

Full Length Research Paper

Population morphological variation of the Nile perch (*Lates niloticus*, L. 1758), of East African Lakes and their associated waters

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Accepted 24 October, 2011

In this study an attempt was made to determine whether there are morphological variations associated with the different geographical populations of the Nile perch of East Africa. Analyses of the levels of morphological differentiation based on morphological characterisation and variation were carried out. The study was based on 864 Nile perch sampled from 25 different locations from different Lakes in the region and 10 morphological characters. Also determined were the length – weight relationships and condition factor of sampled Nile perch. The log transformed data of all sampled Nile perch were subjected to multivariate analysis, using ‘PAST’ statistical software. Findings showed that peduncle form and size, of all the variables used in this study, contributed most to the variance. The analysis clustered the Nile perch into two groups, which were found to be as characterised by earlier morphological description of this species and most probably are representatives of two distinct taxa of Nile perch in the East African waters. The LWRs and condition factor conformed to the fish isometric growth formula $W = aL^b$ with the value for the pooled data being $W = 0.6664L^{0.3264}$. The existence of 2 morphs agrees with earlier taxonomists (Harrison, 1991; Ribbink, 1987; Bwathondi, 1985; Holden, 1967) who proposed that Nile perch exists in two populations – a bigger shallow water dwelling morph and a smaller deep open water dwelling morph. This calls for identification and mapping of the 2 populations in the different waters of East Africa that may require application of different management regimes.

Key words: Nile perch, taxa, morphological variation, East Africa.

INTRODUCTION

Nile perch *Lates niloticus* (Linnaeus, 1782) is an important commercial freshwater fish species in East Africa. It is endemic to Lakes Albert and Turkana and was introduced into Lakes Victoria, Kyoga and Nabugabo over five decades ago (Hamblyn, 1961; Gee, 1964; EAFFRO, 1967; Welcomme, 1988; Pringle, 2005) with intention of bolstering the then failing fishery of these

Lakes and as a potential for sport fishing (Gee, 1969, Acere, 1985; Barlow and Lissle, 1987; Achieng, 1990).

After its introduction, the Nile perch slowly colonized its new environs and then exploded in the 1980s (Arunga, 1981; Okaronon et al., 1985; Goudswaard and Ligetvoet, 1988). This increase in Nile perch population coincided with the disappearance of close to 50% of the endemic fish species in the new environs and Nile perch has been labelled the villain (Barel et al., 1985). Nile perch has established itself in the new environs and currently dominates the fishery in these Lakes. Despite this

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ecological wrath, due to the lucrative international and regional markets, the Nile has boosted the economies of the three riparian countries of Lake Victoria – Kenya, Uganda and Tanzania, where most Nile perch is harvested, bringing in a hefty USD \$250 million from the international markets alone (Odongkara et al., 2009).

Due to its high demand in the market, this fish species has been put under increased fishing pressure in this region, leading to a great decline in its stocks (Environment for Development, 2008). The decline in Nile perch stocks is further compounded by habitat degradation, water pollution and changes in prey for Nile perch (Mkumbo and Ligtoet, 1992; Ogutu-Ohwayo, 1990). One way to mitigate this problem is to domesticate and culture this species so as to supplement the supplies from the wild and reduce the pressure on the natural stocks. This study is part of a bigger project whose overall goal is to domesticate, breed and culture the Nile perch based at Aquaculture Research and Development Center – Kajjansi, Uganda.

To culture any species from the wild it is prudent that the species is characterized taxonomically, ecologically and geographically as the first step. This enables one to define this species and to determine the performance of the different taxa that are in the wild so as to aid selection of the best suited taxon for culturing (Liao and Haung, 2000). Earlier efforts (Worthington, 1929, 1932; Harrison, 1991; Hauser et al., 1998) failed to unambiguously define the Nile perch in this region. For example what was being taken as one species – *Lates niloticus*, turned out to be considered as two different species - *Lates albertiensis* and *Lates macrophalamus* for the Lake Albert Nile perch (Worthington, 1929; Worthington, 1940), and interestingly the Lake Turkana Nile perch were taken to be two different subspecies - *Lates niloticus rudolfianus* and *Lates niloticus longispinus* of the riverine species *Lates niloticus* (Worthington, 1932; Greenwood, 1966). Later this grouping was revised to subspecies level and not species of *Lates niloticus* as the specimens from Lakes Albert and Turkana were seen as intermediates and also thought to interbreed (Worthington, 1940). The other school of thought is that the observed differences in morphology of the Nile perch may be arising from the extremities of a normal population curve. According to Harrison (1991) the Lake Victoria Nile perch has been and is wrongly referred to as *Lates niloticus*, yet its taxonomic status has never been resolved. This paper is part of a bigger study that is attempting to taxonomically characterise the Nile perch using a combination of both morphological and molecular techniques. The paper examines the morphological variation among Nile perch of East Africa and determines which morphological characteristic contributes most to this variation as well as deciphering its morphological phylogenetics. In this paper, results of the analysis of the Nile perch populations and subdivisions based on measurement of 10 morphological characteristics, done using the 'PAST'

statistical software are presented and discussed.

METHODOLOGY AND STUDY AREA

Nile perch samples were taken from Lakes Albert in Uganda and Turkana in Kenya where the fish is endemic and the putative origins for the introduction of this species into Lakes Victoria, Kyoga and Nabugabo in Uganda. Lakes Albert and Turkana are rift valley lakes, with Lake Albert found on the western border of Uganda with Democratic Republic of Congo and Lake Turkana on the north western border of Kenya with Ethiopia. Lake Victoria is the second largest fresh water lake in the world, and is shared between three countries: Uganda (41%), Kenya (6%) and Tanzania (53%). Lake Kyoga is in Central Uganda connected to both Lake Victoria and Lake Albert by the Victoria Nile River. There are waterfalls on either side of Lake Kyoga - Owen Falls and Murchison Falls, which act as a buffer to the movement of adult Nile perch due to their size. Lake Nabugabo is a small (24 km²) satellite lake, formerly a bay on the western shore of Lake Victoria separated from the main lake by a sand bar more than 5,500 years ago (Chapman et al., 1996). It is alleged that before introduction of Nile perch from Lake Albert into Lake Victoria, the fish were first rested and tried out in Lake Nabugabo before eventually being introduced into Lake Victoria (Barlow and Lissle, 1987).

Sample collection

In Lakes Albert, Turkana, Kyoga and Nabugabo (Figure 1) fish were caught using seine nets. In these lakes, the sampling followed different eco-zones (shallow offshore waters and the deep open waters) because different Nile perch morphs are believed to inhabit different eco-zones. In Lake Victoria, samples were caught from 22 different geographical locations (Figure 2) by bottom trawls. Sampling followed transects pre-determined by hydroacoustics experts after consideration of a number of factors including traditional fishing grounds, history as told by the local fisher folk, previous knowledge of Nile perch distribution, findings of tagging experiments, and the Lake topography. Trawls were done after the hydroacoustics experts on board detected signals indicating abundance of relatively big size fish on their computer screen. For the trawls the depth of sampled sites ranged from as low as 4.5m to a maximum 50.4m (Table 1). The seining of Nile perch from both deep open and shallow offshore waters and trawling from the deep open waters toward the shallow offshore waters ensured that if there are differences in habitat for different morphs as alleged, then all morphs would be sampled and included in the analyses. A total of 864 Nile perch fish were sampled from all lakes (Table 1).

Biometric measurements and data analysis

Morphological characters studied included - total length (TL), standard length (SL), body depth (BD), peduncle length (PL) and peduncle depth (PD) (Figure 3), so for every sampled fish measurements of these characteristics were taken immediately after capture/trawl. Ratios of TL to all other variables - SL, BD, PL and PD, and ratio of PL to PD for each sampled fish were calculated and also used in the analyses. The study also considered the length – weight relationships (LWRs) and the condition factor of the fish and establishes whether these are affected or affect the morphological variation of this fish. Condition factor refers to a mathematical formula for determining the physiological state of a fish, including its reproductive capacity. The heavier a fish is for a given length, the higher its condition factor (K), which is one factor that is considered when determining the

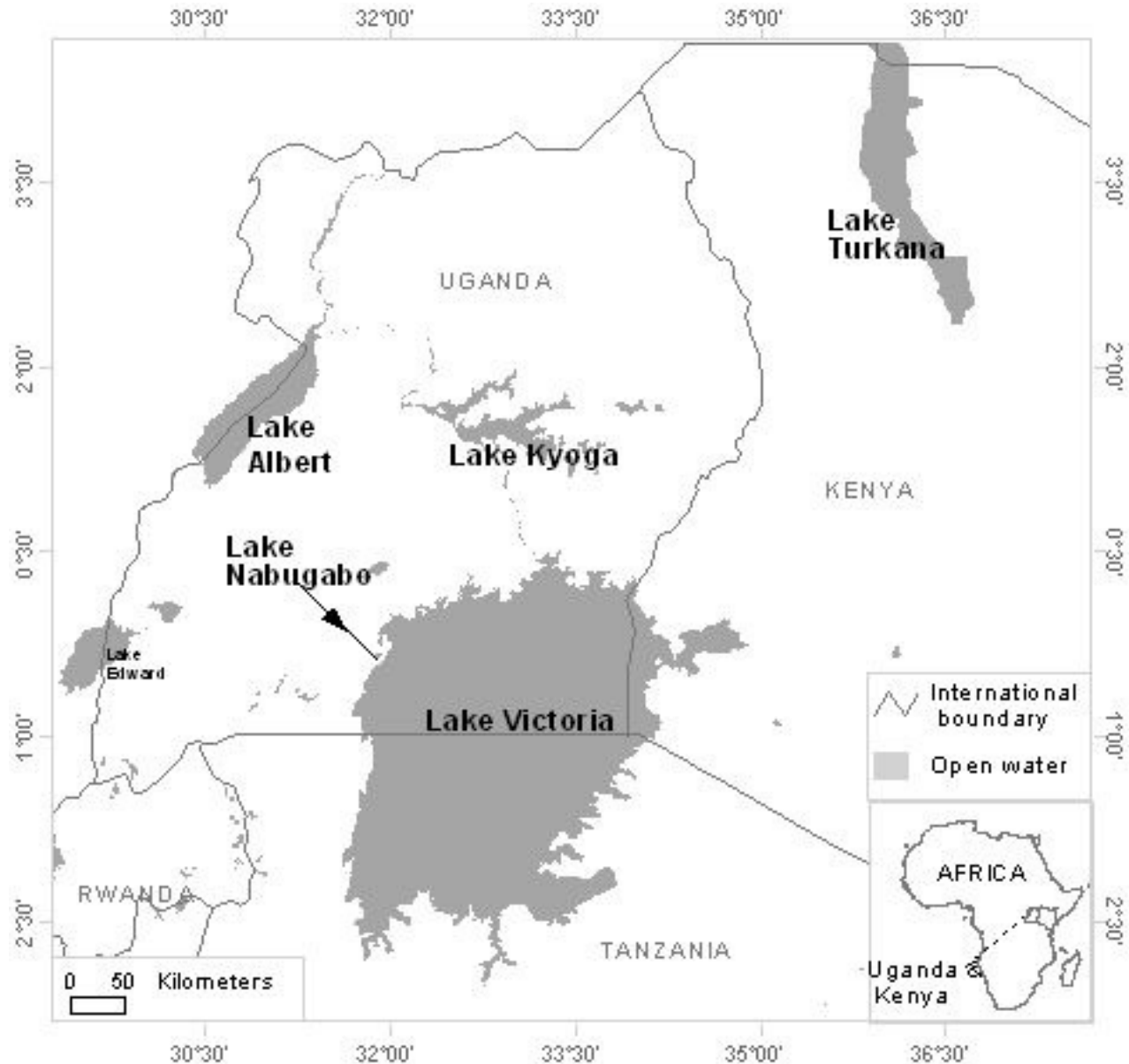


Figure 1. Map showing the East African lakes from which Nile perch was sampled for this study.

health of a fishery. The LWRs of pooled data for all fish were estimated using the equation $W = aL^b$ (Pauly, 1983), where W = weight of fish in grams, L = TL in cm, b = length exponent (slope) and a = proportionality constant (intercept). The 'a' and 'b' values were obtained from a linear regression of length and weight of fish. The correlation or degree of association between length and weight (r^2) was calculated from linear regression analysis, $R = r^2$. The condition factor 'K' was determined using the equation, $K = 100W/L^3$. In order to standardize the data, all variables taken including SL, BD, PL and PD were expressed as a percentage of TL. Also since different strains of the Nile perch are thought to differ in PL and PD, the ratios of these two variables were expressed as percentage and the condition factor 'K' was determined for each sample. To ensure normality and homogenous variances, all values were \log_{10} – transformed before statistical analyses were performed. The outcomes (PL/PD%, BD/TL%, BD/SL% and 'K') were then used as the variables in the consequent multivariate data

analysis using the PAST software. Principal component analysis (PCA) was used to extract principal components from the four variables. The 'PAST' (PALaeontology STATistical) software package was originally aimed at palaeontology but currently has become popular in ecology and other fields (Hammer et al., 2001). Using PAST, the measured morphological characters were subjected to multivariate analysis, a tool highly recommended for determining relationships between populations of a species (Thorpe, 1987) and for use in stock identification of freshwater fish and investigating taxonomical problems in sympatric populations (Cawdery and Ferguson, 1988). The most significant component that contributed most to the variance was then used in determining the morphological phylogenetic relationships of the Nile perch in the East African waters. Based on the outcome of the mixture analysis in 'PAST', all data were subjected to K-means clustering to determine non-hierarchical clustering of all the samples into the number of groups (2) specified under the mixture analysis. For all

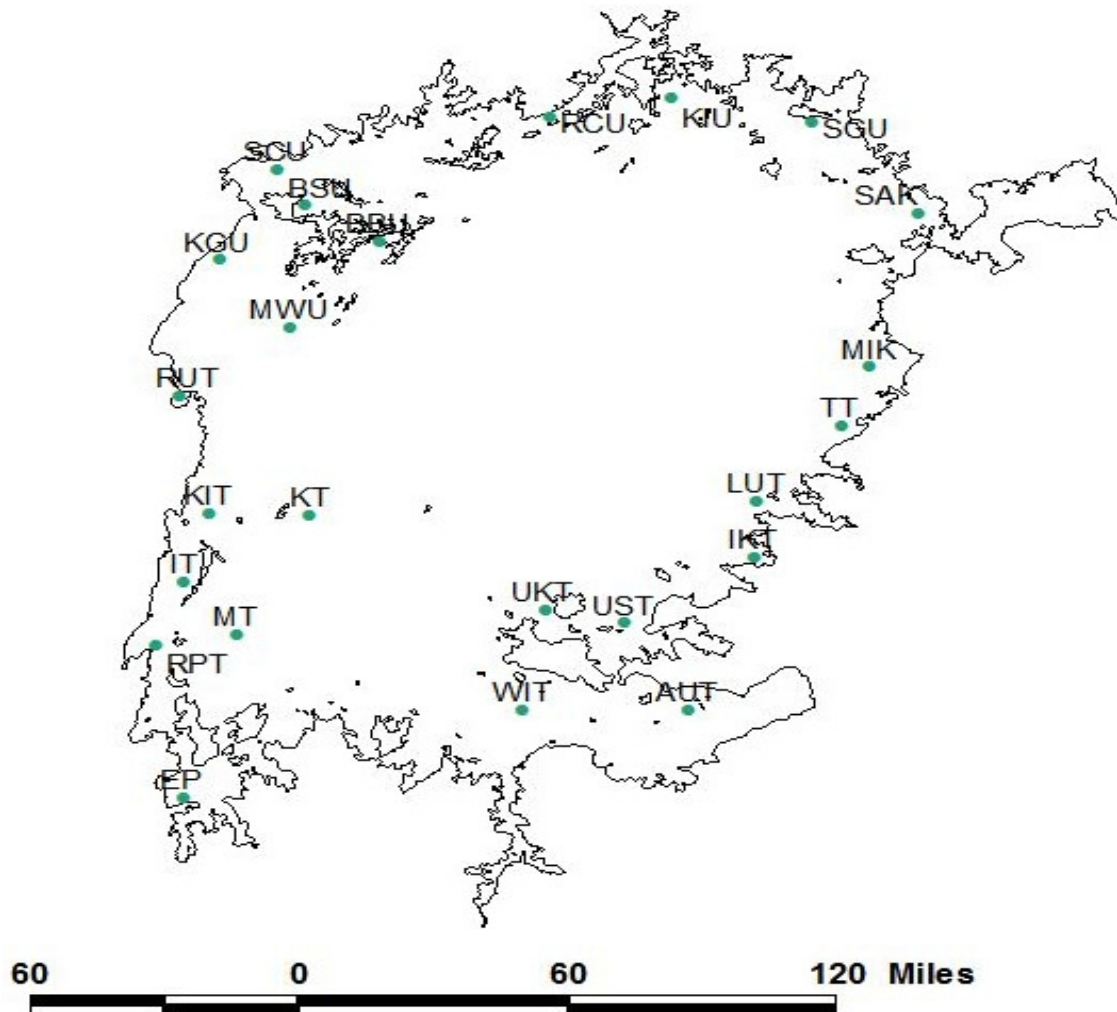


Figure 2. Map of Lake Victoria showing the sampled sites.

analyses the significance level considered was 0.05.

RESULTS

The LWRs of Nile perch was found to be $\text{Log}_{10}W = 0.6664 + 0.3264\text{Log}_{10}TL$, corresponding to $W = 0.6664L^{0.3264}$, indicating an isometric growth pattern. The regression coefficient for the pooled data was $r^2 = 0.9832$ (Figure 6). The relative condition factor ranged from 0.57 to 2.28 with average for pooled data at 1.16. Principal component analysis of the data from the four variables revealed that approximately 96.8% of the total variation was explained along two components 1 and 2, that is PD/PL% and BD/TL% respectively. With most of the variance provided by the component 1 - PD/PL% (73.457%) followed by BD/TL% (23.300%) then BD/SL% (3.2239%) and condition factor 'K' (0.017%) making the smallest contribution to morphological variation of the Nile perch (Table 2). All the Eigen values for all

components were positive (Table 2) indicating all used variables have some effect on the morphological variation of the Nile perch with the most significant contribution from the variable percentage ratio PD/PL (Figure 5). When subjected to mixture analysis, the fish clustered into two groups (Figure 4). From the K-means clustering, the majority of the individuals (583) belonged to one group, that is, cluster 1 and the rest (281) belonged to the other group, that is, cluster 2. The mixture analysis curve (Figure 4) for all data pooled together showed two major groupings. The Neighbour-Joining clustering using Euclidean similarity measure generated by 'PAST' using the \log_{10} -transformed data from the principal component 1 also revealed two clades.

DISCUSSION

These findings indicate that Nile perch fish growth is isometric and obeys the cube law ' $W = L^3$ ', that is, the

Table 1. Showing the Sampling sites, number (N) of fish sampled from each site, the eco-zone of the sample site, and for Lake Victoria depth at the start and end of each fishing trawl.

Population ID	Number (N)	Lake	Country	Eco - zone	Depth start – End of trawl
Emin Pasha /EPT	22	Victoria	Tanzania	Deep/ open	9.0 – 9.0 m
Ruega point /RPT	50	Victoria	Tanzania	Deep/ open	25.0 – 24.0 m
Mazinga /MT	38	Victoria	Tanzania	Deep/ open	45.0 – 48.0 m
Kerebe/KT	31	Victoria	Tanzania	Deep/ open	50.0 – 50.4 m
Ikondo/IT	40	Victoria	Tanzania	Deep/ open	30.0 – 30.0 m
Kishoka/KIT	40	Victoria	Tanzania	Deep/ open	33.0 – 29.0 m
Rubafu /RUT	20	Victoria	Tanzania	Deep/ open	9.4 – 9.4 m
Lukuba/LUT	50	Victoria	Tanzania	Deep/ open	30.2 – 30.2 m
Ushengere /UST	42	Victoria	Tanzania	Deep/ open	40.0 – 37.5 m
Ukara /UKT	33	Victoria	Tanzania	Deep/ open	32.5 – 32.0 m
Wiru /WIT	20	Victoria	Tanzania	Deep/ open	40.0 – 40.0 m
Augustus /AUT	20	Victoria	Tanzania	Deep/ open	13.2 – 14.0 m
Mwena /MWU	28	Victoria	Uganda	Deep/ open	32.0 – 31.0 m
Kagege /KGU	15	Victoria	Uganda	Deep/ open	5.5 – 4.5 m
Bugabu/BBU	46	Victoria	Uganda	Deep/ open	4.8 – 4.5 m
Bumangi Ssese/BSU	39	Victoria	Uganda	Deep/ open	8.0 – 8.0 m
Rosebery Channel/RCU	16	Victoria	Uganda	Deep/ open	24.0 – 24.6 m
Kifudwe/KIU	41	Victoria	Uganda	Deep/ open	20.0 – 24.0 m
Sigulu /SGU	12	Victoria	Uganda	Deep/ open	20.0 – 18.0 m
Saga/SAK	50	Victoria	Kenya	Deep/ open	30.0 – 25.0 m
Migingi/ MIK	35	Victoria	Kenya	Deep/ open	43.0 – 43.0 m
Turkana /TLK	19	Turkana	Kenya	Deep/open and shallow/offshore	–
Albert Kaiso /AKU	95	Albert	Uganda	Deep/open and shallow/offshore	–
Kyoga - Bukungu /KYU	50	Kyoga	Uganda	Deep/open and shallow/offshore	–
Nabugabo /NAU	18	Nabugabo	Uganda	Deep/open and shallow/offshore	–

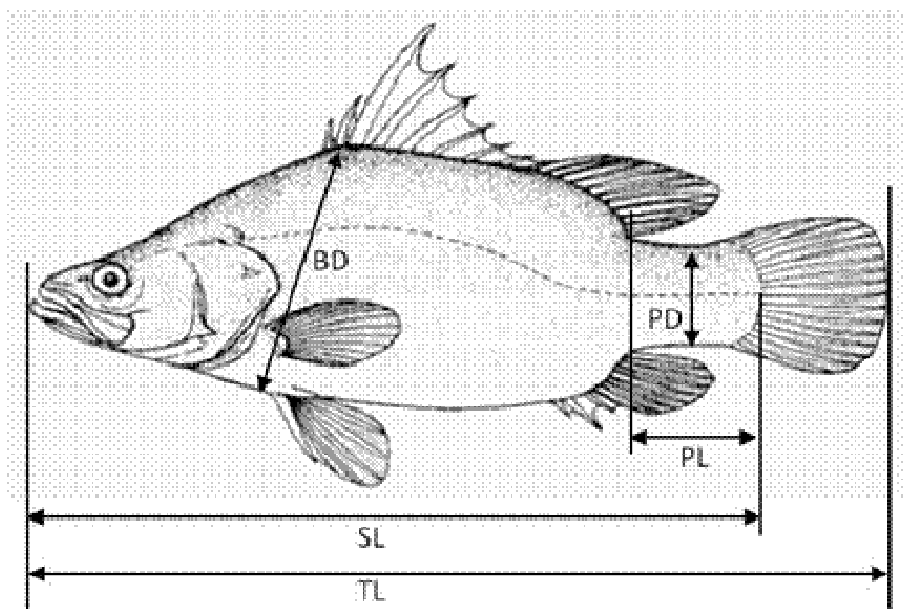


Figure 3. The morphological characteristics of the Nile perch fish that were measured during this study including total length (TL), standard length (SL), body depth (BD), peduncle length (PL) and peduncle depth (PD). In addition, the wet weight of each sampled fish was also taken. (Source of photo – FAO Fish Finder (1994).

Table 2. Eigen values and the distribution of variance among the different components.

Morphological character	Component ranking	Eigen value	Variance (%)
PD/PL%	1	71.965	73.457
BD/TL%	2	22.827	23.300
BD/SL%	3	3.160	3.226
K	4	0.016	0.017

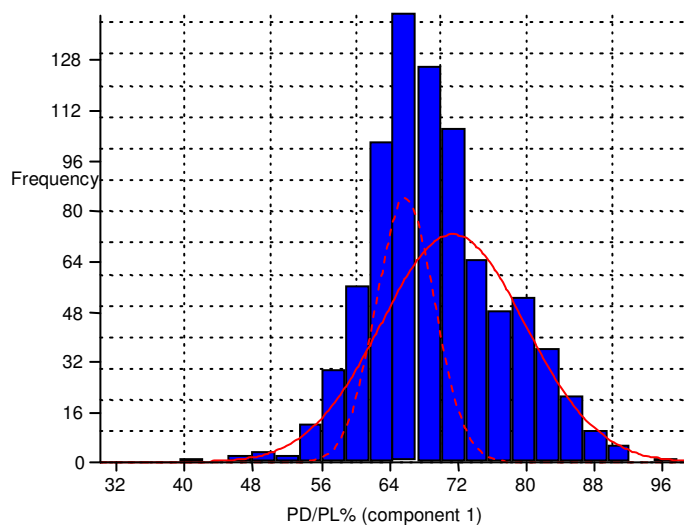


Figure 4. A graph of Frequency Vs PD/TL% of all data from the principal component (component one) showing normal curves of the probable 2 major groupings of sampled Nile perch generated after PCA under 'PAST'. The unbroken line curve represents cluster one the most dominant and the broken line represents cluster 2.

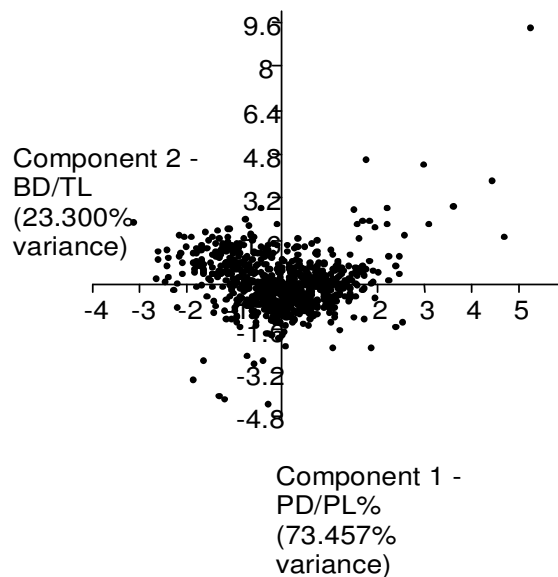


Figure 5. Scores of the first two most significant principal components in this study. Component 1 represents the PD/PL percentage ratio whereas Component 2 represents the BD/TL percentage ratio.

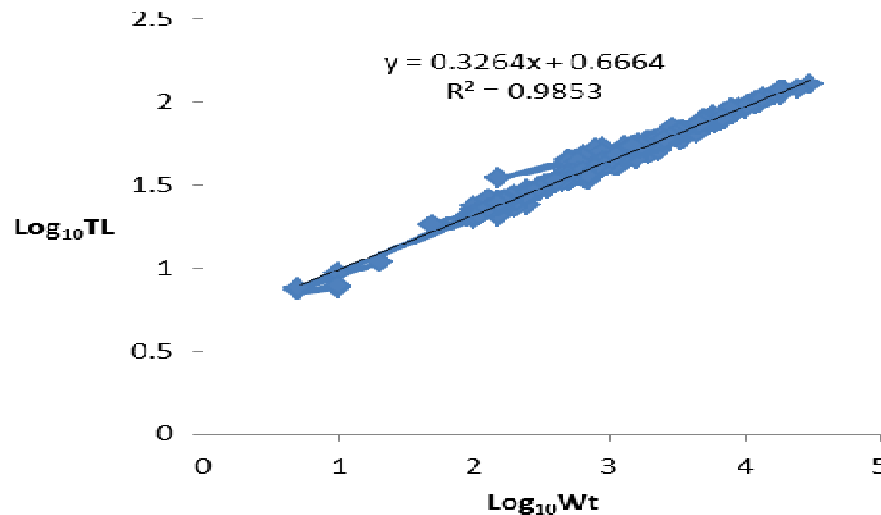


Figure 6. Regression graph for pooled data for Log_{10}TL versus Log_{10}Wt showing regression coefficient ' R^2 ' and regression equation.

weight of the Nile increases in proportion to the cube root of its length. Also from the regression coefficient $r^2 = 0.9853$ all the LWRs of Nile perch were strongly significant. The results of the PCA indicate that of all the variables used in this study, the percentage ratio of PD/PL (73.457%) contributed most to the variance in the Nile perch. This suggests that the different morphs of the Nile perch most probably may be largely be differentiated by their characteristic difference in the form and size of their peduncle. The ratio BD/TL% also contributes significantly (23.3%) to the variation in morphology of the Nile perch, this ratio is an indicator of the body form, whether the fish is lean and long or stout and short. Therefore the peduncle and body size and form are responsible for the variation in morphology of the Nile perch, which agrees with what is known by the local fisher folk around the different lakes (personal communication from the interviews conducted during the sampling). The fisher folk recognize two general morphotypes of Nile perch, one stout (deeper body) with a short and thick peduncle, and the other lankier, with a long and slender peduncle. From the mixture analysis using PAST software and the generated tree the fish clustered into two groups/branches. This most probably suggests that there are probably two major morphs of Nile perch in East African waters. The local fisher folk further attested that the stout form, with a short and thick peduncle, is more common than the lankier form, which agrees with the mixture analysis and K-means analysis that places the sampled fish in two groups with one (583 samples) more prominent than the other (281 samples). The lankier morph most probably uses its slender and longer peduncle to swim faster and forages in the deep open waters where rare availability of prey may not permit formation of a deep body, but this keeps it away

from easy capture by fishermen, whereas the stout morph with the short and thick peduncle is thought to be slower, and as such this morph forages in the shallower open offshore waters where it can hunt easily, a situation that leads to its easier capture by the fishermen and therefore its predominance in the catch. The two clusters/groups differentiated largely by variation in peduncle morphs, despite the spatial separation from the putative lakes of origin they are as clearly distinct in their new environments in which they were introduced over five decades ago. Therefore it is most likely that the two Nile perch groupings are most probably from two different populations of even taxa at subspecies level, thus calling for further work using a combination of both morphological and molecular markers to properly classify the Nile perch and provide the basic (taxonomic status) prerequisite tool for its effective management. Most of the Nile perch fish in the sampled lakes belonged to one of the taxa, with the stout morph as the most dominant in the East African waters of lakes - Albert, Turkana, Victoria, Kyoga and Nabugabo. The contribution to morphological variation of the Nile perch by the condition factor can be ignored as the value (0.017%) is insignificant. The differences in condition factor are mainly due to the wellbeing of the fishery in certain environments and how fish best exploit those particular environments rather than the morphology of the fish.

Conclusion

The exhibited isometric growth implies that Nile perch does not increase in weight faster than the cube of their total lengths. The Nile perch of East Africa has two distinct morphotypes, the stout and lankier forms, an

indicator that there are most probably two different subspecies of this species. The stout form is currently the major contributor to the Nile perch fishery on the East African Great lakes and their associated waters. Given that morphological and molecular data are only complementary and not in competition with one another (Chang, 2004), this outcome of morphological phylogeny analysis will be compared, contrasted and combined with the on-going analysis of the molecular phylogenetics of the very same samples of Nile perch in a bid to more clearly define the taxonomical status of the Nile perch of East African waters. The findings of this study are largely in conformity with earlier descriptions of this species by Holden (1967), Hopson (1972), Bwathondi (1985) and Harrison (1991). The implications to the management of the Nile perch fishery in the East African region is that the probable two populations or taxa may have different biology, prey preferences, environmental conditions, sizes at first maturity fecundity, life expectancy and other differences that will require developing different management regimes for each morph/population.

About the choice of taxon of Nile perch most suitable for domestication and culturing in the region, there is need for further work to determine the comparative advantage of the two morphs such as easy of adaptability to on-farm environmental conditions, breeding in captivity, stress tolerance, disease resistance and uptake of artificial diets. The two morphs need to be first mapped out in the different lakes and then further studied.

ACKNOWLEDGEMENTS

This study is part of the bigger project Nile perch technologies sponsored by the World Bank Millennium Science Initiatives (MSI) under the Uganda National Council of Science and Technology (UNCST). We are thankful to Dr. Rob Skilton of BECA - Nairobi, Kenya for reading the correcting the final manuscript. We are grateful to Lake Victoria Fisheries Organisation for having allowed us on board during their Lake wide stock assessment on Lake Victoria and to the crew of the Explorer vessel of Tanzania Fisheries Resources Research Institute (TAFIRRI) that was used during the bottom trawls on Lake Victoria. We are also indebted to technicians Mapunda and Ogaro from TAFIRRI, Odada from Kenya Marine and Fisheries Research Institute (KEMFRI), Opiri and Mutebi of Uganda for their assistance during morphometrics measurements on Lakes Victoria, Turkana, Nabugabo and Kyoga respectively.

REFERENCES

Acere TO (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: CIFA report of the third session of the subcommittee for the development and

- management of the fisheries of Lake Victoria. Jinja, Uganda. 4-5 Oct. 1984. Fish. Rep. 335. FAO, Rome, pp. 42-61.
- Achieng AP (1990). The impact of the introduction of Nile perch, *Lates niloticus* (L) on the fisheries of Lake Victoria. J. Fish Biol., Supp. A: 17-23.
- Arunga JO (1981). A case study of lake Victoria Nile perch *Lates niloticus* (Mbuta) fishery. In: Proceedings of the workshop of the Kenya Marine and Fisheries Research Institute on aquatic resources of Kenya, 13-19 July, Mombasa. Kenya Marine and Fisheries Research Institute and Kenya National Academy for Advancement of Arts and Sciences, pp. 165-184.
- Barel CDN, Dorit R, Greenwood PH, Fryer G, Hughes N, Jackson PBN, Kawanabe H, Lowe-McConnell RH, Nagoshi M, Ribbink AJ, Trewavas E, Witte F, Yamaoka K (1985). Destruction of fisheries in Africa's lakes. Nature, 315: 19-20.
- Barlow GC, Lissle A (1987). Biology of The Nile perch *Lates niloticus* (Pisces: Centropomidae) with Reference to its Proposed Role as a Sport Fish in Australia. Biol. Conserv., 39: 269-289.
- Bwathondi POJ (1985). The future of the fisheries of the Tanzania part of Lake Victoria, in view of the predominance of the Nile perch *Lates niloticus*. F.A.O. Fish. Rep., 335: 143-145.
- Cawdery SH, Ferguson A (1988). Origins and differentiation of three sympatric species of trout (*Salmo trutta* L.) in Lough Melvin, Ireland. Polskie Archiwum Hydrobiologii, 35: 267-277.
- Chang ML (2004). Phylogenetics analysis of morphological data (Review). Hum. Biol., 76(1): 165-168.
- Chapman LJ, Chapman AC, Ogutu-Ohwayo R, Chandler M, Kaufman L, Keiter AE (1996). Refugia for Endangered Fishes from an Introduced Predator in Lake Nabugabo, Uganda. Conserv. Biol., 10(2): 554-561.
- EAFFRO (1967). East Africa Freshwater Fisheries Organization Annual Reports, 1961-1967; Entebbe, Uganda.
- Environment for Development (EFD) (2008). Over fishing of Nile perch in Lake Victoria. EFD Tanzania press release 02nd- 11 - 2008. At: http://www.efdinitiative.org/news-press/copy_of_job-openings/job-openings-archive/press-releases-2009/over-fishing last accessed on 05th/01/2009.
- FAO Fish Finder (1984). At:http://www.fao.org/fi/common/format/pop/Uplmage.jsp?xp_imageid=698261&xp_showpos=1.
- Gee JM (1964). Nile perch investigations. Annual Reports of East African Freshwater Research Organisation, 1962/63, pp. 14-24.
- Gee JM (1969). A comparison of certain aspects of the biology of *Lates niloticus* (Linne 1758) in some East African lakes. Rev. Zool. Bot. Afr., 80: 244-262.
- Greenwood PH (1966). The Fishes of Uganda. Kampala (Uganda): Uganda Society.
- Goudswaard PC, Ligtoet W (1988). Recent developments the fishery of Haplochromines (Pisces: Cichlidae) and the Nile perch *Lates niloticus* (L.) (Pisces: Centropomidae) in Lake Victoria, pp. 101-112. In: CIFA. Report of the fourth session of the Subcommittee for Development and Management of the Fisheries of Lake Victoria, 6-10 April, 1987, Kisumu, Kenya. FAO Fish. Rep. 388. FAO, Rome.
- Hambalyn EL (1961). The Nile perch project. EAFFRO Annual Report, 1960, pp. 26-32.
- Hammer O, Harper DAT, Ryan PD (2001). Paleontological statistics software package for education and data analysis. In: Paleontol Electronica, 4(1): 4-9.
- Harrison K (1991). The taxonomy of East African Nile perch, *Lates* spp. (*Perciformes Centropomidae*). J. Fish Biol., 38(2): 175-186.
- Hauser LG, Carvalho GR, Pitcher TJ, Ogutu-Ohwayo R (1998). Genetic affinities of an introduced predator: Nile perch in Lake Victoria, East Africa. Mol. Ecol., 7: 849-857.
- Holden MJ (1967). The systematics of the genus *Lates* (Teleostei: Centropomidae) in L. Albert East Africa J. Zool. (London), 151: 329-342.
- Hopson AJ (1972). A study of the Nile perch, *Lates niloticus* (L.), in Lake Chad. HMSO Overseas Research Publications, 19; Foreign and Commonwealth Office, London.
- Liao IC, Haung YS (2000). Methodological approach used for the domestication of potential candidates of aquaculture. In: Recent advances in Mediterranean aquaculture finfish species diversification Zaragoza: CIHEAM-IAMZ, pp. 97-107.
- Mkumbo OC, Ligtoet W (1992). Changes in the diet of Nile perch,

- Lates niloticus* (L), the Mwanza Gulf Lake Victoria. In: *Hydrobiologia*, 232(1): 79–83.
- Odongkara OK, Abila OR, Luomba J (2009). The contribution of Lake Victoria Fisheries to National Economies. *Afr. J. Trop. Hydrobiol. Fish.*, 12: 47-51.
- Ogutu-Ohwayo R (1990). Changes in prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and Northern waters of Lake Victoria (Uganda). *J. Fish. Biol.*, 37(1): 55-63.
- Okaranon JO, Acere TO, Ocenodongo DL (1985). The current state of the fisheries in the northern portion of lake Victoria, pp. 89-98. In: CIFA. Report of the third session of the Subcommittee for Development and Management of the Fisheries of Lake Victoria, 4-5th October, 1984, Jinja, Uganda. FAO Fish. Rep. 335. FAO, Rome.
- Pringle RM (2005). The origins of the Nile perch in Lake Victoria. *BioSci.*, 55(9): 780-787.
- Thorpe RS (1987). Geographic variation: A synthesis of cause, data pattern and congruence in relation to subspecies, multivariate analysis and phylogenies. *Bull. Zool.*, 54: 3–11.
- Welcomme RL (1988). International introductions of inland aquatic species. FAO Fish Technical Paper, 249, FAO Rome.
- Worthington EB (1929). A Report on the Fishing Survey of Lakes Albert and Kyoga, March to July, 1928. London: Crown Agents for the Colonies
- Worthington EB (1932). Scientific results of the Cambridge expedition to the East African Lakes, pp. 30–31.
- Worthington EB (1940). Geographical differentiation in freshwaters with special reference to fish. In the Systematics (J. Huxley, ed.), London: Oxford University Press, pp. 287–302.