



Differential recovery and spatial distribution pattern of haplochromine cichlids in the Mwanza Gulf of Lake Victoria



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ABSTRACT

Lake Victoria had a fish fauna dominated by 500+ species of haplochromines. In the 1980s, the haplochromines from sub-littoral areas of the Mwanza Gulf vanished almost completely. In the 1990s, a recovery of some haplochromine species was observed. To establish the status of the recovery, we studied their relative abundance and distribution pattern in the northern part of Mwanza Gulf in the years 2006 (monthly trawl hauls at 6 stations) and 2008 (bi-monthly trawl hauls at the same stations); the period after environmental changes. The data were compared with those of 1979/80 collected at the same stations before the period of environmental changes. The number of trophic guilds decreased from 12 in 1979/80 to nine in 2006 and 2008 with detritivores, zooplanktivores and oral mollusk shellers being the most abundant guilds. Detritivores were the dominant guild in 1979/80 (average 602 fish/haul) and 2008 (422 f/h) and the second most abundant guild in 2006 (175 f/h). Zooplanktivores were the dominant guild in 2006 (594 f/h) and the second most abundant guild in 1979/80 (159 f/h) and 2008 (270 f/h). Both in 2006 and 2008, oral mollusk shellers were the third dominant guild (27 f/h and 49 f/h respectively). Moreover, the study revealed that the resurgent trophic guilds were more widely distributed in the 2000s than in the 1970s. Possible causes for the recovery of the haplochromines including a decline in the Nile perch population, eco-morphological adaptations of the haplochromines and habitat extension are discussed.

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Introduction

Lake Victoria is among the world's best known examples of a lake with high fish species richness. Prior to the expansions of exotic fish species, Lake Victoria supported a multispecies fishery comprised of several families (Garrod, 1960). More than 90% of the species in the lake belonged to a single family, the Cichlidae (Snoeks, 2000). This family was represented by a few tilapiine species and more than 500 endemic haplochromine species (Witte et al., 2007a) that made up more than 80% of the fish mass (Kudhongania and Cordone, 1974) with the dominant groups of detritivores, zooplanktivores, insectivores, molluscivores and piscivores (Witte et al., 1992a).

In the past 40 years, environmental changes have occurred in Lake Victoria including amongst others the upsurge of the introduced

predatory Nile perch (Pringle, 2005; Goudswaard et al., 2008) and the decline of the cichlids in the sub-littoral and offshore areas during the 1980s (Witte et al., 1992a,b). At the same time, the eutrophication in the lake strongly increased and was associated with more frequent algal blooms (Hecky, 1993; Mugidde, 1993), a decrease in dissolved oxygen (DO) (Hecky et al., 1994; Wanink et al., 2001) and lower water transparency (Seehausen et al., 1997a; Witte et al., 2005; Hecky et al., 2010). In the sub-littoral waters of the Mwanza Gulf, long lasting periods (3–5 months) of hypoxia ($2\text{--}3\text{ mg L}^{-1}$) were observed during the late 1980s (Wanink et al., 2001; Witte et al., 2005). Secchi depth values in this part of the lake decreased from 1.7–2.5 m in 1980 (van Oijen et al., 1981) to 0.7–1.2 m in 1986–1987 (Seehausen et al., 1997a; Witte et al., 2005). Light limits primary production in shallow areas where phytoplankton biomass is high and in deep water where the mixed depth is greater than the euphotic depth (Hecky, 1993; Guildford et al., 2003). In addition, the densities of macro-invertebrates, such as insects, mollusks, shrimps and small cyprinid fish *Rastrineobola argentea* (dagaa) increased (Kaufman, 1992; Wanink, 1999; Goudswaard et al., 2006).

During the second half of the 1990s, Nile perch stocks declined, likely due to intensive fishing (Pitcher and Bundy, 1995; Ntiba et al., 2001). Signs of over-fishing such as a decline in the biomass and a decrease in the age of first maturity were observed in 2000s (Mkumbo, 2002; Matsuishi et al., 2006; Mkumbo et al., 2007; Kayanda et al., 2009).

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However, other causes for the decline of Nile perch in Lake Victoria have been suggested, including eutrophication and the resulting hypoxia/anoxia (Kolding et al., 2008). Concomitant with the decline in Nile perch stocks, a recovery of some haplochromine species was observed in the sub-littoral area of the Mwanza Gulf (Seehausen et al., 1997b; Witte et al., 2000, 2007a,b) and other areas of the lake (Balirwa et al., 2003; Getabu et al., 2003). In the Mwanza Gulf, only a restricted number of zooplanktivorous and detritivorous/phytoplanktivorous (hereafter referred to as detritivorous species) cichlids recovered. From 1987 to 2005, the zooplanktivores rather than the detritivores were the dominant haplochromine group (Witte et al., 1992a,b, 2007a,b). To investigate the ongoing changes, the differential recovery, distribution pattern and relative abundance of haplochromine trophic guilds and species were studied in the southern part of Lake Victoria in 2006 and 2008 and compared with observations in 1979/80; when this research transect was first sampled.

Materials and methods

Study area

The haplochromines were collected from sub-littoral waters in the northern part of the Mwanza Gulf on a research transect, between Butimba Bay and Kissenda Bay (Fig. 1). The haplochromine species composition along the transect was monitored prior to and during the environmental changes by the Haplochromis Ecology Survey Team (HEST) from 1979 till 2002. The transect is approximately 5 km long and includes six sampling stations (E [6 m], F [9.5 m], G [13 m], H [12.5 m], I

[9.5 m] and J [5.5 m]; Fig. 1). In the study, stations of depths <9 m (E, J) were considered as shallow stations while those of >9 m (F, G, H, I) were considered as deep stations. Distance between the stations ranged from 500 m to 1 km. The bottom of these stations is covered with a thick deposit of organic mud (Witte, 1981).

Fish sampling

Haplochromines were collected during two different periods; in 1979/80 (prior to severe environmental changes which took place from 1983 to 2002; van Rijssel and Witte, 2013), 2006 and 2008 (after the severe environmental changes). The division into prior to and after the severe environmental changes is based on the following observations: 1) a strong decline of haplochromines in the period between 1983 and 1988 (Witte et al., 2007b) 2) phytoplankton blooms that were first observed in 1986 (Witte et al., 1992a) and 3) low DO concentrations and low Secchi depth values observed in 1987/88 (Witte et al., 1992a, 2005; Wanink et al., 2001).

Fish were sampled during daytime with 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. In 1979/80, the stations were sampled monthly from February 1979 to January 1980. During that period, no samples were taken at stations H, I and J in April and November 1979 and at station I in February 1979. Similarly, in 2006 the stations were sampled monthly (except for station F in January) while in 2008 each station was sampled once every two months. In all periods, trawling

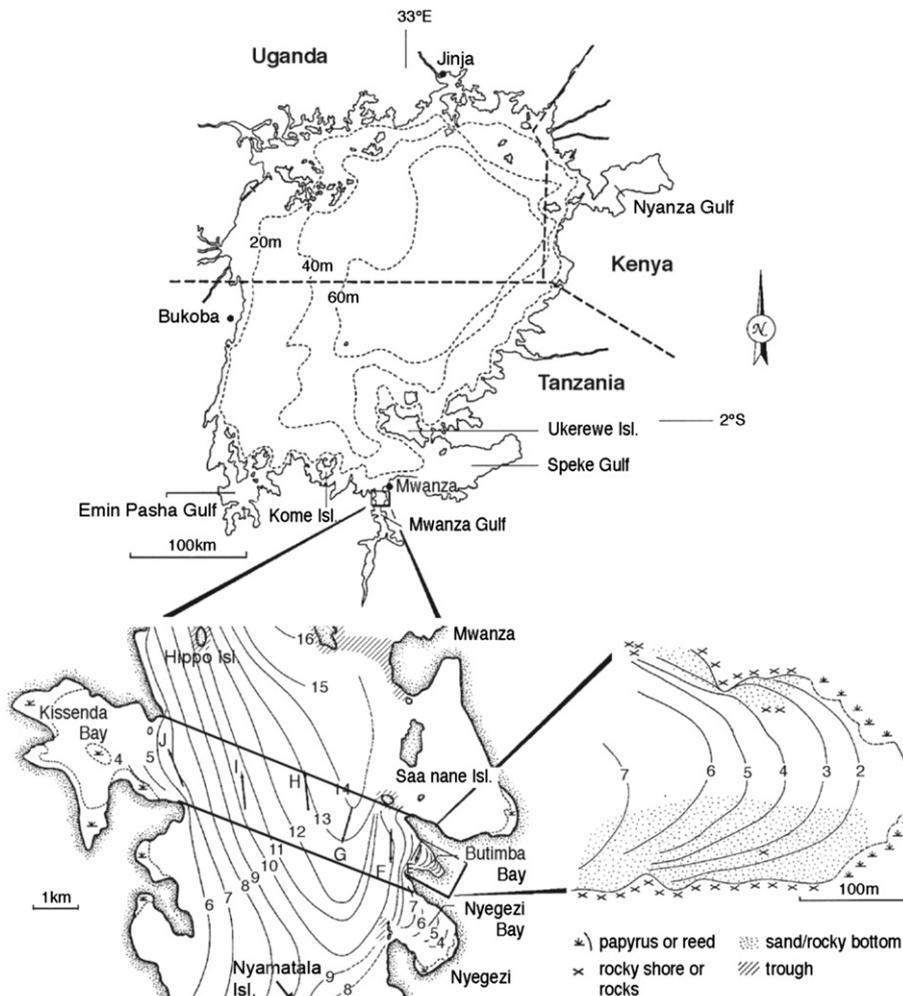


Fig. 1. Map of Lake Victoria showing the sampled stations in the northern part of Mwanza Gulf. The research transect is indicated with black lines from the east to the west shore.

was performed with the same type of bottom trawl net and trawl shots at each station lasted 10 min.

Fish identification

In 1979/80 and 2006/08, fish >5 cm and ≥ 4.0 cm standard length (SL) respectively were considered adults and were used to identify species and/or trophic composition. During the 1980s, size at first maturity was 5.0 cm SL (Witte et al., 1995) but decreased to 4.0 cm SL in 2006/08 (Kische-Machumu pers. obs.).

Lake Victoria cichlids were classified into trophic groups as most species are specialized in eating and processing a certain type of food. Generally, species within a trophic group share morphological characters that are related to the capture and processing of their dominant food type (Greenwood, 1974; Witte and van Oijen, 1990). In some cases, subgroups can be identified based on feeding techniques, location of prey in the environment and the prey eaten. However, the diet of the recovering haplochromine cichlids differed from that of the past (van Oijen and Witte, 1996; Katunzi et al., 2003; Kische-Machumu et al., 2008; Kische-Machumu, 2012). Therefore, the trophic group classification of the haplochromines used in this paper corresponds with that based on morphological features as presented by Witte and van Oijen (1990) and by Seehausen (1996), and consequently, corresponds with their diet in the past, not with their current diet.

The morphology of some haplochromine species has changed (Witte et al., 2008; de Zeeuw et al., 2010; van Rijssel and Witte, 2013; van Rijssel et al., 2015) making these species difficult to identify. In case of doubt as to whether a species 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 group. In addition, species of rare trophic groups (insectivores, pharyngeal crushers, phytoplanktivores, epiphytic algae grazers, paedophages) as well as some females of the detritivores which could not be easily identified to species level were collectively grouped under the rest group. Following Witte et al. (1992b), species that are not yet formally described were given nicknames enclosed in single (") quotation marks. With exception of a few un-identified detritivorous females, individuals belonging to detritivores, zooplanktivores and oral mollusk shellers were identified to the species level.

Data analysis

Monthly catch data (numbers) from the three years were not normally distributed (Kolmogorov–Smirnov test). Therefore, to test if the catches differed significantly between the sampling years and stations, a Kruskal–Wallis test (KW) was employed. When significant, Dunn's Multiple Comparisons Test was used to test for differences in the number of fish among sampling years and stations. All tests were done with Instant statistical software, version 3.06 (GraphPad Instat, 2003).

Results

Abundance of trophic groups along the transect 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 different groups were encountered at stations E–J along the research transect (Table 1). This is a strong reduction compared to the more than 72 species belonging to 12 different groups found in 1979–82 (Witte et al., 1992b). The strongest reduction in species occurred in the piscivores and the paedophages.

Detritivores

In 1979/80, the detritivores were the dominant guild on the research transect (602 fish per haul; Table 2) while in 2006, they were the second

Table 1

Total number of haplochromine species per trophic group collected at stations E to J in the northern part of the Mwanza Gulf before (source: Witte et al., 1992b), and after the environmental changes (source: present study). A + indicates uncertainty about identification of one or more species that morphologically would be assigned to the trophic group.

	1979–1982	2006 and 2008
Detritivores	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+

most abundant group (175 f/h). In 2008, their abundance increased (422 f/h) making them the dominant guild as they were in 1979/80. The differences in abundance of detritivores were significant among years ($P < 0.001$; Electronic Supplementary Material (ESM) Table S1), but not among sampling stations (ESM Table S2).

Zooplanktivores

In 1979/80, zooplanktivores were the second most abundant group (159 f/h; Table 2). In 2006, their abundance had increased (594 f/h) and surpassed the abundance of the detritivores making them the most abundant guild. In 2008, their mean number dropped (270 f/h) and they became the second abundant group as they were in 1979/80. However, these fluctuations in abundance were not significant (ESM Table S1) due to the great variation in catches among the three sampling periods. The differences in abundance of zooplanktivores among the sampling stations were significant in 1979/80, 2006 and 2008 ($P = 0.03, 0.002$ and 0.03 respectively; Table 2; ESM Table S2).

Oral mollusk shellers

The oral mollusk shellers were more abundant in 2006 and 2008 (27 and 49 f/h respectively; $P < 0.001$) than in 1979/80 when they were very rare with an average of one f/h (Table 2). The significant differences in distribution of the oral mollusk shellers with relation to depth was observed over all three sampling years (Table 2), but differences were much more pronounced in 2006 and 2008 ($P < 0.001$ in each year) when the abundance was significantly higher at shallow stations E and J than at deeper stations F, G and H (ESM Table S2).

Piscivores

In 2006 and 2008, the abundance of piscivores (only two species; *H. 'green dentex'* and *H. 'big teeth'* were found) was significantly lower (1.5 and 2.2 f/h, respectively; $P < 0.001$) than in 1979/80 (5 f/h). In 2006, their number was significantly higher at shallow station E than at deeper station G (ESM Table S2).

Rest group

This group mainly comprised unknown haplochromines, unidentified detritivorous females, insectivores and pharyngeal crushers. The abundance of the rest group was significantly lower in 1979/80 (37 f/h; $P < 0.001$) than in 2006 and 2008 (43 and 67 f/h, respectively). In 2006 and 2008, their number was significantly higher at shallow stations E and J than at deeper stations F, G, H and I ($P < 0.001$; ESM Table S2).

Table 2
 Number (mean \pm standard deviation) and percentages of haplochromines per trophic group in bottom trawls of 10 min duration per station at the research transect in 1979/80, 2006 and 2008. Letter combinations in superscript with no overlap represent statistically significant differences among sampling stations (Dunn's Multiple Comparisons Test, $P \leq 0.05$), n-values represent number of catches. Sources: HEST (for 1979/80 data) and present study (2006 and 2008). The rest group comprised insectivores, pharyngeal crushers, phytoplanktivores, epiphytic algae grazers, paedophages, some un-identified detritivorous females, un-identified and unknown haplochromines.

Trophic group	Year	E (6.0 m)	F (9.5 m)	G (13 m)	H (12.5 m)	I (9.5 m)	J (5.5 m)	Transect
n-Values	1979/80	12	12	12	10	9	10	65
	2006	12	11	12	12	12	12	71
	2008	6	6	6	6	6	6	36
Total haplochromines	1979/80	973 \pm 654	672 \pm 673	1097 \pm 977	874 \pm 764	599 \pm 483	521 \pm 457	804 \pm 707
	2006	412 \pm 375	1146 \pm 1885	692 \pm 965	1573 \pm 2687	563 \pm 859	679 \pm 612	840 \pm 1465
	2008	340 \pm 215	1518 \pm 3289	227 \pm 195	139 \pm 64	822 \pm 1227	1809 \pm 1606	809 \pm 1604
Zooplanktivores	1979/80	210 \pm 127 ^a	235 \pm 417 ^{ab}	170 \pm 336 ^{ab}	123 \pm 189 ^{ab}	66 \pm 77 ^b	113 \pm 138 ^{ab}	159 \pm 253
	2006	22% 50 \pm 85 ^a	35% 899 \pm 1638 ^b	15% 629 \pm 973 ^b	14% 1410 \pm 2325 ^b	11% 333 \pm 644 ^{ab}	22% 269 \pm 242 ^{ab}	20% 594 \pm 1291
	2008	12% 17 \pm 27 ^a	78% 938 \pm 2237 ^{ab}	91% 151 \pm 206 ^{ab}	90% 90 \pm 58 ^{ab}	59% 197 \pm 226 ^{ab}	40% 226 \pm 158 ^b	71% 270 \pm 911
Detritivores	1979/80	5.1% 698 \pm 534 ^a	62% 411 \pm 328 ^a	67% 867 \pm 849 ^a	64% 699 \pm 549 ^a	24% 508 \pm 404 ^a	12% 384 \pm 315 ^a	33% 602 \pm 548
	2006	72% 114 \pm 198 ^{ab}	61% 225 \pm 267 ^{ab}	79% 58 \pm 64 ^a	80% 157 \pm 386 ^{ab}	85% 180 \pm 219 ^{ab}	74% 321 \pm 296 ^b	75% 175 \pm 262
	2008	28% 88 \pm 84 ^a	20% 573 \pm 1053 ^a	8.40% 72 \pm 53 ^a	10% 47 \pm 29 ^a	32% 576 \pm 925 ^a	47% 1175 \pm 1101 ^a	21% 422 \pm 790
Oral mollusk shellers	1979/80	26% 2.0 \pm 3.7 ^{ab}	38% 1.7 \pm 1.8 ^a	32% 0.5 \pm 1.7 ^{ab}	34% 0 ^b	70% 0.8 \pm 2.5 ^{ab}	65% 1.1 \pm 1.2 ^{ab}	52% 1.1 \pm 2.2
	2006	0.2% 68 \pm 75 ^a	0.2% 11 \pm 16 ^{ab}	0.1% 4.2 \pm 9.7 ^b	– 4.7 \pm 12 ^b	0.1% 19 \pm 25 ^{ab}	0.2% 52 \pm 61 ^a	0.1% 27 \pm 47
	2008	16% 60 \pm 48 ^a	0.9% 0.7 \pm 1.2 ^b	0.6% 2.5 \pm 4.0 ^{ab}	0.3% 0.2 \pm 0.4 ^b	3.3% 47 \pm 87 ^{ab}	7.7% 181 \pm 278 ^a	3.2% 49 \pm 129
Piscivores	1979/80	18% 13 \pm 21 ^a	0.04% 2.2 \pm 2.4 ^a	1.1% 2.8 \pm 7.1 ^a	0.1% 4.0 \pm 7.1 ^a	5.7% 5.3 \pm 4.2 ^a	10% 1.8 \pm 1.9 ^a	5.9% 5.0 \pm 10
	2006	1.3% 4.2 \pm 8.3 ^a	0.3% 4.3 \pm 9.9 ^{ab}	0.3% 0 ^b	0.5% 0.1 \pm 0.3 ^{ab}	0.9% 0.7 \pm 2.3 ^{ab}	0.3% 0.3 \pm 0.6 ^{ab}	0.6% 1.5 \pm 5.4
	2008	1.0% 0.2 \pm 0.4 ^a	0.4% 3.0 \pm 6.4 ^a	– 0 ^a	0.01% 0.2 \pm 0.4 ^a	0.1% 1.3 \pm 3.3 ^a	0.04% 8.7 \pm 12 ^a	0.2% 2.2 \pm 6.2
Rest group	1979/80	0.1% 50 \pm 62 ^a	0.2% 22 \pm 34 ^a	– 57 \pm 39 ^a	0.1% 48 \pm 45 ^a	0.2% 19 \pm 16 ^a	0.5% 19 \pm 19 ^a	0.3% 37 \pm 42
	2006	5.2% 176 \pm 184 ^a	3.3% 8.0 \pm 12 ^b	5.2% 0.4 \pm 1.2 ^b	5.5% 1.5 \pm 4.6 ^b	3.2% 31 \pm 70 ^{ab}	4.0% 37 \pm 101 ^{ab}	4.6% 43 \pm 108
	2008	43% 175 \pm 147 ^a	0.7% 2.8 \pm 6.5 ^{bc}	0.1% 1.3 \pm 2.4 ^{bc}	0.1% 2.5 \pm 3.3 ^{abc}	5.5% 0.7 \pm 1.6 ^b	5.4% 219 \pm 508 ^{ac}	5.1% 67 \pm 221
		51% 0.4%	0.4%	0.6% 1.8%	0.1%	12%	8.3%	

Table 3
Number (mean \pm standard deviation) of adult haplochromine species in bottom trawls of 10 min duration at stations E to J in 1979/80 and in 2006 and 2008. Letter combinations in superscript with no overlap represent statistically significant differences among sampling stations (Dunn's Multiple Comparisons Test, $P \leq 0.05$), n-values are the same as in Table 2. Sources: HEST (for 1979/80) and present study (2006 and 2008).

Species	Year	E (6.0 m)	F (9.5 m)	G (13 m)	H (12.5 m)	I (9.5 m)	J (5.5 m)	Transect
<i>H. pyrrhocephalus</i>	1979/80	0 ^a	1.7 \pm 3.6 ^{ac}	112 \pm 251 ^b	27 \pm 53 ^{bc}	7.3 \pm 12 ^{abc}	6.0 \pm 19 ^{ac}	27 \pm 113
	2006	36 \pm 76 ^a	859 \pm 1571 ^b	631 \pm 951 ^b	1358 \pm 2319 ^{bc}	275 \pm 614 ^{abc}	175 \pm 207 ^{ab}	551 \pm 1271
	2008	1.7 \pm 3.2 ^a	937 \pm 2238 ^{ab}	136 \pm 173 ^{ab}	78 \pm 45 ^{ab}	147 \pm 148 ^b	78 \pm 137 ^{ab}	230 \pm 912
<i>H. laparogramma</i>	1979/80	0 ^a	0 ^a	0.5 \pm 1.8 ^a	0.2 \pm 0.6 ^a	0 ^a	0.1 \pm 0.3 ^a	0.1 \pm 0.8
	2006	0.6 \pm 1.4 ^a	30 \pm 61 ^a	15 \pm 25 ^a	43 \pm 74 ^a	9.8 \pm 17 ^a	2.2 \pm 4.6 ^a	17 \pm 42
	2008	0.7 \pm 1.6 ^a	0.7 \pm 1.6 ^a	14 \pm 34 ^a	12 \pm 23 ^a	2.3 \pm 4.4 ^a	0.2 \pm 0.4 ^a	5 \pm 17
<i>H. tanaos</i>	1979/80	0.7 \pm 1.9 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0.1 \pm 0.8
	2006	12 \pm 22 ^{ab}	9.7 \pm 13 ^{ab}	2.4 \pm 5.5 ^a	9.1 \pm 18 ^{ab}	48 \pm 56 ^b	90 \pm 108 ^b	29 \pm 59
	2008	15 \pm 27 ^{ab}	1.2 \pm 2.4 ^a	0.8 \pm 1.6 ^a	0.2 \pm 0.4 ^a	47 \pm 89 ^{ab}	148 \pm 144 ^b	35 \pm 84
<i>H. 'paropius-like'</i>	1979/80	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0.4 \pm 0.8 ^a	0.1 \pm 0.3
	2006	72 \pm 165 ^a	191 \pm 213 ^a	32 \pm 43 ^a	106 \pm 290 ^a	74 \pm 88 ^a	145 \pm 194 ^a	102 \pm 184
	2008	40 \pm 74 ^a	408 \pm 717 ^a	50 \pm 46 ^a	24 \pm 7.4 ^a	74 \pm 91 ^a	33 \pm 49 ^a	105 \pm 308
<i>P. degeni</i>	1979/80	1.8 \pm 3.8 ^{ab}	1.7 \pm 1.8 ^a	0 ^b	0 ^{ab}	0.8 \pm 2.5 ^{ab}	1.0 \pm 1.1 ^{ab}	0.9 \pm 2.1
	2006	20 \pm 21 ^{ab}	9.6 \pm 15 ^{ab}	4.2 \pm 9.7 ^{ab}	4.7 \pm 12 ^a	19 \pm 25 ^{ab}	52 \pm 61 ^b	18 \pm 33
	2008	27 \pm 24 ^{ab}	0.7 \pm 1.2 ^a	2.5 \pm 4.0 ^a	0.2 \pm 0.4 ^a	47 \pm 87 ^{ab}	181 \pm 278 ^b	43 \pm 128
<i>H. xenognathus</i>	1979/80	0	0	0	0	0	0	0
	2006	41 \pm 71 ^a	0.9 \pm 3.0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	7 \pm 32
	2008	26 \pm 44 ^a	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	4 \pm 19

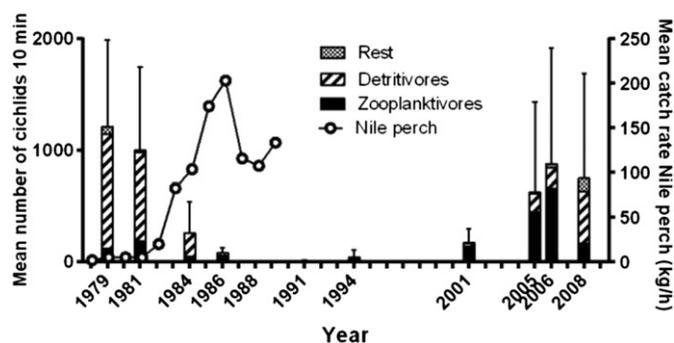


Fig. 2. Mean number of haplochromine cichlids (and standard deviation) in catches of 10 min duration with the small bottom trawler at stations G–J in the Mwanza Gulf from 1979–2008. Sources: Witte et al. 2007a (1979–2005) and present study (2006 and 2008). Nile perch catches in the Mwanza Gulf (kg/h) were derived from Goudswaard et al. (2008). Note that the number of haplochromines in this figure differ from those in Table 2; Table 2 shows the mean number of haplochromines at station E–J.

Abundance and spatial distribution of the main recovering species along the transect prior to and after the environmental changes

Detritivorous species

In 1979/80, *Haplochromis (enterochromis)* 'paropius-like' was caught twice (two fish per haul) on the transect. In 2006 and 2008, a highly significant increase of this species ($P < 0.001$) made it the dominant detritivorous species and the second most abundant species of all haplochromine cichlids on the transect (102, 105 f/h, respectively). Detritivorous species (especially *H.* 'paropius-like') dominated mainly at the deeper stations (9–13 m; Table 3). However, the difference in abundance of this species among the stations was not significant (ESM Table S2). Apart from *H.* 'paropius-like', other un-identifiable detritivorous species including individuals that resembled *Haplochromis (Enterochromis) antleler*, *Haplochromis (Enterochromis) cinctus*, *Haplochromis (Enterochromis) katunzii* and *Haplochromis (Enterochromis) coprologus* were found along the transect in 2006 and 2008.

Zooplanktivorous species

Among the zooplanktivorous species, only *Haplochromis (Yssichromis) pyrrocephalus* was common on the transect in 1979/80 (27 f/h). In 2006, the number of the three zooplanktivorous species (*H. pyrrocephalus*, *Haplochromis tanaos*, *Haplochromis (Yssichromis) laparogramma*) had increased strongly ($P < 0.001$; Table 3). *H. pyrrocephalus* constituted by far the most abundant species (551 f/h) followed by *H. tanaos* (29 f/h) and *H. laparogramma* (17 f/h). The abundance of these three zooplanktivorous species remained similar in 2008 (Table 3). Occasionally, a few individuals of *H. argens* and an unidentified zooplanktivorous species were also found in this area both in 2006 and 2008.

In 1979/80, *H. pyrrocephalus* mainly occupied the deeper stations of the transect especially at station G (Table 3; Goldschmidt et al., 1990). In contrast, in 2006 and 2008 *H. pyrrocephalus* was distributed both in shallow and deep stations but more common at deep stations (Table 3). *H. laparogramma* mainly occurred outside the Mwanza Gulf at depth >20 m during the 1970s and 1980s (Goldschmidt et al., 1990), but in 2006 and 2008 it became a common species along the transect and showed a similar trend in distribution as *H. pyrrocephalus* (though not significant). *H. tanaos* mainly occurred at the shallow sand stations in Butimba Bay (see *H.* 'double stripe' in Witte et al., 1992b; van Oijen and Witte, 1996); but, after its recovery, it became common at the mud stations (mainly station I and J; Table 3). In all sampling years, the abundance of *H. pyrrocephalus* was significantly different among the sampling stations (Table 3; ESM Table S2) while the differences in

abundance among stations for *H. tanaos* were only significant in 2006 and 2008 (ESM Table S2).

Oral mollusk shelling species

In 1979/80, oral mollusk shellers *Platytaeniodus degeni* and *Haplochromis xenognathus* were extremely rare (Table 3). In 2006 and 2008, abundance of *P. degeni* had significantly increased compared to 1979/80 ($P < 0.001$), and it became the most abundant oral mollusk shelling species along the transect (18, 43 f/h in the latter years, respectively; $P < 0.001$) whereas abundance of *H. xenognathus* only increased slightly ($P = 0.014$) and was caught in small numbers mainly at station E (Table 3). In 1970s oral mollusk shelling species mainly occurred in shallow waters over sand bottoms (Witte et al., 1992b) except for *P. degeni* which used to be common both over shallow sand and mud bottoms (Witte et al., 1992b). In 2006 and 2008, this species was common at shallow mud stations E and J but also extended their distributions to deeper stations (Table 3; ESM Table S2). The abundance of *P. degeni* was significantly different among the sampling stations in all the sampling years (ESM Table S2) while for *H. xenognathus* the differences in abundance among the sampling stations were significant only in 2006 and 2008 (ESM Table S2). Occasionally, other oral mollusk shellers species e.g. *Haplochromis (Ptyochromis) fischeri* and *Haplochromis (Paralabidochromis) plagiodon* were found at station E in 2006 and 2008.

Discussion

This study shows that at least 27 out of 72 haplochromine cichlid species had recovered by 2006/2008 to levels observed in 1979/80; period prior severe environmental changes occurred in the 1980s.

The trophic composition decreased from 12 to nine trophic guilds with detritivores, zooplanktivores and oral mollusk shellers being the most abundant. The originally dominant detritivores declined faster than the zooplanktivores (Fig. 2) during the period of severe environmental changes. In 1986, just before the complete collapse of the haplochromines, the zooplanktivores were the most common trophic guild (Fig. 2). From the beginning of the recovery of haplochromines in the early 1990s, zooplanktivores had remained the dominant trophic group along the transect and their densities became even higher than in the 1970s. In 2008, however, the composition reversed back to a dominance of detritivores (Table 2; Fig. 2). The relative abundances of zooplanktivores and detritivores in 2011 (J.C. van Rijssel and F. Witte, pers. obs.) 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.

In the 1970s, distribution patterns of haplochromines with relation to depth were more distinct at the species level than at the trophic group level (Witte, 1981; Witte et al., 1992b). Within each trophic group, species specific distribution patterns seemed to be determined by bottom type and water depth which suggested that species were (partly) excluding each other (Witte, 1981; Goldschmidt et al., 1990; Witte et al., 1992b). All the species of the three abundant trophic groups have shown an extension of their habitat to shallower and/or deeper waters. The detritivores *H.* 'paropius-like' (mainly responsible for the increase of the detritivores) extended their habitat from shallow station J to all other stations on the transect and dominated the deeper stations. A similar distribution pattern was observed in 2011 (J. C. van Rijssel and F. Witte, pers. obs.). The zooplanktivores *H. pyrrocephalus* and *H. laparogramma* extended their habitat to shallower stations while the zooplanktivore/insectivore *H. tanaos* also extended its habitat to deeper stations. *P. degeni* (mainly responsible for the increase of oral mollusk shellers) and *H. xenognathus* both showed an extension of their habitat from shallow sand habitat (Witte et al., 1992b) to deeper mud habitat. In contrast, the least abundant trophic group, the piscivores, showed a reduced habitat range compared to that before

the environmental changes. The rest group was more abundant in 2006 and 2008 than in 1979/80 and there seems to be a habitat shift towards the shallower mud stations. However, the increase in abundance is 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, especially at the shallow stations E and J. This partly may have been caused by hybridization due to the environmental changes (De Zeeuw et al., 2010).

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

Impacts of Nile perch predation

The catches of the Nile perch started rising sharply in the 1980s in the Mwanza Gulf and concomitantly the haplochromines declined (Fig. 2; Goudswaard et al., 2008; Witte et al., 2007a). Since the turn of the century, Nile perch biomass in Lake Victoria has declined substantially (Mkumbo, 2002; Matsuishi et al., 2006; Kayanda et al., 2009). However, Kolding et al. (2008) reported no significant fluctuations in the catch per unit effort of Nile perch since 1997 for the Tanzanian waters. This may indicate that, despite increased fishing effort, Nile perch numbers remained relatively high in this part of the lake. Unfortunately, the only study that quantified Nile perch catches in the Mwanza Gulf shows data up to 1990 only (Goudswaard et al., 2008). As there are no reasons to expect trends in Nile perch abundance in the Mwanza Gulf to be different from elsewhere in the lake, we assume that the increase in catches up to 1990, as shown in Fig. 2, was followed by a decrease after the year 2000. Hence, the observed resurgence of some haplochromine species during the 2000s, could well be a response to a decline of Nile perch in Mwanza Gulf.

Our observations from the Mwanza Gulf do not form the only support for Nile perch predation as a cause of haplochromine recovery. A similar pattern of haplochromine loss and recovery in relation to Nile perch up-surge and decline was also observed in other areas of the Lake Victoria basin (Balirwa et al., 2003; Getabu et al., 2003; Chapman et al., 2003; Paterson and Chapman, 2009). In Lake Nabugabo for instance; a small lake which was isolated from Lake Victoria about 5000 years ago and where Nile perch had also been introduced (Pringle, 2005), the haplochromines also declined strongly with increasing Nile perch population (Ogotu-Ohwayo, 1993; Chapman et al., 1996) and haplochromine resurgence coincided with a decline of Nile perch (Chapman et al., 2003; Paterson and Chapman, 2009).

Adaptive responses

Despite the severely changed environmental conditions, some haplochromines were able to recover (Witte et al., 2007b) by adjusting ecologically and morphologically to the altered environment in the Mwanza Gulf (Witte et al., 2008; van der Meer et al., 2012; van Rijssel and Witte, 2013; van Rijssel et al., 2015). The environmental and ecological change seems to have induced fast (within 3 years) adaptive responses of the studied haplochromines in the Mwanza Gulf (van Rijssel, 2014; van Rijssel et al., 2015). The increased predation by Nile perch is suggested to have inflicted a smaller head-caudal peduncle region in several haplochromine species (van Rijssel and Witte, 2013). A smaller head-caudal peduncle region has been shown to be beneficial for survival in a predatory environment in several fish species like three-spined sticklebacks, guppies and mosquitofish (Hendry et al., 2006, 2011; Langerhans et al., 2004; Langerhans, 2009). The increase of macro-invertebrates and the small cyprinid fish dagaa (Witte et al., 1992a; Wanink, 1999; Goudswaard et al., 2006) created an opportunity for detritivorous and zooplanktivorous haplochromines to switch to these larger-sized preys (van Oijen and Witte, 1996; Katunzi et al., 2003; Kishe-Machumu et al., 2008). These larger preys are likely the reason why several haplochromine species showed a larger cheek depth and a premaxilla adapted to a more biting like feeding style (Witte et al., 2008; van Rijssel and Witte, 2013; van Rijssel et al.,

2015). Eutrophication also resulted in lower dissolved oxygen levels (Wanink et al., 2001) which are suggested to be responsible for the increase in gill surface of several haplochromine species (Witte et al., 2008; van Rijssel, 2014). The decrease in water transparency could be another reason for why the haplochromines shifted towards larger prey. In addition, the eyes of two haplochromine species showed possible adaptive responses in their retinal features as a response to the murky water (van der Meer et al., 1995, 2012). The effect of turbid water on the feeding strategy is well illustrated by the oral mollusk shelling species. The oral mollusk shellers *P. degeni* and *H. fischeri* revealed a strong decline in shelling efficiency at low light intensities during a laboratory experiment (88% and 76% respectively; Witte et al., 2013). It should be noted that in the pre-collapse period, *P. degeni* was not exclusively a mollusk sheller species because its diet consisted of a considerable amount of detritus and fewer mollusks (6–32% of food volume) than for the other oral mollusk sheller species *H. fischeri*. Thus, *P. degeni* was not as dependent on high light for shelling, and this may have facilitated its extension into deeper water.

It is still unclear whether the observed morphological changes are the result of genetically based changes or phenotypic plasticity. Nonetheless, the ability of these haplochromines to respond ecologically and morphologically very fast to environmental changes (van Rijssel, 2014) is likely to have facilitated their recovery. In addition, some of the environmental changes seem to be less harsh during the 2000s including higher oxygen levels and water transparency (Sitoki et al., 2010; van Rijssel, 2014) which also might have played a role in the continuation of recovery of the haplochromines.

Habitat extension

The resurgent species of the three trophic groups (detritivores, zooplanktivores and oral mollusk shellers) showed an extension of their habitat. Before the environmental changes in 1980s, the zooplanktivore *H. tanaos* mainly occurred at the shallow sand stations in the transect (see *H. 'double stripe'* in Witte et al., 1992b; van Oijen and Witte, 1996), but in 2000s after its resurgence it became common at the shallow mud stations especially stations I and J (Table 2; van Oijen and Witte, 1996; Seehausen et al., 1997b). The detritivorous *H. 'paropus like'* was only caught twice in 1979/80 along the transect; whereas, in 2006, 2008 and 2011, it was abundant at all stations without a clear distribution pattern. In 2011, the species dominated especially at the deeper stations G, H, I. The oral mollusk sheller *H. xenognathus*, was a typical sand dweller. However, in 2006, 2008 and 2011, it was common at mud bottom stations. In contrast, *P. degeni* was caught over both sand and mud at stations up to 10 m depth in 1979–1982 (Table 2; Witte et al., 1992b). In 2006, 2008 and 2011, the number of *P. degeni* had increased strongly and they were caught at all shallow mud stations of 9–10 m deep. Ecological adaptations, for example the retina structure in some resurgent species that have become adapted to the relatively low light conditions (van der Meer et al., 2012), may have facilitated its extension into mud and in deeper water. Habitat extensions could be among the factors responsible for the recovery of some haplochromine species.

In conclusion, this study reveals a strong resurgence of some haplochromine species along a research transect in Mwanza Gulf. The study suggests that a successful recovery of some haplochromine trophic guilds and species may possibly be a consequence of a decline in Nile perch population, morphological and ecological adaptations to the altered environment and habitat extension. However, it is not yet possible to draw a final conclusion on the status of the recovery of haplochromines and their differential in recovery in Lake Victoria at large. Thus, further studies in other areas with different degrees of environmental changes and different stages of Nile perch colonization should be conducted to evaluate the recovery status lake-wide and for management of the lake.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2015.03.005>.

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