Fishing down and fishing hard: ecological change in the Nile perch of Lake Nabugabo, Uganda


Abstract – Fishing is a potent ecological force. In Lake Victoria, East Africa, Nile perch, Lates niloticus contributes to a multi-million dollar fishing industry but is threatened by over-exploitation. We quantified spatial and temporal trends in the distribution, diet and size of Nile perch in Lake Nabugabo, Uganda, a satellite of Lake Victoria. From 1995 to 2007, we detected a decline in catch per unit effort of Nile perch, a shift in their distribution and diet, and a decrease in their body size. A greater proportion of Nile perch were found near wetland ecotones than in the 1990s. This may reflect intensive size-selective fishing in open waters, and encroachment of Vossia cuspidata, an emergent macrophyte that has expanded across the lakeshore. Results highlight the strength of fishing in inducing phenotypic changes in target stocks as well as large-scale changes to the aquatic community and are of value in understanding changes in Lake Victoria.

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Key words East Africa; fish habitat use; haplochromine cichlids; invasive species; Lake Victoria; Lates; piscivory

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Introduction

Size-selective predation on fish stocks

There is overwhelming evidence that wild animal populations are capable of rapid phenotypic change in response to anthropogenic stressors (Hendry & Kinnison 1999; Palumbi 2001; Stockwell et al. 2003), and there is no question that such change can be induced by fishing pressure (Law 2000). Fishing-induced mortality is almost always nonrandom in terms of size and location (where the harvest will be the greatest), thus generating selection on yield-determining traits that can lead to shifts in life-history traits (e.g., favouring the survival of smaller, slower-growing phenotypes) and other responses to size-selective predation. Many studies have attributed such phenotypic shifts in fished populations to over-exploitation. Examples include the northern pike (Esox lucius) (Diana 1983), the brown trout (Salmo trutta) and the arctic char (Salvelinus alpinus) (Hegge et al. 1991). In a lab-rearing study, Walsh et al. (2006) subjected the Atlantic silverside, a heavily harvested marine fish, to size-selective mortality regimes over five generations. The silverside showed dramatic declines in fecundity, egg volume, larval size at hatch, larval viability, larval growth rates, food consumption rate and conversion efficiency, and willingness to forage. Such changes may increase fitness by reducing intra-specific competition or selecting for morphotypes more resistant to fishing pressure, but may also be an impediment to population recovery (Walsh et al. 2006). For example, some collapsed fisheries fail to recover even when fishing pressure decreases or ceases (Hutchings & Reynolds 2004), and this may be due, at least in part, to smaller and slower-growing individuals being unable to restock the population to original levels i.e., fish may become smaller and slower growing making them more fit under large-sized selected fishing, but less fit under natural conditions. In this study, we looked for evidence of phenotypic change in the intensively harvested Nile perch (Lates niloticus) that is consistent with predictions of nonrandom fishing mortality.

Paterson & Chapman

The Lake Victoria story – overfished and/or overproductive?

In Lake Victoria, Africa’s single most important source of inland fisheries production, anthropogenic stressors, in particular, overfishing, species introductions and eutrophication, have contributed to massive ecological changes in the system (Graham 1929; Hecky et al. 1994; Kaufman et al. 1997; Oguttu-Ohwayo 1990). After it was fished down in the first half of the 20th century, a series of food fishes were introduced into the lake basin, including the predatory Nile perch, *L. niloticus*, to compensate for depleting commercial fisheries and to boost a sport fishing industry (Jackson 2000; Balirwa et al. 2003; Pringle 2005). A dramatic increase of Nile perch in the 1980s coincided with the disappearance of ≈40% of the 500+ endemic haplochromine cichlid species (See-hausen et al. 1997a,b; Balirwa 2007; Witte et al. 1992). At the same time, the Nile perch fishing industry attracted unparalleled levels of national and international capital investment, sparked the development of 90 fish freezing factories (Balirwa et al. 2003), and fuelled a fish export market that reached $250 million in 2003 (LVFO 2005; Balirwa 2007). Management of the Lake Victoria fisheries has been informed by research initiatives and empirical models predicting the impacts of fishing regimes on Nile perch and the cascading effects to native species. Recommendations derived from these models included restricting gill nets mesh sizes to maximise sustainable catch while preserving native species, and ubiquitous caution to manage fishing effort in order to avoid a collapse in the Nile perch fishery. Despite fishing regulations, as an open-access resource, the level of exploitation of Nile perch has been difficult to control; in recent years, yield has declined as fishing effort has increased (Balirwa et al. 2003; Matsuishi et al. 2006; Mkumbo et al. 2007). Decline in Nile perch yield has coincided with a resurgence of native species suggesting that fishing on Nile perch may enhance biodiversity (Balirwa et al. 2003). These trends support fishing as an important driver of change in the Lake Victoria system; however, it has also been argued that the main drivers of ecological changes in Lake Victoria over the last several decades are the bottom-up effects of eutrophication— not fishing pressure (Kolding et al. 2008).

Eutrophication has increased in Lake Victoria since the 1920s as population density expanded in the riparian countries bordering Lake Victoria primarily through industrialisation and land-use change (Verschuren et al. 2002). Kolding et al. (2008) argue that the role of eutrophication on the Nile perch fishery is monumental in Lake Victoria, relative to fishing pressure. Based on expected and observed trends in length-based and catch per unit effort (CPUE) indicators of over-exploitation, Kolding et al. (2008) reasoned that there are no signs of overfishing in the indicators used and thus, that the top-down effects of fishing cannot be influencing the system in a substantial way. One approach to grasp the extent to which fishing impacts Nile perch populations is to monitor Nile perch in response to intensive fishing in a lake not as strongly influenced by anthropogenic inputs. Lake Nabugabo is a small satellite of the larger Lake Victoria (Greenwood 1965), and has experienced a similar pattern of faunal collapse and resurgence in response to the introduction of Nile perch without the dramatic increases in nutrient loadings and productivity seen in Lake Victoria. It is thus a useful system for exploring the response of Nile perch to environmental change (food web alterations, fishing pressure) coincident with its own invasion. The objective of this study was to quantify phenotypic change in the introduced Nile perch of Lake Nabugabo of East Africa in response to decades of intensive fishing pressure. Specifically, we investigated temporal (12 years from 1995 to 2007) and spatial variation (wetland habitats versus open water habitats) in the CPUE, size and diet of Nile perch in Lake Nabugabo during a period of intensive fishing.

Methods

Study site

Lake Nabugabo is a small water body (5 km long and wide; surface area 25 km²; mean depth = 4.5 m) just south of the equator in Uganda that became separated from Lake Victoria ≈5000 years ago (CNBS 1962, Greenwood 1965; Beadle 1981; Stager et al. 2005). The major source of water inflow to Lake Nabugabo is through the Juma River (Fig. 1). Lake water flows eastward through Lwamunda Swamp and into Lake Victoria (Beadle 1974). The lake is described as a nutrient-deficient system; the bedrock and soils are very old with low salt content (Kateyo 2006). Much of the lake margin is isolated from any significant form of human-induced nutrient input by a dense wetland. Developments along the west side of the lake (three vacation centres/hotels and small bays where cattle farmers lead their herds to drink) are clearly point sources of nutrient input; however, the change in trophic state of the lake has been modest compared to Lake Victoria. In her study of post 1880 sediment and phosphorus accumulation rates in Lake Nabugabo using a sediment core, Cangelosi (1998) reported increasing organic matter and phosphorus accumulation throughout the past century; however, there is no record in recent history of dramatic changes in water transparency or algal blooms that characterise the
larger Lake Victoria, and there has been no invasion of water hyacinth. In addition, Secchi depth (water transparency) in open-water areas has remained at a similar level (~70 cm) for over a decade (Schofield & Chapman 1999; Effire et al. 2001).

The fish community within Lake Nabugabo has changed dramatically over the past half century coincident with the introduction of Nile perch in the early 1960s. In 1962, the Cambridge Nabugabo Biological Survey (CNBS 1962) catalogued the native fauna of Lake Nabugabo and reported 20 noncichlid species (including, as examples, *Protopterus aethiopicus*, *Bagrus docmak*, *Schilbe intermedius* and *Clarias gariepinus*) and 10 cichlids: two tilapias, *Oreochromis esculentus* and *Oreochromis variabilis*, and eight haplochromine cichlids. Nile perch were introduced into Lake Nabugabo in 1960 (85 individuals), but were absent in a sampling survey in 1962 (CNBS 1962). Three years later, approximately 180 more Nile perch were introduced into Lake Nabugabo (Gee 1964). The latter two introductions led to its successful invasion that resulted in the development of an important fishery, but also coincided with collapse of the native fish community. By 1991–1992, many of the native species of Lake Nabugabo had disappeared from the open waters (Ogutu-Ohwayo 1993). Before the Nile perch fishery, *P. aethiopicus*, *B. docmak*, *S. intermedius*, *C. gariepinus*, *O. esculentus*, *O. variabilis* and haplochromines were the most important commercial catches; by the early 1990s, they were rare and replaced in the fishery by introduced Nile perch, introduced Nile tilapia, and the native *S. intermedius*, *Brycinus sadleri* and *R. argentea* (CNBS 1962, Ogutu-Ohwayo 1993).

Changes in the main lake fauna were dramatic, however, remnant populations of several fish species in Lake Nabugabo have persisted with Nile perch through the use of wetland refugia and/or other mechanisms. Studies in the 1990s demonstrated that wetlands serve as structural and low-oxygen refugia for fishes that can tolerate wetland conditions, and limit dispersal of Nile perch (Chapman et al. 1996a,b; Schofield & Chapman 1999; Chapman et al. 2002). Some haplochromines and some noncichlids are relatively tolerant of hypoxia, while Nile perch is not (Schofield & Chapman 1999; Chapman et al. 2002), thus permitting some indigenous species to persist in wetlands under reduced predator pressure. Ecotonal wetlands have been particularly important refugia in Lake Nabugabo because interaction with the main lake waters elevates dissolved oxygen (DO); Nile perch have been rare in these ecotonal habitats, and species richness is higher than in the interior swamp (Chapman et al. 1996a,b; Schofield & Chapman 1999; Chapman et al. 2002). In the early 1990s, the emergent wetland grass *Miscanthidium violaceum* was a dominant wetland macrophyte along the wetland/open water ecotone; however, since that time, the emergent hippo grass *Vossia cuspidata* has proliferated from small patches extending from the *M. violaceum* margin to extensive zones that now dominate the perimeter of the wetland ecotone.

The fisheries of Lake Nabugabo are both commercial and artisanal, and fishing is an open-access resource. Nile perch and Nile tilapia are the most important catches in the lake and are fished intensively (Ogutu-Ohwayo 1994; Chapman et al. 2003). Size-selective gill netting is the predominant method of catch, while long-lining is carried out in the deeper offshore waters (Mbabazi 2006).

**Sampling of Lake Nabugabo, 2007**

In June and July of 2007, the habitat type of 54 transects along the western half of Lake Nabugabo was characterised as wetland or exposed (i.e., rocky and forest edge) ecotone. Wetlands were further categorised based on the dominant shoreline macrophyte being either *M. violaceum* or *V. cuspidata*. To quantify the relative abundance of Nile perch and their...
prey among the major habitat types of Lake Nabugabo, five 20-m long transects were randomly selected for each of the three ecotonal habitats. All sampling was done using a combination of metal minnow traps and 30-m experimental gill nets (four panels: 25.4, 50.8, 76.2, 101.6 mm stretched mesh). At each transect, 10 minnow traps were set at 5-m intervals along the shoreline (adjacent to M. violaceum or V. cuspidata in wetland ecotones and beside rocky or forest edge for exposed ecotones). Experimental gill nets were then set approximately 5, 20 and 100 m from the shoreline structure (e.g., emergent macrophytes, forest deadfall) and parallel to the shoreline and staggered to minimise overlap with respect to the shoreline, producing a total sample size of 45 gill nets set in the lake (three per transect). All traps and nets were set mid morning to early afternoon (10:00 AM to 2:00 PM) at which time environmental data were taken, and the physical characteristics of sampling sites were recorded. Traps and nets were pulled between 7:00 and 10:00 hours the following morning. Active feeding of Nile perch occurs predominantly at dawn and dusk (Olowo et al. 2004) such that specimens collected for stomach content analysis represented a range of digestive stages.

The following environmental data were recorded at each trap sampling site and at both ends of the gill nets: water column depth, water transparency, DO (mg l⁻¹), water temperature (°C), dominant vegetation, and bottom type. Water transparency was quantified using a Secchi disk. DO and water temperature were measured with an YSI oxygen meter (model 51B) (Yellow Springs, Ohio, USA) in the upper 20 cm of the water column when water was <1 m deep, and at both the surface and directly above the lake bottom when water depth was >1 m.

All fishes were identified in the boat to the lowest taxonomic category possible, measured for total length (TL), and released alive at the site of capture whenever possible. Nile perch across a wide size range (5–55 cm TL) were retained for stomach content analyses. Fish were killed either by emersion in buffered MS222 (tricaine methanesulfonate), or for larger fish, with a stunning blow to the head. Nile perch caught fresh on a given sampling day were purchased from local fishers in order to increase the number of nonempty stomachs used for the diet study. Retained specimens were brought back to shore where stomachs were removed. Stomach contents of Nile perch were analysed following methods used in Schofield & Chapman (1999) and Chapman et al. (2003) to facilitate direct comparison across these studies. Prey items were identified, blotted dry and weighed to the nearest 0.01 g. Identification was done to the smallest taxonomic classification possible and was limited when stomach contents were extremely digested. The following parameters were used to assess dietary patterns of Nile perch: (1) relative abundance (% N = the number of times each type of food item is found as a percentage of all food items), (2) frequency of occurrence (% F = the number of Nile perch containing each prey taxon, divided by the total number of nonempty stomachs) and (3) per cent mass (% M = the mass of each type of food category expressed as a percentage of the total mass of the stomach contents). Relative abundance, frequency of occurrence and per cent mass were combined to yield the (4) index of relative importance (IRI) of each food category that provides a single estimate of dietary importance.

To assess temporal changes in the distribution, size and diet of Nile perch over the past 12 years, published data collected in 1995 and 2000 (Schofield & Chapman 1999; Chapman et al. 2003) were compared with data from our 2007 habitat survey. Only fish that were ≤35 cm TL were used for these comparisons to standardise for size across studies. To assess temporal shifts in the ecotonal macrophytes (M. violaceum vs. V. cuspidata), we calculated the percentage of each wetland habitat dominated by M. violaceum and V. cuspidata based on habitat characteristics recorded for randomly selected transects in 1995, 2000 and 2007 (Paterson 2009).

Statistical methods

Environmental data

Split-plot two-way ANOVA was used to test for an effect of habitat (M. violaceum, V. cuspidata, forest edge), distance (5, 20 and 100 m), and their interaction on DO and water temperature in the upper 20 cm of the water column for all transects sampled in 2007. Sidak post hoc tests were used when main effects were significant; and the statistical analyses were based on data collected at the gill net sites. DO and water temperature values collected at trap sites were compared across habitats with ANOVA; values were averaged for the 10 trap sites in each transect.

Fish distribution and abundance

The CPUE of Nile perch and haplochromines were treated as separate dependent variables in a split-plot two-way ANOVA to test for effects of habitat (M. violaceum vs. V. cuspidata vs. exposed), distance from shore (5, 20 and 100 m), and their interaction. Mean values for the CPUE of haplochromines were transformed (log₁₀ + 1) for analysis and back transformed for presentation.

To compare CPUE data from 2007 to earlier sampling years (1995 and 2000), the fish captured in experimental gill nets from M. violaceum and V. cuspidata transects were combined as one group.
representing wetland fish (2007 wetland transects; \( N = 10 \), exposed transects \( N = 5 \)) and compared to fish captured in 1995 and 2000 (wetland transects; \( N = 10 \), exposed transects \( N = 10 \)). Sampling for all years was done in the May–July period (May–July for 2005, May for 2000, June–July for 2007). As data for 100 m offshore were not available in 1995, we compared data for 5 and 20 m from shore for the two major ecotonal types (wetland, exposed). A repeated-measure approach was not applied, because randomly selected transects in 2007 differed from those in 1995 and 2000. Rather, we treated each randomly selected transects in 2007 as a separate data set and used one-way ANOVA to test for effects of year (1995, 2000 and 2007) on CPUE for the four habitat and distance combinations: (1) wetland inshore (2) wetland offshore (3) exposed inshore and (4) exposed offshore. When there were overall year effects, the Sidak post hoc test was used to compare specific years. The data for Nile perch were square root transformed, and the data for the haplochromine cichlids were log transformed (log 10 + 1) to normalise the data and stabilise the variance across years; both data sets were back transformed for presentation.

Size

Size frequency histograms were created by calculating the percentage of Nile perch in 5-cm size classes from the total Nile perch for each habitat type in 2007. ANOVA was used to test for an effect of habitat (\( M. \) violaceum, \( V. \) cuspidata, forest edge), distance (5, 20 and 100 m), and their interaction on the TL of Nile perch for transects run in 2007. All distances were combined for each habitat type; and a one-way ANOVA with Sidak post hoc tests was then used to further explore habitat effects.

To compare the 2007 size trends for Nile perch to earlier years, we first quantified the size–frequency distributions of Nile perch in each year for all habitats combined. Given the change in the distribution across years, we used the distribution-free Kruskal–Wallis test to detect a difference in median total length of Nile perch over time. Mann–Whitney U-tests (corrected for multiple comparisons) were used as post hoc tests to explore inter-year differences. A one-way ANOVA was used to test the effect of habitat type on the mean TL of Nile perch within each sampling year.

Results

Environmental data

There were strong effects of habitat (\( F = 35.073, P < 0.001 \)), distance (\( F = 14.007, P < 0.001 \)), and the habitat by distance interaction (\( F = 5.420, P = 0.001 \)) on DO. It was lowest in \( M. \) violaceum (mean DO = 6.1 mg\( \text{L}^{-1} \)), highest in exposed habitats (8.1 mg\( \text{L}^{-1} \)), and intermediate in \( V. \) cuspidata (DO = 6.8 mg\( \text{L}^{-1} \), Fig. 2a). DO increased with distance from shore in \( M. \) violaceum (\( P = 0.001 \)) and \( V. \) cuspidata (\( P = 0.015 \)) but did not vary with distance in exposed habitats (\( P = 0.148 \)). Data collected at trap stations indicated the lowest DO values in \( M. \) violaceum followed by \( V. \) cuspidata, and exposed habitats (mean DO: 4.6, 5.6 and 7.3 mg\( \text{L}^{-1} \), respectively, ANOVA, \( F = 82.4, P < 0.01 \)).

It was more difficult to get accurate DO measures near the bottom of the gill nets because of disturbed soft mud sediments in some habitats; however, bottom DO in the \( V. \) cuspidata transects averaged 3.1 mg\( \text{L}^{-1} \) and was lower than in either the \( M. \) violaceum transects (5.1 mg\( \text{L}^{-1} \)), or exposed transects (8.0 mg\( \text{L}^{-1} \)).

Water temperature was higher in both wetland habitats (\( M. \) violaceum and \( V. \) cuspidata) than in the exposed habitats (\( F = 7.714, P = 0.007 \) (\( M. \) violaceum, average across distances, 25.1 °C; \( V. \) cuspidata, 25.1 °C; exposed, 24.0 °C; Sidak post hoc, \( F = 39.69, P < 0.001 \)).
Within all three habitat types, temperature did not vary strongly with distance from shore, but overall there was more variation in water temperature at wetland sites than in the exposed habitat. Trap data supported the gill net data with the highest inshore temperatures in the wetland habitats ($F = 73.37, P < 0.01$).

Fish distribution and abundance

**Nile perch**

Split-plot ANOVA indicated no effect of habitat ($F = 1.235, P = 0.325$), distance ($F = 0.018, P = 0.982$), or the habitat x distance interaction on the CPUE of Nile perch in experimental gill nets ($F = 2.265, P = 0.092$, Fig. 3a). However, the total number of small Nile perch captured in minnow traps tucked into the shoreline structure (macrophytes, deadfall) was greatest in *V. cuspidata*, followed by *M. violaceum*, and exposed ecotones ($N = 11$; $N = 5$; $N = 2$ respectively). We calculated the mean DO level in the minnow traps that captured Nile perch. DO varied from an average of 4.4 mg l$^{-1}$ (range 3.1–5.4 mg l$^{-1}$) in the *M. violaceum* habitat to 5.8 mg l$^{-1}$ (range 3.1–7.6 mg l$^{-1}$) in the *V. cuspidata*, to 6.0 mg l$^{-1}$ (sole data point) in the forest edge.

Between 1995 and 2007, there was no evidence for a decline of Nile perch abundance in either the inshore areas of wetland ecotones ($F = 0.689, P = 0.511$) or the inshore areas of exposed transects ($F = 0.746, P = 0.486$, Fig. 4a). However, Nile perch showed a significant decline in abundance in both the offshore area of wetlands ($F = 4.508, P = 0.020$) and the offshore areas of exposed transects ($F = 5.752, P = 0.010$). The decline was most pronounced in the exposed offshore sites, where the CPUE of Nile perch declined from an average of 10.95 Nile perch per transect in 1995 to 1.40 in 2007 (Fig. 4a).

**Haplochromines**

There was a strong effect of habitat ($F = 16.054, P < 0.001$), distance ($F = 7.481, P = 0.003$), and the habitat by distance interaction ($F = 3.243, P = 0.029$) on the CPUE of haplochromine cichlids in 2007 (Fig. 3b). Overall, haplochromine cichlids were more abundant in *V. cuspidata* than in both *M. violaceum* and exposed habitats (Sidak post hoc, $P < 0.001$) and less abundant 100 m offshore than either 20 m ($P = 0.023$) or 5 m ($P = 0.001$). Because there was a significant interaction between distance and habitat, we used post hoc comparisons to detect differences in distance from shore within each habitat type.
Haplochromine cichlids were most abundant 20 m offshore in the *V. cuspidata* habitat (Fig. 3b).

Between 1995 and 2000, haplochromine cichlids increased in abundance in both the inshore (*F* = 4.639, *P* = 0.019) and offshore (*F* = 3.923, *P* = 0.032) areas of wetland ecotones (Fig. 4b). There was evidence of a marginal increase between 1995 and 2000 in offshore areas of exposed transects, but no change in CPUE in inshore areas of exposed transects. There was no significant change in the CPUE of haplochromines between 2000 and 2007 in the exposed sites, but weak evidence for a decline in the wetland sites (Fig. 4b). Overall the resurgence of haplochromines was most pronounced in the wetland ecotones, where the CPUE of haplochromines increased in the inshore areas from an average of 4.5 haplochromines per transect in 1995 to 18.6 in 2000.

**All species**

Overall the total number of fish caught in traps and experimental gill nets was highest in *V. cuspidata* habitats (*M. violaceum* *N* = 241, *V. cuspidata* *N* = 1239, exposed *N* = 231). Taxa richness was also higher in *V. cuspidata* relative to *M. violaceum* and exposed habitats; however, in *V. cuspidata*, several species were relatively low in abundance due to the exceedingly high number of haplochromines present (Table 1). In all habitats, a majority of fish were haplochromines (*M. violaceum sp.* *N* = 156, *V. cuspidata* *N* = 964, exposed *N* = 151, Table 1). We did not differentiate among the haplochromine species because of the difficulty of field identification, particularly of females. This is the subject of an associated investigation.

<table>
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<tr>
<th>Species</th>
<th>$M$. violaceum</th>
<th>$V$. cuspidata</th>
<th>Exposed</th>
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Table 1. Relative abundance (% of fishes) captured in *Miscanthidium violaceum*, *Vossia cuspidata*, and exposed habitats in Lake Nabugabo in June and July of 2007.

There was a strong effect of habitat on the total length of Nile perch in 2007 (*P* = 4.961, *P* = 0.009). Nile perch were larger in *V. cuspidata* than in exposed sites (Sidak post hoc, *P* = 0.018) and marginally larger than in *M. violaceum* sites (*P* = 0.058). In addition, there was a greater proportion of smaller juveniles (5–10 cm TL) in *M. violaceum* and exposed ecotones relative to *V. cuspidata* where there was a higher proportion of larger fish (15–35 cm TL, Paterson & Chapman 2009).

Overall, the size structure of Nile perch captured in experimental gill nets in wetlands and exposed ecotones of Lake Nabugabo between 1995, 2000 and 2007 shifted from a normal distribution to one skewed towards smaller fish; however, this pattern was more pronounced in exposed ecotones. In 2007, there was a greater percentage of larger fish (>20 cm TL) in wetlands relative to exposed sites (Paterson & Chapman 2009). There was a strong effect of sampling year (1995, 2000 and 2007) on the median TL of Nile perch across all habitats of Lake Nabugabo (Kruskal–Wallis test, *P* < 0.001). The median TL of Nile perch was significantly higher in 1995 than in either 2000 or 2007 (Mann–Whitney U-tests, *P* < 0.002). However, there was no difference in the median TL of Nile perch between 2000 and 2007 (*P* = 0.953). ANOVA indicated very similar results, and we therefore report the parametric means in Fig. 5. Within-year analyses revealed a marginal difference in mean TL of Nile perch between wetland and exposed habitats in 1995.
(P = 0.076) and no difference for the year 2000 (P = 0.968). In 2007, Nile perch in wetlands were significantly larger than conspecifics in exposed habitats (P = 0.009, Fig. 5).

Diet

Nile perch sampled in the habitat-wide transect study were used for detailed stomach content analysis (total Nile perch with nonempty stomachs = 90; 29 from exposed areas, 27 from M. violaceum and 34 from V. cuspidata). An additional 86 Nile perch with nonempty stomachs that were freshly caught by local fisherman were purchased in order to supplement diet data (M. violaceum = 31; V. cuspidata = 18; exposed = 37), producing a total of 176 nonempty stomachs (totals M. violaceum = 58; V. cuspidata = 52; exposed habitat = 66). Nile perch consumed a combination of invertebrates and fishes (Table 2); however, the size at which Nile perch shifted from invertebrate feeding to piscivory and the relative importance of fishes in the diet of Nile perch differed across habitat types.

For each of the three habitats, Nile perch with nonempty stomachs were grouped into 5-cm size classes to detect the size at which Nile perch undergo an ontogenetic dietary shift from invertebrate feeding to piscivory. The % mass and IRI results suggest that an ontogenetic dietary shift occurs at different sizes depending on habitat type. In V. cuspidata, fish are the predominant food item in all size classes and invertebrate feeding was extremely rare, thus the dietary shift probably occurs at a smaller size than was included in our sampling (Fig. 6). In M. violaceum and exposed habitats, prominent piscivory did not occur until Nile perch reached between 15 and 20 cm TL. Per cent mass showed fish to be more important than IRI as the latter incorporates frequency of occurrence of each prey item and thus, accounts for large numbers of small invertebrates (Schofield & Chapman 1999). However, both metrics of piscivory indicated a similar ontogenetic size shift.

The relative importance of fish prey when size classes of Nile perch were combined differed among habitat types. Of the fishes that were identifiable i.e., intact or only partly digested, cichlids (including haplochromines, unidentified cichlid species and tilapia species) were the most important fish prey in terms of % mass of Nile perch in V. cuspidata and M. violaceum habitats; Nile perch juveniles were the most important prey item of Nile perch in exposed habitats (Fig. 7). Based on the relative abundance of haplochromine cichlids versus tilapiines in our capture

| Table 2. Relative importance of prey species in terms of percentage of total mass of prey taxa (fish prey and invertebrate prey) of Nile perch sampled in June and July of 2007. |
|---------------------------------|-----------------|
| Habitat | M. violaceum | V. cuspidata | Exposed |
| Fish prey |
| Cichlids | 55.73 | 70.32 | 24.69 |
| Latrolinebola argentea | 3.69 | 1.08 | 6.24 |
| Lates niloticus | 13.76 | 6.60 | 40.92 |
| Barbus sp. | 0.00 | 0.56 | 0.00 |
| Aethiomastacembelus frenatus | 0.72 | 0.00 | 0.00 |
| Unidentified fishes | 21.40 | 20.80 | 16.85 |
| Invertebrate prey |
| Suborder Anisoptera | 2.96 | 0.48 | 2.71 |
| Family Chironomidae | 0.06 | 0.03 | 6.54 |
| Order Ephemeroptera | 1.50 | 0.06 | 0.95 |
| Order Heptoptera | 0.03 | 0.04 | 0.05 |
| Order Odonata | 0.00 | 0.00 | 0.05 |
| Unidentified insect remains | 0.00 | <0.01 | 0.60 |

Fig. 6. Per cent mass and index of relative importance (IRI) of fishes and invertebrates in the stomach contents of Nile perch in Miscanthidium violaceum, Vossia cuspidata, and exposed habitats of Lake Nabugabo in 2007.
data, it is likely that most of the unidentified cichlids were haplochromines.

In 2007, the diet of Nile perch in Lake Nabugabo was dominated by cichlids; this has been the case since the mid-1990s. There were a few Barbus sp. ($N = 3$) and $R. argentea$ ($N = 10$) supplementing the cichlid-dominated diet. Before the mid-1990s, Rastrineobola argentea and Nile perch juveniles were the most important prey item (Schofield & Chapman 1999). In 2007, the size at which Nile perch switched from invertebrate feeding to piscivory when habitats were combined occurred when Nile perch were between 10 and 15 cm TL. This is similar to the size at shift in 2000 when haplochromines were resurging in the system, however, it is dramatically different than in 1995 when haplochromines were rare (Fig. 8).

Discussion

The future of the Nile perch fishery in Lake Nabugabo is difficult to predict; however, if current levels of fishing continue, future stocks may consist of smaller fish with lower commercial value. Based on data collected over a 12-year period (1995–2007), we detected a decline in CPUE of Nile perch, a shift in their distribution and diet, and a decline in their body size. In addition, a larger proportion of Nile perch are now found near wetland ecotones than in the mid-1990s. This may reflect both direct and indirect results of intensive size-selective fishing in more open waters; as well as the encroachment of $V. cuspidata$, an emergent macrophyte that has expanded to cover much of the lake’s perimeter over the past decade (Kateyo 2006).

Transformation of ecotonal wetlands: implications for predator–prey overlap

Identifying key habitats of fishes is important to understanding dynamics among species, particularly interactions between predator and prey that may be modulated by habitat complexity (Crowder & Cooper 1982; Sih 1984; Savino & Stein 1989; Tyler & Kenneth 1997) and/or the relative tolerance of predator and prey to the physicochemical conditions of the habitat (Cockrell 1984; Wellborn et al. 1996; Moore & Townsend 1998; Anderson et al. 2001). Small prey will often reside in structurally complex habitats to minimise risk of predation by reducing predator–prey encounter rates and predator capture success (Stein & Magnuson 1976; Mittlebach 1981; Savino & Stein 1982, 1989; Werner et al. 1983; Persson & Eklöv 1995; Stuart-Smith & White 2008). In Lake Nabugabo, shifts in the structurally complex wetland ecotones and in the habitat distribution of the Nile perch may have important implications for predator–prey interactions. In 1995, the low abundance of Nile perch in wetland ecotones was attributed to low levels of DO in $M. violaceum$ habitats and the high structural complexity in these areas (Schofield & Chapman 1999). At that time, it was argued that dense wetlands and wetland ecotones minimise interaction between Nile perch and haplochromine prey and thus serve as important habitat refugia for some indigenous fishes (Chapman et al. 1996a,b; Schofield & Chapman 1999).

Fig. 7. Per cent mass of dominant fish prey in the stomach contents of Nile perch in Miscanthidium violaceum, Vossia cuspidata, and exposed habitats in 2007.

Fig. 8. Per cent mass of fishes and invertebrates in the stomach contents of Nile perch in wetlands and exposed habitats in Lake Nabugabo in 1995, 2000 and 2007. Data from 1995 and 2000 were adapted from Schofield & Chapman (1999) and Chapman et al. (2000).
Over a 12-year period (1995–2007), approximately 70% of the Miscanthidium-dominated wetland ecotones along the western shores of Lake Nabugabo were encroached upon by *V. cuspidata*. In Lake Nabugabo, *M. violaceum* aggregates in very dense stands of emergent grass, while *V. cuspidata* is found in deeper water with grass fronds of sufficient spread to facilitate penetration by larger fishes. From 1995 to 2000 haplochromine cichlids resurfaced in wetland habitats of Lake Nabugabo (Chapman et al. 2003). In 2007, we found haplochromines to be most abundant in *V. cuspidata* habitats, although their overall CPUE in wetland ecotones shows a marginal decline since 2000. For haplochromine cichlids, *V. cuspidata* habitats may provide structural complexity that minimises predation risk and a rich foraging spot where macroinvertebrate densities and detrital materials are high (Mwebaza 1994; Efitre et al. 2001; Kateyo 2006). For Nile perch, *V. cuspidata* may be more accessible in terms of physicochemical conditions and penetrability than the much denser, more hypoxic *M. violaceum* while also housing the greatest supply of optimal food (viz. haplochromines, Kaufman & Schwartz 2002).

Sixty-seven per cent of the diet of Nile perch in *V. cuspidata* was comprised of cichlids, and over 80% of cichlids captured in nets set in *V. cuspidata* were haplochromines. In *M. violaceum* and exposed ecotones, haplochromines were far less abundant; and Nile perch consumed less cichlids. Nile perch juveniles were the most important prey item in exposed ecotones. Interestingly, the capture of small Nile perch juveniles (3.0–13.5 cm TL) in minnow traps was highest in the *V. cuspidata* habitat, which may reflect their use of high structural complexity to minimise cannibalistic encounters with larger Nile perch. This high number of small juveniles captured in wetland ecotones versus exposed ecotones also suggests that Nile perch juveniles may be more resistant to wetland conditions than previously thought and/or the lakeward extension of hippo grass is providing a more desirable habitat for juvenile perch.

The *V. cuspidata* succession is not unique to Lake Nabugabo. In Lake Victoria, *V. cuspidata* has become common in the Nyanza Gulf of Kenya where water hyacinth once congested littoral waters (Omondi & Mwendi 2006). In Lake Victoria, it has been argued that the recent spread of *V. cuspidata* reflects succession after the invasion of water hyacinth (Omondi & Mwendi 2006). Alternatively, the demise of the haplochromines that had previously hindered establishment of macrophytes through their constant disturbance of the substrate could have facilitated invasion of *V. cuspidata* (Witte et al. 1992). Lake Nabugabo has not experienced water hyacinth invasion to date, but has suffered collapse of its haplo-

Could overfishing select for smaller, swampy Nile perch? The shift in the distribution of Nile perch in Lake Nabugabo is also consistent with differential mortality between wetland and exposed habitats that may reflect intensive size-selective fishing pressure on Nile perch. Although the CPUE of Nile perch was similar across inshore habitats in 2007, the size distribution differed. In 2007, there was a greater proportion of large Nile perch in *V. cuspidata* relative to *M. violaceum* and exposed habitats. For fishes, inter-habitat variation in size structure is often due to ontogenetic habitat shifts (Werner & Gilliam 1984; Lecchini & Galzin 2005); however, Nile perch in Lake Nabugabo are not known to undergo ontogenetic habitat shifts within the size range sampled in our experimental gill nets (Schofield & Chapman 1999). The most parsimonious explanation for variation in size distribution across habitats is the top-down effects of size-selective predation on the Nile perch. Gill nets with mesh sizes ranging from 3.5 to 8 inches (approximately 10–85 cm TL) are the dominant fishing gear, followed by long-lines (hook size 7–12) that supplement yield by harvesting
larger-sized fish (up to 120 cm TL) in the offshore waters (Mbabazi 2006). The mean body size of Nile perch has declined over the past few decades in Lake Nabugabo, and the decline in body size has been habitat specific. In 1991–1992, Ogutu-Ohwayo (1993) used gill net fleets that ranged up to 305 mm stretched mesh to capture Nile perch in Lake Nabugabo; 26% of the Nile perch he reported in his diet analysis were >40 cm TL, and 9% were >60 cm TL. In 1998, Chapman and colleagues sampled four of the locations used in Ogutu-Ohwayo’s study using the same range of mesh sizes; the Nile perch captured were small, averaging 22.5 cm TL and not exceeding 39 cm. A fisheries stock assessment in 2006 revealed that the mean size of Nile perch harvested in Lake Nabugabo at that time was 25 cm TL in gill nets (range 11–74 cm TL) (Mbabazi 2006). Between 1995 and 2007, the mean size of Nile perch in our experimental gill nets declined, reflecting a decrease in the proportion of the larger size classes, a pattern most pronounced in exposed habitats. Our results suggest that fishing is cropping off large-sized individuals and is doing so more effectively in exposed habitats relative to enclosed wetlands. This could be associated with differences in behaviour of fishes and catchability of Nile perch in gill nets across habitats; however, this would require more empirical studies to confirm.

In Lake Nabugabo, the advantage of occupying wetland ecotones may be twofold for Nile perch – they may provide optimal prey and refuge from fishers, although we do not have direct evidence that Nile perch ‘prefer’ *V. cuspidata* ecotones. Fish using open waters, if more vulnerable to effects of size-selective predation, could exhibit phenotypic responses to fishing pressure more rapidly than those in wetland ecotones (e.g., smaller size, lower growth rate). If Nile perch inhabiting *V. cuspidata* experience lower mortality; this may ultimately select for a more wetland resistant Nile perch. Over the past few years, there have been increasing numbers of juvenile Nile perch found within *V. cuspidata* (this study) and even within dense stands of more hypoxic *M. violaceum* (Chapman, Paterson, Twinomugisha, unpublished data). Small Nile perch (<7.0 cm TL) captured in hypoxic wetlands within Nabugabo exhibit a larger gill size than conspecifics captured in open water sites (Paterson & Chapman 2009), suggesting morphological divergence in the small juveniles that may facilitate increased exploitation of hypoxic habitats.

The extent to which habitat characteristics influence Nile perch phenotypes in this system will depend, at least to some degree, on the amount of time that is spent in wetlands and exposed ecotones and the strength of divergent selection pressures between the habitats. A shift in habitat use of the Nile perch may reflect a range shift in individuals and/or a shift in the time that individuals spend in different habitats. Whether the home range of Nile perch has shifted or not remains unknown. However, we believe that the small juvenile Nile perch may be site tenacious given the finding of a significant difference in gill morphology between juvenile Nile perch from wetland and exposed sites (Paterson & Chapman 2009). Larger Nile perch are likely to have a larger home range than the juveniles and may move between wetland and exposed ecotones. Movement studies on individual Nile perch will need to be done in order to better understand the home range patterns for Nile perch in this system and to better predict the extent to which habitat characteristics will drive phenotypic patterns in this species. However, if Nile perch are subject to higher fishing pressure in open waters, selection for more wetland-resistant perch may occur if individuals either move routinely into wetland ecotones or inhabit wetlands ecotones.

**Lake Nabugabo: lessons learned**

Changes in the size and distribution of Nile perch in Lake Nabugabo may reflect the interaction of both fishing pressure and shifts in macrophyte distribution; both drivers also seem relevant to changes that have occurred in the much larger Lake Victoria. However, one fundamental difference in the environmental trajectories of the two lakes is the extent of culturally induced eutrophication in Lake Victoria, a bottom-up driver not as evident in Lake Nabugabo. In Lake Victoria, eutrophication over the past several decades is apparent from the increase in nutrients (Hecky 1993; Verschuren et al. 2002), a shift from a system dominated by diatoms in the 1980s to cyanobacteria (Verschuren et al. 2002), and increases in the depth and extent of the anoxic bottom layer (Hecky 1993; Hecky et al. 1994). Kolding et al. 2008 argue that eutrophication is primarily responsible for the observed trends in Nile perch stocks – increased eutrophication resulted in an increase in biological production and the yield of Nile perch. Based on experimental trawl data taken from offshore waters in Tanzania and Uganda at different depth intervals, Kolding et al. (2008) found no evidence for overfishing based on a set of verifiable indicators. For example, in Tanzania, there were declines in length indices at all depths that one might think is due to overfishing. However, Kolding et al. (2008) found that the CPUE<40 cm (portion of the population unexploited by commercial fisheries) remained stable or increased and CPUE>40 cm (commercially exploited) remained relatively stable at all depths, suggesting that declines in length were due to an increase in the proportion of juveniles and not a decline in large spawners. In addition, they identified patterns of annual and
seasonal vertical migration of Nile perch (CPUE$_{>40\ cm}$) that they attributed to anoxia along the bottom layer. Both the high recruitment of juveniles and temporal variation in CPUE$_{>40\ cm}$ with depth was attributed to eutrophication supporting survival of offspring in the former and controlling habitat availability (i.e., depth of the anoxic bottom layer) in the latter. Other recent studies suggest that there has been an influence of fishing pressure on the Nile perch population, at least locally. Njiru et al. (2006) quantified the CPUE of Nile perch in depths up to 20 m between 1998–2000 and 2004–2005 in Nyanza Gulf (Kenya) using bottom trawl data. They reported no change in the proportion of fish $<50\ cm$ between sampling periods; however, they found a decrease in the asymptotic length, size at maturity and maximum age over the same time frame and an increase in both total and fish mortality. Based on the length frequency distribution of Nile perch captured by commercial trawlers (12,539 trawling hours) in Speke Gulf (Tanzania), Goudswaard et al. (2008) reported a decline in the catch rate of Nile perch $>35\ cm\ TL$ and an increase in the catch rate Nile perch $<35\ cm\ TL$. They suggest that fishing may have caused the reduction in the numbers of large Nile perch; whereas the increase in the small Nile perch may reflect growth of recruits born in the area after the initial invasion and reduced predation pressure by large Nile perch as their densities declined.

As in Lake Victoria, Lake Nabugabo experienced faunal collapse following the expansion of the introduced Nile perch population (Ogutu-Ohwayo 1993; Chapman et al. 1996a,b) and faunal resurgence coincident with intensive fishing of Nile perch (Chapman et al. 2003). Although there is evidence that Lake Nabugabo has eutrophied over the past century (Cangelosi 1998), the lake has not experienced the dramatic increases in primary production, hypoxia, cyanobacteria blooms or the invasion of water hyacinth that characterises the recent history of Lake Victoria. Yet, our results suggest that intense fishing has coincided with phenotypic change in the Nile perch. For Lake Victoria, unless studies can isolate eutrophication as a driving force, it may be prudent for managers to assume that both fishing pressure and eutrophication are influencing the fishery.

The fundamental management goal in the Lake Victoria basin is to establish a sustainable Nile perch fishery while conserving native species (UNENCIA 2001), and much effort has gone into model development to predict effects of fishing on the food-web and the fishery (Kitchell et al. 1997; Schindler et al. 1998; Matsuishi et al. 2006). For example, Matsuishi et al. (2006) used ECOPATH and ECOSIM to model the trophic dynamics of important fishes in Lake Victoria over a 10-year period given elevated levels of fishing pressure. Predation by Nile perch on fishes in the Matsuishi et al. models was allocated to Nile perch over 40 cm TL. However, diet and ontogenetic shifts in Nile perch can be very dynamic as evidenced in Lake Nabugabo over the past 12 years and more generally in lakes where Nile perch have been introduced. Ogutu-Ohwayo (1994) compared the relative prey importance for Nile perch across 20-cm size classes between systems where Nile perch were native or introduced. The author found that when haplochromines were rare, Nile perch fed more on invertebrates and larger numbers of small pelagic species and had similar diet, growth rate and condition as Nile perch in native lakes. On a diet dominated by haplochromines, early in the invasion process, the growth rate and condition of Nile perch was relatively high (Ogutu-Ohwayo 1994, 1999). In Lake Nabugabo, the size at which Nile perch shift from feeding on invertebrates to fishes has also varied with the stage of the invasion process. Nile perch were primarily insectivorous until 30 cm TL when haplochromines were rare, but shifted to a haplochromine-dominated diet as cichlids recovered, and now exhibit a much smaller size at shift to piscivory. In general, in lakes where Nile perch have been introduced, the relative size of the dietary shift to piscivory is very low when haplochromines are abundant (Ogutu-Ohwayo 2004) or resurging (Chapman et al. 2003; this study), but the dietary shift occurs at a much larger size when haplochromines are rare (Ogutu-Ohwayo 1993, 1994; Schofield & Chapman 1999; Katunzi et al. 2006). This has important implications for predicting the outcome of Nile perch invasions and cascading effects to native species under different management regimes. Predation rates may be higher than predicted under scenarios defined by available models.

Conclusions

This study highlights the need to understand more about the ecology of Nile perch, its interaction with other species, and their dynamics in response to fishing pressure and other environmental changes. Currently, fisheries managers acknowledge the power of the top-down effects of fishing on food-webs, specifically how different management strategies will impact Nile perch and native prey. Models of predator–prey dynamics in the system should account for adaptive responses of aquatic systems to environmental change including shifts in Nile perch behaviour, habitat choice and life-history traits. As previously acknowledged, the Nile perch is a moving target that will demand adaptive management of both native and introduced fish stocks in the Lake Victoria basin; strategies should evolve with the system (Kaufman &
Schwartz 1992; Kaufman et al. 1997). Lake Nabugabo has been a useful model for understanding change in Lake Victoria by controlling for effects of severe eutrophication and hypolimnetic anoxia, and in revealing potential refuge habitats (V. cuspidae) that may potentially stabilise the interaction between predator and prey, depending on the ecological and evolutionary response of both.

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