Patterns of the Remnant Cichlid Fauna in Southern Lake Victoria

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Abstract: *During the years 1984–1987 Lake Victoria in East Africa experienced what is probably the largest mass extinction of contemporary vertebrates. Within a decade about 200 endemic species of haplochromine cichlids disappeared. The extinctions that occurred in the 1980s have been documented predominantly on species of offshore and sub-littoral waters in the Mwanza Gulf of southern Lake Victoria. Although the littoral fauna of southern Lake Victoria had not been examined in detail, their diversity seemed less affected by the changes in the ecosystem. We give results of the first comprehensive inventory of the littoral cichlid fauna in southern Lake Victoria and discuss its conservation status. We also report on new developments in the sub-littoral fauna after 1990. More than 50 littoral and 15 sub-littoral stations were sampled between the years 1991 to 1995. Of the littoral stations, 34 were sampled for the first time. One hundred sixty three species of haplochromines were collected. Of these, 102 species were previously unknown. About two thirds of them live in rocky areas that were sampled for the first time. Littoral rocky habitats harbored the highest diversity. Since 1990, however, 13 more species disappeared from established sampling stations in littoral habitats. Fishing practices, spreading of exotic fishes, water hyacinth, and eutrophication are considered important threats to the littoral fauna. Also in the upper sub-littoral the number of species declined further. On deeper sub-littoral mud bottoms individual and species numbers increased again, although they are nowhere close to those found before the Nile perch (*Lates niloticus*) upsurge. This fauna differs from the well studied pre-Nile perch fauna. At well-established sampling stations, the sub-littoral zone is dominated by previously unknown species, and some known species have performed dramatic habitat shifts.*

Patrones de la Fauna de Cíclidos Remanentes en el Sur del Lago Victoria

Resumen: *Probablemente el Lago Victoria en Africa oriental está experimentando la mayor extinción de vertebrados contemporáneos. Durante una decada desaparecían aproximadamente 200 especies de cíclidos haplochrominos. El proceso de extinción en los años 80 se documentaba predominantamente, de especies que habitan aguas de mar adentro y sublitorales del Golfo de Mwanza situado en el sur del Lago Victoria. La fauna litoral de esta zona no se consideraba en detalles y ella parece menos afectada por cambios en el ecosistema. Aqui estamos dando el primer resumen general sobre la fauna litoral del Lago Victoria de sur y su estado de conservación. Además informamos sobre desarollos importantes en la fauna sublitoral desde 1990. Comparamos nuestros datos con datos recién publicados respecto al norte del Lago Victoria. Desde 1991 hasta 1995 investigábamos más de 50 estaciónes litorales (34 for the first time) y 15 estaciónes sublitorales. Colectábamos 163 especies haplochrominos de las cuales 102 especies antes eran desconocidas. Aproximadamente dos tercer partes de las nueves especies habitan estaciónes rocosas investigadas por primera vez. El habitat rocoso litoral aloja la mayor diversidad. No obstante investigaciónes siguientes revelaron que la diversidad de especies en aguas poco profundas decrecía considerablemente avanzados añs 80. Desde el último reportaje que trataba el período hasta 1990, 13 especies más han desaparecido de establecidos estaciones de investigación de HEST. Prácticas de pesca, extensión de malezas y peces exoticos y eutroficación son consid-*

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erados como los impactos más importantes a la fauna litoral. Por contraste el número de individuos y especies subía sobre fondos fangosos sublitorales, pero la composición se distingue de la fauna que existía antes de la explosión demográfica de la Perca de Nil. Ahora la fauna está dominada por especies previas desconocidas y algunas especies conocidas desempeñan un dramatico cambio del habitat.

Introduction

The spectacular decline of one of the world's largest vertebrate species assemblages, the cichlid species flock of Lake Victoria, has been the subject of many publications since 1985 (Barel et al. 1985). However, only much more recently quantitative details of the extinction process became available for southern Lake Victoria (Witte et al. 1992; Goldschmidt et al. 1993). Sound conservation planning and management of this lake requires a geographically comprehensive biotic inventory (Kaufman & Ochumba 1993). Kaufman (1992) and Kaufman and Ochumba (1993) present an overview of the results obtained by Uganda and Kenya-based Lake Victoria Research Team (LVRT) during the years 1989–1992, which describes the current state of the indigenous fauna of littoral, sub-littoral, benthic, and pelagic communities in northern parts of the lake. Unfortunately, solid data from the pre-Nile perch (*Lates niloticus*) situation in that region are scarce. Thus changes from the pre-Nile perch to the post-Nile perch ecosystem can only partly be documented (Kaufman & Ochumba 1993). In the south the upsurge of the Nile perch and the concomittant decline of the haplochromines started several years later than in the northern part of the lake (Witte et al. 1995). Both the pre- and post-Nile perch situation is rather well known, at least for the sub-littoral communities, allowing us to quantitatively examine the extinction process (e.g., van Oijen et al. 1981; Witte 1981). However, the data only extends to 1990. Furthermore, no studies had been made to date about the littoral communities. We sought to bring our knowledge of the southern situation up to date and to collect information from southern littoral communities.

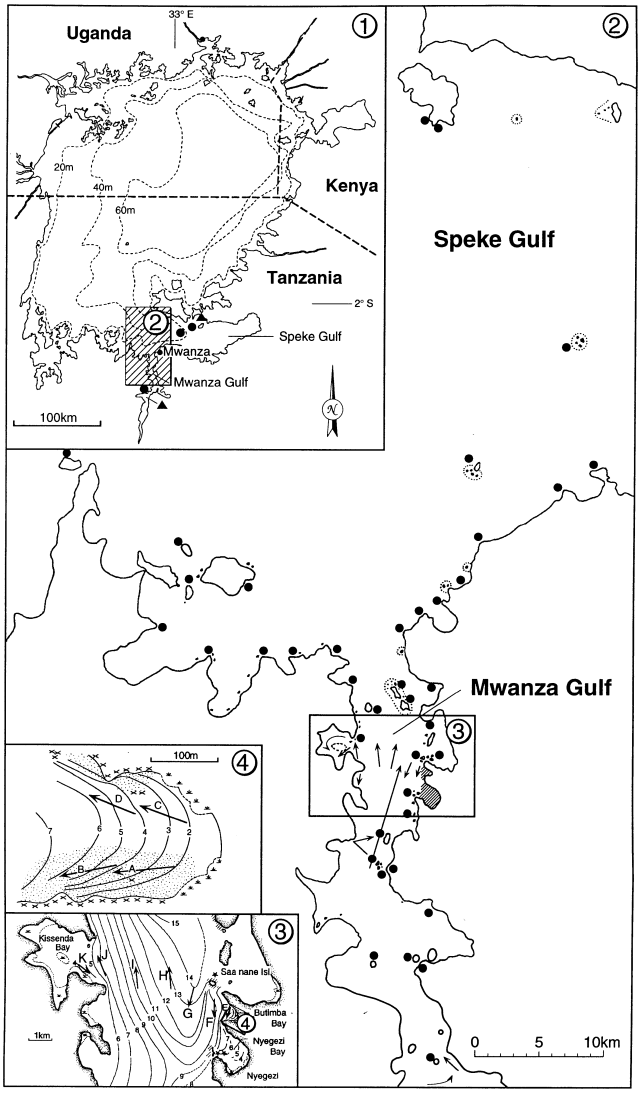

Figure 1. Lake Victoria (1), the research area with the sampling stations (2), and the research trawl transect (3 and 4). Numerals indicate the position relative to the research area and Lake Victoria of areas shown enlarged in the insets. Black dots indicate littoral sampling stations. Arrows and triangles indicate sub-littoral trawl sampling stations, the length of arrows indicates the approximate length of trawl shots. Butimba and Nyegezi Bays (hatched area in 2) were sampled all over, so individual stations are not indicated apart from those that are part of the trawl transect (3, 4).

Methods

Sampling was done by trawl, seine, gill net, and angling rod. The trawl sampling stations along a transect across the Mwanza Gulf (Fig. 1) as well as gear and sampling techniques are described in van Oijen et al. (1981), Witte (1981), and Witte et al. (1992). These stations were sampled twice in 1991 (June and November), one time in 1992 (March), five times in 1993 (September, October two times, November, December), and once in 1995 (February). In total 87 trawl shots were done, all between 900 and 1300 hours. Four night surface trawl shots were conducted at two stations (E and F on the transect) in October 1993. Additional trawl shots were done in southern parts of the Mwanza Gulf in 1991 and 1993 and in the Speke Gulf in 1993. Twenty four rock islands and 19 locations at rocky mainland shores were fished by gill nets and angling. Fourteen of these stations were sampled over several years, and 32 had not been sampled before this survey. Three sandy shores were sampled by beach seine in 1991 and 1993. One weed bed and one reed margin were sampled by gill nets in 1991, 1992, 1993, and 1995, and several others were sampled only in one year. Underwater observations and fish censuses were conducted annually since 1991 at two rock islands and at three more in 1993. Stations are given in Fig. 1. After 1990 trawling has not been conducted in depths beyond 15 m. Thus our data cover only the littoral and sub-littoral fauna.

We used the species recognition criteria outlined by Ribbink (1986) and Witte and Witte-Maas (1987). Undescribed species are indicated by working names in quotation marks (Witte et al. 1992; Seehausen 1996*a*; E. Witte-Maas personal communication). With regard to generic taxonomy of Lake Victoria cichlids, considerable heterogeneity is shown in recent publications in which some authors follow Greenwood's last general revision (Greenwood 1980), and others do not. To avoid confusion we adopt a compromise here, using *Haplochromis* for all species and giving Greenwood's new genera in parentheses. Because we think the definitions and limitations of several of them have to be revised and because taxonomical affinities of many of the "new" species are not yet studied in detail, our assignment of undescribed species to these genera must be considered tentative. The (sub)genus *Astatotilapia* is used between quotation marks because it has been shown to be polyphyletic (Lippitsch 1993). A large number of new species cannot be assigned to any of these genera. In such cases we use only the old generic name *Haplochromis* followed by a question-mark in parentheses.

Our species count is conservative in several ways. (1) Species known from a single individual and species for which male live coloration is not known have been omitted, except in cases of morphologically very distinct species (marked with an asterisk in Table 1). (2) Although it is likely that more than six species of piscivores were found, we treat several similar populations together as species groups and none of them as new because we are not familiar enough with the taxonomy of piscivores. (3) In case of doubt as to whether a species was new or identical to a previously known species, the latter case was assumed.

Preserved material of all species is currently deposited in the Haplochromis Ecology Survey Team (HEST) collection at the University of Leiden/Netherlands and in the collection of the Tanzania Fisheries Research Institute in Mwanza/Tanzania and will finally be deposited at the National Natural History Museum Leiden, The Netherlands, as well as at a suitable institute in Tanzania. Statistical calculations were done in Statgraphics Statistical Graphics System version 5.0.

Results

We found 163 haplochromine species between 1991 and 1995 (Table 1). With the exception of *Haplochromis ("Astatotilapia") nubilus*, *Astatoreochromis alluaudi*, and *Pseudocrenilabrus multicolor* all are supposedly endemic to Lake Victoria and its satellite lakes. Furthermore, relict populations of both indigenous *Oreochromis* species (*O. esculentus* and *O. variabilis*) were found. Of the 157 non-piscivorous haplochromine species 19% were previously described, whereas another 16% were known before 1991 but remained undescribed. One hundred and two non-piscivorous species were collected for the first time. In species number they represent 65% of the current non-piscivorous haplochromine fauna. Of the new species, 71% live over rock and rock-pebble-sand mixed substrates. Ten percent were recovered from sub-littoral mud bottoms, 7% from weed beds, 6% from rock-reed interfaces, 4% from sand beaches, 2% from a satellite lake and 1% from the mouth of a small creek. A small population of *Oreochromis variabilis* was discovered at an offshore rock island in the Speke Gulf, where it coexists with the introduced *O. niloticus* and *O. leucostictus*. A population of *Oreochromis esculentus* was discovered in a satellite lake that has not been invaded by the introduced species.

Figure 2 gives information about distribution of recorded species over different habitats and habitat restriction of species. We distinguish between eight macrohabitat types. Several of them can be further broken down into a number of habitats, microhabitats, and depth zones (e.g., the rock shore macrohabitat can be broken down into large and small boulder, steeply and gently sloping habitats). Within each there are microhabitats like more versus less wind exposed areas, caves among the rocks versus rock surface, etc. Of the 163 haplochromine species found, 81% are in their occurrence exclusively restricted to one type of macrohabitat. The most restricted species are those that live in a rock bottom habitat. Nineteen percent of the species were encountered in two or three macrohabitats. Even topographically very restricted habitats, like the rock-reed interface and the rock-pebble-sand habitat, have species exclusively attached to them.

Forty two percent of the species were found at only one locality; 23.5% could be naturally endemic to these localities. The other 18.5% are known to have been more widely distributed before the Nile perch upsurge or are previously unknown sub-littoral mud bottom dwellers

Table 1. Haplochromine taxa collected in southern Lake Victoria between 1991 and 1995.

Species[a]	_Years of records_	_Habitats_[b]	_Distribution_[c]
Piscivores			
H. (Prognatho.) cf. _mento_*	95	w	x
H. (Harpago.) cf. _serranus_	93, 95	r	
_H. (H.)_ sp. _quiarti_ group	91	s	
_H. (H.)_ sp. Nyegezi Bay*	93	s	x
_H. (H.)_ "almost piscivore"*	91	s	x
H. ("Astatotilapia") "2 stripe yellow-green"*	91	s	x
Paedophages			
H. (Lipo.) cf. _melanopterus_	91, 92, 93, 95	r,rr	
H. (L.) obesus-complex	92, 95	r	x
_H. (L.)_ cf. _parvidens_	95	w	x
H. (L.) cryptodon-complex*	92	w	x
_H. (L.)_ "Matumbi hunter"[d]	95	r	x
_H. (L.)_ "blue microdon"[d]	95	r	x
Crab eaters?			
H. (Harpago.) sp. _bowesi_-complex	95	r	
_H. (H.)_ "orange rock hunter"[d]	92, 93	r	E
Insectivores			
Pseudocrenilabrus cf. multicolor	93	c	
H. ("Astatotilapia") nubilus	91, 92, 93, 95	r, w, l	
H. ("A.") cf. brownae	91, 93	s, rs	
_H. ("A.")_ "diversicolor"	91, 93	s, m	
_H. ("A.")_ cf. "cherry flank"	91	s	x
_H. ("A.")_ "small blue zebra"	91	s, r	
_H. ("A.")_ "red & blue insectivore"[d]	95	s	
_H. ("A.")_ "creek"[d]	93	c	
_H. ("A.")_ "incurved dorsal head profile[d]	92, 93, 95	r	E
_H. ("A.")_ "black long snout"[d]	93	rs, r	E
_H. ("A.")_ "black cave"[d]	92, 93	r	
H. (Gauro.) empodisma-group*	93	r	x
_H. (G.)_ "dwarf hiatus"[d]	95	m	
_H. (G.)_ "simpsoni like"[d]	93	I	E
H. (Psammo.) riponianus	91, 92, 93, 95	s, r, rs	
H. (P.) cf. saxicola	93	rs, r	
H. (P.) cf. aelocephalus	91, 93, 95	s, r	
_H. (P.)_ "red riponianus"[d]	91	w	E
_H. (P.)_ "rock riponianus"[d]	93, 95	r	
_H. (P.)_ "red zebra"[d]	93	r	
_H. (P.)_ "Ruti-Psammo"[d]	93	r	E
H. (Paralabido.) crassilabris	91, 93, 95	w, s	
H. (P.) chilotes	91, 92, 93, 95	r, rs	
H. (P.) cf. chromogynos	93, 95	rs	
_H. (P.)_ "fleshy lips"[d]	93	rs	E
_H. (P.)_ "rockkribensis"	91, 92, 93, 95	r, rs	
_H. (P.)_ "rockpicker"	91	r	x
_H. (P.)_ "pseudorockpicker"	91, 93, 95	r	
_H. (P.)_ "elongate rockpicker"*	93	r	x
_H. (P.)_ "orange anal picker"[d]	95	r	
_H. (P.)_ "red pseudorockpicker"[d]	93, 95	r	
_H. (P.)_ "yellow rockpicker"[d]	91, 92, 93, 95	r	
_H. (P.)_ "blue rockpicker"[d]	91, 92, 93, 95	r	
H. (?) theliodon	91, 93	s	
_H. (?)_ "thick skin"	91, 93, 95	s, m	
_H. (?)_ cf. "curvicephalus"	93	s, m	x
_H. (?)_ "long female"[d]	91	s	x
_H. (?)_ "red insectivore"[d]	95	w	E
_H. (?)_ "beak lip"*[d]	92	w	E
_H. (?)_ "blue giant insectivore"*[d]	95	rr	E
_H. (?)_ "duck snout"[d]	95	r	E
_H. (?)_ "black pseudonigricans"	91, 93, 95	r	
_H. (?)_ "black & yellow pseudonigr."	91, 92, 93, 95	r	
_H. (?)_ "red pseudonigricans"[d]	93, 95	r	

(_continued_)

Table 1. Continued.

Species[a]	*Years of records*	*Habitats*[b]	*Distribution*[c]
H. (?) "yellow chin pseudonigr."[d]	91, 93, 95	r	
H. (?) "Ukerewe pseudonigricans"[d]	95	r	
H. (?) "black Ukerewe"[d]	95	r	
H. (?) "blue deepwater"[d]	93, 95	r	
H. (?) "zebra nyererei"[d]	91, 92, 93, 95	r	
H. (?) "Bwiru nyererei"[d]	93, 95	r	
H. (?) "all black nyererei"[d]	93	r	
H. (?) "red head nyererei"[d]	93, 95	r	
H. (?) "blue nyererei"[d]	92, 95	r	
H. (?) "red chest nyererei"[d]	91	r	E
H. (?) "red anal nyererei"[d]	95	r	E
H. (?) "red rim anal"[d]	95	r	
H. (?) "yellow insectivore"[d]	93	r	E
H. (?) "ladies lake deep"[d]*	93	l	E
Sponge/insect eaters			
H. (?) "deep water"	91, 92, 93, 95	r	
Oral shelling molluscivores			
Macropleurodus bicolor	91, 95	s, rs	
Platytaeniodus degeni	91	s	x
Hoplotilapia retrodens	91	s, w	x
H. (Ptyo.) xenognathus	91, 92, 93, 95	s, m, rs	
H. (P.) sauvagei	91, 92, 93, 95	s, rs, w	
H. (P.) "striped rock sheller"[d]	91	r	
H. (P.) "bright red sheller"[d]	91, 93	s	x
H. (P.) "red giant sheller"[d]	93, 95	rr, r	
H. (P.) "deep water rock sheller"[d]	93, 95	r	E
H. (P.) "parrot mouth"[d]*	91	w	E
H. (P.) "Zue sheller"[d]	95	r	E
H. (?) "red rock sheller"[d]	93, 95	rs, r	
H. (Paralabido.) plagiodon	91, 92, 93, 95	s, m, rr	
Pharyngeal crushing molluscivores			
Astatoreochromis alluaudi	91, 92, 93, 95	r, w, rr, l	
H. (Labro.) ishmaeli	91	s	
H. (L.) "stone"	91, 92, 93, 95	r	
H. (Psammo.) "striped crusher"[d]	91, 92, 93, 95	r	
H. (?) "yellow giant crusher"*[d]	93	rs, r	
H. (?) "Zue crusher"[d]	95	r	E
Epilithic algae scrapers			
H. (Neo.) nigricans	91, 92, 93, 95	r	
H. (N.) "velvet black"	91, 92, 93, 95	r	
H. (N.) "black nigricans"[d]	93	r	
H. (N.) "Vesi scraper"[d]	95	r	E
H. (N.) "blue scraper"[d]	91, 92, 93, 95	r	
H. (N.) "eastern blue scraper"[d]	93, 95	r	
H. (N.) "yellow anal scraper"[d]	93, 95	r	
H. (N.) "large eye nigricans"[d]	92, 93	r	E
H. (N.) "giant scraper"[d]	91, 92, 93, 95	r	
H. (N.) "long black"[d]*	95	r	
H. (N.) "labeo scraper"[d]	95	r	E
H. (N.) "Bihiru scraper"[d]	95	r	E
H. (N.) "unicuspid scraper"[d]	92, 93, 95	r	
H. (Xysti.) "large eye black"[d]	93	r	E
H. (X.) "copper black"[d]	91, 92, 93, 95	r, rs, rr	
H. (X.) "short scraper"[d]	93, 95	r	E
H. (X.) "carp"[d]	91, 92, 93, 95	r, rr	
H. (X.) "red carp"[d]	91, 95	r, rr	
H. (Paralabido.) "short snout scraper"[d]	93, 95	r	
H. (P.) "blue short snout scraper"[d]	93, 95	r	
H. (P.) "red short snout scraper"[d]	95	r	
H. (P.) "rockmacula"	91, 93	r	E
H. (?) "pseudoblack"[d]	91, 93, 95	r	E
H. (?) "scraper pseudonigricans"[d]	93, 95	r	
H. (?) "big blue nyererei"[d]	93	r	

(*continued*)

Table 1. Continued.

Species[a]	*Years of records*	*Habitats*[b]	*Distribution*[c]
Epiphythic algae scrapers			
H. (Haplo.) obliquidens	92, 95	w	x
H. (H.) “macula”	91, 93	rr, r, m	
H. (H.) “red lividus”	91	rr	
H. (H.) “purple yellow”	91, 92, 93, 95	r, w, rr	
H. (H.) “red fin lividus”[d]	91, 93, 95	s, w	
H. (H.) “blue obliquidens”[d]	92, 93, 95	rr	E
H. (H.) “orange chest silvery scraper”[d]	91, 92, 93	rr, r	
H. (H.) “red back scraper”[d]	92	rr	E
H. (H.) “black and red fins”[d]*	91	rr	E
H. (?) cf. “serpentine”*	91	w	x
H. (?) “Anchor scraper”[d]	91	rr	E
H. (?) “red blue scraper”[d]	95	w	E
H. (?) “all red weed scraper”[d]	95	w	E
Plant eaters			
H. (Psammo.) acidens	(89), 91?	w	x
Pelagic zooplanktivores			
H. (Yssi). pyrrhocephalus	91, 92, 93, 95	m	
H. (Y.) laparogramma	91, 92, 93, 95	m	
H. (Y.) cf. “plumbus”	91	m	x
H. (?) tanaos	93, 95	m	x
Planktivorous/insectivorous rock-dwelling			
Species from deeper water			
H. (?) nyererei	91, 92, 93, 95	r	
H. (?) “black & orange nyererei”[d]	93, 95	r	
H. (?) “orange anal nyererei”[d]	95	r	E
H. (?) “Ukerewe nyererei”[d]	95	r	
H. (?) “yellow deepwater”[d]	93, 95	r	
H. (?) “slender deepwater”[d]	93	r	E
H. (?) “brown narrow snout”[d]	93	r	
H. (?) “pink anal”[d]	93, 95	r	
H. (?) “blue pseudonigricans”[d]	91, 92, 93, 95	r	
H. (?) “long snout pseudonigricans”[d]	95	r	
H. (?) “large eye pseudonigricans”[d]	91, 95	r	E
H. (?) “pseudoblue”[d]	91, 93, 95	r	
Phytoplanktivores			
H. (?) “kribensis”	93	m, r	
Detritivores/phytoplanktivores			
H. (Entero.) “dusky wine red fin”	93, 95	m	
H. (E.) cf. “75”	93	m	
H. (E.) cf. “nigrofasciatus”	93	m	x
H. (E.) “straight cinctus”[d]	91, 93, 95	m	
H. (E.) “broken bar”[d]	93	m	
H. (E.) “vertical blotch”[d]	91, 93, 95	m	
H. (E.) “slender orange”[d]	93	m	x
H. (E.) “yellow bloody chest”[d]*	93	m	x
H. (I?.) “red tridens”	93	m	x
H. (?) “grey blue”[d]	93	m	x
H. (?) “broad lower jaw”[d]	91	m	
Trophic group unknown			
H. (?) “shovel mouth”[d]*	93	r	E
H. (?) “mud all red”[d]	91	m	x
H. (?) “deep body red”[d]	93	m	x
H. (?) “parrot obesus”[d]*	92	s	E
Missing trophic groups			
Prawn eaters			
Egg stealers			
Scale eaters			
Parasite eaters			

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[a] *Species known by a single individual are excluded except if the species was morphologically very distinct (marked with an asterisk behind the name).* H. *in front of parentheses* = Haplochromis. *The generic names of Greenwood 1980 are given in parentheses (*Harpago. = Harpagochromis, Lipo. = Lipochromis *etc.).*

[b] *The habitat in which the species was found between 1991 and 1995 is given as r = rocks; s = sand; rs = rock-sand-pebble mixed substrate; rr = rock-reed interface; w = weeds; m = organic mud; l = satellite lakes; c = entrance of creeks.*

[c] *Distribution symbols are as follows: x = caught at a single place but known or likely to have been formerly more widely distributed; E = caught at a single place and possibly naturally endemic to it; others were found in a number of localities.*

[d] *Previously unknown species.*

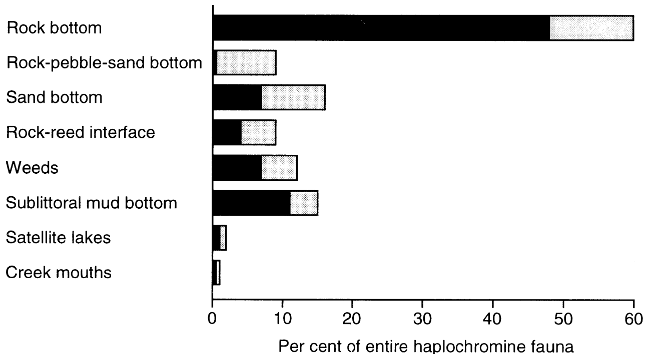

Figure 2. Proportional representation of the currently known and still existing haplochromine fauna in eight macrohabitats. Bars indicate the proportion of species that have the given habitat as one of their major habitats (= 10% or more of its individuals in our samples caught in the habitat). The black part of the bars indicates the proportion of species that are restricted to the given habitat. Eighty one per cent of the species are restricted to one macrohabitat.

of which it is likely they are or were somewhat more widely distributed.

Table 2 gives information about patterns of diversity on the level of trophic groups (Witte & van Oijen 1990). Insectivores and molluscivores are the most widely distributed trophic groups and are present in most habitats. On the other extreme, pelagic zooplanktivores and demersal detritivores are restricted to sub-littoral areas with mud bottom, some trophic specialists (crab and sponge eaters) to rocky shores, and the larger predators (piscivores, paedophages) are largely restricted to littoral habitats that provide hiding places. The rock bottom habitat harbors the highest number of trophic groups, likely reflecting complex food webs in that habitat, a large diversity of microhabitats (Seehausen & Bouton 1997*a*, *b*, in press) but also the best refuge for fishes preyed upon by Nile perch. New taxa were discovered predominantly in littoral and sub-littoral demersal communities, reflected by the proportions of new species in the different trophic groups (Table 2). The trophic group of sponge eaters is for the first time observed (Bouton, Seehausen, van Alphen & Witte in press). Whereas the high numbers of new insectivores, algae scrapers, and rock-dwelling zooplanktivores/insectivores are reflective of our sampling many littoral stations for the first time, the high proportion of new sub-littoral detritivores is not reflective of our sampling.

Only 20 (12%) of the haplochromine taxa encountered in the southern part of Lake Victoria between 1991 and 1995 have been reported also from the northern part between 1989 and 1992 (Kaufman & Ochumba 1993). However, the overlap may be bigger if some new species of the two regions turn out to be identical. It is possible that some of the populations now considered specifically distinct, belong to one species. On the other hand, because many of the rock restricted species do exhibit strong geographical variation, both in coloration and dentition characteristics, some of the populations may indeed turn out to be distinct species. So are differences in head shape and dentition among allopatric populations of *H. (Neochromis)* "velvet black" bigger than those between populations of this species and other sympatric algae scrapers.

In Table 3 frequencies of occurrence of haplochromine species at the transect stations across the Mwanza Gulf are given for 1993. Differences among species reflect

Table 2. Distribution of trophic diversity over eight macrohabitats in southern Lake Victoria.

	*Species numbers per macrohabitat**								
Trophic group	*r*	*rs*	*s*	*rr*	*w*	*m*	*l*	*c*	*New spp. (%)*
Piscivores	1	—	4	—	1	—	—	—	?
Paedophages	4	—	—	1	2	—	—	—	33
Crab eaters	2	—	—	—	—	—	—	—	50
Insectivores	38	8	12	1	5	4	3	2	62
Oral shelling molluscivores	5	4	7	2	3	2	—	—	54
Pharyngeal crushing molluscivores	5	1	1	1	1	—	1	—	50
Epilithic algae scrapers	25	1	—	3	—	—	—	—	88
Epiphythic algae scrapers	3	—	1	8	6	1	—	—	62
Macrophyte eaters	—	—	—	—	1	—	—	—	0
Pelagic zooplanktivores	—	—	—	—	—	4	—	—	0
Zooplanktivores/insectivores	12	—	—	—	—	—	—	—	92
Sponge/insect eaters	1	—	—	—	—	—	—	—	100
Phytoplanktivores	1	—	—	—	—	1	—	—	0
Detritivores/Phytoplanktivores	—	—	—	—	—	11	—	—	64
Unknown	1	—	1	—	—	2	—	—	100
Number of trophic groups per habitat	11	4	5	6	7	6	2	1	

**Macrohabitat abbreviations are defined as follows: r = rock bottom, rs = rock-pebble-sand bottom, s = sand bottom, rr = rock-reed interface, w = weed beds, m = sub-littoral mud bottoms, l = satellite lakes, c = creeks.* Oreochromis esculentus *was found only in satellite lakes, and* O. variabilis *was found only over rocky substratum.*

Table 3. Percentage of occurrence of haplochromine species and Nile perch in bottom trawl catches during daytime over the period September to December 1993.

Stations (from east to west)	*A/B*	*C/D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*
Depth (m)	*2–6*	*2–6*	*7–8*	*10–11*	*13–14*	*13–14*	*10–11*	*7–8*	*4*
Substrate	*sand*	*mud*	*sand/mud*	*mud*	*mud*	*mud*	*mud*	*mud*	*mud*
n[a]	*4*	*4*	*4*	*5*	*4*	*6*	*5*	*6*	*6*
Species[b]									
Detritivores									
H. (Entero.) "straight cinctus" (49)[c]	0	0	0	20	0	17	40	17	0
H. (Entero.) "vertical blotch" (37)[c]	0	0	0	0	25	33	20	0	17
H. (Entero.) "broken bar" (26)[c]	0	0	0	0	0	33	20	0	0
H. (Entero.) "dusky wine red fin" (18)	0	0	0	0	0	17	20	17	67
H. (?) "red tridens" (9)	0	0	0	0	0	17	20	0	0
H. (Entero.) cf. "75" (4)	0	0	0	20	0	17	20	17	0
H. (Entero.) "slender orange" (3)[c]	0	0	0	20	0	0	0	0	0
H. (?) "grey blue"(2)[c]	0	0	0	0	0	0	20	0	0
H. (Entero.) cf. "nigrofasciatus" (1)	0	0	0	0	0	0	0	0	+
Epiphytic algae scrapers									
H. (Haplo.) "macula" (1)	0	0	0	0	0	0	0	0	17
Oral mollusc shellers/crushers									
H. (Paralabido.) plagiodon (57)	25	0	25	0	0	0	40	33	67
H. (Ptyo.) xenognathus (33)	50	25	25	20	0	0	40	0	17
Zooplanktivores									
H. (Yssi.) pyrrhocephalus (472)	0	0	25	60	100	100	100	67	17
H. (Yssi.) laparogramma (140)	0	0	25	60	75	83	80	50	0
H. (?) tanaos (17)	0	0	0	0	0	0	0	33	50
Insectivores									
H. (?) "thick skin" (16)	0	0	50	0	0	0	0	0	17
H. (?) cf. "curvicephalus" (6)	0	0	25	0	0	0	0	0	0
Unknown species	75	50	75	67	25	50	60	50	67
Nile perch (>10 cm SL) (125)	0	0	0	20	25	33	60	50	50

[a] *n = number of trawl shots.*

[b] *Only adult individuals were counted. Behind each species the number of individuals caught is given. Species that were caught on the transect but not in the standard samples are indicated by +. Generic abbreviations as in Table 1.*

[c] *New species.*

differences in abundance. The pelagic zooplanktivores *H. (Yssichromis) pyrrhocephalus* and *H. (Yssichromis) laparogramma* were the most abundant species. At the same time, they were less microhabitat restricted than insectivores and detritivores, which were much more concentrated on a few stations. Witte et al. (1992) described a habitat shift of *H. (Yssichromis) laparogramma* after the Nile perch boom. We present here two further cases of habitat shifts: the zooplanktivore *H. (?) tanaos* (*H.* "double stripe" in Witte et al. 1992) and the oral shelling molluscivor *H. (Paralabidochromis) plagiodon* were in the pre-Nile perch system restricted to littoral sand bottom habitats on the east side of the Mwanza Gulf (Witte et al. 1992, Fig. 3). *H. (?) tanaos* had disappeared there from the catches by 1987. In 1993 we found it again but now over littoral and sub-littoral mud bottoms on the west side (Fig. 3). *H. (Paralabidochromis) plagiodon* had never completely disappeared from the littoral sand bottom although the catches decreased dramatically. In 1993 it was caught frequently over littoral and sub-littoral mud bottoms particularly on the west side of the Mwanza Gulf where it had never been caught before (Fig. 3). Samples from April 1995 confirm the establishment of these two species in their new habitats.

In terms of both individual and species numbers, a slight revival of the sub-littoral haplochromines has been observed on the research trawl transect across the Mwanza Gulf (Fig. 4, 13–15 m depth). However, this holds only for two trophic groups (detritivores and zooplanktivores) out of the 10 that used to be caught in the same area at the end of the 1970s (Witte et al. 1992). Whereas demersal detritivores reappeared and pelagic zooplanktivores increased in abundance, species numbers at the shallower stations continued to decrease (Fig. 4, 2–6 m and 7–8 m depth) and 16 further species disappeared from the research transect (Table 4). Ten of these recently lost species have not been seen elsewhere in the research area since the last survey and may be extinct. They are littoral as well as pelagic and demersal species, and among them is the last piscivore that was found in 2–6 m depth on the transect in the 1987/1990 survey. At least 24 other haplochromine species, not recently known from the transect, were found so rarely in spite of repeated sampling of their habitats, that we consider them critically endangered as well (Table

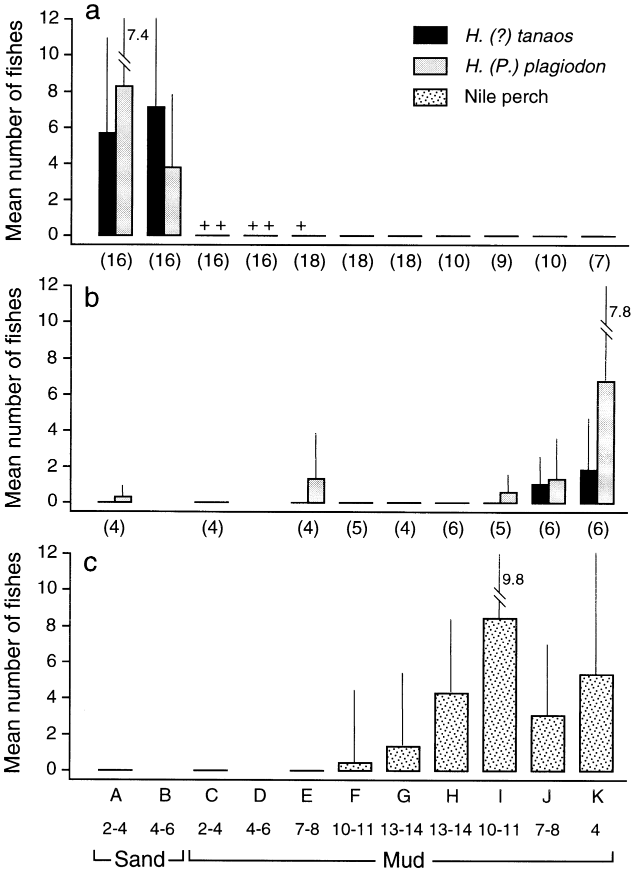

Figure 3. Mean number and standard deviation of H. tanaos *and* H. (Paralabidochromis) plagiodon *before (a) and after (b) the Nile perch upsurge in trawl catches of 10 minutes duration at stations on a transect (from east to west) across the Mwanza Gulf. For the second period the mean number and standard deviation of Nile perches of more than 10 cm standard length are also given (c). The stations are given on the abcissa. The number of trawl shots per station is given in parentheses under the abcissa of the upper two diagrams. The water depth in meters is given for each station under the abcissa of the bottom diagram. Stations A, B, as well as stations C, and D, were treated in the second sample period as a single station, fished by one trawl shot. A + indicates values less than 0.1. The left + stands for* H. tanaos *and the right for* H. (P.) plagiodon.

4). Among them are four of the six fish predators, several sub-littoral insectivores (e.g. species of *Gaurochromis*-type), detritivores, a pelagic zooplanktivore, a snail crusher, and several rock-dwelling species.

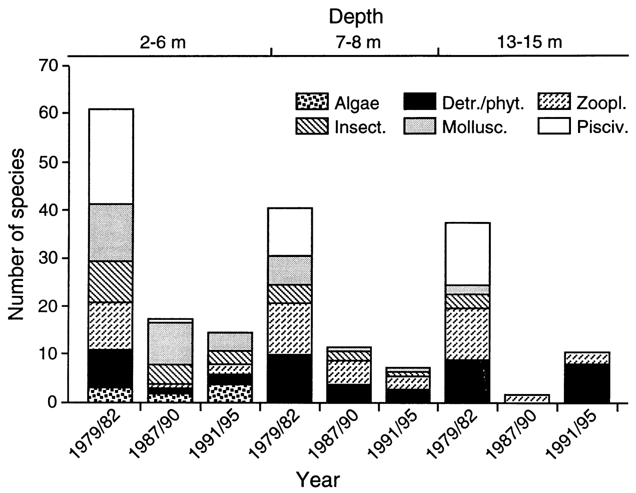

Figure 4. Number of haplochromine species in 1979-1982, 1987-1990, and 1991-1995 at the same stations in three different depth ranges along the research transect across the Mwanza Gulf based on samples from bottom trawl, surface trawl, and gill nets. Extended from Witte et al. (1992). Algae = algae scrapers; Detr./phyt. = detritus and phytoplankton eaters; Zoopl. = zooplanktivores; Insect. = insectivores; Mollusc. = molluscivores; and Pisciv. = piscivores.

Twice during our survey work we happened to witness fish kills in littoral waters, likely caused by the application of the insecticide Thiodon for fishing purposes, at two of our sampling stations: a weed bed in the Butimba Bay and a rocky islet at the entrance of the Nyegezi Bay. In the first case about 500 dead *Haplochromis*, 16 dead *Oreochromis*, 1 *Barbus*, 1 *Lates*, and one toad (*Bufo* sp.) were found. Only small individuals of fish were found. Strong slime secretion of the gills of dead *Oreochromis* indicated toxication. In the second case no dead fish were found. Instead, not a single fish was caught at the islet (Fig. 6) and moribund small *Haplochromis* and *Rastrineobola* were observed. According to fishermen who made similar observations at another islet, some 50 m from ours, Thiodon fishing had been practiced in the preceding night. A third islet, 100 m off the other two, was not affected by the fish kill. Neither in the weed bed nor at the rocky islet was the original condition of the community restored within our research period. Catches in the weed bed remained lower than they were before the fish kill (Fig. 5). However, we cannot exclude repeated application of the insecticide as a causal factor in the weed bed. At the rocky islet the fish density 12 days after the kill outside of the rocks was still extremely low, whereas in rocky crevices it had resumed the old level (Fig. 6). Considerable changes in species composition seem to explain this phenomenon (Fig. 7). The *H. (?)* "pseudonigricans" group had almost completely vanished. This group is a complex of undescribed rock-restricted animal *Aufwuchs*, insect and zooplankton eating cichlid species, that before the fish kill, were the numerically dominant inhabitants of the rocky slope outside of crevices, and comprised two or three species at the islet. *H. (Labrochromis)* "stone," a

Table 4. Species that disappeared from the research transect across the Mwanza Gulf after 1987/1990 and other very rare and probably critically endangered species.[a]

Disappeared	*Rare*[b]
H. (Entero.) "morsei" (D)[c]	*H. (Entero.)* cf. "nigrofasciatus" (D)
H. (Entero.) "purple head" (D)[c]	*H. (Entero.)* "yellow bloody chest" (D)
H. (?) "kribensis" (Ph)	H. (*Nea.*) "cruising" (As)
H. (Ptyo.) granti (O)[c]	*H. (Paralabido.)* "rockmacula" (As)
Hoplotilapia retrodens (O)	*H. (Ptyo.)* "parrot mouth" (O)
Macropleurodus bicolor (O)	*H. (Labro.) ishmaeli* (Cr)
Platytaeniodus degeni (O)	*H. (Yssi.)* cf. "plumbus" (Z)
H. (?) "argens" (Z)[c]	*H. ("Astatotilapia")* "small blue zebra" (I)
H. (Yssi.) piceatus (Z)[c]	*H. (Gauro.) empodisma*-group (I)
H. (Yssi.) heusinkveldi (Z)[c]	*H. (Gauro.)* "dwarf hiatus" (I)
H. ("Astatotilapia") brownae (I)	*H. (?)* "beak lip" (I)
H. ("Astatotilapia") "diversicolor" (I)	*H. (Paralabido.) cf. chromogynos* (I)
H. (Prognatho.) percoides (P)[c]	*H. (Paralabido.)* "rockpicker" (I)
H. ("Astatotilapia") "orange cinereus" (?)[c]	*H. (Paralabido.)* "elongate rockpicker" (I)
H. (?) "stripmac" (?)[c]	*H. (Paralabido.)* "red pseudorockpicker" (I)
H. (?) "purple rocker" (?)[c]	*H. (Harpago.) howesi* (C)
	H. ("Astatotilapia") "two stripe yellow-green" (P)
	H. (Prognatho.) cf. mento (P)
	H. (Harpago.) sp. Nyegezi Bay (P)
	H. (Harpago.) "almost piscivore" (P)
	H. (Lipo.) obesus-complex (Pa)
	H. (Lipo.) cf. parvidens (Pa)
	H. (Lipo.) cryptodon-complex (Pa)
	H. (?) "shovel mouth" (?)
	H. (?) "parrot obesus" (?)

[a] *Letters or symbol following species are defined as follows: As = algae scraper; C = crab eater; Cr = pharyngeal crushing molluscivore; D = detritivore; I = insectivore; O = oral shelling molluscivore; P = piscivore; Pa = paedophage; Ph = phytoplanktivore; Z = zooplanktivore; ? = unknown trophic group. "A". =* "Astatotilapia"*. Abbreviations for other subgeneric names as in Table 1.*

[b] *Recorded by no more than two individuals between 1991 and 1995, except those that were recorded by more than two individuals in 1991 but never again since, and "rock macula" that was not caught after 1993.*

[c] *Disappeared from the entire research area. The others disappeared from the transect but were seen elsewhere at least once after 1990.*

crevice dwelling molluscivore that was not very abundant before the fish kill, became the dominant species afterwards and *H. (Psammochromis)* cf. *aelocephalus*, a possibly not rock-restricted species, invaded.

To investigate Kaufman and Ochumba's (1993) hypothesis that schools of the pelagic cyprinid *Rastrineobola argentea* might be utilized as a shelter by haplochromines, we calculated correlations between the abundances of the cyprinid and various cichlids in the trawl catches of 1993 across the Mwanza Gulf. Furthermore, we calculated correlations between the cichlid species themselves. Using the data from all transect stations collected in 1993 ($n = 44$ trawl shots) a weak positive correlation (Spearman rank correlation coefficient +0.32, $p < 0.05$) between abundances of adult and subadult *Rastrineobola* and zooplanktivorous haplochromines can be demonstrated. However, this reflects the restriction of both taxa to the sub-littoral part of the transect (7 to 15 m depth). An analysis restricted to catches from the sub-littoral part of the transect ($n = 30$) revealed no correlation between the abundances of *Rastrineobola* and either *H. (Yssichromis) pyrrhocephalus*, *H. (Yssichromis) laparogramma*, *H. (?) tanaos,* or all zooplanktivores combined (correlation coefficient +0.22, $p = 0.24$). A further delimitation to the catches at the stations H, I, and J ($n = 17$), which had the highest abundances of zooplanktivorous cichlids, did not change this pattern (correlation coefficient +0.08, $p = 0.76$). A separate analysis of abundances of juveniles revealed that juvenile *Rastrineobola* (<25 mm SL) were most abundant in the littoral and sub-littoral parts on the east side of the Mwanza Gulf (stations A to G), whereas juvenile zooplanktivorous haplochromines of similar size occurred predominantly in sub-littoral waters on the other side (stations H to J).

Among 44 trawl shots, 6 brought exceptionally large numbers of adult and subadult *Rastrineobola* to the surface (between 800 and 3626, compared to a mean of 81+/−133), suggesting that the net passed through dense schools. From two of these catches zooplanktivorous cichlids were completely absent, in two their abundance was below average, and in two it was exceptionally high. No other cichlid was correlated in any detectable way with *Rastrineobola* either. In contrast, correlations between cichlids and the cyprinid were lower than between any two cichlid species (but see discussion). However, also among the cichlids we found only one significant correlation on all levels of analysis. This was between the two zooplanktivores *H. (Yssichromis) pyrrhocephalus* and *H. (Yssichromis) laparogramma* (correlation coefficient +0.70, $p < 0.01$)

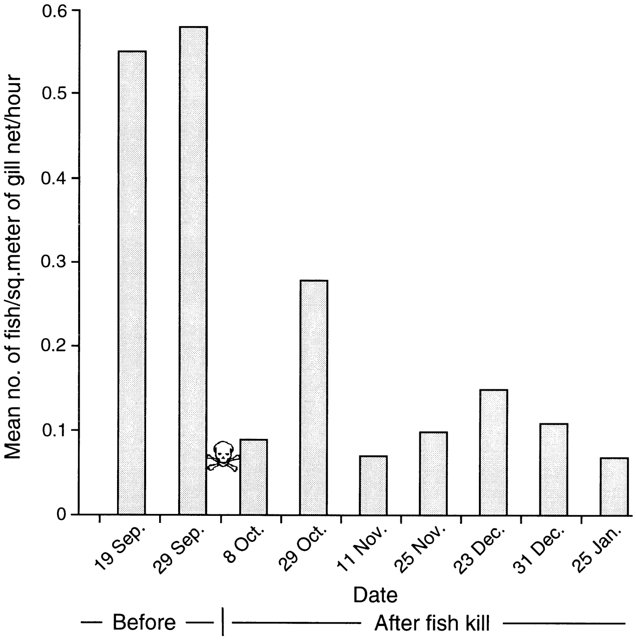

Figure 5. Densities of haplochromine cichlids in a weed bed before and after a fish kill that was likely caused by fishing with the insecticide Thiodon. The fish kill was observed on 2 October 1992 (indicated by the skull and crossbones between 29 September and 8 October).

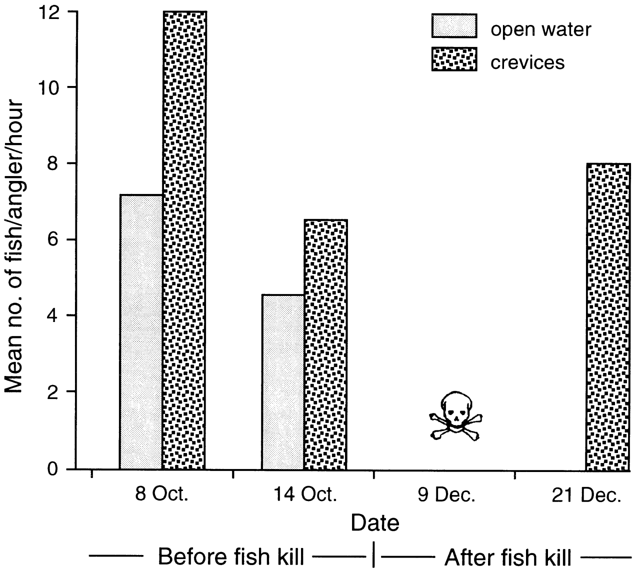

Figure 6. Densities of haplochromine cichlids at a rocky islet before and after a fish kill that was likely caused by fishing with the insecticide Thiodon. The fish kill was observed on 9 December 1993 (indicated by the skull and crossbones). The recovery observed on 21 December was restricted to species living in crevices between the rocks (H. [Labrochromis] *"stone"*, H. (?) nyererei, H. [Psammochromis] cf. aelocephalus).

which apparently live in mixed schools. These two morphologically very similar species were parapatric in the pre-Nile perch system (Witte & Witte-Maas 1987).

Discussion

Species Richness and Population Dynamics

The discovery of 102 new cichlid species within 5 years of research is an impressive demonstration of how little is known about the littoral Lake Victoria cichlid fauna. Certainly species numbers were far underestimated in previous publications. With the 102 new taxa and the 31 new taxa found in the northern part (Kaufman & Ochumba 1993) added to the 302+ reported by Witte et al. (1992), the total number of actually known haplochromine cichlid species in Lake Victoria rises to over 430. Recently collected, and not yet evaluated samples from previously unsampled localities include at least 20 more new species. Patterns of endemicity, mainly among the rock restricted cichlids, and the fact that only about 10% of the lake shore has been investigated, make it almost certain that the real number well exceeds 500 species (Seehausen 1996*b*).

Our observations in the south of the lake certainly confirm Kaufman and Ochumba's (1993) observation that the haplochromine fauna is still changing rapidly. Since the end of the eighties (Witte et al. 1992) major changes have taken place. Sixteen more species disappeared from the established research transect that was sampled annually since 1978 (Table 4) and a few reappeared (compare our Table 3 with Appendix 1 in Witte

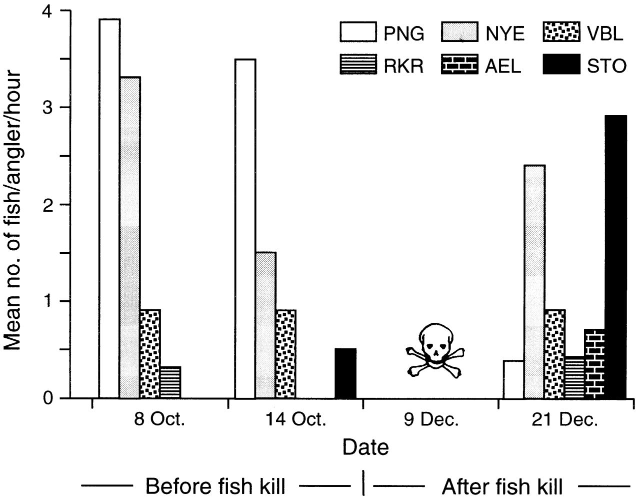

Figure 7. Species composition at the rocky islet before and after the fish kill: PNG = H. (?) *"pseudonigricans", RKR* = H. (Paralabidochromis) *"rockkribensis", NYE* = H. (?) nyererei *AEL* = H. (Psammochromis) cf. aelocephalus, *VBL* = H. (Neochromis) *"velvet black", STO* = H. (Labrochromis) *"stone"*.

et al. 1992). Though the large number of new species is partly due to the extension of the research area along rocky shores, a number of new species were found at sampling stations that had frequently been sampled before. This holds for five of the new sub-littoral detritivores (Table 3) and for several of the new rock-dwellers. Kaufman and Ochumba (1993), citing R. Welcomme, ask whether some of the newly discovered species in Lake Victoria are currently coming into existence. In the cases of the five detritivores we can say with certainty that the species were not present in the samples before the Nile perch upsurge. By the years 1991 to 1993, three of them had become abundant in their habitats. Several explanations are possible (Witte et al. 1995, extended): (1) the species lived in other, unstudied, areas before the Nile perch upsurge and invaded the Mwanza Gulf afterwards; (2) previously known species responded through phenotypic plasticity to changes in the environment; (3) the "new" forms are hybrids; and (4) surviving populations of previously known species, surpassing a bottle neck in population density, have undergone rapid genetic changes. Perhaps several of these possibilities contribute to the observed patterns. The invasion hypothesis is supported by the three cases of habitat shifts described above. The other hypotheses are supported by the circumstance that in 1991, 1993, and 1995 large numbers of individuals were caught in the sub-littoral that resemble species previously known from the same stations but do not fully match them (*H. [Enterochromis]* cf. "nigrofasciatus," *H. [E.]* cf. "75"). In cases where new forms were abundant (*H. [E.]* "broken bar," *H. [E.]* "vertical blotch," *H. [E.]* "straight cinctus"), it appears to us unlikely that they consist simply of F1 hybrids of two species that are not found anymore in the area by themselves.

As a consequence of above discussed population dynamics, the observed changes in trophic group composition on the research transect are not merely a continuation of previously recorded trends. Rather they reflect two opposed developments: the revival of sub-littoral detritivores and zooplanktivores and the further decline of other trophic groups in the littoral zone.

Causes of Decline and Differential Survival

Witte et al. (1992) showed a strong correlation between haplochromine decline and Nile perch upsurge and suggested that Nile perch predation is the major factor causing the extinction of most of the cichlids of the open water. They concluded that different cichlid species exhibit different sensitivity to extinction: (1) rare species are more sensitive than abundant species; (2) bigger species are more sensitive than smaller species; and (3) species are more sensitive in proportion to their habitat overlap with Nile perch. Our recent observations on habitat shifts in surviving species indicate that more factors may play a role. Several of the species that survived in the sub-littoral changed their spatial distribution after the Nile perch upsurge. The idea that spatial flexibility is advantageous for survival in a heavily perturbed system seems plausible but raises questions. By changing spatial distribution, *H. (?) tanaos* and *H. (Paralabidochromis) plagiodon* increased rather than reduced their habitat overlap with Nile perch (Fig. 3). From previous observations this was at least unexpected. The spatial niches now occupied by the shifting survivers, were previously occupied by other, now extinct species that did not differ from the survivers in size or in abundance. Why didn't these species survive if others that shifted into their niche survived? It seems likely that species like *H. (Yssichromis) laparogramma*, *H.* (?) *tanaos* and *H. (Paralabidochromis) plagiodon* survived for unknown reasons or for a combination of unknown reasons with flexibility in spatial behavior. It may be that they rushed into their new spatial niche after the predation pressure that created a spatial void had somewhat relaxed, allowing species that survived elsewhere to invade. But, it then remains unclear why the invaders gave up their original habitats.

Though we consider Nile perch predation the primary cause of extinction of many sub-littoral cichlids, we agree with Kaufman and Ochumba (1993) that a number of other causes of extinction can be identified. The littoral fauna in the Mwanza region is currently under severe pressure due to (1) increasing eutrophication; (2) the spreading of the exotic water hyacinth; (3) the spreading of exotic fish species; (4) heavy use of insecticides for fishing; and (5) strong exploitation of rock fish populations for long line baits. These threats are complementary to Nile perch predation. They affect primarily the habitats in which overlap with Nile perch is minimal and which harbor unique fish faunas and function as refugia for several species that used to have a wider distribution in the lake. Unfortunately their impact is yet very poorly understood, however, the effect of two or more threats posed together may be much greater than any single threat (Beverton 1992; Kaufman & Ochumba 1993).

Little if any attention has been paid so far to the problem of fishing with insecticides. Although use of insecticides for fishing purposes is prohibited in Tanzania, the use of one (Thiodon) has spread rapidly. It is applied at rocky shores and macrophyte rich habitats to obtain *Oreochromis niloticus*. Large *Haplochromis* are collected as well, whereas small fish are left behind and are probably poisoning otters, birds, and bigger fish that eat them. Symptoms of poisoning after human consumption of fish have recently been reported in many cases at Mwanza hospitals (M. Komba/Mwanza district fisheries officer pers. comm.). Very few quantitative data are available about the impact of Thiodon on the fish communities. Our data of 9 December 1993 suggest that populations at an islet that had about 1600 m^2 surface area were completely or nearly completely destroyed.

The change in species composition that we observed afterwards may reflect differential immigration rates. This islet was just 50 m off the rocky mainland shore. Repeated application of insecticides may favor species with high dispersal rates over stenotopic low dispersal species and must be particularly deleterious for local endemics. Our observations in weed and rock bottom habitats indicate the potential threat posed upon littoral cichlid communities by fishing with insecticides. Their use may be one explanation for the loss of species diversity in some littoral habitats.

Rock-dwelling cichlids have become a prime target of fishermen as baits for Nile perch longlines (Ligtvoet et al. 1995). Fishermen collect them using a line and hook in the morning hours before they go out onto the lake to set the long lines in sub-littoral waters. A group of four can collect between 100 and 200 cichlids in 1 hour. Populations of rock dwelling cichlids are easily depleted by frequently repeated angling on a spot (Y. Fermon personal communication.; N. Bouton & O. Seehausen personal observation), and here are indciations that population densities are negatively correlated with fishing pressure (S. Kangwe & O. Seehausen unpublished data). We would like to endorse the suggestion made by Kaufman and Ochumba (1993) to introduce pond culture of bait fish in order to reduce pressure on haplochromine stocks. Moreover, we believe that an upcoming ornamental fish trade, when based on export of wild caught fishes, can be deleterious for locally endemic rock cichlids, if not very well managed.

Apart from Nile perch, several tilapiine cichlids were introduced into Lake Victoria, and particularly *Oreochromis niloticus* is likely to interact with haplochromine cichlids at rocky shores. Rocky shores are now a major habitat of all age classes of *O. niloticus*. We observed them in large shoals, often mixed with haplochromines, scraping *Aufwuchs* from rocks in shallow waters. Frequently outnumbering haplochromine algae scrapers in the shoals, we assume that they exert considerable competition pressure upon the latter.

Water hyacinth (*Eichhornia crassipes*), first reported in Lake Victoria in 1989 (Njuguna 1989), has rapidly spread throughout our research area. Already in 1993 it covered large parts of the water surface in sheltered bays in the Mwanza Gulf. Since then it has gone through an explosive expansion phase in the Mwanza Gulf. In early 1995 the Gulf was sometimes blocked by water hyacinths on its entire width (about 5 km). At several localities it was observed that species composition under an *Eichhornia* layer differs considerably from that of the same habitat without *Eichhornia* (Seehausen unpublished data).

Symptoms of eutrophication were reported from several sides of the lake (e.g., Ochumba & Kibaara 1989; Hecky 1993; Witte et al. 1995). Water transparency in our research area decreased over the last decade from 2.5 m Secchi disc reading in sub-littoral waters of the northern Mwanza Gulf (van Oijen et al. 1981) to 0.9–1.2 m (De Beer 1989). A number of rock restricted haplochromines that went extinct in the Mwanza Gulf (Witte et al. 1992) were recently rediscovered at islands in the Speke Gulf and the open lake, where water transparency is still higher than in the Mwanza Gulf (Seehausen in press). These observations suggest that the decrease of water transparency plays a role in species extinction.

Faunal Refugia

Kaufman and Ochumba (1993) found six faunal refugia in the northern parts of the lake, defined as areas that harbor larger numbers of indigenous haplochromine species: (1) rocky reefs; (2) marginal swamps; (3) satellite lakes; (4) schools of *Rastrineobola argentea*; (5) benthic microbial mats in deep water; and (6) water column and benthos near the oxycline. Patterns of species diversity and population dynamics encountered in our study make it rather difficult to define refugia. Certainly some macrohabitats do harbor much more diverse and less depauperate faunas than others and should be considered refugia of diversity. However, if the term “refugium” implies an area in which species find retreat that once were more widely distributed but did not survive elsewhere, we hesitate using species richness per se as a criterion upon which to define faunal refugia. By far the highest species richness was found in rocky habitats, but most of the species that live there have never occurred in other habitats. For others, rocks indeed function as the last refugium. *H. (Paralabidochromis) chilotes*, *H. (Paralabidochromis) chromogynos*, *H. (Harpagochromis) serranus*, *Oreochromis variabilis*, some catfishes, and cyprinids are examples of species that once occurred in other habitats (Greenwood 1959; Trewavas 1983; Witte & van Densen 1995) but survived only at some rocky shores and islands. On the other hand, certain types of rock habitat themselves have lost a major part of their fauna. Little attention has been paid to sub-littoral rock bottoms. We have evidence from scattered individuals in our catches that such habitats once harbored specific haplochromine communities, completely different from those of shallow water rock habitats. On steeply sloping shores they are now rather void of cichlids which might be due to Nile perch predation, upwelling of deoxygenated waters (cf. Kaufman & Ochumba 1993) or a combination of the two. We measured oxygen concentrations as low as 2mg/L in water as shallow as 5 m along rocky shores (N. Bouton, O. Seehausen, J. van Alphen & F. Witte unpublished data). However, a refugium for rock-dwelling fishes from deeper water has been found in a narrow 7–8 m deep trough between two small islands in the Mwanza Gulf. About 10 species of planktivorous, insectivorous, and molluscivorous cichlids were found there, many of which were never or rarely found elsewhere, and do not occur in shallower water.

To define the importance of a habitat as a refugium, one has to consider in every case the ecology, current and former distribution of the inhabitants, as well as species and trophic diversity. Species richness is highest in rocky habitats but each of the habitat types in Fig. 2 still harbors unique faunal elements that are worth being protected. The second highest species number was encountered on sand bottoms, the third highest on sub-littoral mud bottoms. The almost extinct phytoplanktivores (collected in no more than three individuals since 1991) and the detritivores (Goldschmidt et al. 1993) are now largely restricted to the sub-littoral mud bottoms. They are of high conservation priority because of their role in the ecosystem. Remnant populations of previously more widely distributed species were found primarily at rocky shores and islands, on rock-pebble-sand mixed substrates, in weed beds, on sub-littoral mud bottoms, and in satellite lakes. Thus we consider these habitats the major refugia, in the strict sense of the word, in our research area.

That the majority of the species over mud bottoms in our research area are detritivores contrasts with results from the northern lake where few detritivores were found (Kaufman & Ochumba 1993). The concentration of the demersal detritivores at the stations H and I on the Mwanza Gulf transect, compared to the less concentrated distribution of pelagic zooplanktivores (Table 4), lends support to Kaufman and Ochumba's (1993) hypothesis that some kind of local benthic refugia exist in deeper water. It is unclear, however, why detritivores were not found in abundance at the equally deep stations F and G.

We could not find evidence supporting Kaufman and Ochumba's (1993) hypothesis that schools of the pelagic cyprinid *Rastrineobola argentea* function as a refugium for zooplanktivorous or other pelagic haplochromines. The distribution of the latter seems independent from that of the cyprinids. However, we have quantitative data only for the Mwanza Gulf and only from bottom trawl samples. Furthermore, our data do not rule out the possibility of behaviorally significant associations between pelagic cyprinids and pelagic haplochromines on a much smaller spatial and temporal scale than those detectable with our test.

Conservation Planning

The idea of establishing fish parks to safeguard refugia for endangered indigenous fishes has been brought forward (e.g., Kaufman & Ochumba 1993). The diffuse diversity patterns, however, make a choice of suitable areas difficult. Some rocky islands are candidates for special protection due to their high species and trophic diversity and extreme abundance of haplochromine cichlids. However, protecting such habitats is just half the story. Many of the haplochromine species at rocky shores are endemic to small geographical regions. Though there are nine trophic groups at the rocks, some are extremely rare and the maximum number on one island is seven. Good populations of piscivores are known only from a few islands, the few remaining populations of crab eaters from other islands, and good populations of paedophages from yet again other islands. Areas that protect such priority species are not always contiguous with areas of high diversity. Often it is difficult to understand why a species that went extinct in most of its former range survived on a particular small spot. Such real refugia, even if they do not harbor high diversities, are well worth protecting as refugia. However, their importance is usually not predictable prior to the discovery of the rare species, and they are widely scattered, so that traditional conservation strategies will be difficult to implement.

Other problems arise from the question of how to protect the sub-littoral diversity, recently reestablished in the Mwanza Gulf. The catches of the sub-littoral detritivores fluctuated extremely even within a few weeks in 1993 and it is possible that some of the species perform seasonal migrations. Clearly too little is known about such movements to define areas for conservation of the sub-littoral mud bottom fauna.

In view of the population dynamical developments in southern parts of Lake Victoria, we warn against restocking of captive propagated haplochromines at this moment. Although population growth curves generally pointed downwards over the last decade, this is not the case in all species anymore: a slight revival of a limited number of sub-littoral haplochromines has been documented over the last 5 years. The reviving stocks are not identical with those before the decline. They are dominated by previously unknown species and known species that underwent morphological changes (*H. [Enterochromis]* "dusky wine red fin," *H. [E.]* "nigrofasciatus," *H. [E.]* "75," *H. [?] tanaos*; Witte et al. 1995; Oijen & Witte 1996). These developments are not yet understood. It might be that the reviving stocks are able to cope better with the altered environmental conditions, including Nile perch predation, than the extinct stocks could. Reintroductions of ex-situ maintained pre-Nile perch populations could even be counterproductive. We are not at all against ex-situ maintenance of at least a part of the former diversity but we warn against restockings as long as the developments in the lake are not better understood. Rather than using satellite lakes for breeding of Lake Victoria cichlids we suggest constructing ponds for aqua culture of cichlids. We are afraid that introduction of alien cichlids into satellite lakes, even if they do not retain intact faunas, may destroy more as yet unknown faunal and floristic remnants of the Lake Victoria basin biota.

In our view the diversity to be conserved in Lake Victoria is too diffusely distributed to be successfully safeguarded by geographically restricted conservation measures (i.e., fish parks) alone. We consider it an important step to establish fish parks that need to conserve both areas of high diversity and areas harboring important trophic groups. At the same time we urge (1) intensified lake-wide control of fishing practices and aqua culture (which frequently led to unintentional introductions) and (2) intensified efforts to minimize further pollution by industry, agriculture, and human households.

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