

WETLAND ECOTONES AS REFUGIA FOR ENDANGERED FISHES

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Abstract

Wetlands may serve as refugia for indigenous fishes from introduced predatory fishes because of their structural complexity, which may reduce hunting efficiency, or if the low oxygen conditions that prevail in many swamps limit exploitation by the predator. The vegetated ecotone between lake shores and open water may be extremely important, relative to the dense interior of swamps, because of the accessibility of ecotones for lacustrine fishes, and the less extreme physicochemical conditions generally encountered along lake margins. This paper examines the role of wetland ecotones as refugia for prey species from the introduced Nile perch *Lates niloticus* in Lake Nabugabo, Uganda, where increased numbers of Nile perch coincided with the disappearance or decline of many species from the open waters of the lake. Patterns of ecotone use were examined by comparing fish communities in wetland ecotones with fish communities in exposed ecotone areas with no wetland. Results suggest that wetland ecotones may protect some fishes from Nile perch predation. Nile perch were less abundant in wetland ecotones relative to exposed inshore areas, and were found less frequently in areas of low dissolved oxygen. A negative relationship was found between species richness among ecotones and dissolved oxygen, and a positive relationship between species richness among ecotones and structural complexity. It was difficult to separate the effects of structure and low oxygen on the habitat use of Nile perch. However, tolerance to low oxygen may permit prey species to exploit structured inshore habitats as refugia without adverse effects from the low oxygen conditions that can occur there. Copyright © 1996 Published by Elsevier Science Limited

Keywords: haplochromine cichlids, Nile perch, Lake Victoria Basin, hypoxia, East Africa, wetlands.

INTRODUCTION

The introduction of non-native fish species into new

habitats is a common practice throughout the world, and one which is difficult to regulate. While introductions can be beneficial in maintaining or increasing fisheries' yield, or in biological control, they can also lead to major disruptions and degradation of entire ecosystems (Welcomme, 1984; Balon & Bruton, 1986; Courtenay, 1993). Since fish introductions will continue to be made either for biological management or by accidental transfer, it is important that we learn to predict the consequences of introductions based on environmental characteristics. Two issues are particularly relevant to the introduction of predators into ecosystems. First, we must understand what limits the dispersal of the predator from the site of introduction into new areas. Second, we must learn to identify the characteristics of refugia that can be exploited by prey species when confronted with an introduced predator.

The introduction of Nile perch *Lates niloticus* into waters of the Lake Victoria Basin of East Africa is proposed to have contributed to the disappearance or endangerment of over half of the 300+ endemic haplochromine cichlid species in Lake Victoria (Witte *et al.*, 1992; Kaufman & Ochumba, 1993), in addition to many other indigenous non-cichlids. Similar changes have occurred with the introduction of Nile perch into Lake Kyoga and Lake Nabugabo (Ogutu-Ohwayo, 1990, 1993). The severity of the loss in species richness and diversity has led to studies directed at the identification of faunal refugia. For example, rocky crevices appear to be one important refugium for rock-dwelling haplochromine cichlids in the Mwanza Gulf area of Lake Victoria (Witte *et al.*, 1992). We now believe that wetlands dominated by papyrus *Cyperus papyrus* swamps may represent a second and much more widespread refugium. Wetlands may protect fishes from Nile perch predation because they provide structural complexity which may afford cover for fishes from predators. In addition, the waters of heavily vegetated swamps are often characterized by reduced oxygen levels due to low levels of incident light, minimal mixing of the water beneath the vegetation, and high rates of organic decomposition (Carter, 1955; Chapman & Liem, 1995). This creates a succession of habitats from the dense

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interior to the open water of the lake, with oxygen availability generally increasing towards the open water (Carter, 1955). Swamp habitats are exploited by a community of fishes which themselves vary in their tolerance to deoxygenated water. For example, those species with air-breathing capabilities, such as lungfish and some clariid catfishes, can exploit the anoxic waters of the dense interior of many swamps; while the ecotone area with moderate levels of oxygen seems to be richer in the abundance of non air-breathing fishes (Hickley & Bailey, 1986; Chapman & Chapman, unpublished data). Extensive wetlands may serve as barriers to the dispersal of the Nile perch because Nile perch seem to require water with relatively high dissolved oxygen (Fish, 1956; Chapman and Chapman, unpublished data), and may be inhibited by the structural complexity of the dense wetlands. This permits remnant populations to persist in the lagoons and satellite lakes which are separated from the main lakes by the extensive areas of fringing swamp (Ogutu-Ohwayo, 1993; Chapman *et al.*, 1996). Although these small peripheral refugia are clearly of great importance to the persistence of the lake basin fauna, they seem to harbor only a small subset of the basin diversity (Chapman *et al.*, 1996; L. Kaufman, pers. comm.). The extreme hypoxia that characterizes the fringing swamps may act as a biological filter limiting both colonization and survival (Welcomme, 1970). The vegetated ecotone between lake shores and open water may offer a refugium for a more diverse suite of prey species, because of the accessibility of ecotones for lacustrine fishes, and the less extreme physicochemical conditions generally encountered along lake margins.

To examine the role of wetland ecotones as refugia in lakes where Nile perch have been introduced, we documented the community composition and relative abundance of fishes in different ecotone habitats of Lake Nabugabo, a satellite of Lake Victoria. We selected Lake Nabugabo for this study because baseline data are available to make comparisons of the fish community composition prior and subsequent to the increase in the introduced Nile perch population (Worthington, 1932; Cambridge Nabugabo Biological Survey [CNBS], 1962; Greenwood, 1965; Ogutu-Ohwayo, 1993; Chapman *et al.*, 1996). Chapman *et al.* (1996) compared the species richness of wetland areas in Lake Nabugabo (vegetated ecotones, and swamp lagoons and tributaries separated from the lake by extensive wetland) to the 1962 Cambridge expedition to Lake Nabugabo, which was conducted prior to the increase in the Nile perch population; and a 1991–92 survey of the open lake, which reported the disappearance of 16 indigenous species. Nine species not recovered in the 1991–92 survey were found in the wetlands, demonstrating the potential importance of these in the maintenance of fish faunal structure and diversity in the region. In this study, we focus on patterns of ecotone use to identify habitat characters that relate to the species richness and abundance at the interface between the wetlands and the open waters of the main lake. We compare vegetated ecotones to exposed inshore areas with little vegetation, and microhabitat use within similar ecotone habitats. We predicted that surviving indigenous fish species in Lake Nabugabo would show greater use of highly structured and/or hypoxic ecotones than Nile perch.

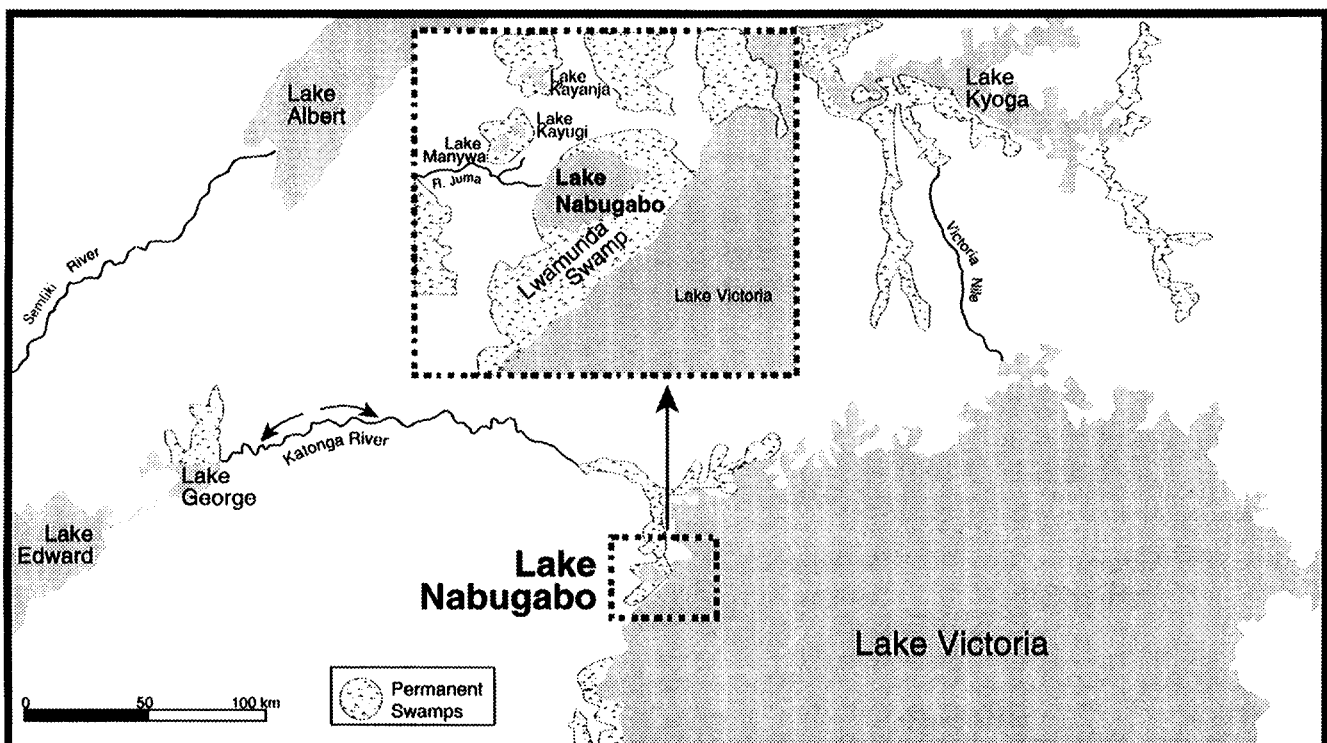


Fig. 1. Map illustrating the location of Lake Nabugabo within the Lake Victoria Basin of East Africa.

METHODS

Study site and recent history

Lake Nabugabo is a small satellite lake (24 km², mean depth 4.5 m), isolated from Lake Victoria c. 4000 years ago (Kendall, 1969). The lake lies within an extensive swamp which was formerly a bay on the western shore of Lake Victoria (Worthington, 1932; Greenwood, 1965; Ogutu-Ohwayo, 1993; Fig. 1). 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 Lwamunda Swamp, an extensive wetland area surrounding much of the lake (approximately 4 km in width), separates Lake Nabugabo from Lake Victoria, and contains several permanent lagoons and small intermittent streams.

The recent history of Lake Nabugabo is one of dramatic change in fish faunal structure and diversity. The Cambridge expedition to Lake Nabugabo in 1962 recorded 20 species of non-cichlids, eight species of haplochromine cichlids, and two tilapiine cichlids (Cambridge Nabugabo Biological Survey [CNBS], 1962; Greenwood, 1965). Five of the haplochromine cichlids were found to be endemic to Lake Nabugabo and three other satellite lakes in the Nabugabo region (Lakes Kanyanja, Kayugi, Manywa, Ogutu-Ohwayo, 1993; Chandler & Kaufman, unpublished data). At the time of the Cambridge expedition, the fishery was dominated (weight) by lungfish *Protopterus aethiopicus*, followed by *Bagrus docmac*, *Schilbe intermedius*, *Clarias gariepinus*, *Oreochromis esculentus*, *O. variabilis*, and species of haplochromine cichlids. A survey conducted in 1991 and 1992 in the open lake, 30 years subsequent to the introduction of Nile perch, showed that many of the native fish species in Lake Nabugabo have either disappeared or declined since the introduction of the Nile perch, the Nile tilapia *Oreochromis niloticus* (Ogutu-Ohwayo, 1993), and other tilapiines (*Oreochromis leucostictus*, *Tilapia rendalli*). Of the species abundant in the pre-Nile perch fishery, only *S. intermedius* remains in large numbers in the open waters. *Oreochromis esculentus*, *O. variabilis*, and *B. docmac* are no longer captured in the lake, and *C. gariepinus* is very rare. *Lates niloticus*, *O. niloticus* (introduced), *S. intermedius*, *Brycinus jacksonii*, and *Rastrineobola argentea* now dominate the open waters of the lake (Ogutu-Ohwayo, 1993).

Sampling protocols

To examine whether fishes were concentrated in ecotones characterized by hypoxia and/or high structural complexity, we selected ecotone areas to maximize the range of structural and physicochemical variation. We use the term ecotone to refer to all inshore habitats defining the edge of the lake adjacent to open water, and we distinguish between wetland ecotones and exposed ecotones with no wetland. Major wetland ecotone types included: papyrus, hippo grass and *Miscanthidium violaceum*, *M. violaceum* with water lilies, and *M. violaceum* in a bay with a heavy growth of submergent

vegetation (*Utricularia*) and water lilies (Table 1). The ecotones were sampled during two field trips to the Nabugabo region: November 1993 and May 1994. Two of these habitat types were sampled in both November 1993 and May 1994. These were treated as independent samples because the physicochemical conditions differed between the sampling periods, and fishes had the opportunity to move in and out of these areas between samples. This produced a total of six wetland transects. We also present the analyses using the mean for the two samples in the wetland ecotones that were sampled twice. We compared the six wetland ecotone transects to two exposed ecotone transects: a sandy area abutting natural forest where structure was limited to deadfall and overhanging branches, and a sandy area abutting a rocky cliff with little structural relief. Sampling was carried out along a 100-m interval of each ecotone habitat. Duplicate minnow traps were set systematically across each transect at an average of 10 locations, and two 30-m test gill nets (four panels, 25.4 mm, 50.8 mm, 76.2 mm, 101.6 mm, stretched mesh) were set along the ecotone close to the vegetation. Traps and gill nets were set in the afternoon and pulled the following morning. The two methods together captured fishes over a broad size range. These quantitative samples were not used to produce absolute density estimates, but rather to compare the relative abundance and richness of species among habitats. To increase the probability of capturing less abundant species, small (3–6 m) seines and A-frame seines were used to sample edge areas qualitatively. Fish captured in seines were only used in calculating estimates of total species richness for wetland ecotones and exposed ecotones.

Vegetation, bottom type, distance from shore, water depth, dissolved oxygen, and water temperature (measured with a portable YSI meter, Model 51B; YSI Incorporated, Yellow Springs, OH) were measured for each trap site, producing an average of 10 duplicate samples of environmental variables for each ecotone transect. Dissolved oxygen concentration and water temperature were measured in the upper 50 cm of water. Characteristics of the vegetation, water depth, and shelter (bay vs open) of each transect were used to rank ecotones by structural complexity. An ecotone dominated by both emergent and dense submergent vegetation was given the highest ranking (5, Table 1), while an inshore area with no macrophytes and little deadfall was given the lowest ranking (1).

All captured fish were identified and measured. Haplochromines were identified on the basis of Greenwood's (Greenwood, 1965) key, as well as recent analyses of morphological data (Chandler & Kaufman, unpublished data). Currently, the nomenclature of haplochromine cichlid species in the Lake Victoria Basin is undergoing considerable revision and debate (Greenwood, 1980; Hougerhoud, 1984; van Oijen, 1991). In this paper, we follow Greenwood's (Greenwood, 1980) revised nomenclature, with the old names given in parentheses when first mentioned. Smaller haplochromine cichlids were difficult to identify to

Table 1. Characteristics of the wetland ecotones and exposed ecotones sampled in Lake Nabugabo, Uganda

Habitat	Month/year sampled	Major structural features (rank of structural complexity)	Mean dissolved oxygen (range) (mg/litre)	Mean depth at trap sites (cm)
1. Wetland	Nov. 93	Emergent vegetation (3) <i>Cyperus papyrus/Vossia cuspidata</i>	4.75 (0.60–6.60)	55.2
2. Wetland	Nov. 93	Emergent vegetation (4) <i>Miscanthidium violaceum/Nymphaea</i> sp.	4.39 (1.30–8.40)	52.3
3. Wetland	Nov. 93	Emergent vegetation (3) <i>M. violaceum/V. cuspidata</i>	3.18 (1.80–4.40)	40.0
4. Wetland	May 94	Emergent vegetation (3) <i>C. papyrus/V. cuspidata</i>	5.81 (4.35–6.80)	82.5
5. Wetland	May 94	Emergent vegetation (3) <i>M. violaceum/V. cuspidata</i>	2.81 (2.30–3.15)	61.6
6. Wetland	May 94	Emergent vegetation (5) <i>M. violaceum/Nymphaea</i> sp. Submergent vegetation <i>Utricularia</i> sp. (sheltered bay)	2.77 (0.80–4.50)	200.00
7. Exposed Forest edge	May 94	No aquatic macrophytes (2) Deadfall (abundant) Submerged branches (abundant)	7.08 (7.00–7.20)	51.5
8. Exposed Rock cliff	May 94	No aquatic macrophytes (1) Deadfall & submerged branches	7.09 (6.90–7.30)	84.4

Major structural features include dominant vegetation types, deadfall, and submerged branches of forest trees. Ecotones are numbered 1–8 for reference, and the rank of structural complexity is indicated in brackets. Two ecotone habitats (1 and 3) sampled in November 1993 were resampled in May 1994 (4 and 5).

species with the exception of *Pseudocrenilabrus multicolor* and *Astatoreochromis alluaudi*, and they were grouped as haplochromines. With respect to the genus *Clarias*, we follow Teugels (1986) in differentiating between *Clarias wernerii* and *C. alluaudi*.

Since structural complexity was a ranked variable, Spearman's rank correlation was used to examine the relationship between both species richness and catch per unit effort of fishes in the ecotones and environmental variables. Pearson correlation was used to determine relationships between the species richness in microhabitats within ecotones and dissolved oxygen concentration at microsites.

RESULTS

A total of 1058 fishes were identified and measured; 855 were captured in the quantitative sampling, and 203 other fishes were captured by seining inshore habitats. Quantitative sampling produced a total of 19 species in wetland ecotones, with an average of 9.5 species per ecotone and nine species from the exposed ecotones, with an average 6.5 species per ecotone (Table 2). Two additional species were captured by seining in the wetland ecotones. Of the species reported as rare or absent in the open lake survey (inshore and offshore) of 1992, *Astatotilapia velifer* (*Haplochromis velifer*), *Gaurochromis simpsoni* (*Haplochromis simpsoni*), *Clarias alluaudi*, *Pseudocrenilabrus multicolor*, and the introduced *Oreochromis leucostictus* were abundant in the

wetland ecotones. Other small species not found in beach seines in 1991–92 in open inshore areas were found to be present in low numbers in wetland ecotones (e.g. *Barbus magdalenae*, *Barbus aploegramma*). A total of nine species taken in earlier surveys of the main lake (Worthington, 1932; Cambridge Nabugabo Biological Survey [CNBS], 1962) were not captured during the 1991–92 survey (Ogutu-Ohwayo, 1993) and were not found in our 1993–94 survey. These include: *Bagrus docmac*, *Oreochromis variabilis*, *O. esculentus*, *Prognathochromis venator* (*Haplochromis venator*), *Barbus kerstenii*, *Barbus neumayeri*, and the three mormyrids, *Gnathonemus longibarbis*, *Marcusenius nigricans*, and *Petrocephalus catostoma*.

Ecotones varied in their structural and physico-chemical conditions (Table 1). Most wetland ecotones exhibited some degree of hypoxia (mean dissolved oxygen = 3.8 mg/litre, range = 0.6–8.4 mg/litre), while the non-structured inshore areas (exposed ecotones) exhibited higher oxygen values (mean dissolved oxygen = 7.1 mg/litre, range = 6.9–7.3 mg/litre). Since dissolved oxygen concentration was measured in the afternoon, these represent values approaching the diurnal maxima.

Among the eight ecotone samples (six wetland areas, two exposed areas), species richness was positively correlated with the structural ranking of the ecotone ($r_s = 0.897$, $p = 0.003$) and negatively correlated with average dissolved oxygen concentration of the ecotone ($r_s = -0.854$, $p = 0.007$; Fig. 2). Similar trends were observed when the mean of the two sampling periods was used for the two ecotones that were sampled twice

Table 2. Relative abundance, expressed as a percent of the total number of fish captured in the quantitative sampling (°) of wetland ecotones and exposed ecotones (inshore areas with no wetland)

Species	Relative abundance (% of total number)	
	Wetland ecotones	Exposed ecotones
<i>Protopterus aethiopicus</i>	0.3	0.0
<i>Schilbe intermedius</i>	14.7	4.5
<i>Clarias alluaudi</i>	2.6	0.0
<i>Clarias wernerii</i>	1.2	0.0
<i>Synodontis afrofisheri</i>	1.5	0.0
<i>Brycinus jacksonii</i>	30.9	57.6
<i>Aethiomastacembelus frenatus</i>	0.7	0.8
<i>Barbus apleurogramma</i>	0.1	0.0
<i>Pseudocrenilabrus multicolor</i>	2.5	0.0
<i>Astatoreochromis alluaudi</i>	1.1	0.0
Other haplochromines ^b	25.4	3.9
Introduced species		
<i>Lates niloticus</i>	6.1	26.5
<i>Oreochromis niloticus</i>	8.3	6.0
<i>Oreochromis leucostictus</i>	3.1	0.0
<i>Tilapia rendalli</i>	0.6	0.8
<i>Tilapia</i> sp.	0.8	0.0

^a*Aplocheilichthys pumilus* and *Barbus magdalenae* were captured in wetland ecotones during supplemental qualitative sampling.

^bFive species of haplochromine cichlids other than *P. multicolor* and *A. alluaudi* were captured (*Gaurochromis simpsoni*, *Astatotilapia velifer*, *Haplochromis annectidens*, *Paralabidochromis beadlei*, and *Astatotilapia nubila*) from wetland sites, and three species from the exposed ecotones (*Astatotilapia velifer*, *Paralabidochromis beadlei*, and *Astatotilapia nubila*). However, many of the small haplochromines other than *P. multicolor* and *A. alluaudi* were not identified to species.

Species lists comparing the Lake Nabugabo community prior to the increase in introduced Nile perch to the later surveys are provided in Ogutu-Ohwayo (1993) and Chapman *et al.* (1996).

(species richness vs structural ranking: $r_s = 0.956$, $p = 0.003$; species richness vs oxygen: $r_s = -0.928$,

$p = 0.008$). The catch per unit effort of smaller fishes (indexed as the number captured in minnow traps) among the eight ecotone samples was positively correlated with structure ($r_s = 0.748$, $p = 0.033$) and negatively correlated with dissolved oxygen concentration ($r_s = -0.952$, $p < 0.001$). Again, similar trends were observed when the mean catch per unit effort of the two sampling periods was used for the two ecotones that were sampled twice (structure: $r_s = 0.868$, $p = 0.025$; oxygen: $r_s = -0.986$, $p < 0.001$).

To examine whether areas of high structure and low oxygen may afford protection from Nile perch predation by minimizing interaction with the predator, we examined the relative abundance of Nile perch and other species in wetland ecotones versus the relative abundance of Nile perch and other species in the exposed inshore areas. We considered all sizes of Nile perch captured (mean = 17.6 cm, range = 6.3–44.7 cm) since fish were found in the stomachs of Nile perch as small as 6 cm (P. J. Schofield, pers. comm.). Among the inshore areas, the relative abundance of Nile perch (number of Nile perch expressed as a percentage of the total numbers of fish captured) was much higher in the inshore areas with no wetland (26.5%) than the wetland ecotones (6.1%; Table 2). In the wetland areas, *Brycinus jacksonii* (30.9%) and haplochromines (29.0%) were very abundant. Of the haplochromines that were identified to species, the most abundant species were two endemics, *Gaurochromis simpsoni* (58.7%) and *Astatotilapia velifer* (11.5%), and the geographically widespread *Pseudocrenilabrus multicolor* (17.3%) and

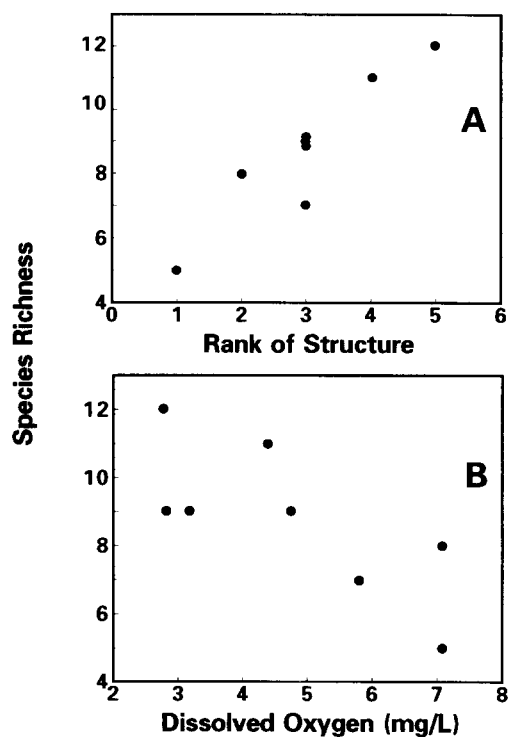


Fig. 2. The relationship between the species richness of fishes in ecotone areas of Lake Nabugabo, Uganda and (A) the rank of structural complexity, (B) the average dissolved oxygen concentration (mg/litre) of the ecotones.

Astatoreochromis alluaudi (7.7%). The other three endemic species were either rare (*Paralabidochromis beadleii* (*Haplochromis beadleii*), 1.0%; *Haplochromis annectidens*, 1.0%) or were not found (*Prognathochromis venator*). *Astatotilapia nubila* (*Haplochromis nubilus*), a widespread haplochromine, was also rare in the inshore areas (1.9%).

Because variation in structure among ecotones was negatively correlated with dissolved oxygen concentration ($r_s = -0.812$, $p = 0.014$), it is not possible to partial out the effects of structure on the relationship between richness and oxygen, using a broadscale analysis between ecotones. It is possible that fish are seeking the structural complexity of wetland areas to minimize predation risk, which places them in areas of lower oxygen concentration. Alternatively, the wetland areas may offer a low oxygen refugium from Nile perch, if they are less tolerant to hypoxia than species using these areas. To examine patterns of habitat use on a finer scale, we divided the six wetland ecotones into two groups; those with lower levels of dissolved oxygen concentration (samples 3, 5, and 6 (Table 1); mean oxygen = 2.92 mg/litre), and those with higher oxygen levels (samples 1, 2 and 4 (Table 1); mean oxygen = 4.98 mg/litre). There was some variation in oxygen levels among trap sites (microhabitats) within both types of ecotone (range for low oxygen wetlands = 0.80–4.50 mg/litre; range for high oxygen wetlands = 0.60–8.40 mg/litre). Correlation analyses were used to examine the association between dissolved oxygen concentration at trap sites (expressed as the mean of the duplicate traps) and fish richness at the trap sites (expressed as the total number of species captured in the two traps). Within the wetland ecotones with low dissolved oxygen, there was no relationship between dissolved oxygen concentration and species richness at trap sites ($r = 0.120$, $p = 0.521$), suggesting that within low oxygen wetland ecotones, fish are not showing differential use of sites with low or high levels of dissolved oxygen. However, within the wetland ecotones characterized by higher average levels of dissolved oxygen, there was a negative relationship between dissolved oxygen concentration and species richness ($r = -0.49$, $p = 0.005$), suggesting that in high oxygen wetlands, fish are showing differential use of microsites with low oxygen.

Fish using wetland ecotones must be tolerant of the extreme conditions that can occur there. We calculated the average oxygen levels associated with different fish species, based on their occurrence in traps (smaller individuals) for species where more than three individuals were captured in traps. Most species were found on average in areas characterized by hypoxic conditions. The lowest average oxygen values were associated with the air breathers *Clarias alluaudi* (mean = 2.51 mg/litre, range = 1.85–4.20 mg/litre) and *Clarias werneri* (mean = 2.68 mg/litre, range = 1.85–5.28 mg/litre), and the two widespread haplochromines *Pseudocrenilabrus multicolor* (mean = 2.77 mg/litre, range = 0.90–4.20 mg/litre), and *Astatoreochromis alluaudi* (mean = 2.99 mg/litre, range = 0.90–4.20 mg/litre). In contrast, juvenile

Nile perch (mean = 3.84 mg/litre, range = 2.73–4.90 mg/litre) were associated with microhabitats having higher dissolved oxygen levels, as was *Aethiomastacembelus frenatus* (mean = 4.95 mg/litre, range = 2.4–7.08 mg/litre). Further, the abundance of Nile perch among ecotone samples was positively related to dissolved oxygen concentration ($r_s = 0.802$, $p = 0.017$). This suggests that fishes tolerant of low oxygen conditions that occur in the dense interior of some wetlands may be able to avoid high densities of Nile perch.

DISCUSSION

It is becoming increasingly important to extend our knowledge of introduced species beyond distributional data, to allow us to predict the consequences of introductions based on characteristics of the environment. We must understand what limits the dispersal of the predator from the site of introduction. There may be particular characteristics of the invaded community that minimize or facilitate dispersal. Such information can be used to predict long-term trends, manage or manipulate barriers, and to formulate recommendations to minimize deleterious effects should future introductions be proposed. We must also identify characteristics of refugia that can be exploited by prey species when confronted with an introduced predator.

These issues are particularly critical in the Lake Victoria Basin given the dramatic impact of the Nile perch on indigenous faunas. In Lake Nabugabo, several lines of evidence suggest that wetland ecotones may protect some fishes from Nile perch predation. These include: a low abundance of Nile perch in wetland ecotones relative to exposed inshore areas, a positive relationship between Nile perch and dissolved oxygen, a negative relationship between species richness among ecotones and dissolved oxygen, and a positive relationship between species richness among ecotones and structural complexity.

Wetland ecotones may serve as refugia for prey species from introduced predators because of their structural complexity which may reduce hunting efficiency. In lakes, fish density is often higher in areas with aquatic vegetation, particularly the densities of smaller species and size classes which may find protection from predation in the structural complexity of the littoral vegetation (Werner *et al.*, 1977, 1983; Keast *et al.*, 1978). In addition, the low oxygen conditions that prevail in many swamps may limit exploitation by some introduced predators. It is difficult to separate the interactive and independent effects of structure and low oxygen on the habitat use of Nile perch. Heavily vegetated wetlands are often characterized by both high structural complexity and low oxygen conditions. However, within the three wetland transects that were characterized by higher oxygen conditions, there was a negative relationship between species richness at trap sites and dissolved oxygen, suggesting differential use of microhabitats with low oxygen conditions in these ecotonal areas.

Fishes observed in the wetland ecotones may represent remnants of larger populations that were once widespread in the lake prior to the increase in numbers of introduced Nile perch, and/or fishes which have shifted their distribution from more open water habitats to wetland areas where the Nile perch are less abundant. In 1962, the endemic haplochromine cichlids *Astatotilapia velifer*, *Gaurochromis simpsoni* and *Prognathochromis venator* were widely distributed in Lake Nabugabo, and abundant offshore (Greenwood, 1965). *Astatotilapia velifer* and *G. simpsoni* are no longer abundant in the open waters of the lake (Ogutu-Ohwayo, 1993); however, both species are still relatively abundant in wetland ecotones. *Prognathochromis venator* has disappeared from the open waters (Ogutu-Ohwayo, 1993) and was not found in our ecotone study. The endemic *Paralabidochromis beadlei* and *Haplochromis annectidens*, and the widespread *Astatotilapia nubila*, were found in the inshore ecotone areas in both the Cambridge survey and in this study; however, they are now extremely rare. A few haplochromines were captured in the exposed ecotone areas. However, in general, the endemic haplochromines are now largely confined to the inshore wetland areas; and their persistence may depend on continued use of ecotone refugia.

There is evidence to suggest that wetlands may limit the dispersal of Nile perch. Although we found some Nile perch in wetland ecotones, their relative abundance was low, and there was a positive relationship between dissolved oxygen and the abundance of Nile perch in inshore areas. Chapman *et al.* (1996) found no Nile perch beyond the margins of Lake Nabugabo in the wetland lagoons that are separated from the main lake by large swampy divides or in the papyrus-choked Juma River which feeds Lake Nabugabo, suggesting a well-demarcated boundary of Nile perch distribution. Three species no longer found in the open waters or ecotone areas of Lake Nabugabo were found in the tributaries and lagoons beyond the margins of the main lake [*Petrocephalus catostoma*, *Barbus kerstenii* and *Barbus neumayeri*; Chapman *et al.* (1996)].

Although the swamp lagoons and papyrus-choked tributaries may offer rigid barriers to the dispersal of Nile perch, areas beyond the margin of the lake may also be inaccessible to some indigenous lake fishes due to the swampy divide and the extreme conditions that can characterize heavily vegetated swamps. In the dense interior of papyrus swamps, deoxygenation can be much more severe than in the lake's ecotone areas, with levels less than 0.5 mg/litre for extended periods (Carter, 1955; Chapman & Liem, 1995). With the exception of *Pseudocrenilabrus multicolor*, which is extremely abundant in wetland lagoons, haplochromine cichlids are rare in lagoons and tributaries beyond the margins of Lake Nabugabo (Chapman *et al.*, 1996). Thus, ecotone areas of the main lake may be extremely important as functional refugia, because of their accessibility to the main lake fishes, and the less extreme physicochemical conditions resulting from interaction with open waters.

The importance of wetland ecotones as potential refugia for some prey species from Nile perch in Lake Nabugabo has implications for the reported mass declines in fish faunal diversity in Lakes Victoria and Kyoga, which have much more extensive zones of papyrus swamp than Lake Nabugabo. Chapman *et al.* (1995) found that some of the cichlids from Lake Victoria can tolerate extremely low levels of oxygen, and that lacustrine cichlids endemic to Lake Victoria were more tolerant of hypoxia than ecologically similar species from Lake Tanganyika. Having evolved in a shallow, swampy basin, the haplochromines from Lake Victoria may be, as a fauna, relatively tolerant of hypoxia. It is possible that in Lakes Victoria and Kyoga, wetland ecotones may serve as refugia from Nile perch predation; and fishes tolerant of hypoxia may use the denser wetlands without adverse effects from low oxygen. However, only certain species may be capable of exploiting these areas. For example, in Lake Nabugabo the abundance of haplochromine cichlids was high in some wetland ecotones; however, haplochromine abundance was dominated by four species: *Gaurochromis simpsoni*, *Astatotilapia velifer*, *Pseudocrenilabrus multicolor* and *Astatoreochromis alluaudi*. The other four haplochromines were rare (*Paralabidochromis beadlei*, *Haplochromis annectidens*, *Astatotilapia nubila*) or absent (*Prognathochromis venator*). This may reflect differential abilities to tolerate both the physicochemical and biological conditions of wetland areas.

The decline of mormyrid species from common to rare or absent in Lake Nabugabo raises questions about the effectiveness of wetland areas as refugia for these fishes. The Cambridge expedition (Cambridge Nabugabo Biological Survey [CNBS], 1962) reported *Gnathonemus victoriae*, *G. longibarbis* and *Marcusenius nigricans* to be common in areas near overhanging swamp, which would seem not to predispose this group to extensive predation by Nile perch. We must therefore consider the possibility that factors other than, or in addition to, the Nile perch introduction may have contributed to the decline of some species in Lake Nabugabo.

It is difficult to draw general rules by which the effects of introduced predators can be predicted. However, it is critical that we identify environmental parameters that may be useful as predictors of introduced predator-indigenous prey dynamics in aquatic systems. Our study suggests that, in the Lake Victoria Basin, species that are more tolerant of low oxygen and inhabit wetland ecotones may be less susceptible to predation by Nile perch. It is likely that the overlap between indigenous fish species and Nile perch in their relative capacities to use wetland ecotones determines the extent of predation in this habitat. This study implicates wetland ecotones as potentially important refugia for some indigenous prey and suggests that some species thought to have disappeared from the open waters of Lake Victoria may still survive in the structural and/or low-oxygen refugia provided by wetland ecotones. Continued anthropogenic disturbance to this region could threaten

remnant populations of indigenous species in Lakes Nabugabo, Kyoga and Victoria.

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