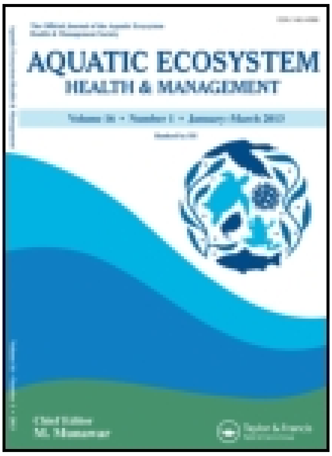

Aquatic Ecosystem Health & Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/uaem20

Feeding ecology of the intensively fished Nile Perch, Lates niloticus, in Lake Victoria, Uganda

Winnie Nkalubo [a] , Lauren Chapman [b] & Fredrick Muyodi [c]
[a] National Fisheries Resources Research Institute , P.O. Box 343, Jinja , Uganda
[b] Biology Department , McGill University , Montreal , Quebec , Canada
[c] School of Biological Sciences , Makerere University , P.O. Box 7062, Kampala , Uganda
Published online: 18 Mar 2014.

To cite this article: Winnie Nkalubo , Lauren Chapman & Fredrick Muyodi (2014) Feeding ecology of the intensively fished Nile Perch, Lates niloticus, in Lake Victoria, Uganda, Aquatic Ecosystem Health & Management, 17:1, 62-69

To link to this article: http://dx.doi.org/10.1080/14634988.2014.880639

AQUATIC ECOSYSTEM
HEALTH & MANAGEMENT

Taylor & Francis
Taylor & Francis Group

Feeding ecology of the intensively fished Nile Perch, *Lates niloticus,* in Lake Victoria, Uganda

Winnie Nkalubo,[1,*] Lauren Chapman,[2] and Fredrick Muyodi[3]
[1]*National Fisheries Resources Research Institute, P.O. Box 343, Jinja, Uganda*
[2]*Biology Department, McGill University, Montreal, Quebec, Canada*
[3]*School of Biological Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda*
**Corresponding author: wnkalubo@yahoo.co.uk*

The diet of Nile Perch (8.0–121.0 cm total length [TL]) from the Ugandan waters of Lake Victoria was quantified through stomach content analysis of specimens collected from experimental catches and fish factory samples. A total of 7824 stomachs (5602 from experimental fishing and 2222 from factory samples) were examined, of which 34.8% contained food. Fish from the experimental catches were smaller (8.0–41.6 cm TL) and had a higher diversity of prey dominated by unidentifiable fish prey, haplochromine cichlids, Rastrineobola argentea*, Odonata and* Caridina nilotica*, while larger fish (30.0–121.0 cm TL) from the factory samples had a predominance of fish remains and haplochromine cichlids. Nile Perch that had a high proportion of fish prey (versus invertebrates) in their stomachs showed a larger size for a given age, and were in a better condition (K = 1.24) than those that had primarily invertebrates (K = 1.10) in their stomachs. Nile Perch exhibited a much smaller size (15 cm versus 30 cm TL) at shift to piscivory in comparison to Nile Perch examined in earlier studies, when haplochromines were rare in Lake Victoria. The recovery of haplochromine cichlids coincident with declining Nile Perch densities illustrates the importance of developing sustainable management options that can define a proper balance between fishing mortality and Nile Perch predation.*

Keywords: Nile Perch diet, haplochromine resurgence, introduced species, ontogenetic shift, piscivory

Introduction

During the 1950s and early 1960s, Nile Perch, *Lates niloticus* (L.) and several Tilapiine species, *Oreochromis niloticus* (L.), *O. leucostictus* (Trewavas), and *Tilapia zillii* (Gervais) were introduced into lakes Kyoga, Victoria, and Nabugabo (Ogutu-Ohwayo, 1990a, 1993, 1994; Pringle, 2005). Nile Perch introduction into Lake Victoria was meant to facilitate the indirect utilisation of the tiny but abundant haplochromines, which the artisanal fishery could not effectively exploit (Acere, 1985; Ogari, 1985; Ogutu-Ohwayo, 1985; Kudhongania et al., 1992) and to improve sport fishing (Pringle, 2005).

The first lake wide bottom trawl survey carried out on Lake Victoria in 1969–1971 before the Nile Perch upsurge indicated that haplochromines formed up to 80% of the fish stocks, while the Nile Perch was negligible contributing <1% (Kudhongania, 1973; Kudhongania and Cordone; 1974, Mkumbo et al., 2005). Subsequent surveys conducted after the establishment of the Nile Perch in the lake registered a marked increase in the Nile Perch catch rates (Okaronon et al., 1985). Although many native fish species had declined in Lake Victoria prior to the Nile Perch introduction, the upsurge of Nile Perch coincided with a further decline or disappearance of hundreds of fish species

Aquatic Ecosystem Health & Management, 17(1):62–69, 2014. ISSN: 1463-4988 print / 1539-4077 online
DOI: 10.1080/14634988.2014.880639

including an estimated 40% of the 500+ species of endemic haplochromine cichlids (Ogutu-Ohwayo, 1990a,b, 1994; Witte et al., 1992a,b; Schwartz et al., 2006) that were the main prey of the Nile Perch (CIFA, 1984; Ogutu-Ohwayo, 1990a,b, 1994; Ogutu-Ohwayo et al., 2002; Barel et al., 1991; Mkumbo and Ligtvoet, 1992). The decline in the haplochromine prey base was followed by changes in the diet and condition of the Nile Perch. The condition factor decreased from 1.4 which was observed in the 1960s (when haplochromines were the main prey base) to 1.2 in the 1990s, the period during which the Nile Perch switched its diet to *Caridina nilotica*, anisopteran nymphs, *Rastrineobola argentea*, juvenile Nile Perch, and *O. niloticus* (Ogutu-Ohwayo, 1994, 2004). In addition, a shift to piscivory at a larger body size (Ogutu-Ohwayo, 1994; Schofield and Chapman, 1999) was observed.

A reported increase in fishing effort targeting Nile Perch fuelled by a high market demand is reported to have led to a continuous decline in the Nile Perch catches in the commercial fishery (Okaronon, 2003; Matsuishi et al., 2006). In turn, the observed resurgence of some native fishes especially the haplochromine cichlids (Kitchell et al., 1997; Witte et al., 2000; Balirwa et. al., 2003; Matsuishi et al., 2006) was associated with decline in Nile Perch catches. Previous modelling efforts suggest that fishing is a strong ecological force in Lake Victoria (Kitchell et al., 1997; Schindler et al., 1998; Mugisha and Ddumba, 2006), and that the specific rate of Nile Perch biomass accumulation should be highest when haplochromines are abundant (Kaufman and Schwartz, 2002; Balirwa et al., 2003). With the recent increase in the proportion of haplochromines in their diet (Budeba and Cowx, 2007; Paterson and Chapman, 2009), it would be expected that Nile Perch response to prey recovery may be reflected in changes in growth and condition (Balirwa et al., 2003). If indeed growth traits vary with prey type, then the key to sustainability of the Nile Perch fishery may depend on defining a proper balance between harvesting and biodiversity recovery, a solution that requires an understanding of the pattern of resurgence, prey selection and growth rate under different prey regimes.

In view of the apparent preference for haplochromine prey when Nile Perch first established itself, this study quantified the diet of Lake Victoria Nile Perch following the observed ongoing resurgence of the haplochromine prey base, and reviewed temporal changes in diet and population traits. It was hypothesized that the size at which Nile Perch shifts to piscivory may have declined in Lake Victoria coincident with haplochromine recovery and that Nile Perch feeding on haplochromine cichlids may benefit from better growth and condition.

Materials and Methods

Fish sampling

The diet of Nile Perch was studied using stomach-content analysis samples obtained from three fish processing factories i.e. Greenfields Uganda Limited, Gomba, Uganda Fish Packers located in Entebbe, Jinja, and Kampala, respectively. Additional samples were collected from experimental gill netting using multi-filament nets (mesh sizes 25.4 to 101.6 mm) carried out in inshore waters of Hannington and Thruston bays, and the Napoleon Gulf of Lake Victoria (Figure 1). Fish samples were collected between March 2006 and May 2008. Fish specimens were measured for total length and weight to the nearest 0.1 mm and 0.01 g, respectively. For each of the specimens examined, fish stomachs were dissected out and stomach fullness was visually evaluated and categorised as: Empty (E), 1/4-Full (Q), 1/2-Full (H), 3/4-Full (T) and Full (F). The stomach contents of the Nile Perch sampled from the fish factories had their prey identification done immediately (consistent with regulations prohibiting preservatives near fish harvested for consumption), while fish stomachs obtained from experimental gill netting were preserved in 10% formaldehyde solution and taken back to the laboratory for further analysis.

Gut content analysis

The total weight of food for each stomach was taken after being blotted dry of moisture, and prey items were identified. Where possible, the length, weight, and number of each type of prey were recorded. The following parameters were calculated for prey taxa: (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 non-empty stomachs), and (3) percent mass (%M = the mass of each type of food

Figure 1. Map of Uganda showing the location of sampled sites in Hannington Bay, Thruston Bay and Napoleon Gulf, Lake Victoria, Uganda. (Color figure available online.)

category expressed as a percentage of the total mass of the stomach contents). From these parameters, the Index of Relative Importance (IRI) of each food category was calculated. This index provides a single estimate of dietary importance by combining relative abundance, frequency of occurrence, and percent mass (IRI = [%N +%M] X%F; Hyslop, 1980). For the different centimetre (total length) size classes of the Nile Perch, the Index of Relative Importance is reported in our results, as well as percent mass as a secondary measure of dietary importance.

Prey items were further categorized as either invertebrates or fish to detect the size at which Nile Perch exhibits an ontogenetic dietary shift and the degree of piscivory. Nile Perch were also placed into one of the following three categories to explore the relationship between major prey type in the stomachs and the condition and age of the fish consumer: Nile Perch with >70% invertebrates in their stomachs, >70% fish (excluding haplochromine cichlids) in their stomachs, and >70% fish that were haplochromine cichlids. Differences in Nile Perch size (i.e. total length) and condition among the three diet categories were compared using the non-parametric Mann-Whitney U test. Statistical tests were performed with SPSS 16.0 for Windows. Transverse-sectioned sagittal otoliths were used to determine the age and growth of the Nile Perch as described in Nkalubo (2012).

Results

Nile Perch response to a resurging prey base

A total of 7824 stomachs (5602 from experimental fishing and 2222 from factory samples) were examined of which 34.8% (n = 2721) contained food. Fish from the experimental catches were smaller (8.0–41.6 cm TL) and had a higher diversity of prey than the factory fish, with their stomach contents dominated by unidentifiable fish prey (fish remains), haplochromines, *Rastrineobola argentea*, Odonata and *Caridina nilotica*. Larger fish (30.0–121.0 cm TL) from the factory samples had a predominance of fish remains and haplochromines. The percent index of relative importance (%IRI) and percent mass (%M) of prey items in the combined stomach samples from the two sources (experimental and factory) are illustrated in Figure 2. Nile Perch of ≥20 cm and <30 cm fed mainly on fish remains, *R. argentea*, haplochromines, and Odonata; while unidentified fish remains and haplochromines dominated the diet of Nile Perch >30 and <100 cm. The few Nile Perch examined that were >100 cm TL had ingested juvenile Nile Perch and *Synodontis* sp. Diet analysis excluding unidentified fish remains showed that the haplochromine cichlids increased in dietary importance with fish size (Figure 2). The average size at shift of the Nile Perch from invertebrate feeding to piscivory was 14.6 cm total length (SE = 0.07 cm; range = 10.0–19.9 cm).

Nile Perch diet and growth

The Nile Perch whose stomach contents were comprised mainly of fish prey such as haplochromines, grew to a larger size at a younger age than those that had more invertebrates in their stomachs (Figure 3). For example Nile Perch that included >70% haplochromines in their diet reached the (40–44) cm TL size class at a younger age (i.e. 1 year) than those which contained a higher proportion of invertebrates, the latter group attaining the same size at 1.5 years later (Figure 3). The total length and condition of the Nile Perch that were characterized by >70% invertebrates as prey in their stomachs were significantly different from Nile Perch with >70% fish in their diet (Mann-Whitney U test, $p < 0.001$). Invertebrate feeding Perch had a lower total length (mean = 40.1 cm TL) and condition (mean = 1.10) than Nile Perch whose diet was comprised of either >70% fish (excluding haplochromine cichlids) (mean TL = 55.2 cm; mean K = 1.24) or >70% fishes that were only haplochromines (mean TL = 51.0 cm; mean K = 1.24). However, there was no significant difference in either total length (Mann-Whitney U test, $p = 0.843$) or condition (Mann-Whitney U test, $p = 0.552$) between Nile Perch whose diet was comprised of either >70% fish (excluding haplochromine cichlids) or >70% fishes that were only haplochromines.

Discussion

Nile Perch response to a resurging prey base

Since its introduction into Lake Victoria in the 1960s, the feeding habits of Nile Perch have been extensively studied (Hamblyn, 1960; Gee, 1962/1963; Okedi, 1970; Acere, 1985; Ogari, 1985; Ogutu-Ohwayo, 1985; Mkumbo and Ligtvoet, 1992; Ogutu-Ohwayo, 1994, 2004; Katunzi et al., 2006; Budeba and Cowx, 2007). A comparison of the current diet of Nile Perch with historical data for Lake Victoria and other lakes in the region, suggests that the diet of Nile Perch is dynamic but predictable based on the phase of the invasion process. The composition of the diet of Nile Perch in Lake Victoria has changed dramatically and appears to reflect an indirect effect of heavy fishing pressure on Nile Perch where by reduced predator pressure by the Perch may have facilitated, to some degree, the resurgence of haplochromine cichlids (Chapman et al., 2008). Between 1968 and 1977, the abundant haplochromines making up 80% of the fish biomass in Lake Victoria (Kudhongania and Cordone, 1974) formed the main prey base of Nile

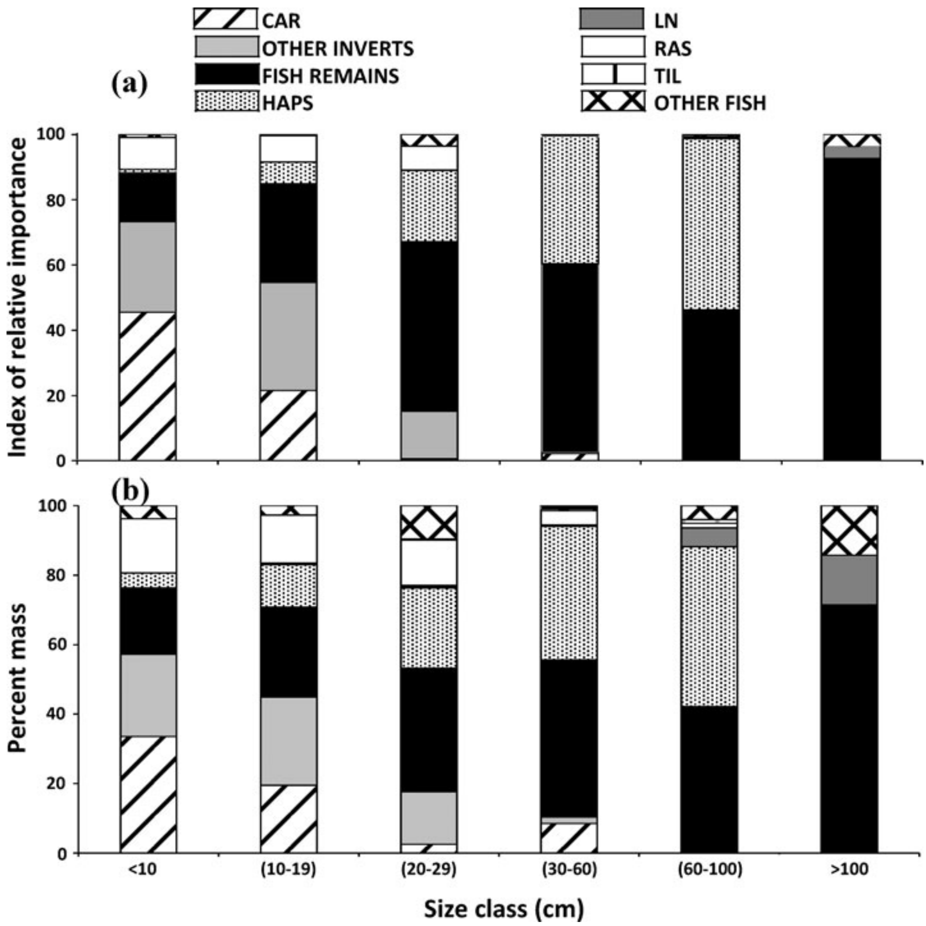

Figure 2. Dietary importance of invertebrate (CAR = *Caridina nilotica*; OTHER INVERTS = other invertebrates) and fish prey (Fish remains; HAPS = haplochromines; LN = *Lates niloticus*; RAS = *Rastrineobola argentea*; TIL = tilapiines) for different size classes of Nile Perch collected from experimental catches from Lake Victoria and fish processing factories between March 2006 and May 2008. (a) Percent index of relative importance (%IRI). (b) Percent mass (%M). Other invertebrates included: bivalves, *Chaoborus* sp., Chironomids, Crabs, Ephemeroptera, Hemiptera, Mollusca, Odonata and *Povilla* sp. while 'Other Fish' included: Fish fry, *Clarias* sp. and *Synodontis* sp.

Perch of 20 to 60 cm size range (Ogutu-Ohwayo, 1994). The growth and condition (K = 1.4) were considered to be high (Ogutu-Ohwayo, 1994). However, by 1988, the major prey eaten by Nile Perch had changed to the freshwater shrimp *C. nilotica*, Anisoptera (dragonfly) nymphs, juvenile Nile Perch, and tilapiines, with very few haplochromines (Ogutu-Ohwayo, 1994, 2004; Balirwa, 2007) and the condition deteriorated to 1.2 (Ogutu-Ohwayo, 1994). These items remained the main type of prey consumed by Nile Perch up to the year 2000, after which the proportion of haplochromines in the diet started to increase coincident with heavy fishing of Nile Perch and resurgence of some haplochromine cichlids (Balirwa, 2007; Budeba and Cowx, 2007).

In addition to the composition of the diet, the size of the ontogenetic dietary shift in Nile Perch (i.e. from feeding on invertebrates to fishes) has also varied with the phase of the invasion and the status of the fishery. After the disappearance or decline of many haplochromine cichlids species, the shift to piscivory occurred at a relatively larger body size (Ogutu-Ohwayo, 1994; Schofield and Chapman, 1999). It thus appears that the intense fishing effort on the Nile Perch stocks (Matsuishi et al., 2006) resulting into a resurgence of a haplochromine-dominated diet, may explain why Nile Perch now exhibits a much smaller size at shift to piscivory. Indeed, the number of fishing crafts on the Ugandan waters of the lake targeting Nile

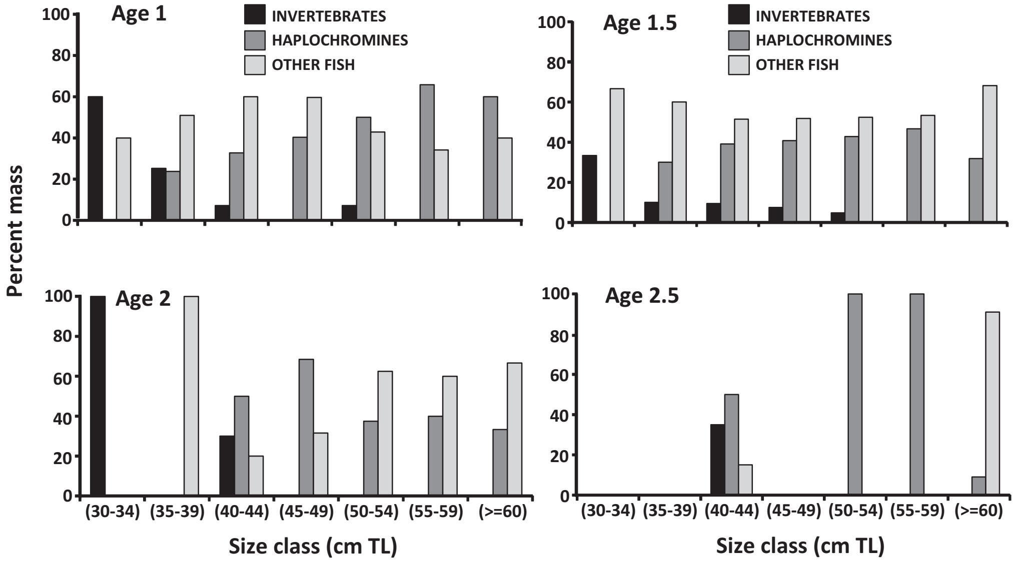

Figure 3. Percent mass of invertebrates and fish prey in stomachs of Nile Perch at different ages collected from commercial catches of Lake Victoria, Uganda between March 2006 and February 2007. 'Other Fish' represents fish other than haplochromines combined with fish remains.

Perch increased from 8107 to 14,692 between 2000 and 2008 (Ministry of Agriculture, Animal Industry and Fisheries [MAAIF], 2010). Hydroacoustic estimates of the haplochromines biomass over the same period indicated an increase from 210,285 t to 518,359 t (Taabu-Munyaho et al., 2011), and our results indicate heavy predation by Nile Perch on haplochromine cichlids during the latter part of this period. Thus, the ontogenetic dietary shifts in Lake Victoria seem to depend on the timing of Nile Perch invasion and level of fishing pressure in the system, and associated changes in the abundance of haplochromine cichlids. The same has also been reported for Lake Nabugabo (Chapman et al., 2003).

Nile Perch diet and growth

Previous modelling efforts on Lake Victoria (Kitchell et al., 1997; Schindler et al., 1998; Mugisha and Ddumba, 2006) exploring the effects of fishing on the foodweb and the fishery, predicted a high Nile Perch biomass accumulation with high haplochromine prey abundance. In this study, the Nile Perch that had a fish-dominated diet (when captured), overall showed a larger size at a young age, and were in a better condition than those that had primarily invertebrates in their stomachs. These findings are based on a point-in-time approach, where the diet of individual Nile Perch is only quantified on one occasion (when captured). Future studies that integrate diet with isotope analysis might provide a stronger basis for interpretation. Nonetheless, these data are interesting because they suggest that the role played by the haplochromines in promotion of faster growth in the Nile Perch could possibly explain their high preference as prey by the predator. Thus, the key to sustainability of the Nile Perch fishery and high production rates would be to maintain sufficient fishing pressure to ensure an abundance of haplochromine prey, but not to fish so hard as to threaten the Nile Perch stock itself (Balirwa et al., 2003).

Conclusions

This study highlights the need to understand the dynamics of predator biomass and its prey for the appropriate management of Lake Victoria fisheries. The proportion of haplochromines in the Nile Perch diet has increased coincident with heavy fishing pressure on, a decline in catches, and haplochromine cichlid recovery. In addition, Nile Perch now exhibit a much smaller size at shift to piscivory in comparison to those examined in earlier studies, when haplochromines were rare in Lake Victoria. A more piscivorous diet may be beneficial to the fishery, as Nile Perch with a high proportion of fish prey in their stomachs, showed a larger size for a given age, and were in a better condition than those that had primarily invertebrates in their stomachs. Clearly, fishing pressure on the Nile Perch can have a cascading effect on the haplochromine prey base, diet, and growth of the introduced predator.

Acknowledgements

Financial support to conduct this study was obtained from the Lake Victoria Fisheries Organization (LVFO) as part of a Ph.D Scholarship. We wish to thank the staff of the National Fisheries Resources Research Institute (NaFIRRI), and of the Department of Zoology, Makerere University, for support given during the course of this study.

References

Acere, T.O., 1985. Observations on the biology, age, growth, maturity and sexuality of Nile Perch, *Lates niloticus* (Linne) and the growth of its fishery in the northern waters of Lake Victoria. In: A Report of the Committee for Inland Fisheries of Africa on development and management of the fisheries of Lake Victoria. FAO Fisheries Report 335, 42–61.

Balirwa, J.S., 2007. Ecological, environmental and socioeconomic aspects of the Lake Victoria's introduced Nile Perch fishery in relation to the native fisheries and the species cultural potential: lessons to learn. African Journal of Ecology 45, 120–129.

Balirwa, J.S., Chapman, C.A., Chapman, L.J., Cowx, I.G., Geheb, K., Kaufman, L., Lowe-McConnell, R.H., Seehausen, O., Wanink, J.H, Welcomme, R.L. and Witte, F., 2003. Biodiversity and fishery sustainability in the Lake Victoria Basin: An unexpected marriage? BioScience 53(8), 703–715.

Barel, C. D., Ligtvoet, W., Goldschmidt, T., Witte, F. and Goudswaard, P.C., 1991. The haplochromine cichlids in Lake Victoria: an assessment of biological and fisheries interests. In: M. Keenleyside (Ed.), *Cichlid Fishes- Behaviour, Ecology and Evolution*, pp.258–279. Chapman and Hall, London.

Budeba, Y.L. and Cowx, I.G., 2007. Contribution of *Caridina nilotica* (Roux) in the Dagaa Fishery in Lake Victoria, Tanzania. Aquat. Ecosyst. Health Mgmt. 10(4), 381–391.

Chapman, L.J., Chapman, C.A., Schofield, P.J., Olowo, J.P., Kaufman, L., Seehausen, O. and Ogutu-Ohwayo, R., 2003. Fish faunal resurgence in Lake Nabugabo, East Africa. Conservation Biology 17, 500–511.

Chapman, L.J., Chapman, C.A., Witte, F., Kaufman, L. and Balirwa, J., 2008. Biodiversity conservation in African inland waters: Lessons of the Lake Victoria Basin. Verhandlungen Internationale Vereinigung Limnologie 30 (Part I), 16–34.

Committee for Inland Fisheries of Africa (CIFA), 1984. Report of the third session of the Sub Committee for development and management of the fisheries of Lake Victoria 1984 October 4–5, Jinja, Uganda, FAO Fish. Rep. 335.

Gee, J.M., 1962/63. Nile Perch investigation. Annual Report 1962/63, East African Freshwater Fisheries Research Organisation, Jinja, Uganda.

Hamblyn, E.L., 1960. The food and feeding behaviour of Nile Perch. In: Annual Report 1960, EastAfrican Freshwater Fisheries Research Organisation, Jinja, Uganda.

Hyslop, E.J., 1980. Stomach content analysis – a review of methods and their application. Journal of Fish Biology 17, 411–429.

Katunzi, E.F.B., Van Densen, W.L.T., Wanink, J.H. and Witte, F., 2006. Spatial and seasonal patterns in the feeding habits of juvenile *Lates niloticus* (L.) in the Mwanza Gulf of Lake Victoria. Hydrobiologia 568, 121–133.

Kaufman, L. and Schwartz, J., 2002. Nile Perch population dynamics in Lake Victoria. Implications for conservation and management. In: M. Ruth and J. Lindholm (Eds). *Dynamic Modeling for Marine Conservation*, pp. 257–313. Springer-Verlag, NY.

Kitchell, J.F., Schindler, D.E., Ogutu-Ohwayo, R. and Reinthal, P.N., 1997. The Nile Perch in Lake Victoria: Interactions between predation and fisheries. Ecological Applications 7(2), 653–664.

Kudhongania, A., 1973. Commercial trawl fishing on Lake Victoria Fisheries Development and Conservation. EAFFRO Annual Report Appendix D. Pages 43–49.

Kudhongania, A.W. and Cordone, A.J., 1974. Batho-spatial distribution patterns and biomass estimate of the major demersal fishes in Lake Victoria. African Journal of Tropical Hydrobiology and Fisheries 3, 15–31.

Kudhongania, A. W., Twongo, T. and Ogutu-Ohwayo, R., 1992. Impact of the Nile Perch on fisheries of Lakes Victoria and Kyoga. Hydrobiologia 232, 1–10.

Matsuishi, T., Muhoozi, L., Mkumbo, O., Budeba, Y., Njiru, M., Asila, A., Othina, A. and Cowx, I., 2006. Are the exploitation pressures on the Nile Perch fisheries resources of Lake Victoria a cause for concern? Fisheries Management and Ecology 13, 53–71.

Ministry of Agriculture, Animal Industry and Fisheries (MAAIF), 2010. National Report of the Frame Survey 2010 on the Uganda side of Lake Victoria.

Mkumbo, O.C. and Ligtvoet, W., 1992. Changes in the diet of Nile Perch, *Lates niloticus* L, in the Mwanza Gulf, Lake Victoria. Hydrobiologia 232, 79–83.

Mkumbo, O.C., Tumwebaze, R. and Getabu, A., 2005. Trends in the Composition, Abundance and Distribution of fishes. In: Proceedings of the Regional Stakeholders' Conference on The State of the Fisheries Resources of Lake Victoria and their management, 2005 February 24th–25. LVFO, Entebbe, Uganda.

Mugisha, J.Y.T., and Ddumba, H., 2006. Modelling the effect of Nile Perch predation and harvesting on fisheries dynamics of Lake Victoria. African Journal of Ecology 45, 149–155.

Nkalubo, W.N., 2012. Life history traits and growth of the Nile Perch, Lates niloticus (L.) in Lake Victoria, Uganda: Implications for management of the fishery. PhD thesis, Makerere University, Kampala.

Ogari, J., 1985. Distribution, food and feeding habitats of *Lates niloticus* in Nyanza Gulf of Lake Victoria (Kenya). A Report of the Committee for Inland Fisheries of Africa on development and management of the fisheries of Lake Victoria. FAO Fisheries Report 335, 68–80.

Okaronon, J.O., 2003. Distribution and abundance of *Lates niloticus* (L.) and *Oreochromis niloticus* (L.) in Lake Victoria, Uganda. PhD thesis, Makerere University, Kampala.

Ogutu-Ohwayo, R., 1985. The effects of predation by Nile Perch, *Lates niloticus* (Linne) introduced into Lake Kyoga (Uganda) in relation to the fisheries of Lake Kyoga and Lake Victoria. In: A Report of the Committee for Inland Fisheries of Africa on development and management of the fisheries of Lake Victoria. FAO Fisheries Report, 335.

Ogutu-Ohwayo, R., 1990a. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of the introduced species, especially the Nile Perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes 27, 81–96.

Ogutu-Ohwayo, R., 1990b. Changes in the prey ingested and the variations in the Nile Perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). Journal of Fish Biology 37, 55–63.

Ogutu-Ohwayo, R., 1993. The impact of predation by Nile Perch, *Lates niloticus* L. on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conservation Biology 7, 701–711.

Ogutu-Ohwayo, R., 1994. Adjustments in fish stocks and in life history characteristics of the Nile Perch, *Lates niloticus* L. in Lakes Victoria, Kyoga and Nabugabo. PhD thesis. University of Manitoba, Winnipeg.

Ogutu-Ohwayo, R., 2004. Management of the Nile Perch, *Lates niloticus* fishery in Lake Victoria in light of the changes in its life history characteristics. African Journal of Ecology 42, 306–314.

Ogutu-Ohwayo, R., Mugidde, R. and Balirwa, J.S. (Eds.), 2002. Technical Guidelines for Management of Fisheries Resources, Biodiversity and Environment of Victoria Basin lakes. Technical document 1. Fisheries Resources Research Institute.

Okaronon, J.O., Acere, T.O. and Ocenodongo, D.L., 1985. The current state of the fisheries in the northern portion of Lake Victoria (Uganda). In: A Report of the Committee for Inland Fisheries of Africa on development and management of the fisheries of Lake Victoria. FAO Fisheries Report 335, 89–98.

Okedi, J. 1970. Further observations on the Ecology of the Nile Perch (Lates niloticus LINNE), in Lake Victoria and Lake Kyoga. In Annual Report 1970, East African Freshwater Fisheries Organisation, Jinja.

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

Pringle, R.M., 2005. The origins of the Nile Perch in Lake Victoria. BioScience 55(9), 780–787.

Schindler, D.E., Kitchell, J.F and Ogutu-Ohwayo, R., 1998. Ecological consequences of alternative gillnet fisheries for Nile Perch in Lake Victoria. Conservation Biology 12(1), 56–64.

Schofield, P.J. and Chapman, L.J., 1999. Interactions between Nile Perch, Latesniloticus, and other fishes in Lake Nabugabo, Uganda. Environmental Biology of Fishes 55, 343–358.

Schwartz, J., Pallin, M., Michener, R., Mbabazi, D. and Kaufman, L. 2006. Effects of the Nile Perch, Lates niloticus, on functional and specific fish diversity in Uganda's Lake Kyoga system. Ecology 44(2), 145–156.

Taabu-Munyaho, A., Kayanda, R., Tumwebaze, R., Nyamweya, C.S., Mroso, H., Sitoki, L., Wabeya, U., Odada, E., and Magezi, G. 2011. Report of the lake-wide hydro-acoustic and environmental survey conducted between 4th September – 3rd October 2011with support provided by the East African Community (EAC) Partnership fund – support to Resource Monitoring for Lake Victoria,

Witte, F., Goldschmidt, T., Goudswaard, P.C., Ligtvoet, W., Van Oijen, M.P.J. and Wanink, J.H., 1992a. Species extinction and concomitant ecological changes in Lake Victoria. Netherlands Journal of Zoology 42, 214–232.

Witte, F., Goldschmidt, T., Wanink, J.H., Van Oijen, M.P.J, Goudswaard, P.C, Witte-Maas, E.L.M and Bouton, N., 1992b. 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.

Witte, F., Msuku, B.S., Wanink, J.H., Seehausen, O., Katunzi, E.F.B., Goudswaard P.C. and Goldschmidt, T., 2000. Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. Reviews in Fish Biology and Fisheries 10, 233–241.