

Hypoxic wetland tributaries as faunal refugia from an introduced predator

Rosenberger AE, Chapman LJ. Hypoxic wetland tributaries as faunal refugia from an introduced predator.
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Abstract – The introduction of Nile perch (*Lates niloticus*) into the Lake Victoria basin of East Africa has coincided with the decline or disappearance of hundreds of indigenous species. To mitigate additional biodiversity loss, we must learn what limits the spread of Nile perch and what habitats serve as refugia for prey species. Heavily vegetated wetlands may protect fishes from Nile perch predation by providing both structural and low-oxygen refugia for prey species tolerant of hypoxia. To examine the potential of wetlands as refugia we quantified the composition, persistence, and stability of fish assemblages in a wetland tributary of Lake Nabugabo, a satellite lake of Lake Victoria in which Nile perch have been introduced. Nile perch were extremely rare in the wetland, and nine of the 18 species that have disappeared from the open waters of the satellite lake were captured in the tributary in this study. Dissolved oxygen was chronically low in the river and may be important in shaping fish community characteristics. Faunal attenuation occurred as the dry season progressed and oxygen levels dropped; however, the most common species remained through seasonal changes. The chronically low oxygen conditions in the wetland tributary may permit persistence of only hypoxia-tolerant species. However, wetland conditions seem to limit exploitation by Nile perch providing critical refugia for a subset of the basin fauna.

Key words: wetland; refugia; East Africa; haplochromine cichlids; Nile perch

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Un resumen en español se incluye detrás del texto principal de este artículo.

The introduction of non-indigenous species into new habitats is common practice throughout the world. Introduced species are potentially useful and have provided sport and recreation, food, ornament, or control of unwanted organisms; however, species introductions are likely to alter the ecology of the indigenous community (Courtenay & Robins 1975; Welcomme 1984; Courtenay 1993). Conservation biologists face critical questions with respect to the consequences of species introductions, and some of the most significant issues relate to introduced predators that impact the abundance and distribution of prey species (Zaret & Paine 1973). In order to understand this impact fully, we must know what qualities of the ecosystem inhibit predation or create distributional barriers for the predator. Areas beyond these boundaries may be exploited by prey species as refugia from predation.

The species flock of endemic haplochromine cichlids in the Lake Victoria basin of East Africa is well known as one of the most diverse and extensive radiations of vertebrates (Greenwood 1980; Kaufman 1992; Kaufman et al. 1997). In addition, a diverse assemblage of non-cichlids inhabits the basin. In the late 1950s and early 1960s, the predator Nile perch (*Lates niloticus*) was introduced into lakes of the Lake Victoria basin in an attempt to increase depleted commercial fisheries (Fryer 1960; Ogutu-Ohwayo 1990, 1993). In Lake Victoria, Nile perch persisted in small numbers until the early 1980s and then underwent a dramatic population increase that coincided with a rapid loss of fish diversity in the lake (Ogutu-Ohwayo 1990; Kaufman 1992; Witte et al. 1992; Kaufman et al. 1997). It is thought that over half of the endemic haplochromines in Lake Victoria, as well as many indigen-

ous non-cichlids, have become endangered or extinct, while Nile perch has radiated throughout the Lake Victoria ecosystem (Ogutu-Ohwayo 1990; Witte et al. 1992; Kaufman et al. 1997). As a result, a fishery that once exploited a diversity of native fishes now rests primarily on Nile perch, with small contributions from an introduced tilapia, *Oreochromis niloticus*, and the native pelagic minnow, *Rastrineobola argentea* (Kaufman 1992; Kudhongania & Chitamwebwa 1995). Similar changes have also occurred with the introduction of Nile perch into Lake Kyoga (Ogutu-Ohwayo 1994) and Lake Nabugabo (Ogutu-Ohwayo 1993; Chapman et al. 1996a, b).

Understanding what allows some native fishes to persist with Nile perch is critical to conservation of the remaining indigenous faunas in lakes Victoria, Kyoga, and smaller lakes in the region that harbor introduced Nile perch. Refugia may act as vital areas for the preservation of fish diversity and could be used for reintroduction programs and/or stocking of aquaculture farms. Well-oxygenated, structurally complex refugia are found in the rocky cliffs and islands of Lake Victoria, where rock crevices shelter endemic haplochromine cichlids from predation (Witte et al. 1992; Seehausen 1996). Small satellite lakes that have not experienced introduction of Nile perch, though less diverse in assemblage than Lake Victoria, may also modulate extinction in the lake basin (Ogutu-Ohwayo 1993; Kaufman et al. 1997). Finally, wetlands dominated by papyrus (*Cyperus papyrus*) or *Miscanthidium violaceum*, may protect prey species from Nile perch predation for two reasons. First, they may provide both structural and low oxygen refugia for prey species tolerant of the hypoxic conditions that prevail in their dense interior. Second, they may serve as barriers to the dispersal of the Nile perch, permitting remnant populations to persist in the lagoons and small tributaries which are separated from the main lakes by extensive areas of fringing swamp (Ogutu-Ohwayo 1993; Chapman et al. 1996b).

Physiological studies suggest that Nile perch are relatively intolerant of low oxygen conditions. Fish (1956) found that Nile perch require water with high dissolved oxygen ($>5 \text{ mg} \cdot \text{l}^{-1}$) because their blood has low oxygen affinity. In addition, both the metabolic rate and the critical oxygen tension of Nile perch are relatively high, which may limit use of oxygen-stressed habitats (Schofield & Chapman in press). However, behavioral experiments (Chapman et al. 1995; Rosenberger 1997), gill morphological analyses (Galis & Barel 1980; Chapman & Liem 1995; Rosenberger 1997), and physiological experiments (Rosen-

berger 1997) suggest a relatively high tolerance to hypoxia in some non-air-breathing haplochromine cichlids and non-cichlids in the basin. Other non-cichlids found in hypoxic waters are air breathers (e.g., *Protopterus aethiopicus*, *Ctenopoma muriei*, *Clarias* spp.) and can meet their oxygen demands using atmospheric oxygen. Such species may find refuge from Nile perch by exploiting hypoxic wetlands.

Lake Nabugabo, a small satellite lake of Lake Victoria, is ideal for addressing the wetland refugium hypothesis. Nile perch were introduced into Lake Nabugabo about the same time as they were introduced into Lake Victoria (Ogutu-Ohwayo 1993). The lake is surrounded by an extensive peat, sedge, and papyrus swamp riddled with passageways and lagoons (Beadle & Lind 1960; Cambridge Nabugabo Biological Survey (CNBS) 1962 unpubl.; Chapman et al. 1996b). It is well documented that many of the native fishes in the open waters of the lake have declined or disappeared since the introduction of Nile perch (Ogutu-Ohwayo 1993). However, survey data in the wetland regions of Nabugabo indicate that some species thought to be rare or extinct in the main lake can be found in the main papyrus-choked tributary of Lake Nabugabo and other wetlands where Nile perch are rare (Chapman et al. 1996a, b).

This study builds on these earlier studies of wetland refugia in the Lake Victoria basin to provide a detailed assessment of the potential of wetland tributaries as refugia for endangered species from Nile perch predation. To fully assess the potential of wetland habitats as refugia, we must ask the following questions: 1) Does the habitat hold a species or assemblage that does not coexist with the introduced predator? 2) Does the habitat effectively exclude the introduced predator or dramatically limit its impact on prey species? 3) Are target species or assemblages consistently present; can the fauna be considered stable or persistent? We examine these issues on the Juma River, the main wetland tributary of Lake Nabugabo. We first describe spatial and temporal variation in environmental characteristics of the river (e.g., dissolved oxygen, depth, and current) that may inhibit colonization and survival of indigenous and introduced species. Second, we describe the fish assemblage of the Juma River and compare our observations to historical data. We relate environmental characters to the diversity and abundance of fishes to identify factors that may account for variation in habitat use. Finally, we examine the stability and persistence of fish assemblages within the wetland tributary across seasonal rainfall and over a 2-year period.

Material and methods

Study area

Lake Nabugabo is a small satellite lake (24 km², 5 km in diameter, mean depth 4.5 m) of Lake Victoria. The lake lies within an extensive wetland that was formerly a bay on the western shore of Lake Victoria (Worthington 1932; Greenwood 1965, Fig. 1). A long sand bar that isolates Lake Nabugabo from Lake Victoria was created during water-level fluctuations about 4000 years ago (Greenwood 1965, 1966). The lake margin is primarily marsh, dominated by hippo grass (*Vossia cuspidata*), *Miscanthidium violaceum*, and water-lilies (*Nymphaea lotus* and *N. caerulea*), with small stands of papyrus (*Cyperus papyrus*). Lake Nabugabo is fed mainly by the Juma River, along with numerous small springs that discharge along the lake shore (Greenwood 1965). Outflow from the lake is eastward via the Lwamunda Swamp, with seepage through the sandbar that forms the east-

ern barrier separating Lake Nabugabo from Lake Victoria (Greenwood 1965, Fig. 1). The Lwamunda Swamp is an extensive wetland area surrounding much of the lake (approximately 4 km wide) and contains permanent lagoons and small, intermittent streams (Fig. 1).

The Juma River is choked with papyrus and other emergent wetland vegetation, and oxygen availability is low (Chapman et al. 1996b). Three locations were repeatedly sampled in the Juma River: 1) the ecotone of the river, where emergent vegetation of the river mouth meets the open waters of the lake, 2) the mouth of the Juma River adjacent to the main lake ecotone, and 3) a site approximately 200 m upstream of the mouth (Fig. 1). The ecotone of the river is dominated entirely by hippo grass and is clearly identified by a marked zonation as the hippo grass is replaced by papyrus, forest, and wetland vegetation characteristic of the deeper swamps. The mouth of the river adjacent to the ecotone is forested wetland, choked

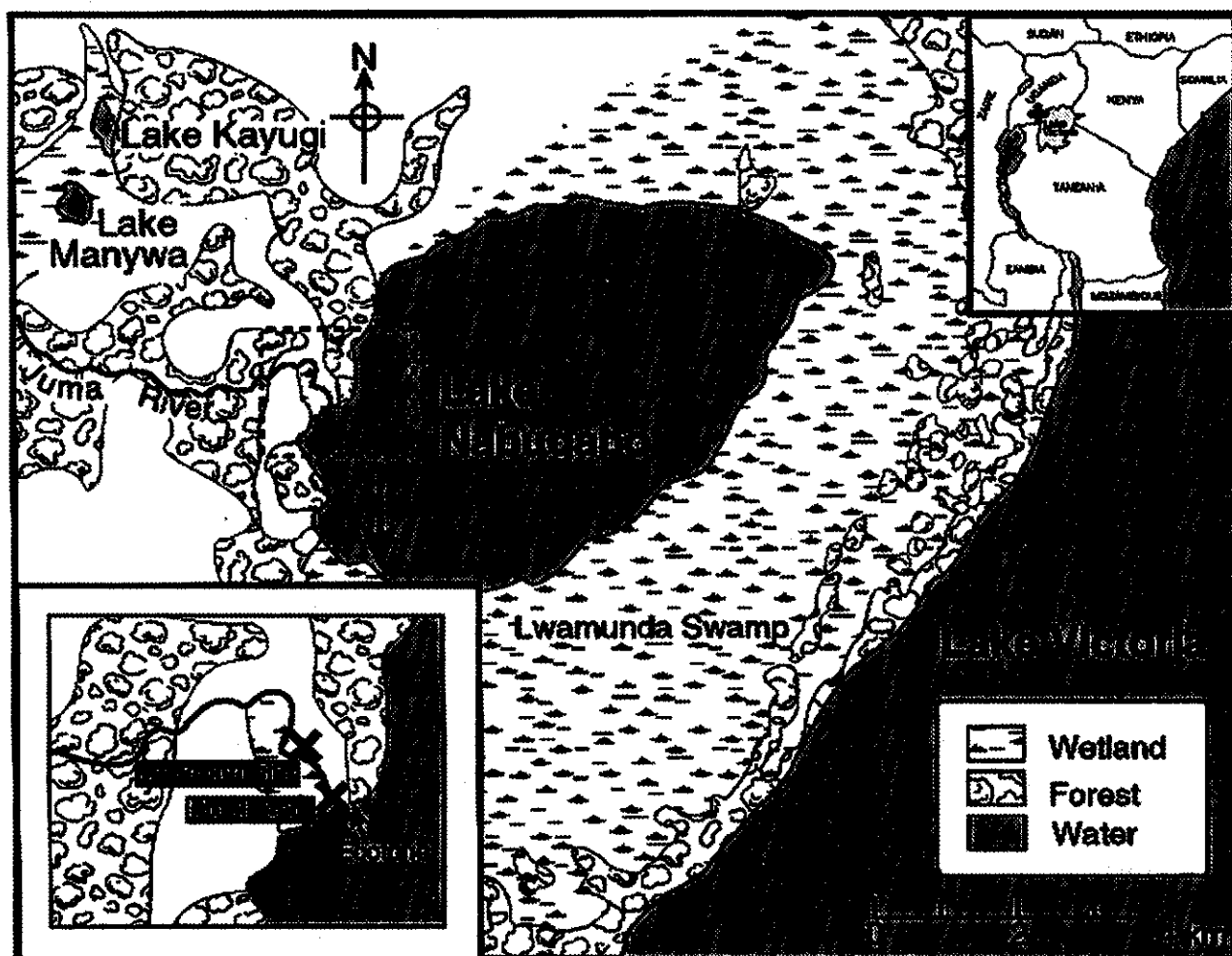


Fig. 1. Map of Lake Nabugabo, Uganda, and its main tributary, the Juma River, with the three sampling sites indicated.

by a diversity of emergent vegetation including *Afromomum* spp., hippo grass, and papyrus. The site approximately 200 m upstream of the river mouth is dominated by papyrus.

Sampling procedures

At each of the three sites, stations were selected systematically for repeat sampling. The tributary was marked off at 5-m intervals for 55 m in the mouth and upstream areas and 15 m at the ecotone area. Every 5 m, one trap was set in heavy vegetation, and one trap was set in more open habitat to produce a total of 22 stations at the mouth (11 distance locations) and upstream sites and 6 stations (3 distance locations) at the ecotone. To increase the probability of capturing all species in each of the three main sites, we carried out additional qualitative sampling with local traps made from papyrus, seine nets, and small experimental gill nets (10-m nets, three panels, 25.4 mm, 50.8 mm, and 76.2 mm). Each site was sampled four times in 1995 and once in 1996. The first year, sampling encompassed the late rainy season and the early dry season, 1995 (late May through early July). In 1996, sampling was repeated once during

the late rainy season (early June). Because the 1996 rainy season was longer and had heavier rains than 1995, we designated the late rainy season as late May, 1995, and early June, 1996.

For each trap or net set, the following environmental data were recorded: dissolved oxygen concentration, vegetative cover, current, depth, and distance from the open waters of Lake Nabugabo. Dissolved oxygen concentration was measured with a YSI model 51B oxygen meter, and vegetative cover was estimated with the aid of line transects used early in the sampling season. Lines marked at 1-m intervals were stretched across the tributary. The presence and type of vegetation were recorded every meter for 2 m on either side of the line transect. These data were used to create a grid map of the study site and to estimate vegetative cover for systematically set traps. Water current was ranked on a scale of 0 to 4 (0=no current, 1=visible but low flow, 2=fast flow with little water perturbation, 3=fast flow with water perturbation, 4=white water). In addition, we collected oxygen readings at 2-h intervals from 0730 h to 1730 h to characterize diurnal changes in oxygen levels. Diurnal data were collected on one occasion in the drier period of 1995 at 10 sites in the upstream

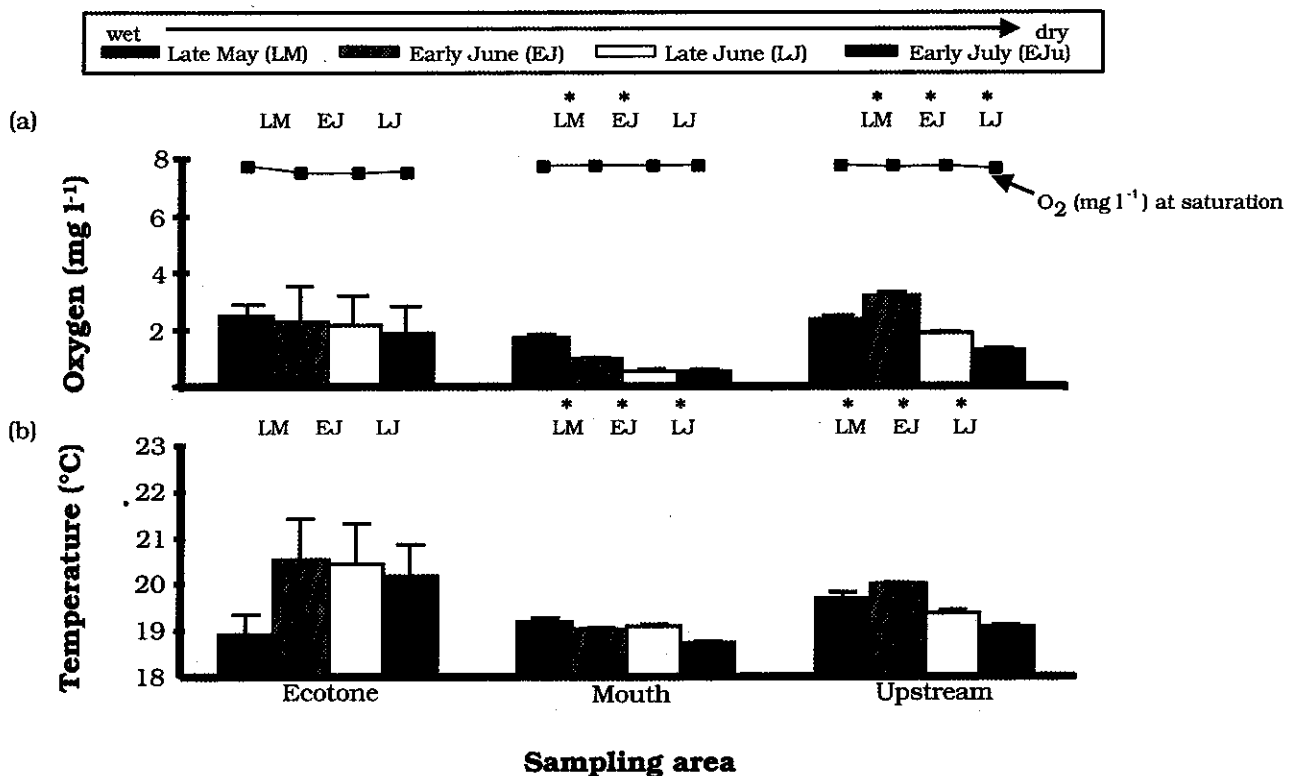


Fig. 2. Average oxygen content ($\text{mg} \cdot \text{l}^{-1}$) (a) and temperature ($^{\circ}\text{C}$) (b) of sites in the Juma River over the 1995 sampling season. Error bars indicate one standard error. The oxygen saturation values for each site and time period are also indicated for reference. * indicates that the sampling period differs from the subsequent sampling period (repeated measures analysis of variance, repeated contrasts $P < 0.05$).

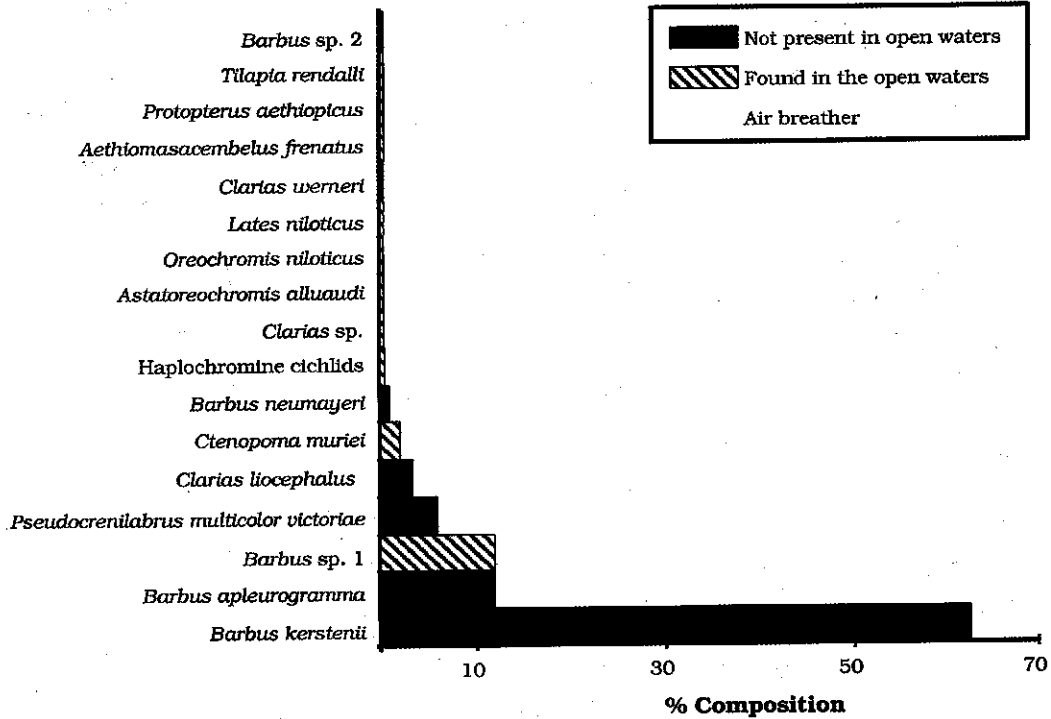


Fig. 3. Relative abundance of fish species in the Juma River (1995) indicating air-breathing species and species no longer captured in the open waters of Lake Nabugabo. *Clarias sp.* include small *C. liocephalus* and *C. werneri*. Haplochromine cichlids include *Astatotilapia velifer*, *Gaurochromis simpsoni*, and *Paralabidochromis beadlei*.

area, eight in the mouth area, and two in the ecotone.

Each captured fish was identified, measured, and returned to the site of capture. Field identification is very difficult for some endemic haplochromine cichlids and very small clariid catfishes. To minimize the number of collected individuals, we grouped small *Clarias liocephalus* and *Clarias werneri* as *Clarias spp.*; endemic haplochromines were grouped as haplochromine cichlids. A small sample of haplochromine cichlids and clariid catfishes were collected to verify species present in the system.

Statistics

Repeated-measures analysis of variance was used to test for significant differences in environmental characters among sampling periods for each of the three sites. Because the variance among stations was much higher in the ecotone area than at the mouth and upstream sites, between-site effects were not examined in the repeated measures analyses. Following Potvin et al. (1990), Mauchley's criterion was used to test for the compound symmetry of the variance covariance matrix. When Mauchley's criterion was rejected an alternative test (Greenhouse-Geisser), which relaxes the spher-

icity assumption was used to adjust the degrees of freedom and significance levels. Repeated contrasts were used to test for differences among the time periods (SPSS Inc., 1997). The repeated contrast compares the mean of each time period to the mean of the subsequent time period. The nonparametric Kruskal-Wallis test was used to detect differences among sites within sampling periods.

Measures of assemblage composition included species richness, diversity, and similarity. Fish abundance was compared among sites and over time using catch per unit effort. Species richness was compared to historical data (CNBS 1962 unpubl.) and current data (Ogutuh-Ohwayo 1993) on the species composition of the open lake waters. Diversity was measured using the Shannon-Wiener index following Krebs (1989). Morisita's index (Morisita 1959, Wolda 1981) was used to examine the similarity between adjacent distance locations for data combined over the four sampling periods in 1995. A repeated measures analysis of variance was used to test for significant differences in species diversity and catch per unit effort among sampling periods for each of the three sites, and repeated contrasts were used to test for differences among time periods. The nonparametric Kruskal-Wallis test was used to detect differences among sites within sampling periods.

The relative importance of dissolved oxygen and vegetative cover in shaping community parameters within the river (catch per unit effort and diversity) was examined through multiple regression. Samples for each station were averaged over the four sampling periods in 1995. Partial correlation analysis was used to determine the relationship between each dependent variable and one environmental parameter after removing the linear effect of the environmental variable. Ecotone data were excluded from this analysis due to the dissimilarity in species composition between the ecotone and the other two sites.

In this study, we follow Connell & Sousa (1983), Ross et al. (1985) and Matthews (1986) in defining persistence as the continued presence of species, and stability as constancy in the relative abundance of species over time. We use the percentage of fish species in an area that were found in the same area the next sampling period to represent seasonal and inter-annual variation

in persistence. Following Grossman (1982) and Matthews (1986), the stability of the assemblage structure was examined for each area by comparing the relative abundance of fish species from any adjacent or paired time periods (late May vs early June; early June vs late June; late June vs early July; late May vs early July; and the late rainy season in 1995 vs the late rainy season in 1996). The Spearman's rank correlation (r_s) was used to compare the relationship between paired collections in the relative abundance of the 10 most common species in the Juma River. Because the analysis included many comparisons, we adjusted the alpha levels to ensure that all tests would detect significance at the 0.05 level using the Dunn-Sidak formula (Ury 1976, Grossman et al. 1985). Following Ross et al. (1985), Matthews (1986), and Matthews et al. (1988), Kendall's test of concordance was also used to test for constancy in the relative abundance of species over multiple sampling periods.

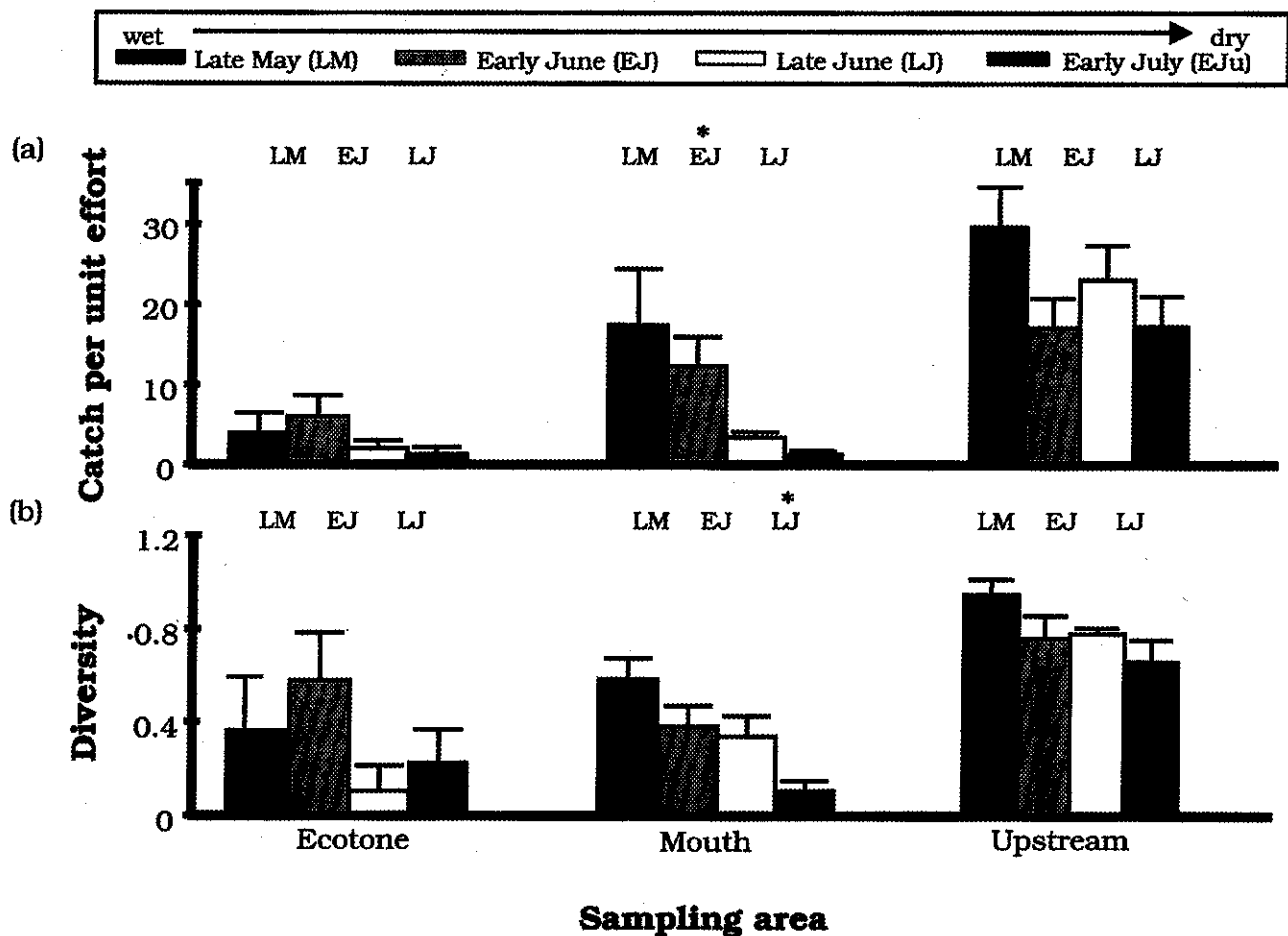


Fig. 4. Catch per unit effort (a) and species diversity (Shannon-Wiener index) (b) for sites in the Juma River over the 1995 sampling season. Error bars indicate one standard error. * indicates that the sampling period differs from the subsequent sampling period (repeated measures analysis of variance, repeated contrasts $P < 0.05$).

Results

Environmental conditions

Water depth did not vary significantly over the sampling periods in 1995 (repeated measures ANOVA, ecotone: $F_{3,15}=1.27$, $P=0.32$; mouth: $F_{3,63}=1.62$, $P=0.19$; upstream: $F_{3,63}=0.99$, $P=0.40$), nor did ranks of water current (ecotone: $F_{3,15}=0.63$, $P=0.61$; mouth: $F_{3,63}=1.46$, $P=0.23$; upstream: $F_{3,63}=2.16$, $P=0.10$). Given the shallow gradient of the wetland tributary, increased water flow associated with seasonal rains is reflected in expansion into shallow marginal areas rather than any great increase in water depth or current. Water depth was greater at the ecotone (10910 cm, SE) than either the mouth (462 cm) or upstream areas (64 ± 3 cm, Kruskal-Wallis, $\chi^2=15.65$, $df=2$, $P<0.001$, multiple comparisons, $P<0.05$). Current was faster at the upstream site (1.1 ± 0.1 , SE) than at the mouth (0.6 ± 0.1) and ecotone areas (0.25 ± 0.1 , Kruskal-Wallis, $\chi^2=14.53$, $df=2$, $P<0.001$, multiple comparisons, $P<0.05$).

Dissolved oxygen concentration decreased as the dry season progressed at the mouth and upstream sites in the Juma River (repeated measures ANOVA, mouth: $F_{1,5,32.5}=123.19$, $P<0.001$; upstream: $F_{3,63}=72.04$, $P<0.001$, repeated contrasts, $P<0.05$, Fig. 2a), but remained relatively stable at the ecotone ($F_{1,6,7.7}=0.194$, $P=0.774$). Oxygen concentration was lower at the mouth of the Juma River than at either the ecotone or upstream areas in all three sampling periods (Kruskal-Wallis tests, $P<0.05$); however, at all three sites, dissolved oxygen was well below saturation (Fig. 2a). Microhabitat variation among sampling stations within sites was much higher in the ecotone area than in either the mouth or upstream sites, reflecting interaction between the main lake and swamp waters at the ecotone. Water temperature also decreased as

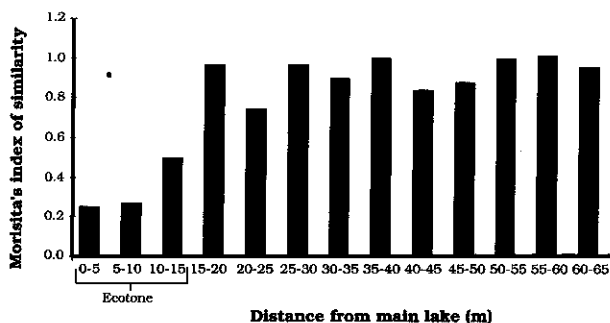


Fig. 5. Morisita's index of similarity for adjacent distance locations in the Juma River mouth and ecotone with a clear indication of the ecotone boundary. The indices are based on systematic sampling of the Juma River with metal minnow traps over a 3-month sampling period, 1995.

Table 1. The relationship between two fish community parameters (catch per unit effort and the Shannon Wiener diversity index) and two independent variables: oxygen partial pressure (mmHg) and percent vegetative cover in the Juma River

Community parameter	Total r^2	P	Factor	Partial correlation coefficient	
				coefficient	P
Catch per unit effort	0.44	<0.001	Oxygen (mmHg)	0.64	<0.01
			% Vegetative cover	-0.18	0.25
Diversity	0.19	0.035	Oxygen (mmHg)	0.37	0.02
			% Vegetative cover	-0.18	0.25

the dry season progressed at the mouth and upstream sites (repeated measures ANOVA, mouth: $F_{1,8,37.7}=43.16$, $P<0.001$; upstream: $F_{1,5,31.5}=72.65$, $P<0.001$, repeated contrasts, $P<0.05$, Fig. 2b), but did not differ significantly among sampling periods at the ecotone ($F_{1,2,6}=4.02$, $P=0.09$). Water temperatures were coolest at the mouth and warmest at the ecotone in all sampling periods except the first when the ecotone was coolest site (Kruskal Wallis tests, $P<0.05$, Fig. 2b).

Levels of dissolved oxygen concentration varied little over the day in the Juma River. The maximum change ranged from 0.20 to 0.80 $\text{mg}\cdot\text{l}^{-1}$ at the upstream sites (mean= 0.41 $\text{mg}\cdot\text{l}^{-1}$), 0.25 to 0.45 $\text{mg}\cdot\text{l}^{-1}$ (mean= 0.31 $\text{mg}\cdot\text{l}^{-1}$) at the mouth sites, and 1.45 to 1.6 $\text{mg}\cdot\text{l}^{-1}$ (mean= 1.5 $\text{mg}\cdot\text{l}^{-1}$) at the ecotone.

Species composition in the Juma River

Of the 18 species of fish that have disappeared from the open waters of Lake Nabugabo (Ogutu-Ohwayo 1993), nine were found in the Juma River during this study (Fig. 3). The relative abundance (catch-per-unit-effort) of species captured in systematic sampling was highly skewed with six species comprising 93% of the sample (Fig. 3). Five species in the Juma River were air breathers (Fig. 3). Haplochromine cichlids endemic to the Nabugabo region were exclusively ecotonal inhabitants and included *Astatotilapia velifer*, *Paralabidochromis beadlei* and *Gaurochromis simpsoni*. Non-endemic haplochromine cichlids were captured at all sites and included *Pseudocrenilabrus multicolor victoriae* and *Astatoreochromis alluaudi*. Fishes that have disappeared from the main lake and were not found in the Juma River include *Gnathonemus longibarbis*, *Gnathonemus victoriae*, *Marcusenius nigricans*, *Petrocephalus catostoma*, *Barbus magdalenae*, *Barbus radiatus*, *Bagrus docmac*, *Oreochromis esculentus*, *Oreochromis variabilis*, and *Prognathochromis venator*. Nile perch comprised a very small proportion of the catch (Fig. 3) and did not seem to persist under wetland tributary con-

Table 2. **A.** The percentage change in species composition (persistence) of three sites in the Juma River (number of species in common between temporally adjacent samples, expressed as a percentage of the first sample). **B.** The species present in the Juma River in each sampling period. Species are listed in order of abundance in the Juma River. Field identification of endemic haplochromines is difficult; therefore, *Astatotilapia velifer*, *Gaurochromis simpsoni*, and *Paralabidochromis beadlei* are lumped under haplochromines for the purpose of this analysis.

A. Persistence

Site	Late May to early June	Early June to late June	Late June to early July	Late May to early July	May 1995 to June 1996	Average \pm SD
Ecotone	20%	0%	0%	20%	25%	13% \pm 12%
Mouth	60%	39%	26%	24%	56%	41% \pm 17%
Upstream	77%	80%	76%	66%	80%	76% \pm 6%
All sites	81%	57%	100%	73%	91%	80.4 \pm 17%

B. Species

	Late May	Early June	Late June	Early July	June 1996
<i>Barbus kerstenii</i>	+	+	+	+	+
<i>Barbus apleurogramma</i>	+	+	+	+	+
<i>Barbus</i> sp. 1	+	+	+	+	+
<i>Pseudocrenilabrus multicolor victoriae</i>	+	+	+	+	+
<i>Clarias liocephalus</i>	+	+	+	+	+
<i>Ctenopoma muriei</i>	+	+	+	+	+
<i>Barbus neumayeri</i>	-	+	-	+	+
Haplochromine cichlids	+	+	-	-	+
<i>Astatoreochromis alluaudi</i>	+	+	-	-	+
<i>Oreochromis niloticus</i>	+	-	-	+	+
<i>Lates niloticus</i>	-	+	+	+	+
<i>Clarias wernerii</i>	-	+	-	-	-
<i>Barbus</i> sp. 2	-	+	-	-	-
<i>Protopterus aethiopicus</i>	+	+	+	+	+
<i>Tilapia rendalli</i>	+	-	-	-	-
<i>Aethiomastacembelus frenatus</i>	-	+	-	-	-

ditions. Only two Nile perch (averaging 4.95 cm) were found at the upstream site. Capture of these juvenile Nile perch occurred shortly after episodes of heavy rainfall.

There were no significant differences in CPUE over time at the ecotone and upstream sampling sites (repeated measures ANOVA, ecotone: $F_{3,15}=1.15$, $P=0.36$; upstream: $F_{3,63}=2.19$, $P=0.10$, Fig. 4b). However, CPUE decreased at the mouth site as the dry season progressed ($F_{1,9,40}=7.44$, $P=0.002$, repeated contrasts, $P<0.05$). CPUE was highest at the upstream site (Kruskal Wallis tests, $P<0.05$, Fig. 4a) with the exception of early June when CPUE did not differ among sites (Kruskal Wallis, $\chi^2=18.8$, $df=2$, $P=0.13$, Fig. 4a). No seasonal trend was observed in diversity at the ecotone and upstream sampling sites in the Juma River (repeated-measures ANOVA, ecotone: $F_{3,15}=1.32$, $P=0.31$; upstream: $F_{3,63}=1.87$, $P=0.14$, Fig. 4b). However, diversity decreased at the mouth site as the dry season progressed ($F_{3,63}=7.05$, $P<0.001$). Diversity was highest at the upstream sites in all months (Kruskal Wallis tests, $P<0.03$, Fig. 4b).

Similarity in species composition between adjacent distance locations (ecotone to 65 m up-

stream) in the Juma River was very high, with the exception of the ecotone, where there was a sharp transition in species composition (Fig. 5). The ecotone of the Juma River differed from the other major sites in that it received an influx of species typically inhabiting the main lake (i.e., Nile perch and *Oreochromis niloticus*), the fringing wetlands of the main lake (i.e., *Astatotilapia velifer*, *Gaurochromis simpsoni*, and *Paralabidochromis beadlei*), and the deeper swamps (i.e., *Ctenopoma muriei* and *Pseudocrenilabrus multicolor victoriae*).

The relative importance of two environmental characteristics, oxygen availability (partial pressure, mmHg) and vegetative cover, in explaining variation in two community characteristics, diversity and catch per unit effort, was examined among sampling stations for the mouth and upstream sites using multiple regression. The partial pressure of oxygen (mmHg) was positively correlated with both catch per unit effort and diversity (Table 1). Percent vegetative cover did not correlate with either community parameter when the linear effect of oxygen was removed (Table 1).

For all sites combined, the percentage of fish species in the Juma River that was found in the next sampling period (1995) was high, with the exception

Table 3. The relationship between the relative abundance of species for paired collections from the Juma River. Correlations are based on the ten most abundant species.

Comparison (10 most dominant species)	r_s	P
Late May and early June	0.845	<0.01
Early June and late June	0.925	<0.01
Late June and early July	0.922	<0.01
Late May and early July	0.887	<0.01
Late May 1995 and June 1996	0.511	=0.31
Late May 1995 and June 1996 (excluding haplochromine cichlids)	0.954	<0.01

of early dry season comparisons (Table 2). Persistence was also high between 1995 and 1996. Faunal attenuation during the early dry season reflected the loss of rare species; the six most abundant species in the Juma River persisted between the wet and dry season sampling periods (1995) and between years (Table 2). Persistence differed among the three sampling sites. The ecotone, which has the highest amount of interaction with the main lake, had the lowest persistence, while the upstream area had the highest persistence (Table 2).

Spearman's rank correlation (r_s) was used to detect changes in the relative abundance of species over the season and between sampling years. All 1995 comparisons were strongly correlated (Table 3). Kendall's test of concordance also indicated stability in relative abundance of species across sampling periods in 1995 (Kendall's $W=0.878$, $P=0.01$). However, relative abundance of species differed between 1995 and 1996 (Table 3). This reflected an increase in numbers of endemic haplochromine cichlids captured in 1996, rather than a dramatic shift of species composition in the river. The relative abundance of species between years showed no significant difference when the endemic haplochromines were excluded from the analysis (Table 3).

Discussion

Conservation biologists face critical issues regarding the introduction of non-indigenous species into new habitats. In the context of introduced predators that impact prey communities, it is critical to identify refugia that protect prey species by limiting interaction with the introduced predator. We found three lines of evidence to suggest that wetland tributaries may be important refugia for some prey species in Lake Nabugabo. These included: 1) a unique assemblage of species in the Juma River, some of which have disappeared from the open waters of Lake Nabugabo and cannot be found in other wetland refugia habitats, 2) effective, though not complete, exclusion of the introduced pred-

ator, and 3) a stable assemblage, where the most common species were found through seasonal changes and between years. However, loss of rare species did occur at the onset of the dry season, suggesting that the Juma River may not be a permanent refugium for all inhabitants.

The Juma River assemblage

It is important, when targeting wetland areas for conservation in the Lake Victoria region, to include a diversity of habitat types to insure diversity in the species assemblages conserved. Three wetland types have been identified in Lake Nabugabo as potential refugia: wetland ecotones, lagoons, and tributaries (Chapman et al. 1996a, b). Thirteen of the 18 species that have disappeared from the open waters of Lake Nabugabo subsequent to the Nile perch introduction can be found among these habitats (Chapman et al. 1996a, b). These wetland types differ in their habitat characteristics and, although they share species in common, have their own unique composition and relative abundance of species (Chapman et al. 1996a, b). The Juma River's most common species, *Barbus kerstenii* (Fig. 2), is absent from the wetland ecotones of Lake Nabugabo and extremely rare in wetland lagoons beyond the fringing swamp. *Barbus neu-mayeri*, another common species in the Juma River, cannot be found either in the open waters of Lake Nabugabo or in lagoon or ecotone refugia.

Although catch per unit effort and species diversity were higher at the upstream area than at the mouth of the river, these two areas were similar in faunal composition. However both areas differed from the ecotone area which received an influx of species from both the open waters of Lake Nabugabo and the Juma River and, in addition, also held a suite of rare species now unique to the fringing wetlands of Nabugabo (Ogutu-Ohwayo 1993; Chapman et al. 1996a, b). Haplochromine species that were captured in the ecotone, with the exception of *Pseudocrenilabrus multicolor victoriae*, are extremely rare in other wetland types such as lagoons (Chapman et al. 1996a, b). Fluctuating environmental conditions in the ecotone and its interaction with main lake waters may allow the establishment of prey species unable to tolerate chronic upstream conditions. However, persistence of species in the Juma River ecotone was low, and Nile perch were frequently captured in this area. The divergent nature of the Juma River ecotone and its unique suite of species suggest that conservation of this habitat is important; however, the long-term viability of ecotonal refugia may be compromised by the dynamic nature of this habitat and its proximity to open waters with Nile perch.

Nile perch did not seem to persist in areas upstream of the Juma River ecotone. It is likely that dense vegetation choking the mouth of the river inhibits the dispersal and foraging of larger individuals. Although smaller Nile perch may be able to penetrate dense wetland vegetation, the oxygen-scarce waters may limit wetland access for these individuals. However, two juvenile Nile perch were found upstream in the Juma River. A temporary increase in water depth and oxygen content as a result of heavy rains just prior to their capture could account for their presence in the river at that time. Nile perch did not persist when oxygen levels dropped to dry season levels. Still, it should be noted that wetland tributaries may facilitate Nile perch dispersal to new waters during episodes of heavy rainfall.

Stability and persistence of the Juma River assemblage

The relative abundance of the most common species in the Juma River was stable over seasonal changes and over a 2-year period. Monitoring of the Juma River over several years will be necessary to evaluate long-term stability and viability of the system; however, the results of this study suggest low inter-annual variation in species composition. Dissimilarity between sampling years was the result of an increase in haplochromine cichlids captured in the ecotone in 1996. In her detailed study of ecotones in Lake Nabugabo, Schofield (1997) also found a marked increase in the abundance of haplochromine cichlids between 1995 and 1996. These increases could indicate a possible resurgence of haplochromine cichlids in fringing ecotones around the lake. Local fishermen have noted a dramatic decline in the availability of Nile perch over the past decade most likely due to heavy fishing pressure. Overfishing of Nile perch may have reduced predation pressure to the point where haplochromines that survived in ecotonal refugia are recovering. Long-term monitoring of this haplochromine resurgence and Nile perch decline in Lake Nabugabo will be extremely useful in predicting further events in Lake Victoria.

Persistence of the common species in the Juma River was high over the 1995 sampling season and over the 2 years sampled. Only rare species dropped out of the system in the early dry season, which may reflect a decrease in oxygen availability. This concurs with previous studies on the persistence of aquatic species assemblages. Williams & Hynes (1977), Grossman et al. (1985), and Freeman et al. (1988) found that stability in small temperate streams was related to low variation in the abundance of the most common species. In the context of wetland refugia, these results suggest

that seasonal and annual data are needed to ascertain what species can use wetland tributaries permanently. It is possible that the rarer species in this system have to return to more open habitats during dry season conditions and may, as a result, increase their exposure to Nile perch.

Low-oxygen refugia in the Lake Victoria basin

Several lines of evidence suggest that oxygen is an important environmental characteristic in shaping the faunal structure of the Juma River. First, low oxygen is a chronic condition in the river, not alleviated by midday increases. Further, variance among microhabitats in diversity and catch per unit effort within the main river can be explained, in part, by oxygen availability. At the mouth of the river, both catch per unit effort and species diversity decreased as the dry season progressed and oxygen levels dropped. In addition, unique characteristics of the ecotone including a divergent species composition and low persistence and stability corresponded to high variation in oxygen content. Finally, although much of Lake Nabugabo's former diversity persists in wetland refugia (Chapman et al. 1996b), these wetlands contain only a subset of those species that have disappeared in open waters since the increase of Nile perch. Some haplochromine cichlids, such as *Prognathochromis venator*, and other non-cichlids, including several species of mormyrids, are not found in the Juma River. Habitat characteristics such as dense vegetation may limit their predation efficiency and exclude piscivores such as *P. venator*, and low food availability or competition from other benthic invertebrate feeders in the Juma River may limit exploitation by mormyrids. However, severe changes in species composition from the ecotone to the upstream region of the river, the large number of air-breathing fishes found in the river, and the importance of oxygen in shaping community parameters within the wetland suggest that the hypoxic water of the Juma River may be most important in limiting colonization and survival of fishes in this system.

The oxygen values in the Juma River, which averaged $0.95 \text{ mg} \cdot \text{l}^{-1}$ at the mouth and $2.2 \text{ mg} \cdot \text{l}^{-1}$ at the upstream site, are not unusually low for papyrus swamps and other dense tropical wetlands. Carter (1955) reported oxygen values averaging less than $0.1 \text{ mg} \cdot \text{l}^{-1}$ for the shore of littoral papyrus swamps in Lake Victoria and average values of $2.5 \text{ mg} \cdot \text{l}^{-1}$ for areas of papyrus adjacent to main lake waters. Welcomme (1969) reported low early morning oxygen levels (ranging from $1.3 \text{ mg} \cdot \text{l}^{-1}$ to $1.6 \text{ mg} \cdot \text{l}^{-1}$) in lagoons separated from Lake Victoria by dense vegetation. He related the faunal attenuation and depauperate species com-

position in these lagoons to high vegetative density and low oxygen conditions. Chapman & Liem (1995) found that chronically low oxygen averaging $0.67 \text{ mg} \cdot \text{l}^{-1}$ characterized a valley swamp dominated by papyrus in western Uganda.

Hypoxia plays an important role in limiting fish distributions in many ecosystems. For intolerant species such as Nile perch, low oxygen may create as much of a boundary as the absence of water. However, fishes have developed a diversity of adaptations that allow exploitation of hypoxic habitats. These include the development of air breathing organs in several phylogenetically distinct lineages (Jordan 1975; Magid & Babiker 1975; Kramer 1983; Chapman 1995), the use of aquatic surface respiration (ASR, Kramer & McClure 1982; Kramer 1983, 1987; Gee & Gee 1991, Chapman & Liem 1995; Chapman et al. 1995), the development of large gills (Galis & Barel 1980; Palzenberger & Pohla 1992), and various physiological mechanisms such as high hemoglobin (Ultsch et al. 1978; Ulrich 1984). It is often assumed that air breathers have an advantage over non-air breathers under hypoxic conditions, and the species composition of the Juma River supports this idea. Air breathers comprised 15% of the fish species in the Juma River; whereas air-breathing fishes comprise only 1.5% of all fish species (Graham 1997). However, several non-air breathing species also persist in the Juma River. *Pseudocrenilabrus multicolor victoriae* and *Barbus neumayeri* seem to survive by virtue of large gill surface area, a low metabolic rate, a low critical oxygen tension, and a low threshold for aquatic surface respiration (Chapman & Liem 1995, Olowo & Chapman 1996, Rosenberger 1997, Chapman unpubl. data). In a study examining the response of nine cichlid species from Lake Victoria, Chapman et al. (1995) found that many of the cichlids, including *Astatoreochromis alluaudi*, were relatively tolerant of hypoxia and that tolerance was higher among the widespread swamp specialists than in the stenotypic lacustrine forms. Our study of the Juma River and other studies examining the hypoxia tolerance of non-air breathing fishes in the region suggest that yet undiscovered haplochromines and other non-cichlids may survive in fringing wetlands and swamps common in the lake basin.

Resumen

1. La introducción de *Lates niloticus* en la cuenca del Lago Victoria (Tanzania, Africa) coincidió con el declive o la desaparición de cientos de especies indígenas. Para mitigar mayores pérdidas, es necesario conocer los límites de expansión de la especie así como los hábitats que sirven de refugio a las especies presa. Las zonas húmedas con vegetación densa pueden proteger a los peces de la predación de *L. niloticus* al ofrecer refugios

estructurales y bajos en oxígeno a especies tolerantes de hipoxia. Para examinar el potencial de las zonas húmedas como refugio, cuantificamos la composición, persistencia y estabilidad de los ensamblajes de peces en una zona húmeda afluente del Lago Nabugabo (lago satélite del Lago Victoria). Para ello muestreamos tres localidades: el ecotono donde la vegetación emergente de la desembocadura del río se encuentra con las aguas abiertas del lago, la desembocadura del río adyacente al ecotono y una localidad situada a unos 200 m aguas arriba de la desembocadura.

2. La cantidad de oxígeno disuelto fué baja en el río Juma, con una media de $1.6 \text{ mg} \cdot \text{l}^{-1}$. La disponibilidad de oxígeno disminuyó a medida que avanzó la estación seca en la desembocadura y en las localidades aguas arriba, pero se mantuvo relativamente estable en el ecotono. La concentración de oxígeno más baja la encontramos en la desembocadura, aunque en las tres localidades el oxígeno disuelto estuvo por debajo del nivel de saturación.

3. De las 18 especies que han desaparecido de las aguas abiertas del Lago Nabugabo, nueve han aparecido en el Río Juma. *L. niloticus* fué raro en el afluente; la presencia de agua con abundante vegetación y escasos niveles de oxígeno parece inhibir la dispersión y el forrajeo de la especie depredadora. El ecotono del río es único ya que recibe un flujo de especies procedentes de las aguas abiertas del Lago Nabugabo y de las zonas con abundante vegetación del Río Juma, además de las especies características de las zonas húmedas. Sin embargo, la viabilidad del ecotono como refugio a largo plazo puede estar comprometida por la naturaleza dinámica de este hábitat y por su proximidad a las aguas abiertas donde se encuentra el depredador, *L. niloticus*. La disminución faunística se hizo patente en el Río Juma a medida que avanzó la estación seca y bajaron los niveles de oxígeno, lo que sugiere que el río no debe ser un refugio permanente para todas las especies presentes, aunque las especies más comunes permanecieron a lo largo de cambios estacionales e interanuales.

4. Diversas evidencias sugieren que el oxígeno es una característica ambiental de importancia en el modelado de la estructura faunística del río. En primer lugar, el bajo nivel de oxígeno es una condición crónica en el río Juma y un predictor significativo de la abundancia y diversidad de los peces en los microhábitats del sistema. En segundo lugar, los cambios drásticos en el contenido de oxígeno en el ecotono coincidieron con un cambio drástico en la composición de la ictiofauna. Por último, la desaparición de especies raras en el río coincidió con la hipoxia más severa durante la estación seca. Los niveles bajos en oxígeno, crónicos en las zonas húmedas, pueden permitir la persistencia de especies tolerantes a estas condiciones de hipoxia, aunque también limita la explotación por *L. niloticus* al ofrecer refugios críticos para la fauna subyacente en la cuenca.

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