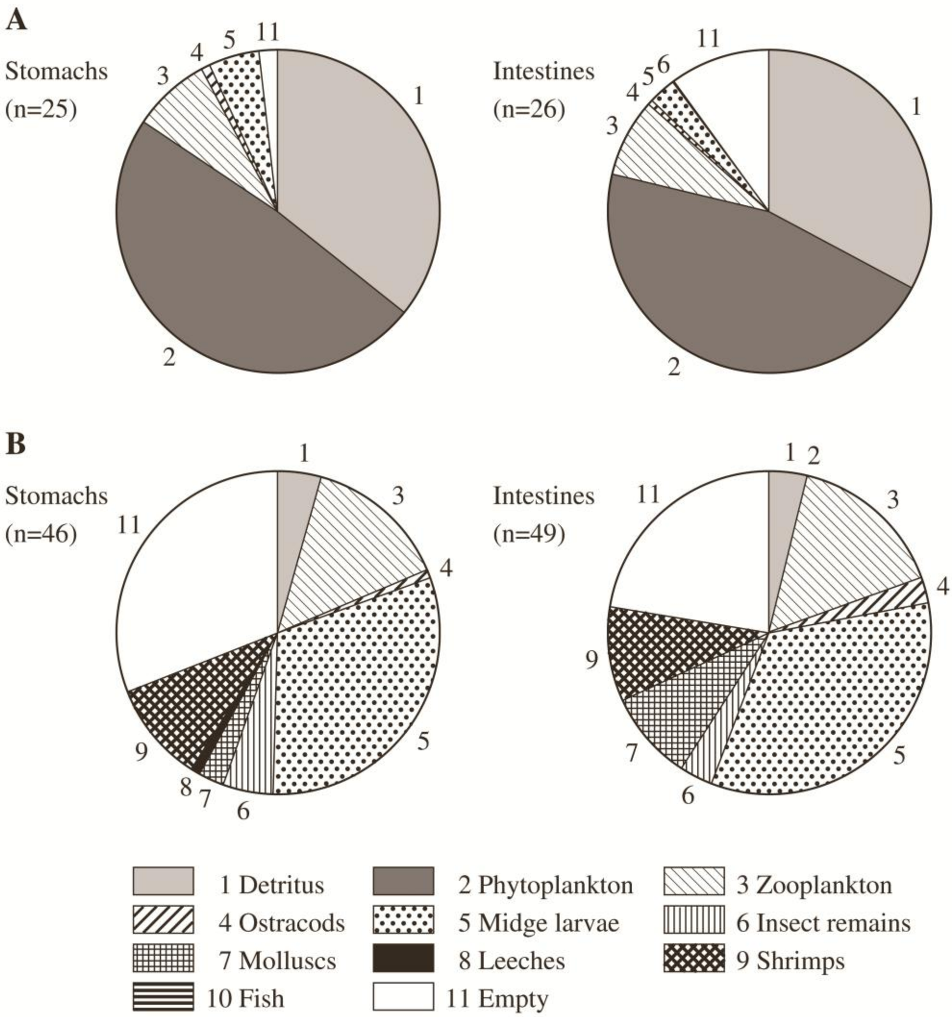

Fig. 3.1 Diet composition (mean volume percentages) by day in stomachs of the pooled "detritivores" in the Mwanza Gulf (a) in the old ecosystem (1977-1982; *H. cinctus*, *H. antleter*, *H. coprologus*, *H.* 'purple head') (b) in the modern ecosystem (2005-2006).

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).

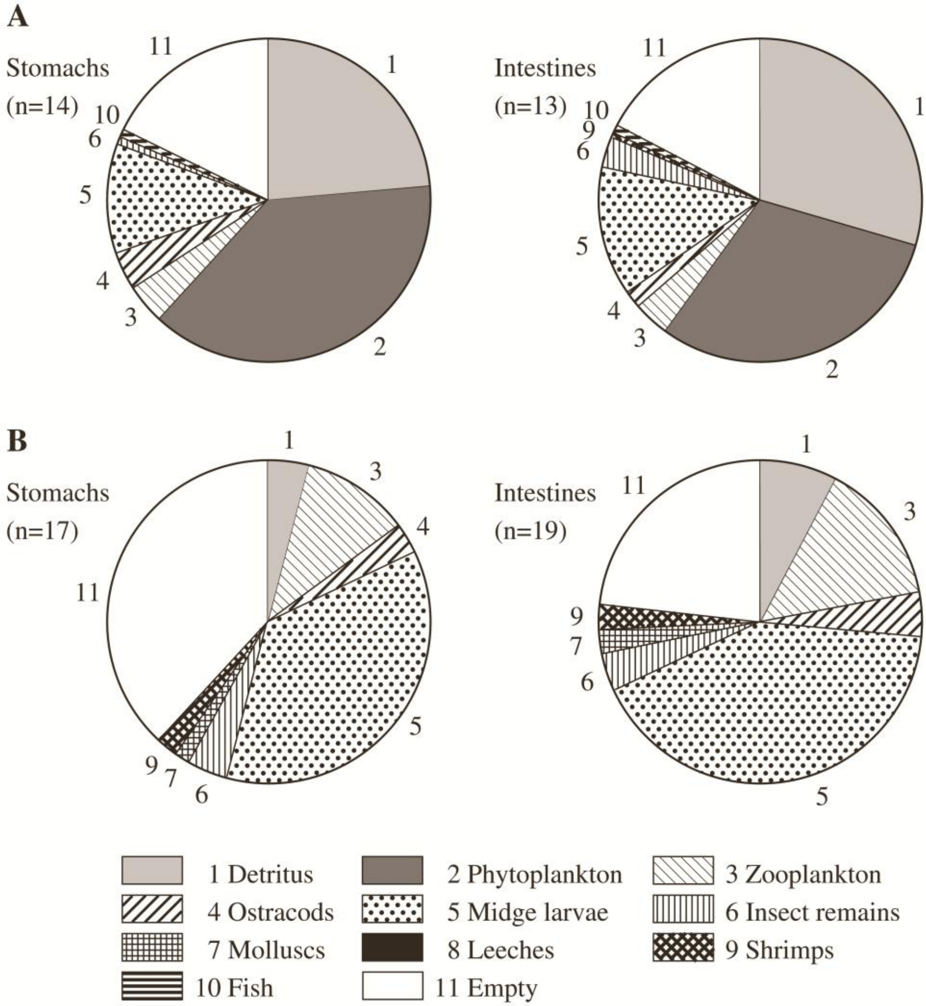

Fig. 3.2 Diet composition (mean volume percentages) in stomachs and intestines of *H.* 'paropius-like' by day in the Mwanza Gulf (a) in the old ecosystem (1977-1982); (b) in the modern ecosystem (2005-2006).

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.

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