Fish Faunal Resurgence in Lake Nabugabo, East Africa

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Abstract: *In Lake Nabugabo, Uganda, a small satellite of the equatorial Lake Victoria, approximately 50% of the indigenous fish species disappeared from the open waters subsequent to establishment of the introduced predatory Nile perch (*Lates niloticus*). However, several of these species persisted in wetland refugia. Over the past decade, Nile perch in Lake Nabugabo have been intensively fished. Herein we report a resurgence of some indigenous species in open waters. In a multiyear study, we used annual transects in inshore and offshore waters of exposed (no wetland) and wetland habitats to document the pattern of resurgence. In 1995, haplochromine cichlids were largely confined to inshore areas, particularly wetland ecotones, and were rare in Nile perch stomachs, as were most other indigenous species. By 2000 haplochromine cichlids were abundant in inshore and offshore areas of both exposed and wetland transects. Several indigenous noncichlids also reappeared in the main lake, including three of the four original mormyrid species. Between 1995 and 1999, there was a dramatic increase in the proportion of haplochromines in the diet of Nile perch. When haplochromines were rare (1995), Nile perch switched from an invertebrate-dominated diet to piscivory at a large size (30 cm total length). In 2000, however, Nile perch were strongly piscivorous by 5–10 cm total length. The pattern of faunal loss and recovery in Lake Nabugabo demonstrates the importance of refugia in providing the seeds of resurgence and provides a model with which to understand some changes in Lake Victoria.*

Resurgimiento de la Fauna Íctica en el Lago Nabugabo, África Oriental

Resumen: *En el Lago Nabugabo, Uganda, un pequeño satélite del lago ecuatorial Victoria, el 50% de las especies indígenas de peces, aproximadamente, desaparecieron de aguas abiertas después del establecimiento de la perca del Nilo (*Lates niloticus*); una especie depredadora introducida. Sin embargo, varias de estas especies persistieron en refugios de humedales. En el transcurso de la última década la perca del Nilo en el lago Nabugabo ha sido pescada intensivamente. En este documento presentamos información sobre el resurgimiento de algunas especies indígenas en aguas abiertas. En un estudio, a lo largo de varios años, usamos transectos anuales en aguas cercanas a la orilla y en aguas abiertas de hábitats expuestos (no humedales) y hábitats de humedal para documentar el patrón de resurgimiento. En 1995, los cíclidos haplocrómicos fueron en su mayoría confinados a las áreas cercanas a las orillas, especialmente ecotonos de humedal, y fueron raros en los estómagos de perca del Nilo, así como lo eran la mayoría de las otras especies nativas. Para el año 2000 los cíclidos haplocrómicos fueron abundantes tanto en las áreas cercanas a las orillas como en aguas abiertas de transectos expuestos y humedales. Muchas especies no-cíclidos también reaparecieron en el lago principal, incluyendo tres de las cuatro especies de mormíridos. Entre 1995 y 1999, hubo un dramático aumento en la proporción de haplocrómicos en la dieta de la perca del Nilo. Cuando los haplocrómicos fueron raros (1995), la perca del Nilo cambió de una dieta dominada*

por invertebrados a una dieta fuertemente piscívora a un tamaño grande (30 cm de longitud total). Sin embargo, en el año 2000, la perca del Nilo fue fuertemente piscívora entre los 5 y 10 cm de longitud total. El patrón de pérdida de fauna y recuperación del lago Nabugabo demuestra la importancia de refugios para proveer las semillas del resurgimiento y provee un modelo para entender algunos cambios en el Lago Victoria.

Introduction

Biodiversity Loss

The equatorial Lake Victoria is the largest tropical lake in the world and supports Africa's largest inland fishery. The lake is best known to scientists for its species flock of haplochromine cichlids (>600 endemic species; Seehausen 1996; Kaufman et al. 1997), representing one of the most rapid, extensive, and recent radiations of vertebrates known (Greenwood 1981; Kaufman 1992; Kaufman et al. 1997). A rich assemblage of noncichlids also inhabits the basin.

Throughout the twentieth century, Lake Victoria experienced large-scale ecological changes. Fishing intensified and generally resulted in successive loss of the largest individuals and species in favor of smaller, shorter-lived fishes. In the late 1950s and early 1960s, the predatory Nile perch (*Lates niloticus*) and four tilapiine species (*Oreochromis niloticus, O. leucostictus, Tilapia zillii,* and *T. rendalli*) were introduced into the Lake Victoria basin to increase depleted commercial fisheries (Fryer 1960; Ogutu-Ohwayo 1990, 1993, 1994). The Nile perch is a large centropomid fish that can reach over 2 m in length. This predator exhibits an ontogenetic dietary shift from invertebrate feeding to piscivory (Mkumbo & Ligtvoet 1992; Ogutu-Ohwayo 1993, 1994; Schofield & Chapman 1999). Although catches of many species had declined by the 1960s and others declined in the 1970s, probably as a result of overexploitation, the dramatic increase in Nile perch in the 1980s in Lake Victoria coincided with a further decline in populations of several indigenous species (Barel et al. 1985). Over 50% of the nonlittoral haplochromines, or about 40% of the endemic haplochromine cichlid community, in Lake Victoria disappeared (Kaufman 1992; Witte et al. 1992*a*; Seehausen et al. 1997*a*, 1997*b*). Many indigenous noncichlids, some of which were important in the pre-Nile-perch fishery, also declined or disappeared (Chapman et al. 1996*b*; Goudswaard & Witte 1997; Goudswaard et al. 2002). Haplochromines and mormyrids were the main fish prey ingested by Nile perch in the early stages of the introduction. By 1988, however, haplochromines and mormyrids had declined to the point where the native prawn *Caridina nilotica*, anisopteran nymphs, the open-water cyprinid *Rastrineobola argentea*, and Nile perch juveniles had become the main prey (Ogutu-Ohwayo 1990; Mkumbo & Ligtvoet 1992). Other changes

in the Lake Victoria system, including increasing eutrophication and deoxygenation of deeper waters (Hecky 1993; Hecky et al. 1994), may also have contributed to the faunal collapse (Kaufman & Ochumba 1993; Seehausen et al. 1997*a*). As a result of these changes, the fishery in Lake Victoria was converted from a multispecies system exploiting native fishes of more than a dozen principal target species to one in which three species (the introduced Nile perch, the introduced Nile tilapia, and *R. argentea*) make up almost all the commercial and artisanal catch. Similar changes occurred with the introduction of Nile perch into other lakes in the basin, including Lake Kyoga (Ogutu-Ohwayo 1994), central Ugandan satellite lakes (Kaufman et al. 1997), and Lake Nabugabo (Ogutu-Ohwayo 1993; Chapman et al. 1996*a*, 1996*b*).

The tremendous loss of diversity led to studies directed at identification of faunal refugia. A decade of study has revealed that satellite water bodies around the main lakes harbor small, remnant faunas of the larger lakes (Ogutu-Ohwayo 1993; Kaufman et al. 1997). Within Lake Victoria, rocky shores and offshore rocky islands serve as important refugia because of their high structural complexity and relatively clear waters that facilitate the coexistence of many fish species (Seehausen 1996, 1999; Seehausen et al. 1997*b*). Wetlands also protect prey species by offering both low-oxygen and structural refugia (Chapman et al. 1996*a*, 1996*b*; Rosenberger & Chapman 1999; Schofield & Chapman 1999, 2000). In Lake Victoria, other within-lake refugia, such as the deeper waters near the oxycline, have also been identified (Kaufman & Ochumba 1993; Seehausen et al. 1997*b*; Wanink et al. 2001).

The remnant populations of fishes that have persisted potentially serve as seeds for resurgence. In some lakes of the Lake Victoria basin and some sections of Lake Victoria, the resurgence of some indigenous species has been documented (Seehausen et al. 1997*b*; Witte et al. 2000) and seems to coincide with intense fishing that has reduced the numbers of large Nile perch. This has given new hope for maintenance of fish diversity in the basin and renewed motivation for management options that integrate sustainability of the fishery with conservation of indigenous fishes (Kaufman & Schwartz 2002). Our objectives here were to (1) provide a quantitative picture of faunal collapse and recovery in Lake Nabugabo, a small satellite of Lake Victoria, to demonstrate patterns and rate of faunal change occurring in the Lake

Victoria basin and (2) describe the response of Nile perch to a changing prey base. To address these objectives, we examined the change in the fish assemblage and the diet of Nile perch in Lake Nabugabo between 1991 and 2000, with a focus on the rapid changes that occurred between 1995 and 2000.

Study System

Lake Nabugabo, which lies just south of the equator in Uganda, is a small satellite lake (24 km^2, mean depth = 4.5 m) that became isolated from Lake Victoria approximately 4000 years ago (Greenwood 1965; Fig. 1 in Schofield & Chapman 1999). The lake lies within the extensive Lwamunda Swamp that was formerly a bay on the western shore of Lake Victoria (Worthington 1932; Greenwood 1965; Ogutu-Ohwayo 1993). The lake margin is primarily swamp dominated by hippo grass (*Vossia cuspidata*), *Miscanthidium violaceum*, and water lilies (*Nymphaea lotus* and *N. caerulea*), with small stands of papyrus (*Cyperus papyrus*).

The recent history of Lake Nabugabo is one of dramatic change in fish faunal structure and diversity. Nile perch were introduced into Lake Nabugabo in 1960 and 1963 (Ogutu-Ohwayo 1993). The 1962 Cambridge expedition to Lake Nabugabo recorded 30 species of fishes there: 20 noncichlids, 8 haplochromines (5 endemic to Nabugabo and nearby small lakes), and 2 tilapiines (Cambridge Nabugabo Biological Survey 1962; Greenwood 1965). Although 119 Nile perch were introduced into Lake Nabugabo prior to the Cambridge expedition, none were recorded in their survey (Cambridge Nabugabo Biological Survey 1962). At that time, the fishery was dominated (in terms of mass) by lungfish (*Protopterus aethiopicus*), followed by *Bagrus docmac, Schilbe intermedius, Clarias gariepinus, Oreochromis esculentus, O. variabilis*, and various species of haplochromines. A survey conducted in 1991 and 1992, 30 years after introduction of Nile perch and nonindigenous tilapiines, showed a dramatic change in the fish community. Of the species that formed the basis of the pre-Nile-perch fishery, *O. esculentus, O. variabilis*, and *B. docmac* were extirpated, and *S. intermedius, C. gariepinus,* and *P. aethiopicus* were rare. Nile perch (introduced), Nile tilapia (introduced), *S. intermedius, Brycinus sadleri,* and *R. argentea* dominated the open waters of the lake (Ogutu-Ohwayo 1993). A survey of extensive wetland areas surrounding Lake Nabugabo in 1993–1994 revealed that several species no longer present in the main lake were present in wetland ecotones or habitats deep within the swamp interior (Chapman et al. 1996*a*, 1996*b*). Haplochromines were primarily confined to wetland ecotones, whereas other species, such as the mormyrids *Petrocephlaus catostoma* and *Gnathonemus victoriae,* were recovered in interior swamp refugia (Chapman et al. 1996*a*, 1996*b*; Chapman & Chap-

man 1998; Rosenberger & Chapman 1999; Schofield & Chapman 1999).

Although Lake Nabugabo is much shallower and smaller in area than Lake Victoria, it has several littoral habitats similar to those of its larger neighbor. Both lakes have shorelines fringed by emergent aquatic macrophytes, quiet embayments with water lilies and thick beds of *Ceratophyllum*, and exposed shoreline. Lake Nabugabo, like much of the inshore areas of Lake Victoria, has turbid waters. Both lakes experienced the introduction and subsequent boom in Nile perch populations. Although the fish fauna of Lake Nabugabo is far simpler than that of Lake Victoria, Lake Nabugabo is virtually a small sample of the larger lake, an embayment complete with an original portion of the Lake Victoria littoral biota and hence a very useful model.

Methods

Fish Composition

In 1995 we set up a program to quantify interactions between Nile perch and other fishes in the main lake and ecotonal wetlands of Lake Nabugabo (Schofield & Chapman 1999). The inshore areas of the lake are bordered by either wetland or "exposed" shoreline (forest, rocky cliff, or sand beach). For logistical reasons, we examined habitat use by Nile perch and other lake fishes in only the western half of Lake Nabugabo. The study area was divided into 200-m shoreline sections or transects, and each transect was designated as wetland or exposed. We randomly selected 20 transects (10 wetland, 10 exposed) and sampled them between May and July 1995 with a combination of minnow traps and experimental gill nets. Ten metal minnow traps were set along the shoreline at 5-m intervals to capture small fishes. Two 30-m experimental gill nets (four panels: 25.4 mm, 50.8 mm, 76.2 mm, and 101.6 mm stretched mesh) were set parallel to the shore, one approximately 5 m from the edge of the wetland or forest deadfall and the second approximately 20 m offshore. We also set a series of the same experimental gill nets 100 m offshore at a subset of sites. Traps and nets were set overnight.

We randomly selected 10 transects and sampled them annually between 1996 and 1999. In 2000 we resampled the entire 20-transect survey for detailed comparison with 1995. In addition, we sampled transects 100 m offshore at each transect site in 1998 and 2000 for comparison with the 1995 open-lake data. In 1995 and 2000 we also set a small series of experimental nets in the middle of the lake. We carried out a second sampling method in 1998 to capture a larger size range of Nile perch. We used the same gill-net fleets Ogutu-Ohwayo (1993) used for conducting his 1991–1992 survey. These fleets were

25.4- to 305-mm stretched mesh, and we sampled four of the locations used in his original study.

In the field, fish were identified to the lowest taxa possible (for noncichlids, this was generally species). Because of the complexities of field identification of haplochromines, we lumped species together as "haplochromines" to describe broad patterns of faunal resurgence. To examine trends in haplochromine abundance across years, we calculated the relative abundance of haplochromine cichlids expressed as a percentage of fish captured in the experimental gills nets. We used the 20 transects sampled in 1995 and 2000 to examine more-detailed changes in the fish community. Catch per unit effort (CPUE) of haplochromines was used as the response variable in a split-plot two-way analysis of variance (ANOVA) testing for effects of habitat (wetland vs. exposed), distance from shore (inshore vs. 20 m offshore), and their interaction. The data were square-root transformed for this analysis. We used the nonparametric Mann-Whitney U test to compare the CPUE of small haplochromines in minnow traps between wetland and exposed inshore areas. Results of these two analyses were compared between 1995 and 2000 to detect changes in the distribution and abundance of haplochromines. A paired t test was used to detect differences in the CPUE between 1995 and 2000 for each of the major taxa captured in experimental gill nets. Again, CPUE data for haplochromines were square-root transformed, but this was not necessary for the other taxa.

A subset of haplochromine cichlids was collected and identified following the methods of Greenwood (1965) and with the generic classification of Greenwood (1980). One of us (L.S.K.) had gone over historical Nabugabo material with Greenwood at the Harvard Museum of Comparative Zoology during his visits there. Identification of the haplochromine cichlids from Lake Nabugabo entailed careful examination of the color pattern, tooth form, and body form of these specimens. We report species occurrence across years based on these identifications.

Diet of Nile perch

To examine changes in the diet of Nile perch coincident with the recovery of haplochromines and other native fishes, we examined stomach-content samples between 1994 and 2000. All samples were collected between May and July. In 1995 and 2000, our collections were more extensive, so we could better assess the size at which Nile perch exhibited a dietary shift. In 1994, 1996, 1998, and 1999, we took smaller representative samples of Nile perch to detect interannual variation in diet. The stomach of each fish was removed in the field, and stomachs with food in them were preserved in 10% formalin and later transferred to 50% isopropanol. Prey types were identified, counted, blotted dry, and weighed to the nearest 0.01 g.

Schofield and Chapman (1999) found that Nile perch taken from wetland and exposed transects in Lake Nabugabo differed in diet. Therefore, we used equivalent numbers of exposed and wetland fishes randomly chosen from available data for each year. These were pooled across habitats for interannual comparisons. We examined ontogenetic changes in diet by using the same technique to ensure that each size class had the same number of fish from both habitat types.

Nile perch were grouped by year of capture, and in some analyses these groups were broken down into 5-cm (total length) size classes. Frequency of occurrence (number of Nile perch containing each prey taxon, divided by the total number of Nile perch) and/or percent mass (mass of each type of food category expressed as a percentage of the total mass of the stomach contents) were calculated for prey taxa. Prey were lumped into invertebrates or fishes for the examination of differences in the size of the ontogenetic dietary shift and the degree of piscivory between 1995 and 2000. In addition, we used a more-detailed prey-taxa analysis (family level and below) to examine interannual variation in fish taxa consumed. We used linear regression to examine the relationship between the percent mass of haplochromines in the diet and the relative abundance of haplochromines expressed as a percentage of all fish captured in experimental gill nets.

Results

Temporal and Spatial Patterns of Faunal Resurgence

In 1995 the CPUE of haplochromines in experimental gill nets was very low (mean = 6 fish per transect). At this time, haplochromines were more abundant inshore than offshore, but there was no difference between wetland and exposed sites (analysis of variance [ANOVA]: distance effect, $F = 14.07$, $p = 0.001$; habitat effect, $F = 1.97$, $p = 0.178$; distance × habitat, $F = 1.46$, $p = 0.242$, Fig. 1). The minnow traps set in the inshore areas of wetland and exposed transects captured a smaller size class of haplochromines and showed far greater use of wetland sites (median CPUE per transect = 18, range = 1–64) than those set in exposed sites (median CPUE = 0, range = 0–1, Mann-Whitney U test, $U = 0.500$, $p < 0.001$). In nets 100 m offshore, CPUE was only 0.2 haplochromines per transect (range = 0–1 per net). In the series of nets set in the middle of the lake (approximately 700 m offshore), we captured no haplochromines. Nile perch captured in experimental gill nets in 1995 showed a different pattern of habitat use than the haplochromines. They were most abundant in offshore areas of exposed transects characterized by high levels of dissolved oxygen (Schofield & Chapman 1999).

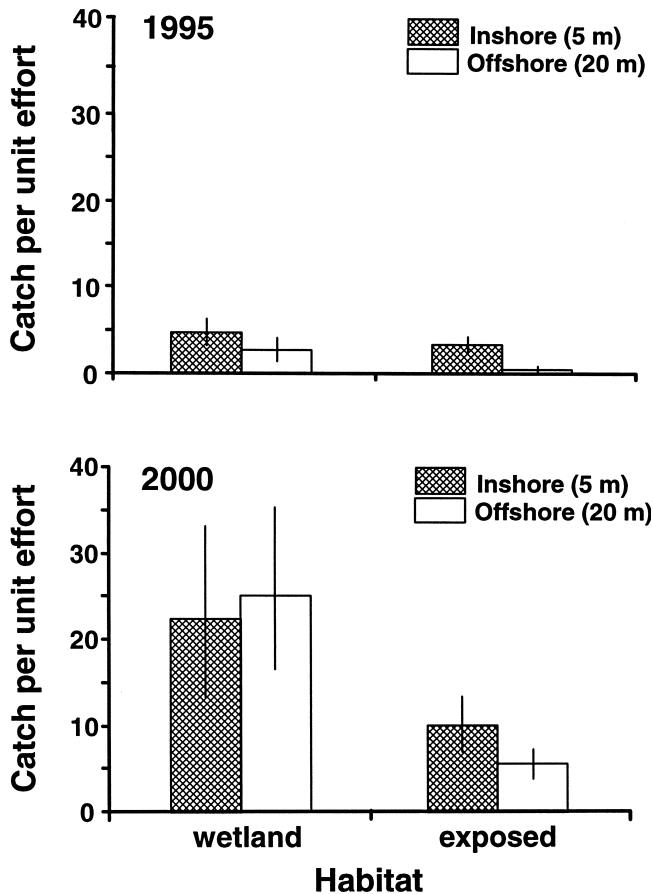The relative abundance of haplochromines, expressed as a percentage of all fish captured in gill nets,

Figure 1. Mean catch per unit effort (CPUE, number of fish per net) of haplochromine cichlids (±SE) in the inshore and offshore (20 m offshore) areas of wetland and exposed ecotones in Lake Nabugabo, Uganda, in 1995 and 2000. Data were collected with experimental gill nets. All data were square-root transformed, and the back-transformed data are presented. In 1995, the CPUE of haplochromine cichlids was higher inshore than offshore (p = 0.001). In 2000, the CPUE of haplochromine cichlids was marginally higher in wetland areas than in exposed areas (p = 0.078).

increased dramatically between the early 1990s and 2000 (Fig. 2). This was the result of an increase in the CPUE of this group to 33 fish per transect in 2000 and a decrease in the CPUE of *Brycinus sadleri*, an open-water characid (Fig. 3). In our experimental gill nets, the CPUE of *B. sadleri* declined dramatically from 92 fish per transect in 1995 to 16 fish per transect in 2000. Our experimental gill nets captured Nile perch between 7 and 50 cm total length (TL). The mean size of Nile perch decreased from 20.6 ± 0.4 cm, SE (TL, range = 8.6–42.2 cm), in 1995 to 18.2 ± 0.4 cm (TL, range = 7.2–50.0 cm) in 2000 ($t = 4.1$, $p < 0.001$). Nile perch showed a marginal decline in abundance ($p = 0.092$) from 14 fish per transect in 1995 to 10 fish per transect in 2000 (Fig. 3). In our resampling of sites sampled by Ogutu-Ohwayo
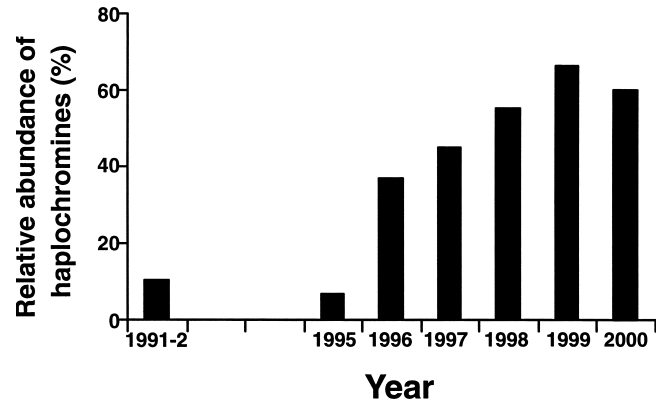

Figure 2. Relative abundance of haplochromine cichlids, expressed as a percentage of all fishes captured in experimental gill nets set at 5 and 20 m offshore between 1991–1992 and 2000 in Lake Nabugabo, Uganda. The 1991–1992 data were derived from Ogutu-Ohwayo (1993) and represent data from gill nets operated inshore and offshore. Comparable data are not available for 1993 and 1994.

(1993) with gill-net fleets up to 305 mm stretched mesh, the average size of Nile perch captured was also small, 22.5 cm (TL, range = 10.5–39.0 cm). These results, in addition to observations at fish landings, indicated that numbers of large Nile perch were relatively low at this time. With respect to rare taxa ("other" category in Fig.

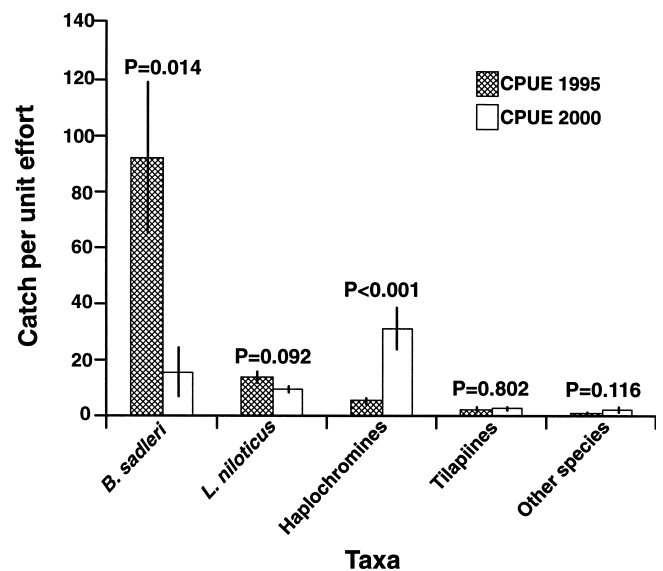*Figure 3. Catch per unit effort (CPUE; number of fish per transect) of major taxa (±SE) captured in experimental gill nets in Lake Nabugabo, Uganda, in 1995 and 2000 (nets from 5 and 20 m offshore were pooled). For each taxon, the difference in mean CPUE between years was determined with a paired t test. The p values are presented at the top of each within-species comparison. Rare taxa were combined as "other" fish because of the very small numbers captured.*

3), only two catfish species, *Schilbe intermedius* and *Synodontis afrofischeri,* were captured in 1995. In 2000 we captured six other rare species in experimental nets, including two mormyrids (*G. victoriae* and *P. catostoma*), three catfishes (*S. afrofischeri, S. intermedius*, and *Clarias werneri*), and the cyprinid *Barbus radiatus.*

Haplochromines not only increased in abundance between 1995 and 2000, they expanded their habitat from primarily ecotonal areas to offshore waters. In 1995, haplochromines were most abundant in inshore areas (mean total length [TL] = 8.9 ± 0.2 cm, SE), and smaller individuals (mean TL = 4.8 ± 0.08 cm) were most abundant in wetland ecotones. In 2000, there was no significant difference in the CPUE of haplochromines between inshore and offshore areas (ANOVA: $F = 0.49$, $p = 0.494$), but there was a marginally higher CPUE in wetland than exposed transects ($F = 3.50$, $p = 0.078$; Fig. 1). Smaller haplochromines were still much more abundant in the inshore areas of wetland habitats (median CPUE per transect = 89.5, range = 2–365) than in exposed habitats (median CPUE = 10.5, range = 0–45, Mann-Whitney U test, $U = 21.5$, $p = 0.031$). In 1995, *B. sadleri* and Nile perch were the two most abundant species captured in the gill nets 100 m offshore. By 1998 the relative abundance of *B. sadleri* and Nile perch had declined 100 m offshore, and haplochromine abundance had increased. The 1998 pattern was similar to that observed in 2000 (Fig. 4). The small cyprinid *R. argentea* was also abundant in offshore areas in all years but was not captured with our sampling gear.

To detect changes in species richness between 1995 and 2000, we combined trap and experimental gill nets and observations at fish landings. These data are presented in Table 1. The major change in species richness was the reappearance, albeit in small numbers, of mormyrid and cyprinid species. Some species have never recovered, including the haplochromine *Prognathochromis venator*, the tilapiines *Oreochromis esculentus* and *O. variabilis*, the mormyrid *Marcusenius nigricans*, the cyprinids *Barbus magdalenae* and *Barbus neumayeri* (although the latter species can be found in deep swamp refugia), and the catfish *Bagrus docmac* (Table 1).

The haplochromine catch over the years consisted of seven described species plus one not previously reported from Lake Nabugabo, which appeared in the more recent catches. The described species included: *Pseudocrenilabrus multicolor victoriae, Astatoreochromis alluaudi, Astatotilapia nubila, Paralabidochromis beadlei, Astatotilapia velifer, Gaurochromis simpsoni, and Haplochromis annectidens.* The unidentified and previously unknown taxon is morphologically assignable to the genus *Psammochromis*; specimens are being placed on deposit at the Harvard Museum of Comparative Zoology. In addition, the most recent collections contained specimens that appear to be of hybrid origin, intermediate in coloration and morphology between *P. beadlei* and the previously unknown, *Psammochromis*-like taxon. This discovery has spawned a detailed analysis of species composition and shifts in haplochromine community composition between 1990 and 2002, the results of which will be published elsewhere. Within the context of this paper, we examined total haplochromine catch per unit effort and relative abundance over time and the presence of species across years.

Predator Response to a Changing Prey Base

The diet of Nile perch changed coincident with change in the fish prey base. The most prominent feature of the dietary change was an increase in the proportion of haplochromines in the diet (Fig. 5). The major prey taxon in 1994 was *Rastrineobola argentea*. In 1995 *R. argentea* and Nile perch were the major prey consumed, and cichlids (unidentified cichlids and haplochromine cichlids combined) composed only 9% of the diet. In 1996 through 2000, however, the major prey taxon was haplochromines (Fig. 5). Linear regression showed that the relative abundance of haplochromines (expressed as a percentage of all fish captured in experimental gill nets) explained 97% of the variance in percent mass of the Nile perch diet composed of haplochromines ($F = 92.83$, $p = 0.002$).

In 1995 Nile perch fed largely on invertebrates until reaching approximately 30 cm, when fish became the dominant prey (Fig. 6). Frequency-of-occurrence data indicated the same trend. Although our sample size of <10 cm for Nile perch is low, in 2000 Nile perch were strongly piscivorous across the entire range of sizes sampled (Fig. 6).
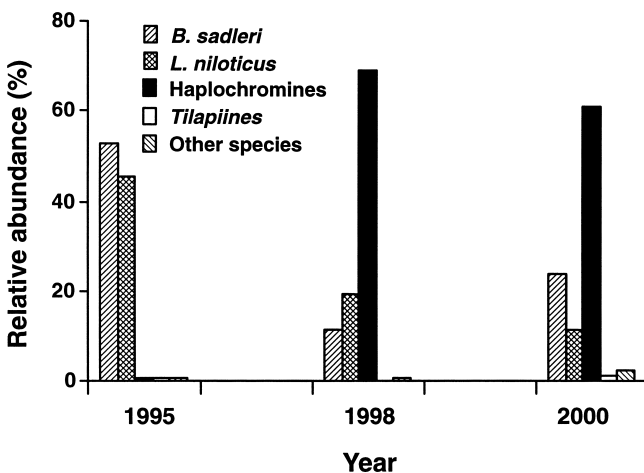

Figure 4. Relative abundance of major taxa, expressed as a percentage of all fishes captured in experimental gill nets, in the offshore waters (100 m offshore) of Lake Nabugabo in 1995, 1998, and 2000.

Table 1.   Changes in the species composition of Lake Nabugabo over the past decade.[a]

Family	Scientific name	1991–1992	1994–1996	1998–2000
Protopteridae	*Protopterus aethiopicus*	+	+	+
Mormyridae	*Gnathonemus victoriae*	+	−	+
	Gnathonemus longibarbis	−	−	+
	Marcusenius nigricans	−	−	−
	Petrocephalus catostoma	−	−	+
Characidae	*Brycinus sadleri*	+	+	+
Cyprinidae	*Rastrineobola argentea*	+	+	+
	Barbus magdalenae	−	−	−
	Barbus apleurogramma	−	−	+
	Barbus radiatus	−	−	+
	Barbus kerstenii	−	−	+
	Barbus neumayeri	−	−	−
	Barbus sp.	+	+	+
Bagridae	*Bagrus docmac*	−	−	−
	Schilbe intermedius	+	+	+
Clariidae	*Clarias gariepinus*	+	−	+
	Clarias alluaudi	−	+	+
	Clarias werneri	−	+	+
Mochokidae	*Synodontis afrofischeri*	+	+	+
Cyprinodontidae	*Aplocheilichthys pumilus*[b]	−	+	+
Cichlidae	*Oreochromis esculentus*	−	−	−
	Oreochromis variabilis	−	−	−
	Astatotilapia velifer[c]	+	+	+
	Gaurochromis simpsoni	+	+	+
	Haplochromis annectidens	+	+	+
	Paralabidochromis beadlei	+	+	+
	Prognathochromis venator	−	−	−
	Psammochromis sp.	−	+	+
	Astatotilapia nubila[c]	+	+	+
	Pseudocrenilabrus multicolor[b]	−	+	+
	Astatoreochromis alluaudi	+	+	+
Mastacembelidae	*Aethiomastacembelus frenatus*	+	+	+
Introduced species	*Lates niloticus*	+	+	+
	Oreochromis niloticus	+	+	+
	Oreochromis leucostictus	+	+	+
	Tilapia rendalli	+	+	+
	Tilapia zillii	+	−	−

[a] *A + indicates that the species was recorded during the designated time period; − indicates the species was not captured but had been recorded prior to the expansion of the introduced Nile perch population. Data for 1991–1992 were abridged from Ogutu-Ohwayo (1993). Data for 1994–1996 and 1998–2000 were based on a survey of Lake Nabugabo using traps, experimental gill nets, and observations at fish landings. These data represent open-water and ecotonal areas and do not include species restricted to deep (interior) swamp refugia.*
[b] *These species were not reported in Ogutu-Ohwayo (1993) but were found in wetland ecotones and interior swamp refugia in 1993–1994 (Chapman et al. 1996a, 1996b).*
[c] *The genus Astatotilapia includes a fluviatile group that forms a monophyletic lineage (Lippitsch 1993). The lacustrine species previously assigned to Astatotilapia are unrelated to the riverine group, as has been shown in a study of scale and squamation characters (Lippitsch 1993). Lippitsch states that it seems probable that the lacustrine species are closely related to other endemic species of the Lake Victoria system rather than to riverine Astatotilapia and suggests that new genera be established for these.*

Discussion

Patterns of Faunal Resurgence

In Lake Nabugabo, there has been a dramatic recovery of a subset of the pre-Nile-perch fauna. Most notably, haplochromines have increased in abundance and expanded their range to offshore waters. A number of noncichlids have shown a modest resurgence, including the catfishes *S. afrofischeri* and *S. intermedius*; the mormyrids *P. catostoma*, *G. longibarbis*, and *G. victoriae;* the clariid catfishes; and the cyprinids *Barbus kerstenii, B. radiatus*, and *B. apleurogramma*. Interestingly, we observed a marked decline in the CPUE of the open-water characid *B. sadleri*. In Lake Victoria and Lake Kyoga, intense fishing of Nile perch has also coincided with faunal resurgence (Ogutu-Ohwayo 1994; Seehausen et al. 1997b; Witte et al. 2000). In the Mwanza Gulf of Lake Victoria, for example, haplochromines increased from 0.2% of the catch in 1987 to 21.3% of the catch in 1997 (Witte et al. 2000). As in Lake Nabugabo, faunal recovery in other areas of the Lake Victoria basin represents
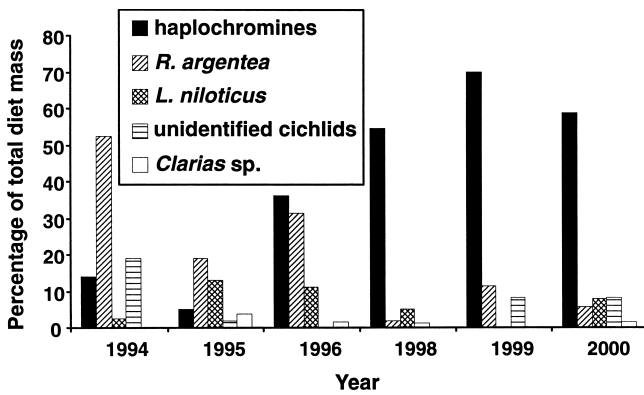
Figure 5. Dietary importance, expressed as percentage of total diet mass, of major fish prey taxa (invertebrate taxa are not included) in the stomachs of Nile perch from Lake Nabugabo, Uganda, between 1994 and 2000. The sample sizes of stomachs with contents was 48, 224, 20, 16, 44, and 152 for 1994, 1995, 1996, 1998, 1999, and 2000, respectively.
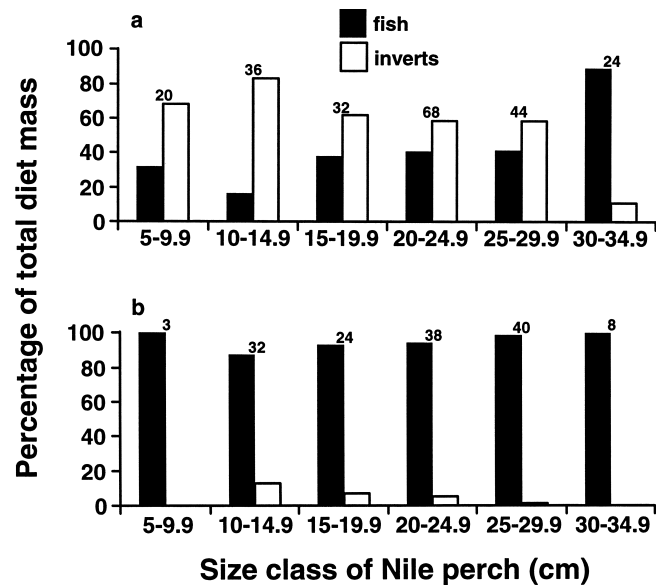

Figure 6. Dietary importance, expressed as percentage of total diet mass, of invertebrate and fish prey taxa in the stomachs of the 5-cm-total-length size class of Nile perch collected from Lake Nabugabo, Uganda, (a) in 1995 when haplochromine cichlids were relatively rare in the lake and (b) in 2000 after haplochromine cichlids had resurged in the system. Sample size is above bars.

only a subset of the species that characterized pre-Nile perch fauna. For example, in the sublittoral zone of the Mwanza Gulf, there has been a resurgence of some species of haplochromines but only a few species in large quantities (Witte et al. 2000).

The resurging fauna in Lake Nabugabo includes species that have persisted with Nile perch and have the flexibility to respond quickly to changing environments. In Lake Victoria, resurging species have persisted in the face of more dramatic changes to the system, among them, eutrophication, deoxygenation of deep water, introduction of Nile perch, and introduction and spread of water hyacinth (*Eichhornia crassipes*). Key refugia in Lake Nabugabo are wetland areas, because rocky refugia and deeper waters are absent in the system. Several species that have reappeared in the open waters of the lake were only recovered in ecotonal wetlands or deep swamp refugia in the early 1990s (e.g., *P. catostoma, B. radiatus, B. kerstenii;* Chapman et al. 1996a). In Lake Victoria, both wetland refugia and rocky refugia are likely to have been key source areas for resurging species, although several of the species that have resurged in the sublittoral are likely to have survived in the sublittoral because they have never been found in either wetlands or rocky areas.

Fishes that persist in faunal refugia may represent remnants of larger populations that were once widespread or species that actively shifted from open-water habitat to areas offering protection from Nile perch predation. In rocky boulder refugia in Lake Victoria, one finds a number of rock-dwelling specialists but also species that were not specialized rock dwellers in the pre-Nile-perch era but either survived only in rocky refugia or shifted to rocky habitat (Witte et al. 1992b; Seehausen 1996; See-

hausen et al. 1997b). In Lake Nabugabo over the past few years, a number of species have expanded from inshore areas to open waters, suggesting that the pre-Nile-perch distribution was much broader. Habitat shifts by fishes in response to predator risk have been reported in several studies (Power et al. 1985; He & Kitchell 1990; Brown & Moyle 1991), and this probably contributes to the current distribution patterns of indigenous fishes in lakes Victoria and Nabugabo.

Although intense fishing pressure on Nile perch has coincided with faunal resurgence in lakes Nabugabo, Kyoga, and Victoria, it is possible that other environmental changes have contributed to the observed patterns. In Lake Kyoga, for example, the increase in certain haplochromine species coincided both with the invasion and spread of water hyacinth (that may have enhanced ecotonal refugia) and heavy fishing pressure on Nile perch (Ogutu-Ohwayo 1994). In Lake Nabugabo, the dramatic decline of the insectivorous *B. sadleri* may have released pressure on the food base for invertebrate-feeding haplochromines. Other environmental characters, such as high water levels, may also influence recruitment by the increasing availability of ecotonal refugia. With their shallow basins and vast valley swamps and swampy margins, Lake Victoria and its satellite lakes are strongly influenced by changes in water level. If regional water-level change was the major driving factor, how-

ever, we would expect similar patterns of resurgence among lakes with introduced Nile perch. This does not seem to be the case, because resurgence was detected earlier in Lake Kyoga (Ogutu-Ohwayo 1994) than in lakes Victoria and Nabugabo.

We can make two general statements about the species composition of the haplochromine assemblage in Lake Nabugabo, pending the results of detailed morphological and genetic analysis. First, the species described by Greenwood (1965) as being in Lake Nabugabo are still present, with the exception of *Prognathochromis venator* (Kaufman & Ochumba 1993; Ogutu-Ohwayo 1993). Second, the resurgent assemblage differs from what we were used to seeing in the early 1990s in several interesting ways that bear closer examination. We are currently conducting detailed morphological and genetic studies of today's Nabugabo haplochromine assemblages.

Predator Response to a Changing Prey Base

Between 1994 and 2000, the Nile perch in Lake Nabugabo showed a major change in diet, most notably an increase in the proportion of haplochromines. When Nile perch were originally introduced into Lake Nabugabo, haplochromines were abundant (Greenwood 1965), and it is likely that perch fed on haplochromines and other indigenous fishes. Because these fishes largely disappeared from the open waters of the lake, Nile perch presumably shifted their diet to include more invertebrates, pelagic species (*R. argentea*), and their own juveniles (Schofield & Chapman 1999). With the recent increase in haplochromine abundance, smaller Nile perch have shifted their diet to include a large proportion of haplochromines. This strong dietary flexibility is characteristic of Nile perch, as evidenced by their history of dietary change in Lake Victoria. Between 1968 and 1977, Nile perch (20–60 cm) in Lake Victoria fed heavily on haplochromines (92% frequency of occurrence, Ogutu-Ohwayo 1994). Between 1988 and 1992, however, haplochromines were rare in the diet of Nile perch (4% frequency of occurrence in Nile perch 20–60 cm TL), whereas invertebrates (primarily *Caradina nilotica*), *R. argentea*, and juvenile Nile perch were more frequent (Mkumbo & Ligtvoet 1992; Ogutu-Ohwayo 1994). This dietary shift coincided with the dramatic decline of haplochromines in Lake Victoria (Kaufman 1992; Witte et al. 1992*a*, 1992*b*).

Between 1995 and 2000, Nile perch in Lake Nabugabo showed a major decrease in proportional mass of invertebrates consumed and were strongly piscivorous at a much smaller size. A similar pattern is evident in Lake Victoria, where the shift to piscivory for Nile perch occurred at a larger body size after the collapse of the haplochromine cichlid fauna (Mkumbo & Ligtvoet 1992; Ogutu-Ohwayo 1994; Schofield & Chapman 1999). Evi-

dence suggests that Nile perch prefer to prey on haplochromines when they are available (Mkumbo & Ligtvoet 1992; Ogutu-Ohwayo 1994; Schofield & Chapman 1999; this study). This pattern of ontogenetic shift should be taken into consideration when the effects of Nile perch on indigenous fish and fisheries are being predicted. Dynamic mass-balance models that take these factors into account predict that haplochromine resurgence following overfishing of perch can provide a crucial cushion against the complete collapse of a Nile perch fishery (Kaufman & Schwartz 2002).

Implications for the Fishery

Fish communities seem to respond to environmental and fishing pressures with a characteristic suite of changes termed the "fishing-down" process, which involves the successive loss of large individuals in favor of smaller, shorter-lived fishes (Welcomme 2003). The changes in the Lake Victoria fish stock observed between 1950 and 1980 conform in a general way to this model. The fishery moved toward the smallest species (haplochromines and *R. argentea*), with the exception of the Ugandan portion of the lake, where a large proportion of the catch was still composed of some larger indigenous species (J. Balirwa et al., unpublished data). Subsequent to 1980, the impact of Nile perch and Nile tilapia on the fishery temporarily reversed this trend, and the fishery drifted back toward larger species. However, recent intense fishing pressure on Nile perch may represent a second "fishing-down" process. Although most fishermen on Lake Nabugabo currently (2001) fish for both Nile tilapia and Nile perch, Nile tilapia is the major catch for more than 80% of the fishermen, whereas Nile perch is the major catch for only 18% (L.J.C., C.A.C., and D. Schindler, unpublished data) and large Nile perch (>60 cm) are currently rare in the catch (L.J.C. and C.A.C., personal observations). In our study we detected a marginal decrease in Nile perch (7–50 cm) between 1995 and 2000 in our experimental gill nets set nearshore and 20 m offshore, but we observed that large Nile perch were quite rare in the lake even by 1995. We also used four sets of gill-net fleets that ranged up to 305 mm stretched mesh in 1998 to facilitate the capture of a larger size range. The Nile perch captured were small, however, averaging only 22.5 cm TL (range = 10.5–39.0 cm). In 1991–1992, Ogutu-Ohwayo and his team captured a higher proportion of large Nile perch; 26% of the fish sampled for stomach contents were >40 cm TL, and 9% were >60 cm TL.

The predator-prey situation in Lake Nabugabo is a moving target, and the degree of faunal recovery will depend to some extent on the direction and intensity of fishing efforts. Prior to Nile perch establishment, other piscivores were abundant in the lake (e.g., *P. venator, C. gariepinus, S, intermedius, B. docmac*), and indige-

nous haplochromines coexisted in abundance with these predators. It is possible that intense fishing pressure on Nile perch could keep their numbers low enough to permit maintenance of the resurging assemblage. Kitchell et al. (1997) used a bioenergetic model of Nile perch predation rates to evaluate the consequences of fishery exploitation patterns in Lake Victoria. They concluded that fisheries based on large-mesh gill nets could reduce predation by Nile perch to approximately 40% of predation estimates in the late 1970s, when Nile perch densities seemed to be the highest. Their model also suggested that increased pressure on Nile perch juveniles (through beach seining and small-mesh gill-net fisheries) could reduce Nile perch predation to approximately 25% (Kitchell et al. 1997). In a similar bioenergetics modeling analysis, Schindler et al. (1998) found that enforcement of a 5-inch minimum mesh size in Lake Victoria would reduce both Nile perch cannibalism and predation on other indigenous fishes by as much as 44% with only a 10% decrease in the yield of Nile perch. Clearly, both the dynamics of the predator-prey situation in Lake Victoria and Lake Nabugabo and bioenergetics modeling (Kitchell et al. 1997; Schindler et al. 1998; Kaufman & Schwartz 2002) suggest that fishing is an extremely potent ecological force in these systems that to some degree can potentially regulate the Nile perch population and therefore the trophic dynamics and patterns of faunal resurgence.

Characteristics of the Resurging Fauna

Resurging populations in lakes Nabugabo, Victoria, and Kyoga are encountering an environmental milieu much changed from that of 20 years ago. Only a subset of the basin fauna now exists, and in Lake Victoria limnological conditions are strongly influenced by intense human land use. Thus, it is reasonable to expect that the resurging fauna will differ in composition and ecosystem function from the pre-Nile-perch fauna (Seehausen 1999). For example, resurging species may experience reduced competitive pressure for food resources, permitting either a higher level of specialization or, alternatively, a broader diet spectrum. In Lake Victoria, some of the resurging species have experienced severe reduction in population size or have survived in refugia with turbid water, and we anticipate that some of these resurging taxa represent genetically mosaic stock derived from more than one pre-refugial species (Seehausen et al. 1997*a*, 1997*b*; Witte et al. 2000). In Lake Nabugabo, we are seeing evidence of hybridization that may reflect recent habitat shifts into open waters with low haplochromine densities. Such conditions relax mate selectivity in females and are conducive to interspecific hybridization (Seehausen et al. 1997*a*). Future studies, using a combination of molecular genetics, morphometrics, and

breeding experiments, should examine gene-flow patterns among the resurging Lake Nabugabo haplochromines.

Species that shifted to hypoxic wetland refugia in response to predation by Nile perch or that are recovering in the currently hypoxic areas of Lake Victoria have potentially experienced strong selection pressure for low-oxygen tolerance over multiple generations. For these species, we might anticipate differences between pre- and post-resurgence populations with respect to such characteristics as gill morphology, body size, and respiratory physiology. Wanink and Witte (2000) documented an increase in the number of gill filaments in *R. argentea* from Lake Victoria between 1983 and 1988. Similarly, Witte et al. (2000) reported that *Yssichromis pyrrhocephalus,* a haplochromine from Lake Victoria, showed an increase in the average number of secondary gill lamellae between 1978 and 1999. It is unknown whether these changes are the result of a heritable response to selection, phenotypic plasticity, or their interaction. It is possible, however, that several generations of strong selection pressure in hypoxic refugia may lead to a heritable change in respiratory traits, among other characters.

The resurgence of some indigenous species in lakes Nabugabo, Kyoga, and Victoria offers hope for the persistence of a subset of the basin fauna and warrants standardized biodiversity monitoring. The faunal resurgence also clearly demonstrates the importance of habitat refugia as seeds of resurgence in the lake basin. These habitats should be preserved through protected-area status or as part of integrative co-management programs. The predator-prey situation in lakes with introduced Nile perch is clearly a fluid one that will demand careful long-term monitoring and both empirical and modeling approaches to estimate future change and inform management decisions. The apparent impact of intense fishing of Nile perch on the food-web structure in lakes of the Lake Victoria basin supports the importance of fisheries in the continued recovery of a subset of the basin fauna and the continuing role of indigenous fishes as the apparently preferred prey of the Nile perch.

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