Refugia for Endangered Fishes from an Introduced Predator in Lake Nabugabo, Uganda

LAUREN J. CHAPMAN,* COLIN A. CHAPMAN,* RICHARD OGUTU-OHWAYO,†
MARK CHANDLER,‡ LES KAUFMAN,§ AND AMANDA E. KEITER*

*Department of Zoology, University of Florida, Gainesville, FL 32611, U.S.A., ljchapman@zoo.ufl.edu
†Fisheries Research Institute, P.O. Box 343, Jinja, Uganda,
‡Edgerton Research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110, U.S.A.,
§Boston University Marine Program, Department of Biology, Boston University, 5 Cummington Street, Boston, MA 02215, U.S.A.

Abstract: *Wetlands may protect fishes from introduced predatory fishes by providing both structural and low-oxygen refugia for prey species tolerant of the conditions that prevail in these habitats. We examined the potential of wetlands as refugia for fishes in Lake Nabugabo, Uganda, where increased numbers of an introduced predator, the Nile perch* (Lates niloticus), *coincided with the decline or disappearance of many indigenous species in the main lake. In 1993 and 1994 we sampled fishes in three wetland habitats: the marginal wetland ecotones of the lake, wetland lagoons separated from the lake by densely vegetated marsh habitats, and a stream separated from the lake by dense papyrus swamp. Fish distributions in these wetlands were then compared to results from two earlier fish surveys: the 1962 Cambridge expedition to Lake Nabugabo, which was conducted prior to the increase in the Nile perch population; and a 1991-1992 survey of the open lake, which reported the disappearance of 16 indigenous species. In our 1993-1994 surveys 9 of the 16 species not recovered in the 1991-1992 open-lake survey were found in the wetland ecotones or beyond the margins of the lake in wetland lagoons and tributaries. Three of these species were found only beyond the margins of the lake in the tributaries and lagoons within extensive wetlands. Three endemic haplochromine cichlids were abundant offshore in 1962. Of these species one has disappeared and the others are now largely confined to inshore areas. Other species that were abundant in the open waters of the lake in 1962 (e.g., the lungfish* Protopterus aethiopicus) *are now found primarily in wetlands. Two species, the characid* Brycinus jacksonii *and the cyprinid* Rastrineobola argentea, *are still abundant in the open waters. This study highlights the need for quantitative survey work to identify wetland refugia in the Lake Victoria Basin and suggests that some species thought to have disappeared in the mass extinction of fishes in Lakes Victoria and Kyoga may still survive in refugia. Some fish populations could recover under effective ecosystem management.*

Refugio para proteger de un de predador introducido a los peces en peligro de extinción del Lago Nabugabo, en Uganda

Resumen: *Los humedales pueden proteger a los peces de otros peces depredadores introducidos al brindar refugio estructural y de bajo contenido en oxigeno para especies predadoras tolerantes a las condiciones que prevalecen en esos ambientes. En el presente estudio, examinamos el potencial de los humedales como refugios para los peces del Lago Nabugabo, en Uganda; donde el incremento en número de un de predador introducido, la perca del Nilo* (Lates niloticus), *coincidió con la declinación o desaparición de varias especies indígenas en el lago principal. En 1993 y 1994 muestreamos peces en tres ambientes de humedales: los marginales ecotonos de humedales del lago, las lagunas de humedales sepapradas del lago por hábitats pantanosos densamente vegetados y un arroyo separado del lago por un pantano con una densa vegetación de*

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papyrus. La distribución de los peces en esos humedales fue comparada con los resultados de dos estudios previos: la expedición de Cambridge al Lago Nabugabo en 1962, que fue llevada a cabo con anterioridad al incremento de la población de la perca del Nilo y un estudio del lago abierto, llevado a cabo en 1991-1992, que reportó la desaparición de 16 especies indígenas. En nuestro estudio de 1993-1994, 9 de las 16 especies no recuperadas en el estudio del lago abierto de 1991-1992, fueron encontradas en los ecotonos de humedales o más alla de los márgenes del lago, en lagunas de humedales o en los tributarios. Tres de estas especies fueron solo encontradas mas allá de las margenes del lago en los tributarios y en laguunas dentro de humedales extensos. En 1962, tres cíclidos haplocrominos endémicos fueron abundantes en áreas costeras. De estas especies una ha desaparecido y las otras se encuentran actualmente confinadas a áreas interiores. Otra de las especies que fueron abundantes en las aguas abiertas del lago en 1962 (por ej. Protopterus aethiopicus*), se encuentran ahora principalmente en los humedales. Son abundantes aún dos especies en las aguas abiertas, el carácido* Brycinus jacksonii *y el ciprínido* Rastrineobola argentea*. Este estudio resalta la necesidad de estudios cuantitativos, que identifiquen los refugios en los humedales de la cuenca del Lago Victoria y sugiere que ciertas especies que se cree desaparecieron durante la extinción masiva de peces del Lago Victoria y Kyoga pueden haber sobrevivido en los refugios. Algunas poblaciones de peces puedrían recuperarse bajo un manejo efectivo del ecosistema.*

Introduction

Fresh waters are increasingly threatened by the overexploitation of existing fish stocks. In many cases this increases pressure for species introductions to increase fish yields (Ogutu-Ohwayo & Hecky 1991). Within Africa the most dramatic and catastrophic fish introduction involves the transfer of the Nile perch (*Lates niloticus*) into the lakes of the Lake Victoria Basin during the 1950s and early 1960s (Hamblyn 1961; Gee 1964; Ogutu-Ohwayo 1990, 1993). This introduction is proposed to have contributed to the extinction or endangerment of approximately 200 of the over 300 endemic haplochromine cichlid species in Lake Victoria (Witte et al. 1992), and similar changes are suggested to have occurred with the introduction of Nile perch into Lakes Kyoga and Nabugabo (Ogutu-Ohwayo 1990, 1993). In a few habitats within Lake Victoria, however, the original communities of fish species seem less affected by the Nile perch. For example, rock-dwelling haplochromine cichlids have shown the most modest decline in the Mwanza Gulf area of Lake Victoria (Witte et al. 1992).

Papyrus (*Cyperus papyrus*) swamps, wetlands dominated by other vegetation, and lagoons within or behind marsh areas may present much more widespread refugia in the Lake Victoria basin. These wetlands may protect fishes from Nile perch predation for two reasons. First, they provide structural heterogeneity in which fish can escape predators. Second, the closed canopy of heavily vegetated wetlands minimizes incident light and the mixing of water below, resulting in reduced oxygen levels (Carter 1955; Chapman & Liem 1995). Because Nile perch seem to require water with relatively high levels of dissolved oxygen (Fish 1956), wetlands may limit their dispersal and serve as refugia for some prey species. Chapman et al. (1995) demonstrated that some of the cichlids from Lake Victoria can tolerate extremely low levels of oxygen, which may permit these fishes to use structured inshore habitats as refugia.

To examine the potential of wetlands as refugia in the lakes affected by the introduction of Nile perch, we documented the community composition of fishes in the wetlands of Lake Nabugabo, a satellite of Lake Victoria, where an increase in the numbers of Nile perch, introduced into the lake in 1960 and 1963 (Gee 1964), has coincided with the decline or disappearance of many indigenous species (Ogutu-Ohwayo 1993). We selected Lake Nabugabo (24 km^2) for this study because it is smaller than Lake Victoria (68,800 km^2), is easily accessible, and can be thoroughly sampled. It also has a relatively well known and simple fish fauna. In addition, baseline data are available for 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, preliminary report; Greenwood 1965; Ogutu-Ohwayo 1993). An assessment of fish-community composition in the Nabugabo wetlands provides a means of evaluating the potential role of wetland refugia in the survival of native species in Lakes Victoria and Kyoga.

We compared the species composition of three habitats characterized by a high degree of structural complexity: the marginal wetland ecotones of the lake; wetland lagoons and their small tributaries, separated from the lake by dense marsh vegetation; and small, open channels of the main tributary separated from the lake by dense papyrus swamp. Our data on the distributions of fishes in wetland areas are compared to the results of the 1962 Cambridge expedition to Lake Nabugabo (CNBS 1962) and to a 1991-1992 survey of the open lake (Ogutu-Ohwayo 1993). Results are considered in light of recent observations on the resurgence of indigenous species in Lakes Victoria and Kyoga (Ogutu-Ohwayo 1994).

Study Area and Methods

Lake Nabugabo is a small satellite lake (24 km^2, mean depth = 4.5 m) of Lake Victoria. It lies within an extensive marsh that was formerly a bay on the western shore of Lake Victoria (Worthington 1932; Greenwood 1965; Ogutu-Ohwayo 1993; Fig. 1). Long shore bars that isolate Lake Nabugabo from Lake Victoria were 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. The main tributaries to Lake Nabugabo are the Juma River (Fig. 1), which is choked with papyrus, and numerous small springs that discharge along the lake shore (Greenwood 1965). Although it is generally recognized that swamps are flooded areas dominated by woody vegetation, we followed the traditional use of the term papyrus swamp to refer to marsh areas dominated by papyrus. Outflow from Lake Nabugabo is eastward via the Lwamunda Swamp, with seepage through the sandbar that forms the eastern 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 several permanent lagoons and small, intermittent streams.

Wetland ecotone areas of the open lake were selected to maximize the range of structural and physicochemical variation among habitats, and sampling was carried out within 100-m-long sampling sites along the ecotone

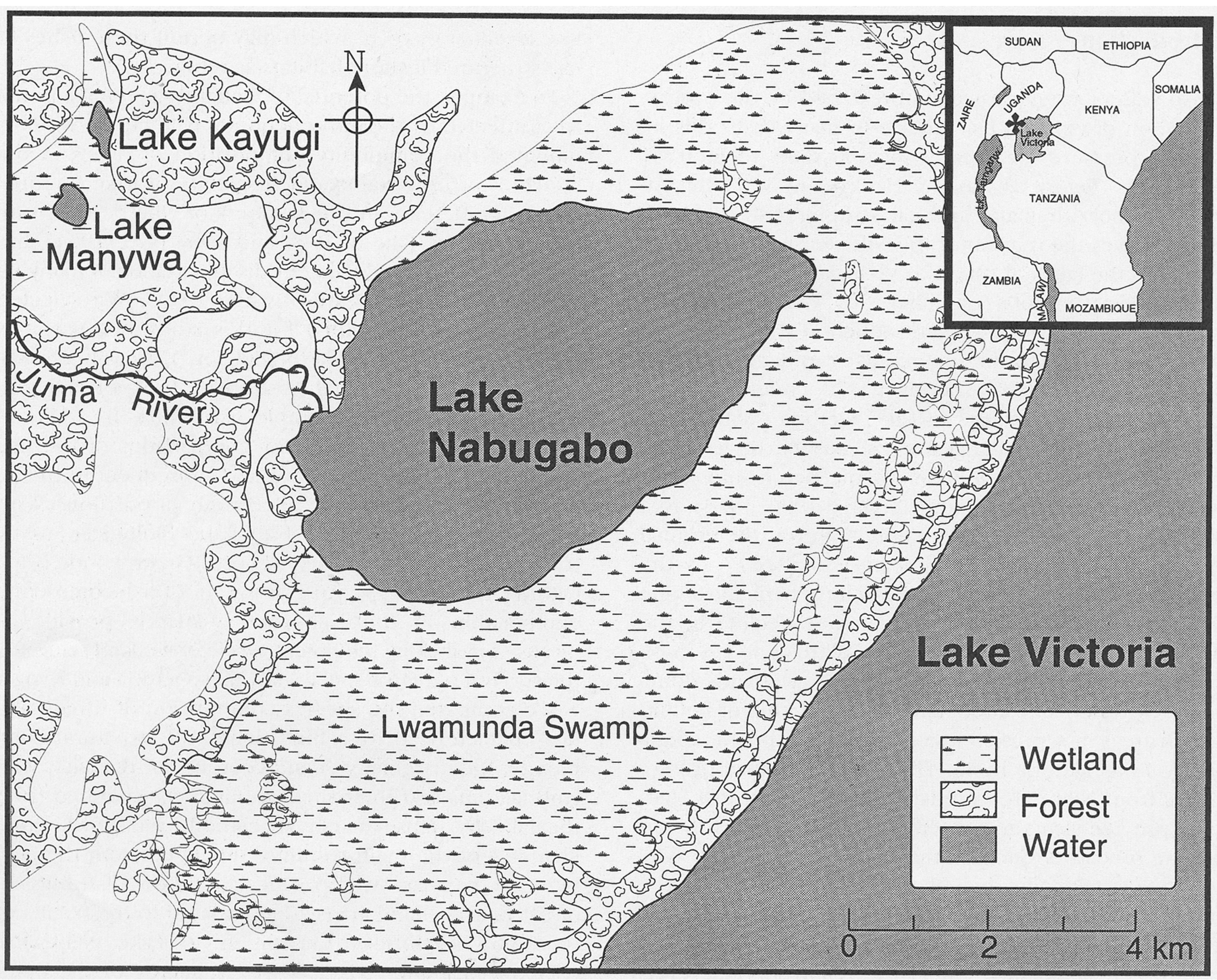

Figure 1. Map illustrating the location of Lake Nabugabo, the Juma River, and the Lwamunda Swamp relative to Lake Victoria, based on a 1:50,000 topographic map done in 1958. The Lwamunda Swamp is an extensive wetland area containing several permanent lagoons and small streams. Many of the forested areas have been reduced since 1958.

habitat. Major 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* spp.) and water lilies. Minnow traps were set systematically across each ecotone area, 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 overnight along the ecotone as close as possible to the vegetation. Small 3-m seines and A-frame seines were used to sample edge areas qualitatively to increase the probablility of capturing less-abundant species. The ecotones were sampled during November of 1993 and May of 1994 for a total of seven ecotone samples. The Juma River was sampled along a 100-m stretch heavily choked with papyrus, and approximately 200 m upstream of the river mouth. Minnow traps and larger local fish traps were placed in open pools, open channels with flowing water, and deep in the papyrus of the main channel. Several small lagoons and tributaries were sampled in the Lwamunda Swamp using a combination of local traps, minnow traps, a 3-m seine, and A-frame seines. Fish from the lagoons were also purchased from local fishermen who regularly fish these sites. Dissolved oxygen and water temperature were measured with a portable meter (YSI, model 51B) for the ecotone areas and the sampling sites on the Juma River. All captured fish were identified and measured (total length). Haplochromines were identified on the basis of Greenwood's (1965) key, supplemented by recent morphological data (Chandler & Kaufman, unpublished data). The nomenclature of the haplochromine species in the Lake Victoria Basin has undergone considerable revision (Greenwood 1980). We follow Greenwood's (1980) revised nomenclature. With respect to the genus *Clarias* we follow Teugels (1986) in differentiating between *Clarias werneri* and *C. alluaudi*. In earlier surveys of Lake Nabugabo these were considered one species (Greenwood 1966). Voucher specimens are deposited at the Museum of Comparative Zoology (cichlids), the Florida Museum of Natural History (non-cichlids), and the American Museum of Natural History (non-cichlids).

We compare our results to the 1962 Cambridge expedition (CNBS 1962) and the 1991-1992 survey of the open lake (Ogutu-Ohwayo 1993). Although we draw our comparisons from surveys that differed in sampling protocols, all surveys used a variety of gears and sampled intensively. From the catch data and the observations made by the sampling teams, we can interpret changes that have occurred in the species richness and composition of the fish fauna of the main lake since the introduction of the Nile perch. We restrict our discussion of abundance to qualitative observations on major changes in habitat use and catch.

The Cambridge expedition (June to August 1962) used a combination of seining in inshore open areas, gill nets (25.4 mm to 229 mm stretched mesh) in the open waters of the main lake, traps, rotenone in small bays, and fishing records from the Ministry of Natural Resources to quantify the richness of species in the main lake and to provide qualitative data on habitat use. They also sampled lagoons and tributaries of the Lwamunda Swamp and noted the species found. Ogutu-Ohwayo (1993) made eight 5-day sampling trips to Lake Nabugabo bimonthly from January 1991 to August 1992. The open waters (inshore and offshore) of the lake were sampled with gill nets of 25.4 mm to 305 mm stretched mesh, and beach seines (51 mm and 5 mm mesh) were used in open inshore areas. The 1991-1992 survey also included fishes found in stomachs of captured Nile perch, which increased the probability of capture for smaller species. Because the surveys differed in intensity and duration, the disappearance of species after the introduction of Nile perch may reflect their decline or extinction. Species may remain in low numbers in areas not sampled or not sampled sufficiently to capture extremely rare fishes.

Results and Discussion

Twenty species of non-cichlids, eight species of haplochromine cichlids, and two tilapiine cichlids were recorded by the Cambridge expedition to Lake Nabugabo in 1962 (CNBS 1962; Greenwood 1965; Table 1). Five of the haplochromine cichlids were considered by Greenwood (1965) to be endemic to Lake Nabugabo. Later work has indicated that their endemic distribution includes Lake Nabugabo and at least one of the other small satellite lakes near Nabugabo (Kaufman & Ochumba 1993; Ogutu-Ohwayo 1993) and that morphological variation within and among sites for *Astatotilapia velifer* and *Gaurochromis simpsoni* is high (Kaufman and Chandler, unpublished data). The 1991-1992 survey in the open lake, 30 years subsequent to the introduction of Nile perch, showed that many of the native fish species in Lake Nabugabo had either disappeared or declined since the introduction of the Nile perch and the Nile tilapia (*Oreochromis niloticus*; Ogutu-Ohwayo 1993). *L. niloticus*, *O. niloticus*, *Schilbe intermedius*, *Brycinus jacksonii*, and *Rastrineobola argentea* were the only species abundant within the open waters of the lake. Although sampling was primarily in open water areas (both inshore and offshore), Ogutu-Ohwayo (1993) noted that many surviving species in the lake were confined to macrophytes along the lake margins.

Our survey of the wetland ecotone areas of the lake and of lagoons and small tributary areas behind the margins of the open lake (1993-1994) revealed a number of species thought to have disappeared from the open lake, as well as species not previously reported in earlier surveys. Nine of the 16 species not recovered in the 1991-

Table 1. A comparison of indigenous and introduced fish species reported in the Cambridge Nabugabo Biological Survey (1962), open lake surveys in 1991–1992 (Ogutu-Ohwayo 1993), and wetland surveys in 1993–1994.

Family/Species	*1962 (Cambridge)*	*1991–1992 (open lake)*	*1993–1994 (wetlands)*
Protopteridae			
Protopterus aethiopicus	+	+	+[a b c]
Mormyridae			
Gnathonemus victoriae	+	+	–
Gnathonemus longibarbis	+	–	–
Marcusenius nigricans	+	–	–
Petrocephalus catostoma	+	–	+[b]
Cyprinidae			
Rastrineobola argentea	+	+	–
Barbus magdalenae	+	–	+[a]
Barbus apleurogramma	+	–	+[a b c]
Barbus kerstenii	+	–	+[c]
Barbus neumayeri	+	–	+[c]
Barbus sp.	–	+	+[b]
Barbus radiatus	+	–	+[b]
Characidae			
Brycinus jacksonii	+	+	+[a]
Bagridae			
Bagrus docmac	+	–	–
Schilbeidae			
Schilbe intermedius	+	+	+[a]
Clariidae[d]			
Clarias gariepinus	+	+	–
Clarias alluaudi	+	–	+[a]
Clarias liocephalus	–	–	+[b c]
Clarias werneri	[d]	–	+[ac]
Mochokidae			
Synodontis afrofischeri	+	+	+[ac]
Cyprinodontidae			
Aplocheilichthys pumilus	+	–	+[a b c]
Nothobranchius sp.	–	–	+[b]
Cichlidae			
Oreochromis esculentus	+	–	–
Oreochromis variabilis	+	–	–
Astatotilapia velifer	+	+	+[a b c]
Gaurochromis simpsoni	+	+	+[a]
Haplochromis annectidens	+	+	+[a]
Paralabidochromis beadlei	+	+	+[a]
Prognathochromis venator	+	–	–
Astatotilapia nubila	+	+	+[a]
Pseudocrenilabrus multicolor	+	–	+[a b c]
Astatoreochromis alluaudi	+	+	+[ac]
Anabantidae			
Ctenopoma muriei	+	–	+[b c]
Mastacembelidae			
Aethiomastacembelus frenatus	+	+	+[ac]
Introduced Species			
Centropomidae			
Lates niloticus	–	+	+[a]
Cichlidae			
Oreochromis niloticus	–	+	+[a b c]
Oreochromis leucostictus	–	+	+[a b c]
Tilapia rendalli	–	+	+[a b]
Tilapia zillii	–	+	–
Total Species	30	20	29

[a] *Wetland ecotone of the open lake.*
[b] *Lwamunda Swamp.*
[c] *Juma River.*
[d] *Greenwood (1966) did not differentiate between* Clarias alluaudi *and* Clarias werneri.

1992 survey were found in the wetland ecotones or beyond the margins of the lake in the Juma River and Lwamunda Swamp (Table 1). Three species were recorded that were not reported from earlier surveys; these species were primarily confined to the Juma River and Lwamunda Swamp (Table 1). Because our sampling of both the Lwamunda area and the Juma River was limited in scope and seasonal duration, the actual number of species is probably greater.

The communities that characterize the ecotone of the open lake differed from those of the areas beyond the margins of the open lake in both species richness and composition. Inshore areas of the open lake contained the most species. We found 21 fish species in wetland ecotones, whereas only 15 species were recovered from the Juma River and 14 species from the Lwamunda Swamp tributaries and lagoons. The ecotone areas varied in their structural and physicochemical conditions, but most wetland ecotones exhibited some degree of hypoxia (mean dissolved oxygen = 3.8 mg/L, range = 0.6 to 8.4 mg/L). Nile perch were recovered from ecotone areas, but they were never abundant in our samples, and most were small juveniles (mean total length = 15.2 cm, range = 6.3 to 39.0 cm). No Nile perch were recovered beyond the margins of the lake in wetland lagoons or in the papyrus choked Juma River. The data suggest a strongly demarcated isocline of Nile perch distribution.

The Juma River was extremely hypoxic (mean dissolved oxygen = 1.3 mg/L, range = 0.2 to 2.1 mg/L). Many fish species found beyond the margins of the lake in the Juma River and Lwamunda Swamp are those with high tolerance to low oxygen conditions. Several possess accessory air-breathing organs (*Clarias liocephalus, C. werneri, Ctenopoma muriei, Protopterus aethiopicus*). Other species are not air breathers but are known to be tolerant of hypoxia. These include *Barbus neumayeri* (Chapman & Liem 1995), *Synodontis afrofischeri* (Chapman et al. 1994), *Pseudocrenilabrus multicolor* (Chapman & Chapman, unpublished data), and *Oreochromis leucostictus* (Welcomme 1970), all of which use aquatic surface respiration in response to low oxygen conditions.

Six species taken in earlier surveys (Worthington 1932; CNBS 1962) were not captured during the 1991–1992 survey or our 1993–1994 wetland survey (*Bagrus docmac, Oreochromis variabilis, O. esculentus, Prognathochromis venator*, and two mormyrids, *Gnathonemus longibarbis* and *Marcusenius nigricans*). Three species recorded in the early surveys were not found in the main lake (open water or wetland ecotones) but were found beyond the margins of the lake in the Juma River or the Lwamunda Swamp: *Petrocephalus catostoma, Barbus kerstenii,* and *Barbus neumayeri*. Together, these two groups represent the species currently thought to have disappeared from the open waters and ecotone areas of Lake Nabugabo.

The report presented by the Cambridge Nabugabo Biological Survey and Greenwood's summary of the distribution of the haplochromine cichlids based on the Cambridge field notes provides the basis for evaluating changes in the distribution of the remaining species in the system. In our recent survey, *Pseudocrenilabrus multicolor*, a widespread haplochromine throughout the Nile Basin, was found in all major wetland habitats sampled but was most abundant in the wetland lagoons and tributaries of the Lwamunda Swamp. It has not been taken from the open lake (Ogutu-Ohwayo 1993). The Cambridge Nabugabo Biological Survey also did not find *P. multicolor* in open lake waters, but it was abundant in a wide range of inshore habitats, the Juma River, and the Lwamunda Swamp (Greenwood 1965). Greenwood (1965) states that the endemic haplochromine cichlids *Astatotilapia velifer, Gaurochromis simpsoni*, and *Prognathochromis venator* were widely distributed in the lake and abundant offshore in 1962. The 1991–1992 surveys and our wetland survey found that *A. velifer* and *G. simpsoni* were no longer abundant in the open lake, but both were common in marginal macrophytes. The endemic *Paralabidochromis beadlei* and *Haplochromis annectidens* and the widespread *Astatotilapia nubila* were found in the inshore ecotone areas during both the Cambridge survey and our recent surveys, but these species are now extremely rare in Lake Nabugabo. In general, the endemic haplochromines are now largely confined to the inshore areas of the open lake and are much more common in wetland ecotones than exposed inshore areas with no wetland (Chapman et al., in press). The one exception is *A. velifer*, which was found on rare occasions beyond the margins of the lake in the Juma River and Lwamunda Swamp. This suggests that haplochromine populations are able to persist today only by continued use of the wetland ecotones; in some cases this may have resulted from a habitat shift to concentrate in ecotone refugia.

Fisheries statistics reported by the Cambridge expedition suggested an annual total of 27 tons at the major fish landing in 1962. At that time the fishery was dominated in weight by the lungfish (*Protopterus aethiopicus*), followed by *Bagrus docmac, Schilbe intermedius, Clarias gariepinus, Oreochromis esculentus, O. variabilis,* and various species of haplochromine cichlids. The lungfish is now extremely rare in both open waters and ecotone areas but is relatively easy to catch in the Lwamunda Swamp. Of the other species that formed the basis of the pre-Nile perch fishery, only *S. intermedius* remains abundant in the open waters; *O. esculentus, O. variabilis,* and *B. docmac* are no longer captured, and *C. gariepinus* is very rare. None of these five species were found beyond the margins of the lake in the Juma River or the Lwamunda Swamp. In 1962 *Synodontis afrofischeri* and *Aethiomastacembelus frenatus* were abundant and confined to the main lake. In our recent sampling these species were found only in the lake ecotone areas and in the Juma River.

The mormyrids seem to have largely disappeared from Lake Nabugabo. The Cambridge expedition reported *Gnathonemus victoriae*, *G. longibarbis*, and *Marcusenius nigricans* as common in areas near overhanging marsh vegetation. *Petrocephalus catostoma* was found in one place in the open lake in 1962, where it occurred together wtih *M. nigricans*. The larger mormyrids were an important component of the local fish catch. In the later surveys (1991-1994) *G. victoriae* was extremely rare in the open lake and not reported from any wetland areas in the main lake or beyond the margins. *G. longibarbis* and *M. nigricans* have not been captured recently. *P. catostoma* is now captured only in the Lwamunda Swamp, where it was also found in 1962. The disappearance of three species of mormyrids from Lake Nabugabo is particularly interesting given their use of marginal areas prior to the Nile perch introduction. Another group that has largely disappeared from the open waters and ecotones of Lake Nabugabo are the *Barbus*. *Barbus apleurogramma*, *B. kerstenii*, *B. neumayeri*, and *B. magdalenae* were reported as abundant in some widely spread localities in the lake. In the recent sampling, *B. magdalenae* and *B. apleurogramma* were found to be extremely rare in the main lake and restricted to marginal macrophytes. The other *Barbus* species were not found in the open lake or ecotone areas but are still found beyond the margins of the lake in the Juma River, where *B. apleurogramma* and *B. kerstenii* are extremely abundant, or the Lwamunda Swamp (*B. apleurogramma*, *B. radiatus*, and *Barbus* sp.). Some of the mormyrid and cyprinid taxa of the basin are still abundant in the small satellite lakes near Nabugabo (Ogutu-Ohwayo 1993).

Some species have shown no appreciable decline over the past 30 years. Although *Brycinus jacksonii* and *Rastrineobola argentea* were not a major component of the fisheries catch because of their small size, the Cambridge expedition reported them as abundant in beach seine catches. These two species are still abundant in Lake Nabugabo and have persisted with Nile perch in Lakes Kyoga and Victoria as well. The question of how these two species coexist with Nile perch in open water habitats remains unanswered. Two other species have shown no change in habitat use and remain abundant today. *Aplocheilichthys pumilus* is still found in shallow water with projecting vegetation, and *Ctenopoma muriei* is still found in high abundance beyond the margins of the lake in the Lwamunda Swamp and the Juma River.

It appears that the fishes observed in the wetland ecotones, lagoons, and tributaries may represent remnants of larger populations that were once widespread in the system prior to the introduction of the Nile perch, as well as fishes that have shifted their distribution from open-water habitats to areas where the Nile perch are rare or absent. Habitat shifts in response to predator risk have been reported for a variety of fish species (Power et al. 1985; Carpenter et al. 1987; He & Kitchell 1990; Brown & Moyle 1991) and may contribute to the current distribution patterns for some species in the Lake Victoria Basin.

The wetland ecotone areas differ from the lagoons and tributaries in their accessibility to fishes, which affects their usefulness as potential refugia. Our data suggest that Nile perch can be found in ecotone areas but may not be able to exploit lagoons and tributaries separated from the open lake by wetland divides. The areas beyond the margin of the lake may also be inaccessible to a variety of indigenous lake species, however, due to the wetland divide and the extreme conditions that can characterize the interior of heavily vegetated wetlands. A tradeoff may exist among accessibility, physicochemical conditions, and predator risk. It is likely that a more-thorough survey of the Lwamunda Swamp at sites close to the margins of either Lake Nabugabo or adjacent to Lake Victoria would reveal higher numbers of species.

Data on the recent changes in the fish catches, stomach contents of Nile perch, and preliminary results of faunal surveys in Lakes Victoria and Kyoga all suggest the potential for a resurgence of some haplochromine species (Ogutu-Ohwayo 1994; Kaufman & Chandler, personal observation). The most parsimonious explanation at this stage is that overfishing of the Nile perch populations has reduced predator pressure to the point where some of the haplochromines that had survived in refugia, such as wetland ecotones, are increasing in numbers. Anthropogenic disturbance to wetlands, particularly ecotonal areas, could be especially damaging to remnant populations of indigenous species threatened by Nile perch. In Lake Victoria, ecotonal impacts are further compounded by the spread of water hyacinth, *Eichhornia crassipes*, which is capable of destroying submerged macrophyte beds along wetland borders by shading. Alternatively, the floating beds of water hyacinth may provide cover for haplochromine cichlids from Nile perch predators or may enhance ecotone refugia by deoxygenating the water column for some distance from the edge of a swamp. The increase in haplochromine stocks in Lake Kyoga has coincided both with the invasion and spread of water hyacinth and heavy fishing pressure on Nile perch (Ogutu-Ohwayo 1994).

Conclusions

In a conservation context, ecologists face several critical needs with respect to the biology of introduced predators. First, we must understand what limits the dispersal of the predator from the site of introduction. Second, we must know the characteristics of refugia that protect prey species from exploitation by an introduced predator. Such information is critical if we are to minimize biodiversity loss through the management or manipulation of refugia. In the Lake Victoria Basin, wetlands may serve as both refugia for prey species from the introduced Nile perch and as barriers to the dispersal of Nile perch. Survey of the wetland ecotones and some areas beyond the margins of the Lake Nabugabo has revealed several species thought to have disappeared from the open waters of the lake. This preliminary study highlights the need for quantitative survey work to identify wetland refugia in the Lake Victoria Basin and for more detailed analyses of the characteristics of wetland habitats that permit them to function as refugia for indigenous species. This study also suggests that some species thought to have disappeared in the mass extinction of Lake Victoria may survive in refugia, and their populations could recover under effective ecosystem management, such as the protection of papyrus swamps and other wetlands.

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