**Nile Perch Research Paper**

Title: *“Changes in the feeding dynamics of an introduced predator when confronted by variable anthropogenic stress”*

**Abstract**

**Introduction**

Freshwater ecosystems harbour some of greatest faunal biodiversity found anywhere on the planet. The diverse nature of these systems leaves them especially vulnerable to human activities including exploitation due to overfishing.1 One example of such a freshwater system which is precariously balanced between anthropogenic pressures and internal ecological dynamics is the Lake Victoria Basin in Central Africa. The introduction of the predatory, non-native Nile perch (*Lates niloticus*) in the 1950s and 60s was meant to increase fish production and help grow the local fisheries. However, the introduction of the Nile perch coincided with the decline and disappearance of select native species. Over the past decades, intense fishing pressure on the Nile perch has supported the resurgence of some native fish populations. In September of 2017, the Ugandan government instituted a fishing ban in parts of the Lake Victoria basin in an attempt to increase the number and size of Nile perch for commercial product. This policy was able to reverse some of the effects of the perch on native species abundance, in part allowing for their resurgence.

In a system that is no stranger to rapid change, from fluctuations in the fishery stock of the Nile perch as well as drastic variations in total fish abundance of native species over the last six decades, Lake Nabugabo has incurred multiple stressors imposed by the local fishery on the natural ecosystem. Yet from 2016, when fishing pressures had reached record levels in Lake Nabugabo, to the implementation of the fishing ban in September of 2017, to the wide-scale resumption of illegal fishing into the present-day, the system has experienced more perturbations in a shorter time span than ever in its recent history.

*Offshore vs. nearshore dynamics which have created divergent characteristics of fish which inhabit wetland areas verses the open waters of the lake.*

**Methods**

*Study system. F*ormerly a bay of the neighbouring Lake Victoria, Lake Nabugabo was isolated from the main lake approximately 5000 years ago by the formation of the extensive Lwamunda Swamp and sandbar on the western shore of Lake Victoria. Lake Nabugabo is however much smaller (surface area = 33km2) and shallower (mean depth = 3.13 m) (Nyober and Chapman 2013) than Lake Victoria but is similarly situated just south of the equator in Uganda. Dense vegetation in the wetland areas of the lake which compose the majority of the lake’s periphery are dominated primarily by the macrophytes hippo grass (*Vossia cuspidata*) and/or the grass *Miscanthidium violaceum*. These emergent macrophytes comprise most of the littoral zone of the lake with the exception of the West side of the lake that is bounded by forest and small human developments including fishing villages, three resorts, and multiple beach landings. Wetland ecotones are characterized by lower dissolved oxygen (DO) concentrations than the forest edge and a higher density of both submerged and exposed macrophytes (Schofield and Chapman 1999; Paterson and Chapman 2009) which result in a more structurally complex habitat than other areas of the lake.

*Fish abundance sampling.* Fish abundance was determined using data collected as part of a multidecade, long-term transect (LLT) of Lake Nabugabo established by L. Chapman conducted on a semi-continuous, monthly basis from 2008 to the present. For sampling purposes, Nabugabo was dived into four major habitat types characterized by the dominate vegetation of the wetland-lake ecotone: three wetland ecotones [*Miscanthidium violaceum* (Miscanthidium), *Vossia cuspidate* (Hippo), and *Nymphaea lotus/N. caerulea* (Lilies) and the forest edge (Forest) (Fig. 1). Fish were sampled at 4 distances from the shoreline in each habitat for a total of 16 sites lake-wide. 30-m experimental gill nets were used with four panels of mesh sizes (25.4, 50.8, 76.2, 101.6 mm). Nets were set approximately 5, 20, and 100 meters offshore with replicate nets placed at the same offshore distance 200 meter apart at each site. Distances from shoreline were considered from the edge of emergent vegetation at wetland ecotone habitats, and from overhanging trees and deadfall at the Forest edge habitat. In the forest edge habitat specifically, nets could not be set immediately adjacent to the forested area due to the presence of deadfall. An additional set of three nets was set father offshore at approximately >600m in each habitat zone to represent the open water of the lake (referred to as Midlake). Gill nets were set parallel to the direction of the shoreline in the mid-afternoon and were pulled from the water between 0700-1000 h the following morning. At all sites, catch per unit effort (CPUE) was standardized by the number of set nets. Our experimental gill nets captured fish ranging from 1.0 cm to 98.22 cm standard length with occasional larger Nile perch or lungfish *Protopterus aethiopicus*. Like many fishing sampling gears, potential biases to the data are introduced with a chosen size of experimental netting. Therefore, our analysis reflects the community assemblage of fishes in the lake that are captured by this gear. Based on our experience with other sampling gears in Lake Nabugabo (e.g., Fyke nets, minnow traps, beach seines), the experimental gill nets allowed us to capture the majority of species currently present in the main lake with the exception of two small and abundant species: the small cyprinids *Rastrineobola argentea* and *Barbus magdalenae*.

Data collection occurred on a monthly basis from 2016 to 2018, up to and including the first 7 months of 2019 (July). The total potential sample size was 43 months (12 months × 3 years + 7 months × 1 year); however, the final sample size was 35 months due to the yearly suspension of data collection in February and May due to other research activities at the Nabugabo station. All fish captured in the LTT were identified in the boat upon being caught to the lowest possible taxonomic level and were reported for each taxonomic group. Relative abundances of each species in the lake over time were calculated using catch-per-unit-effort (CPUE) with a unit effort of 1 net.

Species identification of endemic and non-endemic haplochromines has proved challenging in the field (Greenwood 1965; Barel, Van Oijen, Witte, & Witte-Maas 1976) and was therefore recorded to the level of genus and reported upon after being grouped into a single taxon. Specimens of endemic haplochromine cichlids collected by the Cambridge Nabugabo Biological Survey (CNBS, 1962) were described in Greenwood’s (1965) account of cichlid fishes in Lake Nabugabo as *Haplochromis annectidens*, *Astatotilapia velifer*, *Gaurochromis simpsoni*, *Prognathochromis venator*, and *Paralibidochromis beadlei*. *Prognathochromis venator* has been eradicated from Lake Nabugabo (Chapman et al. 1996). There are three other non-endemic haplochromines that have been reported in Lake Nabugabo, *Astatoreochromis alluaudi, Astatotilapia nubila, and Pseudocrenilabrus multicolor*. In long-term transects since 2008, we have only captured *A. alluaudi* (rarely); *A. nubila* has not be captured, and *P. multicolor* is largely restricted to wetland refugia (Chapman et al., 2002) and was not captured in the gill nets during the 2016-2019 sampling period. Recent studies of haplochromine cichlids in Nabugabo over the last two decades have primarily regarded haplochromines as a single group. We therefore continue to consider all haplochromine cichlids as part of a single group to maintain consistency with previous studies. All fish captured in the gill nets were measured for total length to the nearest 0.1 cm. Mass was measured to the nearest 0.01 g for only Nile perch along with their sex, maturity, stomach fullness, and standard length to the nearest 0.1 cm.

*Diet analysis.* The diet of Nile perch was studied preforming stomach content analysis on samples obtained at Lake Nabugabo. Stomachs analyzed in this study were collected semi-continuously from January 2016 to July 2019 exclusive. A total of 386 stomachs from individual fish were examined. Stomachs from 2016 were dissected on-site in Uganda, while samples from 2017 onward were brought back to Canada for later analysis.

Stomachs were dissected following the protocols outlined by Schofield and Chapman (1999). Contents were identified to the lowest possible taxonomic category, counted, and dry weighed to the nearest 0.01 g. Where possible, the length, weight, and number of each prey type were recorded. Dissection of stomachs was necessary to create an individual index of relative importance (IRI) which included each prey item in the Nile perch diet. IRI was calculated for two prey categories, invertebrates and fish taxa, by grouping identified prey items into either class. IRI was calculated as

where %N is the relative abundance, the number of times each food item is present as a percentage of all food items. %M is percent mass, the mass of each type of food item expressed as the percent of total food mass. The relative abundance and percent mass of fish remains present in the stomach were then added with the result being a fraction on a 0 to 1 scale where 1 represents complete piscivorous feeding and 0 represents complete insectivorous feeding in that individual.

*Characterization of time periods.* In a novel method of defining periods of distinct Nile perch ontogenetic activity and subsequent change, in this study we chose to categorize time by changes in the abundance of endemic haplochromine cichlids in Lake Nabugabo. As documented by Ogutu-Ohwayo (1994), Schofield and Chapman (1999), and Nkalubo et al. (2014) changes in population abundance of haplochromine cichlids has been a long-term driving factor ontogenetic dietary shifts and changes in ecotonal distribution of the Nile perch, as well as a key determinant in the size at which perch’s shift to piscivory. Additionally, it has been well described that when haplochromines are available the Nile perch will preferentially feed on them, selecting for haplochromine prey over all other prey present in the lake (Mkumbo & Ligtvoet 1992; Ogutu-Ohwayo 1994; Schofield & Chapman 1999; Chapman et al. 2003).

The first time period we report is from January 2016 to September of 2017 (referred to as “Pre-Ban Conditions”). During this period, haplochromine populations remained relatively stable with respect to catch per unit effort across all distances from shore and between habitats. The second period of time represents the effects on Nile perch populations after the imposition of a lake wide fishing ban by the Ugandan government beginning in October 2017 and with effects lasting until December 2018 (referred to as “Post-Ban Conditions”). During this period haplochromine populations experienced a relative decline when comparted with pre-ban abundances. The fishing ban was officially instituted in September of 2017 but is reported from October of the same year to account for a lag in effects on the system. The third period of time is from January 2019 to July 2019 (referred to as “Faunal Recovery”) and is defined by a sharp increase in the number of haplochromines caught in experimental gill nets, followed by a steady increase in the abundance of Nile perch.

Offshore and nearshore areas of the lake were categorized based on prevalent structural complexity of the ecotone at each given distance from shore. In this study, we grouped nets set 5 m and 20 m from shore together (referred to as “Nearshore”) due to consistent similarities in emergent macrophytes. Nets set 100 m and >600 m from shore (“Midlake”) were grouped together (referred to as “Offshore) due to consistency in the open-water character of the lake at these distances and a notable absence of vegetative growth when compared to nearshore areas.

*Data analysis.*

*Growth curves*

**Results**

*Temporal and spatial patterns of faunal decline and resurgence.* During the pre-ban period the CPUE of haplochromines was relatively high (mean = 69.1 fish per transect, 43.09% of total CPUE). At this time, haplochromines were more abundant nearshore than offshore, but there was no difference between abundances at specific habitats (analysis of variance [ANOVA]: distance effect, *F* = 16.03, *p* = <0.0001; habitat effect, *F* = 0.74, *p* = 0.389; distance × habitat, *F* = 0.001 , *p* = 0.979, Fig. 1). Nile perch captured in experimental gill nets over the same period of time showed a different pattern of abundance. The CPUE of Nile perch was relatively similar between nearshore and offshore areas (mean offshore = 17.3 fish per transect, mean nearshore = 13.2 fish per transect) but were slightly more abundant in exposed areas characterized by deeper waters and higher levels of dissolved oxygen (Schofield & Chapman 1999). There was a difference between the abundance of Nile perch at specific habitats (analysis of variance [ANOVA]: distance effect, *F* = 2.31, *p* = 0.129; habitat effect, *F* = 25.56, *p* = <0.0001; distance × habitat, *F* = 1.025, *p* = 0.312, Fig. 2). The relative abundance of haplochromines expressed as a percentage of all fish captured in gill nets decreased dramatically during the post-ban period between October 2017 and December 2018 (mean = 15.2 fish per transect, 24.25% of total CPUE). This trend was prevalent in both nearshore and offshore areas (Fig.3). This was the result of an increase in the %CPUE of *Brycinus sadleri*, an open water characid in both nearshore and offshore areas as well as a lake wide increase in the %CPUE of Nile perch. Nile perch showed a decline in absolute abundance during the post-ban period (mean = 8.9 fish per transect) compared to their average CPUE pre-ban. Experimental gill nets placed throughout the lake captured Nile perch between 6.0 and 98.2 cm standard length (SL). The average size of Nile perch increased from 10.5 ± 0.2 cm, SE (SL, range = 6.0-98.2 cm) during the pre-ban period to 18.4 ± 0.4 cm, SE (SL, range = 55.5-6.7 cm) during the post-ban period. During the recovery period the CPUE of haplochromines rose beyond its previous average value during the pre-ban period and increased more over a shorter period of time than it ever has over the last decade (unpublished data) (mean = 218 fish per transect, 83.15% of total CPUE). Haplochromines increased in abundance across the lake but saw the majority of variation in CPUE between wetland habitats and exposed habitats. During the pre-ban period there was no difference between haplochromine abundances at different habitats. Yet, during the recovery period haplochromines returned in the greatest abundance to nearshore regions of the lake with greater structural complexity and to habitats where emergent *Miscanthidium violaceum* (Miscanthidium) and *Vossia cuspidate* (Hippo grass) were expanding in distance from shore. Haplochromine abundance also increased offshore, but to a lesser extent than increases in CPUE observed nearshore at 5 and 20 m nets. Haplochromine CPUE did not return to either offshore or nearshore levels at the Forest edge, the habitat where the majority of the haplochromine population was captured during the pre-ban period. During the recovery period, the abundance of Nile perch decreased by total % CPUE, but saw site specific increases in abundance at all habitats except for the *Nymphaea lotus/N. caerulea* (Lilies) dominated wetland which has experienced a decrease in structural complexity due to the receding of vegetation toward the shoreline (Nyober and Chapman 2013; personal observation). The average size of Nile perch decreased over the same period to 17.9 ± 0.5 cm, SE (SL, range = 6.7-41.5 cm) when compared to a higher average standard length over the post-ban period.

The absolute abundance of *B. sadleri* experienced consecutive decreases over the three time periods observed. During the pre-ban period *B.sadleri* accounted for 43.70% of the total fish populations in the lake by CPUE. *B. sadleri* reached their lowest level by CPUE during the recovery period of haplochromines (4.75% of the total CPUE) when compared to their share of total CPUE during the post-ban period (55.46%) when they accounted for the majority of fish species in the lake by CPUE.

*Dietary changes in response to changing prey base.* The diet of the Nile perch was largely determined by the availability and distribution of their preferred prey item, the haplochromine cichlid. Perch in offshore areas had a much greater variability in their diets and experienced much greater size-selective competitive pressures for fish prey. During the pre-ban period the switch from primarily invertebrate feeding to dominant piscivory occurred around 10 cm SL in offshore areas. Over the same period, Nile perch of all size classes (grouped in increments of 5 cm from 5 cm SL to >25 cm SL) captured nearshore had diets composed by a majority of fish prey. This trend follows in all Nile perch captured near shore for both the post-ban and recovery periods. Offshore, during the post-ban period when haplochromine abundance was very low, perch made the shift to piscivory occurring at a larger size. During this period, Nile perch fed largely on invertebrates at all sizes below 25 cm. Only fish of the largest size class (>25 cm) found in offshore areas (mean SL = 31.1 ± 0.6 cm, SE (SL, range = 25.1-41.2 cm) preyed on primarily fish. In the same size class, approximately one third of Nile perch captured offshore during the post-ban period had an IRI value lower than 0.5, suggesting that even at sizes above 25 cm, there was still interclass competitive pressures to feed on fish. This trend reversed again to match pre-ban conditions during the recovery period in perch caught offshore. As haplochromine populations returned to offshore areas of the lake, the switch from invertebrate feeding to a diet composed of primarily fish occurred at approximately 10 cm SL. Nile perch IRI was related to haplochromine CPUE (p = 0.001). There was a difference between individual IRI values calculated across all time periods, distances, and standard lengths (analysis of variance [ANOVA]: standard length effect, *F* = 16.36, *p* < 0.0001; distance effect, *F* = 36.39, *p* <0.0001; time effect, *F* = 20.82, *p* = <0.0001; distance × time, *F* = 8.56, *p* < 0.0001). Increasing standard length had a positive effect on IRI values (p < 0.0001) suggesting that larger Nile perch were overall better able to feed on fish to meet dietary requirements. Nile perch captured offshore were less likely to be piscivorous (p = 0.04) due to, as we suggest, the increased abundance of haplochromines in the densely vegetative littoral zones of nearshore habitats. During the recovery period, Nile perch captured at any given standard length were more likely to have fed on fish, the cause of this we suggest being the increased abundance of haplochromines across the lake. Nile perch captured offshore during the post-ban period when haplochromine abundance was at its lowest were least likely to have consumed fish prey and more likely to have primarily insectivorous diets (p = 0.003).

Nile perch captured offshore also had a greater diversity of prey found in their stomachs included a higher proportion by mass of juvenile Nile perch*,* and small cyprinids *Rastrineobola argentea,* and *Barbus* spp.

*Nile perch diet composition.* A total of 1715 Nile perch were recovered in experimental fishing nets of which 22.5% (n=386) had non-empty stomachs. Perch recovered from experimental catches ranged in size from 6.0 – 98.2 cm SL. Across all time periods, distances from shore, and standard length’s the major prey item in the perch stomach was haplochromines and other cichlids accounting for 71% of the total mass of prey recovered from stomachs of the Nile perch. Other significant prey recovered were, in order of decreasing prevalence by percent mass: various invertebrates (0.09%), unidentified fish prey (0.05%), juvenile *L. niloticus, Rastrineobola argentea,* and *Barbus magdalenae* (0.03%), assorted vegetation (0.01%) and other species of native fish which include catfish of the family Clariidae and the freshwater eel *Mastacembelus frenatus (<0.01%)*.

Other fish abundance.

Hap habitat specific increases and decreases in CPUE

Expanding macrophytes are perforated habitat types

**Discussion**

**Conclusion**

Distance was statistically significant (p < 0.001) but statistical power was insufficient to identify the pairwise comparison which was driving this relationship (all pair-wise p > 0.05).

**References**

Barel, C., Van Oijen, M., Witte, F., & Witte-Maas, E. L. (1976). An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria. Netherlands Journal of Zoology, 27(4), 333-380.

Cambridge Nabugabo Biological Survey (CNBS). (1962). Preliminary report. CNBS, Makerere College Library, Uganda.

Chapman, L. J., Chapman, C. A., Nordlie, F. G., & Rosenberger, A. E. (2002). Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 133*(3), 421-437.

Chapman, L. J., Chapman, C. A., Ogutu‐Ohwayo, R., Chandler, M., Kaufman, L., & Keiter, A. E. (1996). Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. Conservation Biology, 10(2), 554-561.

Greenwood, P. H. (1965). The cichlid fishes of Lake Nabugabo, Uganda. *Bulletin of the British Museum of Natural History, 12,* 313-357.

Nyboer, E. A., & Chapman, L. J. (2013). Movement and home range of introduced Nile perch (*Lates niloticus*) in Lake Nabugabo, Uganda: implications for ecological divergence and fisheries management. *Fisheries Research, 137*, 18-29.

Paterson, J., and L. Chapman. 2009. Fishing down and fishing hard: ecological change in the Nile perch of Lake Nabugabo, Uganda. Ecology of Freshwater Fish **18**:380-394.

Schofield, P. J., and L. J. Chapman. 1999. Interactions between Nile perch, Lates niloticus, and other fishes in Lake Nabugabo, Uganda. Environmental Biology of Fishes **55**:343-358.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas, and N. Bouton. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes **34**:1-28.