Reviews in Fish Biology and Fisheries **10:** 233–241, 2000.
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Points of view

Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction

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Accepted 14 August 2000

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Key words: biodiversity, eutrophication, extinction, haplochromine cichlids, hypoxia, *Lates niloticus*, predation, reproduction, retinal structures, zooplanktivores

Introduction

Lake Victoria, the world's largest tropical lake by area, had a fish fauna that was dominated until recently by more than 500 species of haplochromine cichlids (Greenwood, 1981; Witte et al., 1992; Kaufman and Ochumba, 1993; Seehausen, 1996). In the 1950s, the Nile perch (*Lates niloticus*, Centropomidae), a large-growing predator, was introduced into the lake. Its population rapidly increased in the 1980s, whereas simultaneously approximately 200 haplochromine cichlid species vanished (Ogutu-Ohwayo, 1990; Witte et al., 1992). Although environmental changes and local overfishing played a role in the decline of the haplochromines (Witte and Goudswaard, 1985; Hecky, 1993; Bundy and Pitcher, 1995; Seehausen et al., 1997a), Nile perch likely was a key factor in this decline in sublittoral (6–20 m deep) and offshore (>20 m) waters (Witte et al., 1992).

More than 110 haplochromine species belonging to 12 trophic groups had been collected from the sublittoral waters in the Mwanza Gulf between 1978 and 1982 (Witte, 1981). By 1987 almost 100 species had vanished and the contribution of haplochromine cichlids to the demersal ichthyomass had decreased from more than 90% to less than 1% (Witte et al., 1992). During the following years, few haplochromines were caught in sublittoral areas, but a slow increase of both individuals and species was observed between 1991 and 1995 (Seehausen et al., 1997b; Witte et al., 1999). Similar observations had been made in other areas of the lake after reduction of Nile perch, without specifying species or trophic groups that recovered (CIFA, 1990). After 1995, the haplochromines in

the Mwanza Gulf were no longer monitored systematically. However, through local fishermen and fishery researchers we heard that the amounts of haplochromines in the catches increased. Examination of several catches in 1997 and 1999 indeed revealed a substantial upheaval of two zooplanktivorous species in the sublittoral areas, whereas other species remained rare or absent. Processes involved in extinction are rarely well documented because ecological data of species in a community *prior to* and *during* the disturbance that causes extinction are often lacking. In particular for tropical ecosystems, the fish fauna of Lake Victoria offers one of the rare cases where these requirements are met. Here, we describe the resurgence of the two zooplanktivores and suggest explanations for differences in survival and extinction among closely related species.

Data on changes in species composition between 1978 and 1999

Bottom trawl catches in the northern part of the Mwanza Gulf

Since 1979, bottom trawl catches have been made by a small research vessel along a research transect in the Mwanza Gulf (Figure 1; Witte et al., 1992). At 4 stations (7–14 m depth), where densities of zooplanktivorous haplochromines were high till the end of the 1970s, almost no haplochromines at all were caught in 1987/88 (Witte et al., 1992). From 1991 on, we observed a recovery of the zooplanktivores *Haplochromis* (*Yssichromis*) *pyrrhocephalus and H. (Y.) laparogramma* at these stations (Table 1; Seehausen et al., 1997b). The same species were the most common haplochromines and the only zooplanktivores in two trawl shots at the entrance of Nyegezi Bay (6–8 m depth) in November 1997 and July 1999.

A bottom trawl catch on 8 November 1997 made with a large trawler in the northern part of the Mwanza Gulf (9–13 m depth), which previously had been thoroughly studied with similar vessels, supported the observations on recent changes in species composition (Table 2): In 1978, haplochromines dominated the demersal stock (92% of the total ichthyomass) and Nile perch was almost absent. In spite of intensive sampling, in 1987 haplochromines were hardly present in the catches and 97% consisted of Nile perch. Concomitantly, the mean total catch rate had decreased from ca. 1100 to 200 kg h^{-1}. In the sample taken in 1997, the contribution of Nile perch had decreased to 76%, while that of haplochromines had increased to 21%, however, the total catch rate (199 kg h^{-1}) remained low.

In 1978, about 60% of the demersal haplochromine biomass consisted of detritivores/phytoplanktivores (more than 10 species, dominated by *H. (Enterochromis)* "nigrofasciatus", *H. (E.) cinctus, H. (E.)* "75" and *H. (E.)* "dusky wine red fin") and 30% of zooplanktivores (12 species, mainly *H. (Y.) heusinkveldi, H. (Y.) pyrrhocephalus, H. (?) piceatus* and *H. (?)* "argens"). In the 1997 sample, the haplochromines were dominated by zooplanktivores (84%), of which *H. (Y.) pyrrhocephalus* and *H. (Y.) laparogramma* were the only representatives. The abundance of *H. (Y.) laparogramma* in the Mwanza Gulf is now higher than before 1982, when the species mainly occurred outside the gulf at depths of 20–30 m (Goldschmidt et al., 1990). Detritivores/phytoplanktivores comprised only 15% of the haplochromine catch in 1997 and consisted mainly of *H. (E.)* "straight cinctus" and *H. (E.)* "dusky wine red fin".

In total, we caught about 20 haplochromine species in the period 1991–1999 in the sublittoral area of the Mwanza Gulf, where formerly more than 110 species were present. Apart from the zooplanktivores and detritivores/phytoplanktivores, these survivors include some species of insectivores and molluscivores (Seehausen et al., 1997b; F. Witte. unpublished data).

Fish landings of nocturnal light fishery in the Speke Gulf

Data of commercial fish landings in the Speke Gulf corroborate the above observations. In 1997 and 1999, we inspected some catches of the nocturnal light fishery on *Rastrineobola argentea*, a zooplanktivorous cyprinid. On 7 November 1997, two samples of ca. 2 kg were taken from the catches of two lift net fishermen at a landing site near Igombe (Figure 1). In one sample, the zooplanktivore *H. (Y.) laparogramma* comprised 64% of the weight, while 33% consisted of *R. argentea* and 3% of juvenile (up to 5 cm TL) Nile perch. In the other sample, *H. (Y.) laparogramma* comprised 30% and *R. argentea* 70%. Three drying fields of fishermen using encircling nets were inspected as well; two on 10 November 1997 at Nyamikoma and one on 25 July 1999 near Kalemera

Table 1. Mean number of haplochromines[a] (± standard deviation) in bottom trawls (head rope 4.6 m, codend mesh 15 or 5 mm[b]) of 10 minutes duration at 4 stations (G to J, 7–14 m deep) on the transect across the Mwanza Gulf

Year	1979	1987–1988	1990–1992	1993–1995	1999
number of hauls	37	18	9	24	1
Main trophic groups					
Detritivores/phytopl.	1096.7 ± 720.4	0.0	0.7 ± 1.4	16.1 ± 39.4	0
Zooplanktivores	149.8 ± 229.1	0.7 ± 1.5	5.0 ± 12.1	24.6 ± 41.6	12
Others	67.5 ± 49.6	0.0	0.0	1.7 ± 3.3	0
Main zooplanktivores					
H. (Y.) heusinkveldi	42.2 ± 84.0	0.0	0.0	0.0	0
H. (Y.) pyrrhocephalus	47.2 ± 149.5	0.0	1.9 ± 4.2	20.0 ± 38.0	12
H. (Y.) laparogramma	0.3 ± 1.1	0.7 ± 1.4	3.1 ± 7.9	4.6 ± 6.1	0
H. (?) piceatus	35.2 ± 71.5	0.0	0.0	0.0	0
H. (?) "argens"	5.9 ± 11.9	0.1 ± 0.2	0.0	0.0	0

[a]Only (sub)adult fish of 4 cm standard length or longer are included, to compensate for different codend meshes. [b]In 1979 an extra 5 mm codend, that was fixed over the 15 mm codend, was left open when trawling at these stations. From 1987 onwards the 5 mm codend was closed, resulting in relatively high numbers of juveniles.

Table 2. Mean catch size and composition of large bottom trawls (codend mesh 20 mm) in the northern part of the Mwanza Gulf (7–15 m deep) between Nyegezi and Kissenda bays

Year	1978	1987	1997
number of hauls	7	69	1
Catch in kg h^{-1}	1156[a]	214[b]	199[c]
% of total catch weight			
Lates niloticus	0.1	97.0	76.2
Haplochromines	92.3	0.2	21.3
Other species	7.6	2.8	2.4
% of total nr of haplochromines[d]			
Detritivores/phytoplanktivores	61.1	3.6	14.9
Zooplanktivores	29.6	96.4	83.9
Others	9.3	0.0	1.2
Nr h^{-1} (± st.dev) of main zooplanktivores			
H. (Y.) heusinkveldi	21 806 ± 15 634	0.1 ± 0.6	0
H. (Y.) pyrrhocephalus	15 987 ± 9 873	0.6 ± 2.3	10 760
H. (Y.) laparogramma	0	18.0 ± 39.5	805
H. (?) piceatus	7 615 ± 14 970	0	0
H. (?) "argens"	2 089 ± 3 326	0	0

Head ropes respectively 25 m[a], 18 m[b], 22.6 m[c]. Catch duration respectively 45[a], 30[b] and 45[c] minutes. All data were transformed to catch per hour with a 22.6 m headrope. Speed of the trawlers was *ca.* 3 nautical miles per hour. [d]Data from 1987 were based on 32 (out of 69) hauls in which haplochromines were identified to the species level.

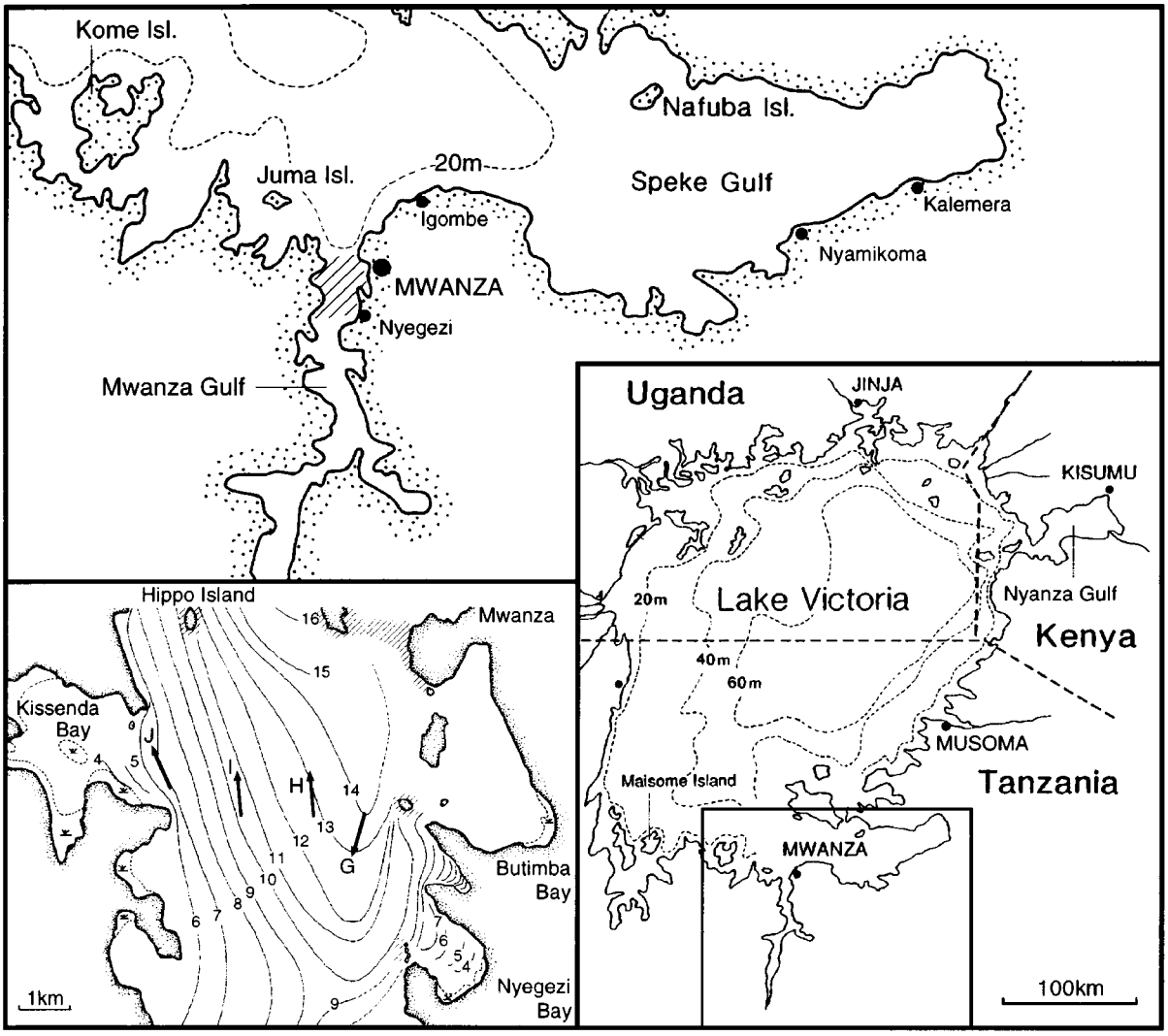

Figure 1. Map of the study area. Left inset corresponds with hatched area in the Mwanza Gulf in the top panel. The area between Nyegezi and Butimba bays was fished with large trawlers (see Table 2). The stations G, H, I, J were sampled with the small trawler (see Table 1).

(Figure 1). Between 50 and 90% of the drying fish consisted of the zooplanktivorous haplochromine *H. (Y.) pyrrhocephalus*, the remainder being mainly *R. argentea* and a few detritivorous haplochromines. The fishermen told us that only during the past few years (as far as we could ascertain since 1995) zooplanktivorous haplochromines had become common in their catches.

Discussion

Effects of predator decline

Before the 1980s all piscivorous fish species together, made up less than 10% of the ichthyomass in the Mwanza Gulf (Witte et al., 1999), but after the Nile perch boom this became more than 90%. Although currently Nile perch still comprises more than 50% of the catch weight, the density has declined due to heavy fishing pressure (Pitcher and Bundy, 1995; O.C. Mkumbo pers. comm.). This decline coincided with the recovery of some haplochromine species. Recent observations in Lake Nabugabo also showed a resur-

gence of haplochromines after a decline in Nile perch due to overexploitation (Rosenberger and Chapman, 1999; L.J. Chapman pers. comm.). In the man made Gatun Lake (Panama) there was a reduction of more than 99% of individual fishes (Zaret, 1979) and a local extermination of 13 of 17 native fish species (Zaret, 1982) after introduction of the predator *Cichla ocellaris*. In Chagres River, a tributary to Gatun Lake, the native species were not exterminated (Zaret, 1979) and, subsequent to a decline in *C. ocellaris* in the lake, all species, except perhaps for one, recolonized the lake (Welcomme, 1988; pers. comm.). Hence, the resurgence of some haplochromine species in Lake Victoria might be a response to the decline in predation pressure.

Predictions about survival and recovery of haplochromines

A bioenergetics model for Lake Victoria did predict the recovery of haplochromines with increasing exploitation of Nile perch (Kitchell et al., 1997), but it could not predict which species were likely to revive. At the onset of the Nile perch upheaval, it was predicted that the partly pelagic distribution of the zooplanktivores would make them relatively insusceptible to predation by bottom dwelling Nile perch (Witte and Goudswaard, 1985). The zooplanktivores were indeed the last haplochromine species surviving in sublittoral areas, but in 1987 they too had almost vanished, including the predominantly surface dwelling *H. (?) "argens"* which had least habitat overlap with Nile perch (Tables 1, 2; Goldschmidt et al., 1990; Wanink, 1991; Witte et al., 1992). The prediction took account of Nile perch predation only, but surviving species must also cope with other environmental changes. Eutrophication, algal blooms and decreased water transparency and oxygen concentrations were observed in the 1980s (Ochumba and Kibaara, 1989; Kaufman, 1992; Hecky, 1993; Hecky et al., 1994; Mugidde, 1993; Seehausen et al., 1997a; Wanink et al., 2000). Hence, rather than predation alone, several factors could affect the risk of extinction – and the potentials for survival – of haplochromines.

Potentials of comparative studies on closely related species

Comparative studies on pairs of closely related species, of which one disappeared and the other survived, may help to understand to what extent survival is stochastic or deterministic and, when deterministic, may elucidate the factors that determine susceptibility to extinction. In our research area *H. (Y.) heusinkveldi*, which disappeared, and the recovering *H. (Y.) pyrrhocephalus* represent such a pair of species. They are morphologically similar, had nearly identical distribution patterns (Goldschmidt et al., 1990) and were equally abundant before the Nile perch upsurge (Tables 1, 2). They differed mainly in male coloration (grey blue versus orange red). A preliminary comparison of features which may be relevant with regard to the observed environmental changes, e.g. the functional morphology of their visual and respiratory apparatus, and aspects of their life history, revealed the following: (1) At the end of the 1970s, viz. before their decline, there was no significant difference in gill surface between the two species (M. Heemskerk, I. van der Stap and F. Witte, unpublished data); (2) The retina of *H. (Y.) pyrrhocephalus* mainly consisted of large double cones in low densities, whereas that of *H (Y.) heusinkveldi* had small double cones in high densities (Figure 2; van der Meer et al., 1995; van der Meer and Bowmaker, 1995). The rod density in *H. (Y.) pyrrhocephalus* was approximately 15% higher than in *H. (Y.) heusinkveldi* (van der Meer et al., 1995); (3) *H. (Y.) pyrrhocephalus* spawned all-year-round with a peak between July and November, at depths less than 9 m, while *H. (Y.) heusinkveldi* had a more distinct spawning peak between June and August, at depths between 8 and 14 m (Figure 2; Goldschmidt and Witte, 1990). Percentages of ripe females in *H. (Y.) heusinkveldi* were significantly higher during the period with relatively clear water (April–September, Mann-Whitney *U*-test, $p = 0.01$), whereas in *H. (Y.) pyrrhocepohalus* this was not the case (Mann-Whitney *U*-test, $p = 0.15$).

The higher number of smaller double cones in *H. (Y.) heusinkveldi* could result in a higher visual resolution, at the cost of a higher photopic threshold, and has been interpreted as an adaptation to detection of small food items (van der Meer et al., 1995). In *H. (Y.) heusinkveldi* 20 to 40% of the diet consisted of relatively small phytoplankton and in *H. (Y.) pyrrhocephalus* less than 5% (Goldschmidt et al., 1990).

Due to its larger double cones, which are long wavelength sensitive, *H. (Y.) pyrrhocephalus* likely had a higher sensitivity to light in general, and red light in particular, than *H. (Y.) heusinkveldi* (van der Meer et al., 1995; van der Meer and Bowmaker, 1995). Also compared to other haplochromine species (including *H. (?)* "argens" and *H. (?) piceatus*), *H. (Y.) pyrrhocephalus* had large double cones, whereas

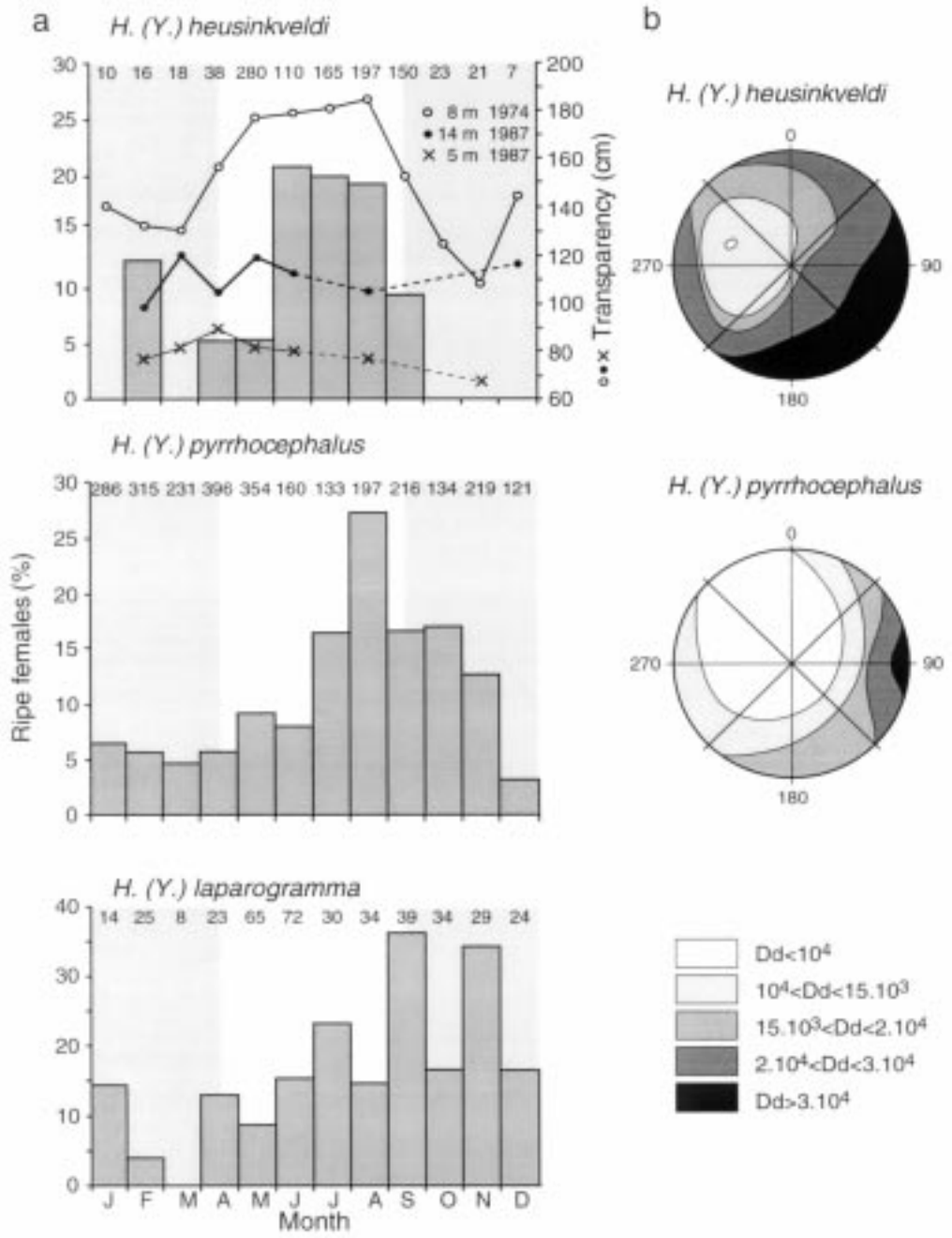

Figure 2. (a) Percentage of ripe females of *H.(Y.) heusinkveldi, H. (Y.) pyrrhocephalus* and *H.(Y.) laparogramma* collected at a station of 14 m depth between March 1983 and October 1984. Mouth brooding females of *H.(Y.) heusinkveldi* (n = 40) collected during the period 1979–1982 at depths between 8 and 14 m confirm the pattern depicted above, as 90% were found between April and September (F. Witte, unpublished data; no data for *H. (Y.) pyrrhocephalus*). Included in top panel: water transparency (Secchi values) per month measured in the Mwanza Gulf in 1974 at 8 m depth (adapted from Akiyama et al., 1977) and in 1987 at stations of 5 and 14 m depth (after J. J. Kashindye and J. H. Wanink, unpublished). At the 14 m station, Secchi values between 20 February and 15 April 1980 ranged from 2.4 to 2.8 m (mean 2.5 $\pm$ 0.2, n = 5). Shaded areas indicate periods with relatively murky water in 1974. Assuming that the measured seasonality in spawning activity and in water transparency are representative for average years, we tested for difference in ripe females in months with relatively high (April–September) and low transparency (October–March): Mann-Whitney U-test, p = 0.01 for *H. (Y.) heusinkveldi*, p = 0.15 for *H. (Y.) pyrrhocephalus*, p = 0.63 for *H. (Y.) laparogramma*. (b) Patterns of double cone density (Dd, number per mm^2) in *H. (Y.) heusinkveldi* and *H. (Y.) pyrrhocephalus*. Patterns of cone size are reversed to those of cone density (adapted from van der Meer et al., 1995).

the spectral sensitivity of its visual pigments in double cones and rods appeared shifted to significantly longer wavelengths (van der Meer and Bowmaker, 1995). These features seem advantageous for visual observation of prey, predators and mates, in areas where eutrophication caused a decrease in light penetration, in particular of short wavelength (Seehausen et al., 1997a). It may also explain why, before the ecological changes, spawning activities of *H. (Y.) pyrrhocephalus* may have been less constrained by water transparency than those of *H. (Y.) heusinkveldi* (Figure 2). Spawning activity of *H. (Y.) laparogramma* did not coincide with periods of high water transparency either (Figure 2). The size of the double cones of this species is intermediate to that in *H. (Y.) heusinkveldi* and *H. (Y.) pyrrhocephalus* (van der Meer et al., 1995), but we have no information on its rods or visual pigments nor on its spawning sites (Goldschmidt and Witte, 1990).

Vision seems to be important in haplochromine reproduction for courtship behaviour, picking up of the eggs by the mouth brooding female, and for fertilization (Fryer and Iles, 1972). The need for fairly clear water for reproduction in Lake Victoria haplochromines is supported by the observation that, before their eradication, most cichlids in the sublittoral area in the Mwanza Gulf spawned during the dry season, when water transparency in this area became temporarily high (Witte et al., 1999). In contrast, in shallow sandy and rocky habitats, which are relatively clear, most haplochromines spawned year-round (Witte, 1981; Seehausen et al., 1998).

Turbidity constrains colour vision and interferes with mate choice, based on male coloration, which maintains reproductive isolation between sympatric closely related species (Seehausen et al., 1997a; Seehausen and van Alphen, 1998). Hence, introgression of *H. (Y.) heusinkveldi* into *H. (Y.) pyrrhocephalus* after strong reduction in water transparency could also provide a possible explanation for the disappearance of the *H. (Y.) heusinkveldi* phenotype.

Apart from extant anatomical and ecological differences, differences in phenotypic plasticity or evolvability of anatomical, ecological, or life history traits may have been crucial in determining survival, recovery or extinction in the changed environment. Preliminary investigations show that between 1978 and 1999 the average number of secondary gill lamellae in *H. (Y.) pyrrhocephalus* increased by ca. 25% (M. Heemskerk, I. van der Stap and F. Witte unpublished data). This is speculated to be a response to increased hypoxia. Indications of an increase in gill surface between 1983 and 1988 have also been observed for *R. argentea* (Wanink and Witte, 2000). The increase in fecundity observed in *H. (Y.) pyrrhocephalus* and *H. (Y.) laparogramma* between 1983 and 1988 (Wanink, 1991) may have been a response to increased predation pressure. It is one of the common reproductive tactics when adult mortality increases (e.g. Stearns, 1992). No sufficient data on fecundity over the same period were available for *H. (Y.) heusinkveldi*.

Possible effects of the recovery of zooplanktivorous haplochromines

The recovery of zooplanktivorous haplochromines is likely to be a lake-wide phenomenon, as *H. (Y.) laparogramma* and *H. (Y.) fusiformis* (a species that was never found in the southern part of the lake) are currently also common in the Ugandan and Kenyan waters (Tumwebaze, 1997; Ogutu-Ohwayo, 1999; L. Kaufman, W. Ojwang and S. Wandera pers. comm.). In contrast to the 1970s, zooplanktivorous haplochromines are now more common than detritivores/phytoplanktivores. The effects on the ecosystem of the recovery of predominantly zooplanktivores are still unknown. Through competition the zooplanktivorous haplochromines may cause a decline of the *R. argentea* population, which had increased substantially after the decline of the haplochromine cichlids in the 1980s (Wanink, 1991, 1999; Wanink and Witte, 2000). Alternatively, an increase of the total zooplanktivorous ichthyomass might, through cascading effects, further enhance phytoplankton growth (Ogutu-Ohwayo, 1999), which in turn may influence water turbidity and oxygen concentrations. However, the current dominance of zooplanktivores may be only an intermediate stage in the process of resurgence of sublittoral cichlid stocks. Detailed field and laboratory studies on the recovering haplochromines are urgently needed to contribute to our understanding of biotic and abiotic factors leading to differential extinction in species rich communities, and to reveal the potential effects of changes in species composition on the ecosystem.

Acknowledgements

We are grateful to Prof. P.O.J. Bwathondi and the staffs of TAFIRI and the Nyegezi Fisheries Training Institute for their support during many years of fieldwork. We thank Kees Barel, Jennifer Nielsen, Jacques

van Alphen and three anonymous referees for comments on earlier drafts of this paper. The fieldwork was financially supported by WOTRO, by the section DPO of the Netherlands Ministry of Foreign Affairs and by the Tetra Company. The visit of F.W. to Tanzania in 1997 was paid by Chubu Nippon Broadcasting Co., Ltd.

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