Exploring the morphological dynamics of Nile tilapia (Oreochromis niloticus Linn. 1758) in Victoria Nile as depicted from geometric morphometrics

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Abstract

Background: Various anthropogenic activities continue to threaten the fish biodiversity of the East African water bodies such as the Victoria Nile. Although the Victoria Nile is a significant source of livelihood to human populations, the biology and ecology of Nile tilapia in this ecosystem remain understudied with little or no information on the morphology of the fish given varying and immense anthropogenic activities. Here, we use geometric morphometrics to examine the morphology/shape variations of Nile tilapia populations in Victoria Nile to gain insights into their current ecological state.

Results: Our results indicate unexpected smaller body weights of Nile tilapia in Victoria Nile than in L. Victoria. Despite this, all the populations displayed condition factors of greater than 2 suggesting a healthy stock. We also report that the Upper and Lower Victoria Nile populations display morphological similarities. We note that Nile tilapia from Nalubale Dam Reservoir is morphologically distinct from the close neighboring Victoria Nile populations which are likely allied to the influence of the Nalubale Hydroelectric power dam as a barrier.

Conclusion: Nile tilapia's morphological variation appears to be influenced by various anthropogenic disturbances notably, overfishing, hydroelectric power dams, and fish translocational history in Uganda. Management should enforce regulatory frameworks to avert human-mediated activities as these are likely to compromise the sustainability of the fisheries. Further studies are required to follow these populations with molecular data to gain a deeper understanding of the fish species for sustainable management and conservation.

Background

Like many global inland freshwater bodies, the lakes and rivers of Uganda are vital for economic development but have at the same time experienced alarming disturbances for virtually a century, since the 1920s, (1–6). The distressing challenges have been mainly mediated by anthropogenic activities as a result of exponential demographic growth that have triggered user conflicts and escalated demands for the fisheries' resources (7). For instance, the high demand for fishery products led to overfishing and a subsequent decline in fish stocks, which influenced the translocation of alien species (Nile tilapia and Nile perch) to various water bodies in Uganda (2, 8). Other than fish translocations, Uganda's major water bodies have been invaded by aquatic weeds which have devastated the water quality resulting into negative effects on the fisheries (9). For instance, the water hyacinth (*Eichornia crassipes*), which was introduced in the Lakes Kyoga and Victoria as well as Victoria Nile in 1988 (6, 9, 10), and more recently (2013), the Kariba weed (*Salvinia molesta*) (11, 12) have caused challenges in these lakes. These weeds have proliferated in the water resources as a consequence of the massive influx of nutrients (mainly phosphates), propelled by various human-mediated activities (11, 13). The anthropogenic activities have dramatically upset fish biodiversity and ecology in nearly all the country's water bodies either directly or indirectly.

Nile tilapia in Uganda is a popular species in both aquaculture as well as capture fisheries and is thus vital for the country's economic development. The fish is the second most economically important species after Nile perch, but the most highly valuable under aquaculture (Balirwa et al. 2003). Traditionally, Nile tilapia is non-native to Lakes Victoria, Kyoga, Nabugabo, the upper Victoria Nile, and various satellite water bodies in Uganda (2, 7, 14–16). The species is native to Lakes Albert, Edward, George, Kazinga Channel, and the lower Victoria Nile (Uganda), and was introduced into Lakes Victoria, Kyoga, Nabugabo, and the upper Victoria Nile in the 1950s to augment the devastated capture fisheries (Balirwa 1992). Albeit the introduction of Nile tilapia triggered increased catches, it also coincided with the many negative impacts in these water bodies. These include the massive stock decline and in some cases, extinction of the native tilapiine species such as *Oreochromis esculentus* (Singinda tilapia, Ngege) and *Oreochromis variabilis* (2, 7, 14–16). These events coincided with the dramatic upsurge of the introduced Nile tilapia catches in the 1980s (Balirwa et al. 2003). As a result, the L. Victoria basin is now predominantly inhabited by three fish species notably, the native small cyprinid silver fish (*Rastrineobola argentea*) and the two non-native (introduced) species; Nile tilapia and Nile perch.

In Uganda, Lakes Victoria, Kyoga, Albert, George, and Edward are the major fish sources and generally the central focus of scientific investigations (6, 8, 17–21). The rather less studied Victoria Nile is also a salient fish source providing employment opportunities and livelihoods to the riparian communities (22). The river drains water from L. Victoria to L. Kyoga and then through Lake Albert to form the Albert Nile (10). The prevalent anthropogenic activities in Vitoria Nile might have compromised the genetic integrity of the fish populations. For instance, in the 1950s, the first hydroelectric power dam, previously referred to as Owen Falls dam and now Nalubale dam was constructed at the source of the Nile, Jinja-Uganda (10, 23). This dam is likely to have inhibited the geneflow of fish species between L. Victoria and other sections of Victoria Nile as well as L. Kyoga (10, 24). Later (in the year 2003), another dam, Kiira, was constructed adjacent to Nalubale and perhaps exacerbated the segregation of the fish populations. In recent years, since 2007, several other hydroelectric power dams, including Bujagali and Karuma, have been constructed across the Victoria Nile, which in the long run, might pose further threats to fish biodiversity through impoundment (25, 26). Usually, the construction of hydroelectric power dams entails the structural reservation for fish-pass-ways as well as mimicking natural bays for fish spawning (26). It is not clear if these mitigation strategies were considered during the hydroelectric power dam construction in Uganda. Ecologically, power dams might promote fish population intraspecific divergent by blocking fish interface or, altering habitat conditions and existing niches. These may subsequently induce selection pressures that promote changes in the organism's behaviour and morphological variations (27).

Recently, it was observed that the genetic diversity of Nile tilapia in Victoria Nile was lower than that of other habitats such as Lake Victoria (Tibihika et al. 2020). This was likely attributed to the consequence of the constructed hydroelectric power dams, loss of diversity through overfishing or water pollution, or founder effects, inter alia, consistent with the historical fish translocations (24). Nevertheless, in the study, the small sample size is likely to have limited the clear understanding of the state of Nile tilapia populations given that only one site in the Victoria Nile was sampled (21, 24). Therefore, in the current study, we sampled multiple sites in the Victoria Nile and stretched to adjacent main water bodies (Lakes). The major focus of this study was to investigate the extent of Nile tilapia morphological variation as a potential consequence of anthropogenic activities in the Victoria Nile. We approached this study by delineating the fish size and condition factor variations, and compared the morphological differences amongst fish from Lakes Victoria, Kyoga, and upper and lower Victoria Nile. Further, we singled out non-native and native fish strains and subsequently tested the underlying morphological differences between the populations. The current study is intended to unveil key information vital for management and sustainable conservation decisions regarding Nile tilapia species in Victoria Nile.

Results

Fish size and condition factor

The comparisons of Nile tilapia populations based on body sizes; weight (g), length (cm), and CS, from the 8 populations indicated that ND Reservoir and L. Victoria individuals had relatively larger body weights and were significantly differentiated from the remaining populations ($p < 0.05$). No significant divergence was found among the remaining populations. Generally, ND_Reservoir indicated the least body size variance within the population, considering CS and length (Fig. 3b; c). Apart from ND_Reservoir, the Victoria Nile populations unveiled the smallest body weights and CS of less than 400g and 10 respectively (Fig. 3). Albeit Albert Nile and below Nalubale Dam (Victoria Nile) demonstrated relatively higher condition factor values, generally, all the Nile tilapia populations presented results higher than two (Fig. 3d).

Geometric morphometrics

PC1and PC2 accounted for 24% and 16.3% of the shape variation respectively (Fig. 4). Nile tilapia population from L. Victoria displayed higher and significant shape divergent ($p < 0.05$), followed by VN_Bukeeka, ND_Reservoir, LMF, and L. Albert, with L. Kyoga indicating the least feature changes as represented on PC1 (Fig. 4, b). On PC2, L. Albert, Albert Nile, L. Kyoga, and VN_Bukeeka presented pronounced shape feature divergence compared to the other populations. On PC2, L. Victoria indicated shape feature variability analogous to ND_Reservoir, LMF, and BN_Dam (Fig. 4a; c). Shape changes on PC1 were mainly associated with the head-to-body depth and the caudal peduncle, without shape deviations on the caudal fin origin, describing a downward pointing head and narrowing body depth, (Fig. 4 PC1; w1), see also the supplementary materials, Figure S.1. On the other hand, PC2 indicated body feature changes linked with mainly the head and body depth, with relatively shape deformations on the caudal fin origin, describing an upward-pointing head and body widening (Fig. 4 PC1; w2).

Based on CV1, Lakes Kyoga and Victoria as well as VN_Bukeeka were morphologically divergent, despite relatively overlapping (Fig. 5, a). On the same axis, two morphotype clusters i) LMF, ND_Reservior, and L. Albert, and ii) BN_Dam and Albert Nile, were observed (Fig. 5a; b). However, with respect to CV2, more clusters were revealed including, i) LMF and Albert Nile and ii) L. Kyoga and ND_Reservior, iii) L. Victoria and ND_Reservior, iv) Albert Nile and L. Albert, v) VN_Bukeeka and Albert Nile, and vi) VN_Bukeeka and LMF). On this axis (CV2), the other populations were indicated morphologically distant (Fig. 5). Despite some overlap, indicated by CV2, generally, BN_Dam and L. Kyoga, were morphologically distinct (Fig. 6). Generally, results regarding population shape differentiation based on CVA were congruent with the dendrogram (Fig. 6).

Following the population pairwise comparisons based on discriminant function analysis (DFA), the results were generally consistent with CVA and Dendrogram. Here, DFA grouped nine population pairs that are morphologically similar (Fig. 7) and 20 divergent population pairs (see supplementary materials Figure S.2). Interestingly, like in CVA and dendrogram, the individual shapes in L. Kyoga and BN_Dam population morphotypes are consistently distanced from the other populations. L. Albert Nile tilapia morphotypes showed close similarity with all the lower Victoria Nile (Albert Nile, and LMF) as well as with those of the upper Victoria Nile (VN_Bukeeka and ND_Reservoir, including L. Victoria), apart from BN_Dam and L. Kyoga (Fig. 7). The upper Murchison Falls Victoria Nile populations (VN_Bukeeka, BN_Dam, and ND_Reservoir) did not appear to associate with each other.

To further gain insights into the extent of morphological divergence between the different categories of Nile tilapia populations, we separated the groups into two; native and non-native and subjected them to CVA within groups. Results showed somewhat clear morphotype separations (Fig. 8). Albeit the non-native Nile tilapia populations were indicated relatively overlapping, the native CVA demonstrated clear separate morphotype groups (Fig. 8).

Discussion

Fish size and condition factor

Our findings show significant differences between Nile tilapia populations based on the body size and condition factor in the studied Victoria Nile ecosystem. We observed a larger body size of Nile tilapia in L. Victoria and ND_Reservoir compared to other populations. This was interesting, particularly, given that ND_Reservoir neighbors BN_Dam suggesting the likely high impact of this dam on this species geneflow. In general, all the sampled sites in Victoria Nile demonstrated small body sizes. Albeit, one may reckon that the sampling artefacts may contribute to the observed variations, centroid size generally demonstrated consistent values.

The observed size variations might be linked with some anthropogenic impacts on Victoria Nile, particularly overfishing, and habitat degradation albeit other factors such as hydroelectric power dams, and water flow rate may play pivotal roles (28). It is widely known that usually fishing targets large-bodied species and as overfishing intensifies, the fish size at maturity reduces which may elucidate the current data (28–30). Overfishing or high fishing mortality exacerbates the contemporary evolution towards the increased allocation of earlier energy to reproduction and consequently smaller-sized fish at age (30). These findings may be correlated with the previous reports which indicate that overfishing is the major cause of the dwindled fish stocks and subsequent fishery collapse in the Lake Victoria basin (15, 31). It should thus be noted that overfishing might be more detrimental in the riverine environs than in wide and open water bodies. For instance, while fisheries activities in large water bodies for example L. Victoria, can be regulated by restricting fishing in certain areas (e.g., inshore breeding areas) to allow fish stocks to recover, it can be problematic and confounding in smaller-sized water bodies like the case of Victoria Nile. This is because riverine fishing activities cannot be localised (e.g., only in the deeper/offshore waters), rather fish harvest is usually conducted throughout the water body, which does not spare areas, for example, important for breeding.

However, one salient point to note is that overfishing in Victoria Nile might have also been influenced by the existence of hydroelectric power dams (HEP). Fundamentally HEP across water bodies serve as fish barriers that subsequently confine the organisms in limited habitats. In Victoria Nile, the HEP might have confined Nile tilapia populations to the limited refugia and hence exposing the fish’s vulnerability to easy and high fishing mortality (overexploitation). Albeit there are also reports of overfishing in L. Victoria (6, 15, 32), the vast openness of water to fish movement coupled with restricted fishing areas (inshore waters) may provide the limited chances for overexploitation. Overall, these results are congruent with the previous studies on Nile tilapia of which indicators of genetic bottleneck were observed in Victoria Nile (despite one sampled site), suspected of overfishing (24). It should be noted that recently more HEP facilities have been constructed along the Victoria Nile stretch and these are likely to impose more and unprecedented threats to fish biodiversity.

Despite the significant variation in condition factor as noted amongst the studied Nile tilapia populations, the overall results demonstrated healthy fish stocks. The current condition factor results are consistent with those of (21, 33) who correlated this to the rich trophic state of the water body. The fact that all the condition factor results were contemporary in the same range (2-2.5), might elucidate that the Nile tilapia populations grow isometrically (34).

Geometric morphometrics

Divergent and significant morphotype changes were generally observed in the lakes; L. Victoria based on PC1, as well as Kyoga, Albert, and Albert Nile on PC2, compared to the other populations in the riverine environment; Victoria Nile populations. Importantly, the current study also shows that generally apart from BN_Bukeeka and L. Kyoga, the Nile tilapia morphotypes from the upper Nile (including L. Victoria) were morphologically similar to the lower Nile populations. It is expected that shape feature changes in the lotic conditions might generally differ from the lentic environment due to the continuous stressing conditions of the fast water current (35). Additionally, the prevailing natural fish barriers like the Murchison falls radically would play a pivotal role to detach the upper Nile populations from the lower ones (36), thus defining different morphotypes. Apparently, these scenarios appear to have no significant role in the morphology of the current studied populations.

This study potentially informs that the observed morphotypic clusters might be influenced by the historical anthropogenic fish translocations between the various water bodies in Uganda (5, 6, 8, 36). Fish translocation in Uganda began in the 1950s through which several tilapiine species, including Nile tilapia, were relocated into Lake Victoria and Kyoga basins from L. Albert (14, 36, 37). These reports were supported by both molecular genetics and geometric morphometric studies (21, 24, 37). It is thus likely that the closely related morphotypes between the L. Albert basin (Lower Nile) with those of the upper Nile might be a consequence of shared genotypes following the historical translocations. However, the observed distant morphotype of L. Kyoga might be associated with the founder effect detected in the previous studies (24) following the past restocking programs. Similarly, the distinct Below Nalubale Dam morphotype might be a result of geneflow constraints caused by the hydroelectric power dams coupled with divergent abiotic conditions.

Nile tilapia shape variations were mainly associated with the head-to-body depth and the caudal peduncle, describing a downward pointing head and narrowing body depth. These observations might be indicators of re-adjusting the body forms for suitability and survival in varying environments. Principally, the shape orientation, size, and structure of the body parts may permit different or same fish species to live in varying habitats or different locations of the same environment. Thus, the phenotypes or external anatomy of a fish may unveil a great deal about how and where it lives. For instance, responses to the predator-prey avoidance (e.g., pressure from Nile perch), and fast-flow water currents, inter alia, might contribute to morphological variations (35, 38, 39).

More importantly, the morphotypic divergence of ND_Reservoir from the neighboring upper Victoria Nile populations, particularly BN_Dam, may be a clear indicator of population detachment through the establishment of Nalubale HEP. Apart from the observed morphological differentiation, the Nalubale HEP might have also altered the genetic integrity of the populations which can be detrimental to the populations. This is consistent with the observed small-sized Nile tilapia in Victoria Nile and the previous studies in which the indicators of genetic bottleneck and genetic drift coupled with low genetic diversity were encountered in the river (24).

Results from the current study also show that the native Nile tilapia populations were more morphological divergent among each other than non-native ones. This suggests admixture promoted by non-native populations, which has already been reported by previous studies (Tibihika et al 2020).

In principle, the Victoria Nile fisheries particularly the upper Murchison Falls, are less or insufficiently studied. Therefore, it is apparent that the fish stocks and perhaps the water quality of this important aquatic system have been compromised which might require crucial management strategies for the sustainability of the ichthyofauna therein.

Conclusion And Recommendations

The Nile tilapia morphology and size variation are likely influenced by various anthropogenic activities ranging from, inter alia, overfishing, dams, and fish translocational history. These may compromise the sustainability of the fisheries. These threats may be mitigated by encouraging connectivity through the dams for fish passages, as well as regulating overfishing and species translocations. However, for a better understanding of how this can be done further studies are necessary. This includes studying how the anthropogenic impacts influence genetic variation and also how they induce the variation of fish species.

Materials And Methods

Study area

Nile tilapia samples were collected mainly from Victoria Nile, with additional specimens from Lakes Victoria, Kyoga, and Albert as well as the Albert Nile (Fig. 1). Field excursions were conducted between January and February 2020.

Field sampling

At the time of field data collection, the Government of Uganda had temporarily designated a quota fishing season for the Victoria Nile system to allow fish recovery following overfishing threats. In this case, prior to sampling, verbal fishing permission was acquired from the Uganda Peoples Defence Forces (UPDF), who were guarding the water bodies in Uganda at the time. Fish samples were collected using experimental gillnets (127mm mesh size), set during the day. Fishing was carried out with due diligence by avoiding any artefacts that could lead to fish shape malformations. Since fish landed when freshly dead, no special animal rights were observed/required. On landing, high-quality and fresh fish specimens were quickly weighed (g), using a digital weighing scale, measured for total length (cm) using a ruler, and subsequently photographed with a digital camera (Canon IXUS 275 HS, 12x optical zoom). The capture of digital images followed the guidelines from Tibihika, Waidbacher (21). A total of 196 individuals from 8 populations were sampled and analyzed (Fig. 1; Table 1). It should be noted that the Nalubale dam reservoir and the below Nalubale dam sampling sites were once one waterbody without any interruptions but are now separated by the Nalubale dam hydroectric power plant (see Fig. 1; between sites 2 and 3).

Table 1
Details of sample sources and sizes.

S/No	Sample source/identity	District/site	Sample size	Coordinates	
1	L. Victoria	Jinja	30	0.124216	33.237244
2	ND_Reservior	Jinja	17	0.412424	33.208296
3	BN_dam	Jinja	21	0.453489	33.181493
4	VN_Bukeeka	Kayunga	29	0.552432	33.082585
5	L. Kyoga	Nakasongola-Tumba	30	1.440512	32.595943
6	L. Albert	Buliisa-Bugoigo	20	1.898907	31.315673
7	LMF	Buliisa-Wanseko	26	2.199049	31.340102
8	Albert_Nile	Pakwach-Kalolo	23	2.45354	31.491157

S/No=Serial number, ND=Nalubale Dam, BN=Below Nalubale, VN=Victoria Nile, LMF = Lower Murchison Falls

Analyses

Fish condition factor

Condition factor/coefficient of condition (K) may be regarded as the general measure of the physical health of fish based on the assumption that heavier organisms of a given length are in better condition (40). K also commonly referred to as Fulton’s condition factor, is considered a useful approach for depicting the organisms’ (fish) physiological status and may relatively be employed as a tool for fisheries management (34, 40). Since K is directly congruent with weight, it can be pertinent and salient in assessing whether an organism is making good use of its environmental trophic resources. Therefore, in the current study, to gain insight into the broad overview of the performance of the Nile tilapia populations in Victoria Nile, we calculate K based on the expression; $K = \frac{W.100}{L^3}$, where K=condition factor, W=individual fish weight in grams and L=fish total length in cm.

Geometric morphometrics: Landmark digitization

Digitization of landmarks followed the procedures in Tibihika, Waidbacher (21). Landmark acquisition was conducted using two thin-plate spline programs (Tps): TpsUtil (utility) and TpsDig (digitizer) (41, 42). TpsUtil was used to build Tps files that were imported into TpsDig for digitizing, sequentially 15 homologous landmarks (Fig. 2) to subsequently generate two-dimensional x,y coordinates (21, 42, 43). Landmark digitization was performed by one scientist to enhance consistency and error minimization. The anatomical description of each landmark is presented in Fig. 2.

Statistical analysis

To test the effect of a given site/locality on the size (weight and length) and condition factor of Nile tilapia population variations, we used a One-Way ANOVA implemented in SPSS IBM version 21. Here, weight and length as well as the condition factor variables were taken as explanatory variables and population sites or locations as independents.

Nile tilapia shape variations were statistically investigated using the MorphoJ program, version 1.07a (45), freely downloadable from http://www.flywings.org.uk/MorphoJ_page.htm. Here, the x,y coordinates generated by the TpsDig, were imported into MorphoJ for subsequent shape extraction based on Procrustes superimposition (21). Procrustes analysis is vital for aligning the landmarks and for filtering any variations that may arise from different specimen sizes between the specimens (35). Following this analysis, a covariance matrix was generated from which various multivariate analyses including, Principal Component Analysis (PCA), Canonical Variate Analysis (CVA), and Discriminant Function Analysis (DFA) were performed. PCA was conducted to investigate and display the main features responsible for shape variation based on different Nile tilapia populations. Here, the first principle component (PC1) delineates the highest amount of variation whilst the second component (PC2) defines the next highest variability, etc. until variability becomes less vital to depict data (46). To optimize the visualization of shape feature changes based on PCA, we exported principal component scores to the SPSS program to test the effect of site/habitat on the shape variability using One-Way ANOVA procedures. CVA was carried out to portray information on the shape features that best distinguish between multiple groups of Nile tilapia through clustering. Related to PCA, we exported canonical variate scores to the SPSS program to enhance the visualization and validation of shape separation based on populations using One-Way ANOVA procedures.

To validate and enhance the effect of habitat/population site on the size variation, we analyzed centroid size (CS) variables based on MorphoJ program procedures. CS is a composite size measure based on all landmarks and is proportional to the square root of the summed squared inter-landmark distances that are employed to estimate body size in geometric morphometrics (35, 47). CS was calculated following the procedures of Procrustes superimposition (35, 45).

To further assess the nature of morphological divergence amongst Nile tilapia populations, we performed DFA for population pairwise comparisons based on wireframes. We further validated the results arising from CVA and DFA by using the SPSS program to construct a dendrogram derived from the MorphoJ averaged Procrustes coordinates program. Because the upper Murchison Falls Victoria Nile, including Lakes Kyoga and Victoria, are radically inhabited by the introduced stocks of Nile tilapia populations contrary to the lower Nile (36), we also compare the CVA results of the Native and non-native strains. Here the native Nile tilapia populations include LMF, Lake Albert, and Albert Nile. The non-natives involve Lakes Victoria and Kyoga, Nalubale Dam Reservior, Below Nalubale Dam, and Victoria Nile Bukeeka.

Declarations

Ethics approval and consent to participate

All the experimental protocols were approved by the Ugandan fisheries regulatory body: the Ministry of Agriculture, Animal Industry and Fisheries (MAAIF). All methods were carried out in accordance with the relevant guidelines and regulations. Additionally, the ethics committee of the Ugandan fisheries regulatory body: the Ministry of Agriculture, Animal Industry and Fisheries approved the study.

Consent for publication

Not applicable

Availability of data and materials

The datasets generated and/or analyzed during the current study are not publicly available due to the big size nature of the data that cannot be uploaded as a supplementary file. However, the dataset is available from the corresponding author on request

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

PDT, MC, and HM developed the research concept. PDT, CA, GM, JSL, CCO, MA, RD and TO, participated in the fieldwork. PDT analyzed, interpreted data, and wrote the initial draft manuscript. MC, HM, JSL, VTN, and CA led the review process with substantial contributions from the other authors.

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References

1. Worthington EB. A report on the fisheries of Uganda investigated by the Cambridge Expedition to the East African Lakes, 1930-31. 1932.
2. Ogutu-Ohwayo R. The reduction in fish species diversity in Lakes Victoria and Kyoga (East Africa) following human exploitation and the introduction of non-native fishes. Journal of Fish Biology.

1990;37:207-8.

3. Marten GG. Impact of fishing on the inshore fishery of Lake Victoria (East Africa). Journal of the Fisheries Board of Canada. 1979;36(8):891-900.
4. Kaufman L. Catastrophic change in species-rich freshwater ecosystems. BioScience. 1992;42(11):846-58.
5. Welcomme R. Recent changes in the stocks of Tilapia in Lake Victoria. Nature. 1966;212(5057):52.
6. Balirwa JS, Chapman CA, Chapman LJ, Cowx IG, Geheb K, Kaufman L, et al. Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? BioScience. 2003;53(8):703-15.
7. Ogutu-Ohwayo R, Hecky RE, Cohen AS, Kaufman L. Human impacts on the African Great Lakes. Environmental Biology of Fishes. 1997;50(2):117-31.
8. Balirwa J. The evolution of the fishery of Oreochromis niloticus (Pisces: Cichlidae) in Lake Victoria. Hydrobiologia. 1992 232(1):85-9.
9. Twongo T, Bugenyi F, Wanda F. The potential for further proliferation of water hyacinth in Lakes Victoria, Kyoga and Kwania and some urgent aspects for research. African Journal of Tropical Hydrobiology and Fisheries. 1995;6(1&2):1-10.
10. Dumont HJ. The Nile: origin, environments, limnology and human use: Springer Science & Business Media; 2009.
11. Andama M, Ongom R, Lukubye B. Proliferation of Salvinia molesta at Lake Kyoga Landing Sites as a Result of Anthropogenic Influences. Journal of Geoscience and Environment Protection. 2017;5(11):160-73.
12. Wanda F, Balirwa J, Ogwanga J, Moro R, Amondito B. A new water weed, giant salvinia (Salvinia molesta), invades Lake Kyoga. http://aquaticcommons.org/id/eprint/20322 National Fisheries Resources Research Institute. 2015:2.
13. Ongom R, Andama M, Lukubye B. Physico-Chemical Quality of Lake Kyoga at Selected Landing Sites and Anthropogenic Activities. Journal of water resource and protection. 2017;9(11):1225-43.
14. Trewavas E. Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia. *London: British* Museum (Natural History); 1983.
15. Njiru M, Getabu A, Jembe T, Ngugi C, Owili M, Van der Knaap M. Management of the Nile tilapia (Oreochromis niloticus (L.)) fishery in the Kenyan portion of Lake Victoria, in light of changes in its life history and ecology. Lakes & Reservoirs: Research & Management. 2008;13(2):117-24.
16. Fuerst P, Mwanja W, Kaufman L, editors. The genetic history of the introduced Nile tilapia of Lake Victoria (Uganda–E. Africa): the population structure of Oreochromis niloticus (Pisces: Cichlidae) revealed by DNA microsatellite markers. Tilapia Aquaculture in the 21st Century Proceedings from the Fifth International Symposium on Tilapia in Aquaculture; 2000.
17. Witte F, Kishe-Machumu MA, Mkumbo OC, Wanink JH, Goudswaard PC, Van Rijssel JC, et al., editors. The fish fauna of Lake Victoria during a century of human induced perturbations. Proc Fourth Int Conf On African Fish and Fisheries 2013; Addis Ababa, Ethiopia.

18. Goudswaard PC, Witte F, Katunzi EFB. The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. Journal of Fish Biology 2002;60:838-56.
19. Graham M. The Victoria Nyanza and its Fisheries: A Report on the Fishing Survey of Lake Victoria, 1927-1928, and Appendices: Crown agents for the Colonies; 1929.
20. Tibihika PD, Curto M, Dornstauder-Schrammel E, Winter S, Alemayehu E, Waidbacher H, et al. Application of microsatellite genotyping by sequencing (SSR-GBS) to measure genetic diversity of the East African Oreochromis niloticus. Conservation Genetics. 2019:1-16.
21. Tibihika PD, Waidbacher H, Masembe C, Curto M, Sabatino S, Alemayehu E, et al. Anthropogenic impacts on the contextual morphological diversification and adaptation of Nile tilapia (Oreochromis niloticus, L. 1758) in East Africa. Environmental Biology of Fishes. 2018;101(3):363-81.
22. Witte F, de Graaf M, Mkumbo OC, El-Moghraby AI, Sibbing FA. Fisheries in the Nile system. The Nile: Springer; 2009. p. 723-47.
23. Green J. Nilotic lakes of the Western Rift. . In: Dumont H.J. (eds) The Nile. Monographiae Biologicae. The Nile. 89: Springer, Dordrecht; 2009. p. 263-86.
24. Tibihika PD, Curto M, Alemayehu E, Waidbacher H, Masembe C, Akoll P, et al. Molecular genetic diversity and differentiation of Nile tilapia (Oreochromis niloticus, L. 1758) in East African natural and stocked populations. BMC Evolutionary Biology. 2020;20(1):16.
25. Dudgeon D. Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity: the construction of large dams will have an impact on the biodiversity of tropical Asian rivers and their associated wetlands. BioScience. 2000;50(9):793-806.
26. Williams JG, Armstrong G, Katopodis C, Larinier M, Travade F. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Research and Applications. 2012;28(4):407-17.
27. Price TD, Qvarnström A, Irwin DE. The role of phenotypic plasticity in driving genetic evolution. Proceedings of the Royal Society of London Series B: Biological Sciences. 2003;270(1523):1433-40.
28. Wilson S, Fisher R, Pratchett MS, Graham N, Dulvy N, Turner R, et al. Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecological Applications. 2010;20(2):442-51.
29. Yanti A, Tresnati J, Yasir I, Rahmani P, Aprianto R, Tuwo A, editors. Size at the maturity of sea cucumber Holothuria scabra. Is it an overfishing sign in Wallacea Region? IOP Conference Series: Earth and Environmental Science; 2020: IOP Publishing.
30. Audzijonyte A, Kuparinen A, Gorton R, Fulton EA. Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. Biology letters. 2013;9(2):20121103.
31. Njiru M, Nzungi P, Getabu A, Wakwabi E, Othina A, Jembe T, et al. Are fisheries management, measures in Lake Victoria successful? The case of Nile perch and Nile tilapia fishery. African Journal of Ecology. 2007;45(3):315.

32. Lowe-McConnell R, editor The changing ecosystem of Lake Victoria, East Africa. Freshwater Forum; 1994.
33. Balirwa JS. Lake Victoria wetlands and the ecology of the Nile tilapia, Oreochromis niloticus Linne. Rotterdam: Balkema; 1998.
34. Ighwela KA, Ahmed AB, Abol-Munafi A. Condition factor as an indicator of growth and feeding intensity of Nile tilapia fingerlings (Oreochromis niloticus) feed on different levels of maltose. American-Eurasian Journal of Agricultural and Environmental Science. 2011;11(4):559-63.
35. Kelley JL, Davies PM, Collin SP, Grierson PF. Morphological plasticity in a native freshwater fish from semiarid Australia in response to variable water flows. Ecology and Evolution. 2017;7(16):6595-605.
36. Ogutu-Ohwayo R. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, Oreochromis niloticus. Environmental biology of fishes. 1990;27(2):81-96.
37. Mwanja WW. Genetic biodiversity and evolution of two principal fisheries species groups, the Labeine and Tilapiine, of Lake Victoria Region, East Africa: The Ohio State University; 2000.
38. Ohlberger J, Staaks G, Hölker F. Swimming efficiency and the influence of morphology on swimming costs in fishes. Journal of Comparative Physiology B. 2006;176(1):17-25.
39. Eklöv P, Svanbäck R. Predation risk influences adaptive morphological variation in fish populations. The American Naturalist. 2006;167(3):440-52.
40. Froese R. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. Journal of applied ichthyology. 2006;22(4):241-53.
41. Rohlf FJ. Geometric morphometrics and phylogeny. Systematics Association Special Volume. 2002;64:175-93.
42. Zelditch ML, Swiderski DL, Sheets HD. A Practical Companion to Geometric Morphometrics for Biologists: Running analyses in freely-available software. Free download from http://booksite elsevier com/9780123869036/content/Workbook pdf. 2012.
43. Park PJ, Aguirre WE, Spikes DA, Miyazaki JM. Landmark-Based Geometric Morphometrics: What fish shapes can tell us about fish evolution. Proceedings of the Association for Biology Laboratory Education. 2013;34:361-71.
44. Ndiwa TC, Nyingi DW, Claude J, Agnèse J-F. Morphological variations of wild populations of Nile tilapia (Oreochromis niloticus) living in extreme environmental conditions in the Kenyan Rift-Valley. Environmental Biology of Fishes. 2016;99(5):473-85.
45. Klingenberg CP. MorphoJ: an integrated software package for geometric morphometrics. Molecular ecology resources. 2011;11(2):353-7.
46. Jolliffe I. Principal Component Analysis and Factor Analysis. In: Principal Component Analysis. Springer Series in Statistics. Springer, New York. 2002.
47. Mitteroecker P, Gunz P, Windhager S, Schaefer K. A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. Hystrix, the Italian Journal

of Mammalogy. 2013;24(1):59-66.

Figures

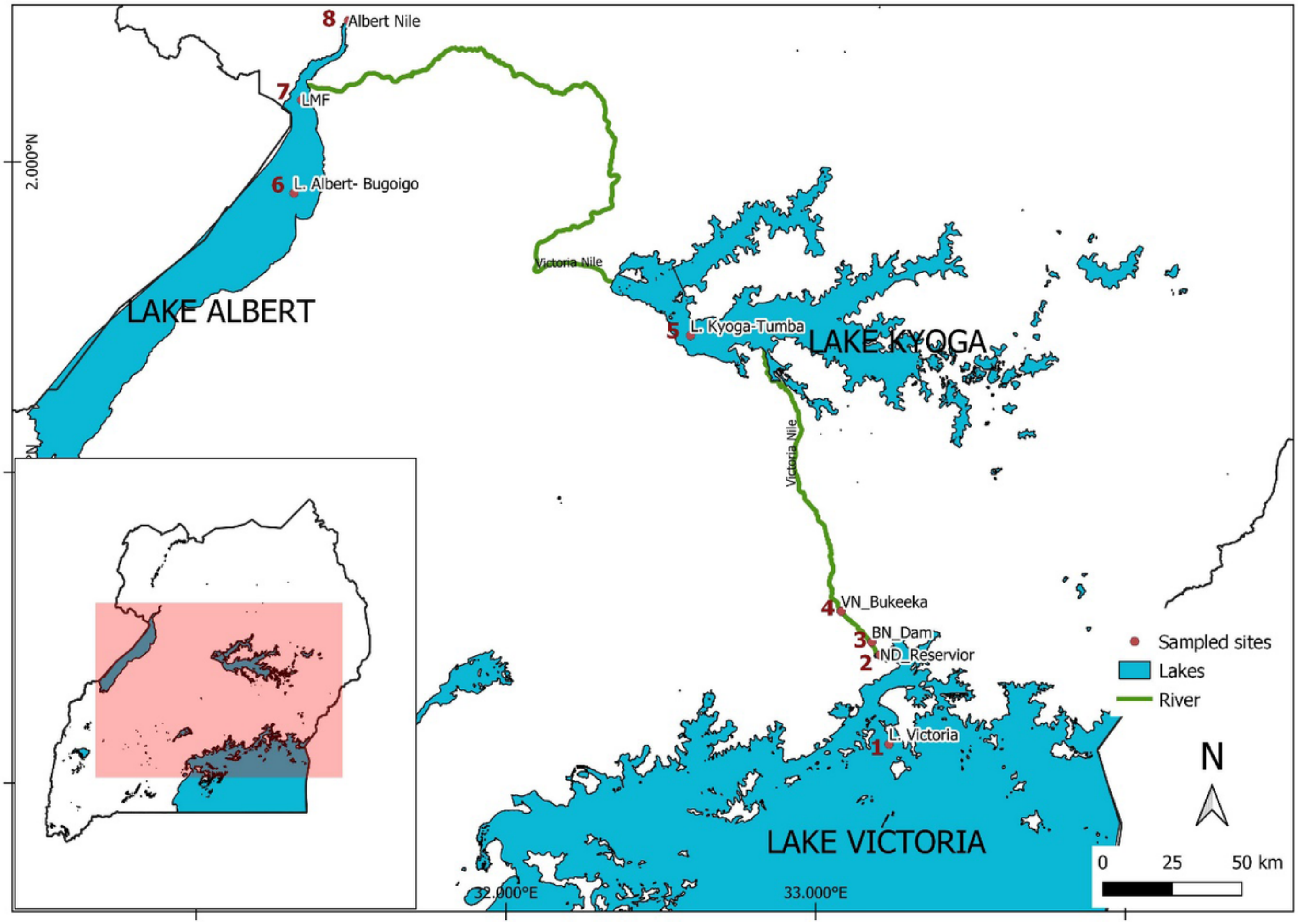

Figure 1

Collection sites of Nile tilapia samples. Numbers from 1 to 8 indicate sample collection sites. The Nalubale hydroelectric power dam lies between sites 2 and 3. See also Table 1 for specific site descriptions.

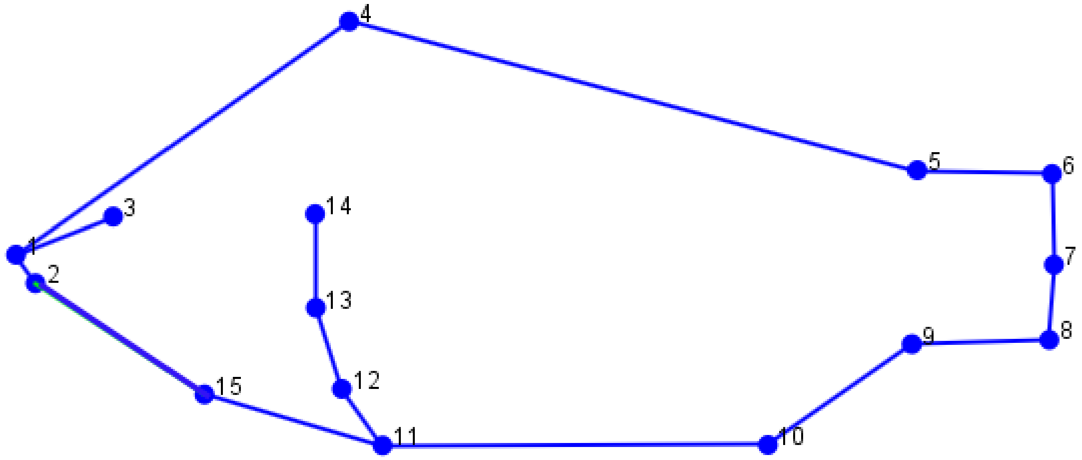

Figure 2

Specimen wireframe illustrating the positions of 15 homologous landmarks: (1) anterior tip of the snout with mouth closed, (2) posterior end of the mouth, (3) Orbit/eye centre, (4 & 5) anterior and posterior insertions of the dorsal fin, (6) the dorsal origin of the caudal fin, (7) mid-dorsal and ventral origin of the caudal fin, (8) the ventral origin of the caudal fin, (9) posterior insertion of the anal fin, (10) the anterior origin of the anal fin, (11) the anterior origin of the pelvic fin, (12) the posterior origin of the pectoral fin, (13) the anterior origin of the pectoral fin, (14) most posterior end of the operculum, and (15) juncture of the ventral edge of the operculum (1, 2).

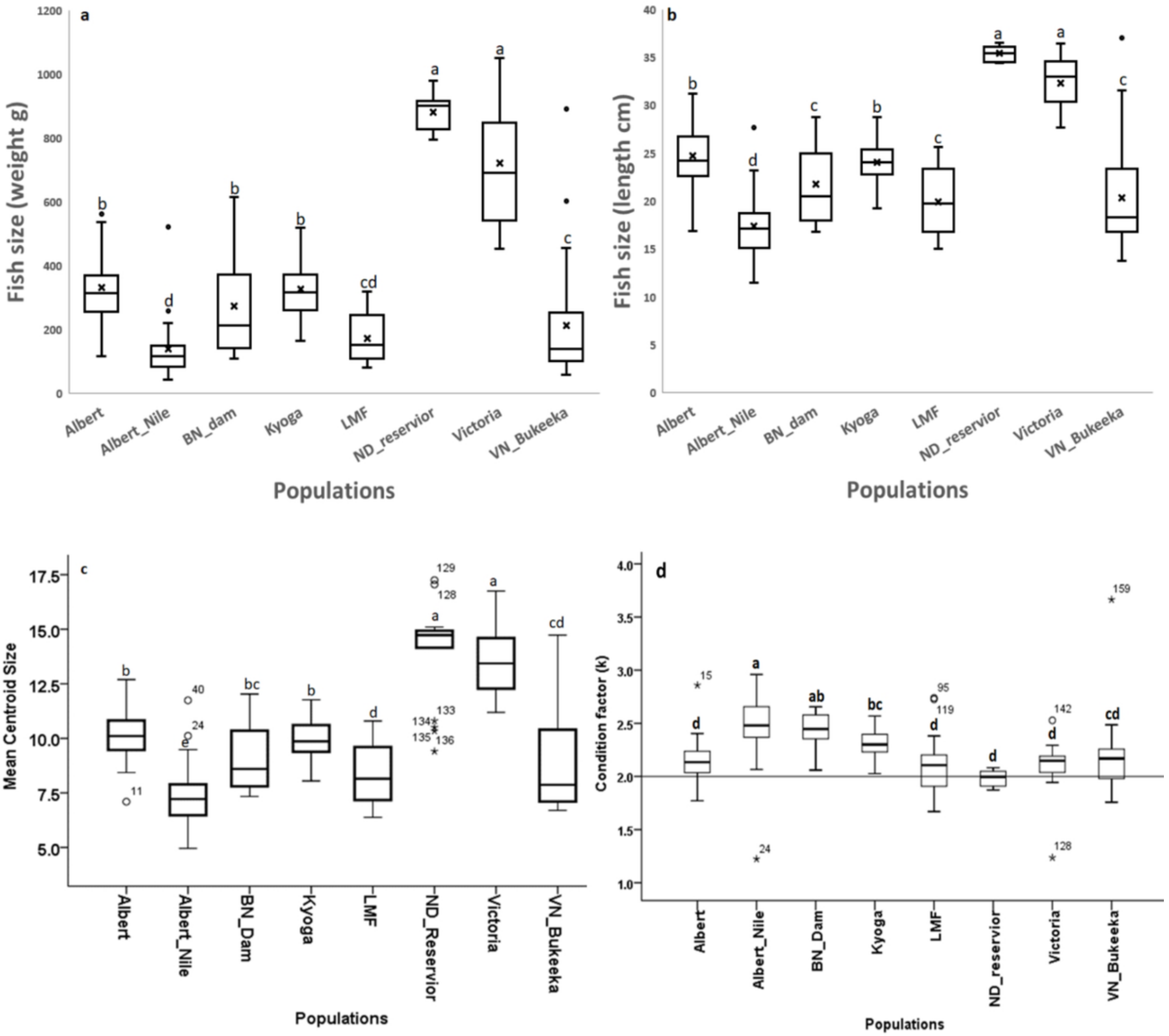

Figure 3

Body size variations of Nile tilapia populations, depicting weight (a), length (b), Centroid Size (c), and condition factor (d). Different superscript letters indicate statistically significant different values ($p<0.05$) and vice versa.

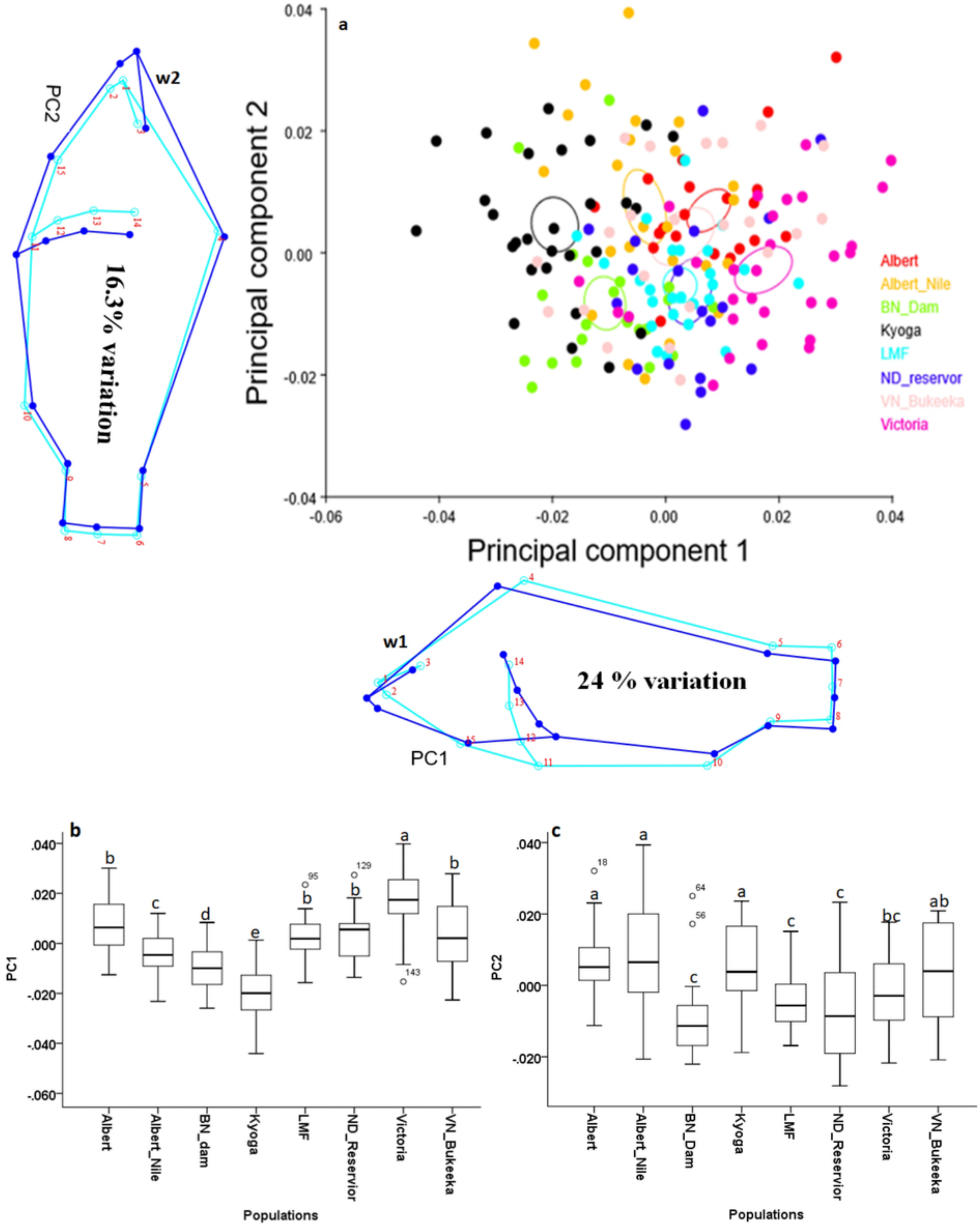

Figure 4

Illustration of PCA for the 8 Nile tilapia populations depicted from principal component (PC) scores. a represents PCA scatter plot, w1 and w2 depict wireframes for PC1 and PC2 respectively, demonstrating deformations for the major features behind the morph variations. Wireframe colors; light green and light blue, show the ideal shape and shape-change respectively. Ellipses in the scatter plot represent a 95% confidence interval for the means. b and c depict PC1 and PC2 scores plotted on bar graphs respectively.

Different superscript letters on the bar graphs indicate statistically significant Nile tilapia shapes (p<0.05) and vice-versa.

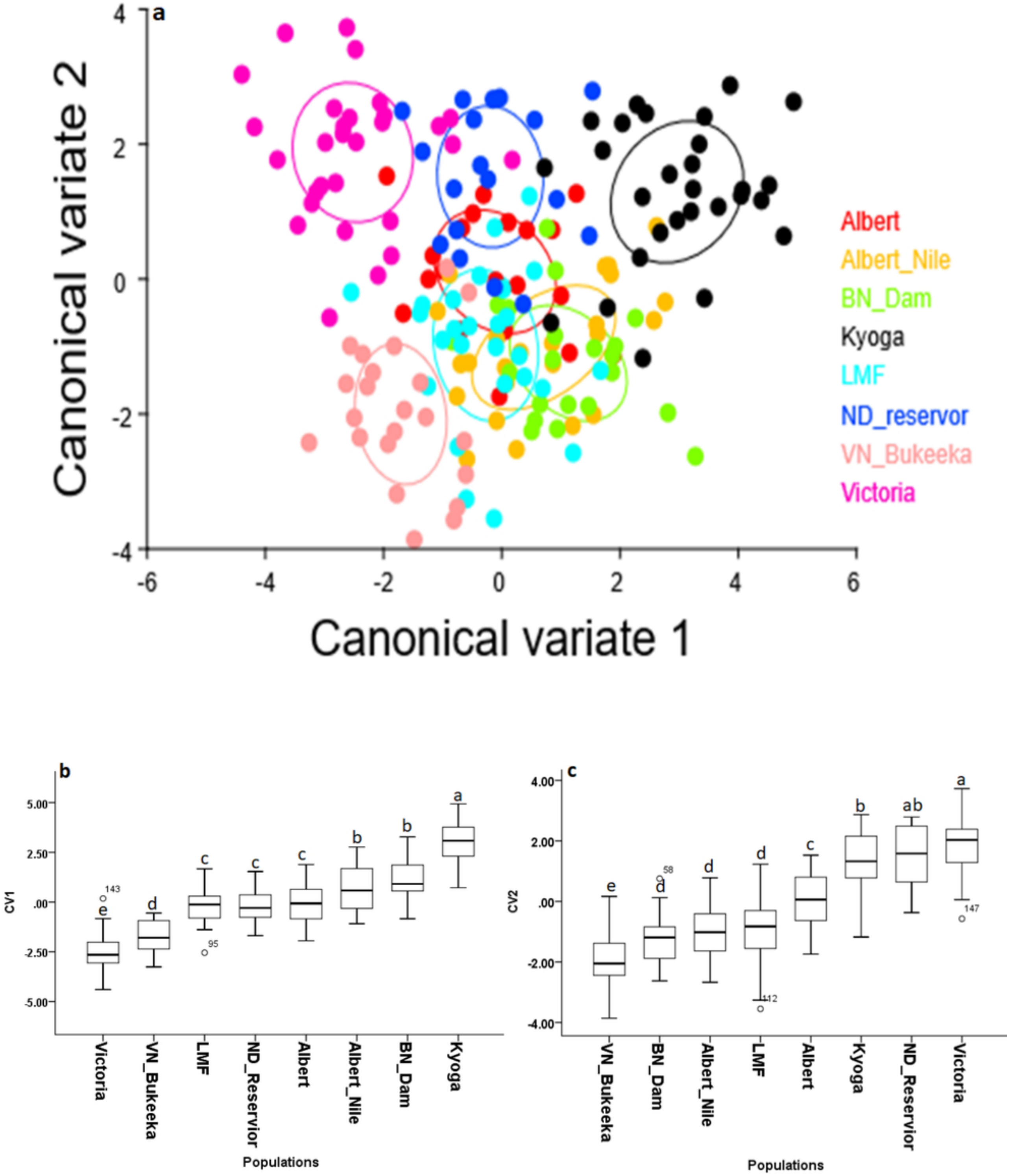

Figure 5

Illustration of CVA for the 8 Nile tilapia populations, depicted from canonical variate (CV) scores. a represents CVA scatter plot, while b and c portray CV1 and CV2 scores plotted on bar graphs respectively.

Ellipses in the scatter plot represent a 95% confidence interval for the means set at 10,000 iterations. Similar superscript letters on the bar graphs indicate that populations are morphologically clustered together and therefore undifferentiated significantly ($p<0.05$) and vice-versa.

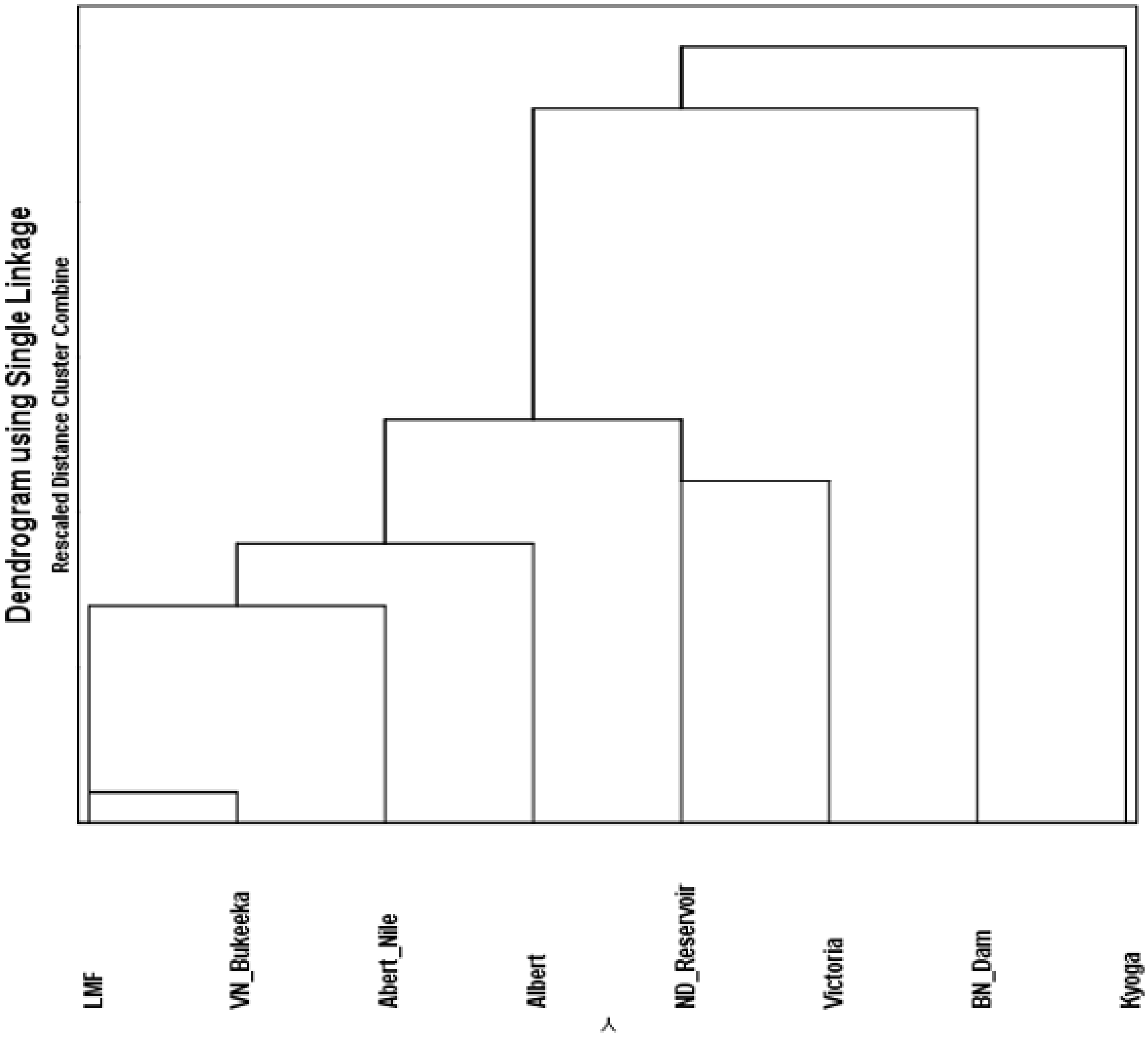

Figure 6

Dendrogram illustrating the Nile tilapia population clusters derived from the Procrustes coordinates.

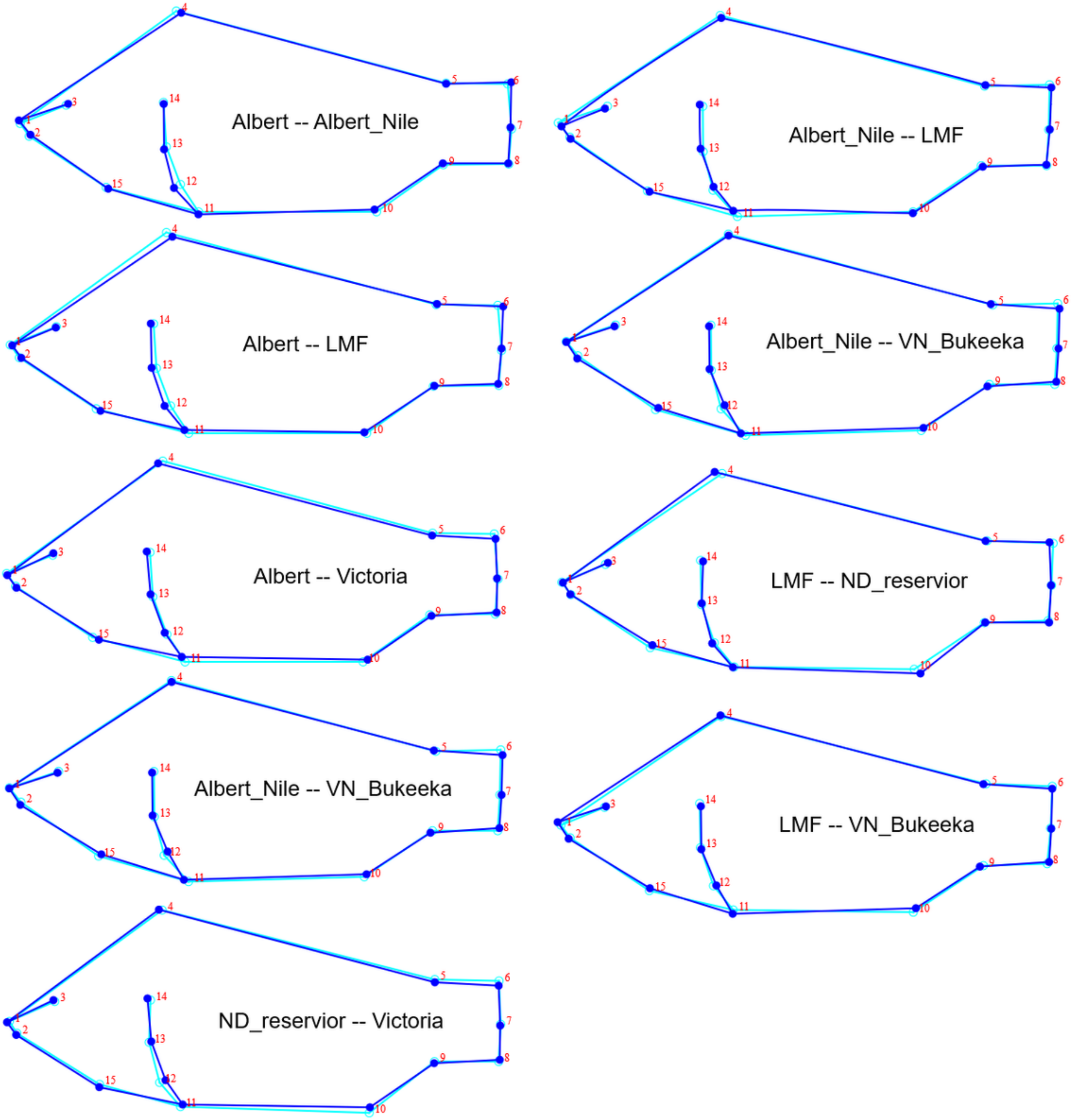

Figure 7

Population pairwise comparison of Nile tilapia morphotypes based on discriminant function analysis (DFA). The wireframe colors; light green and light blue, represent the shapes of the compared population pairs.

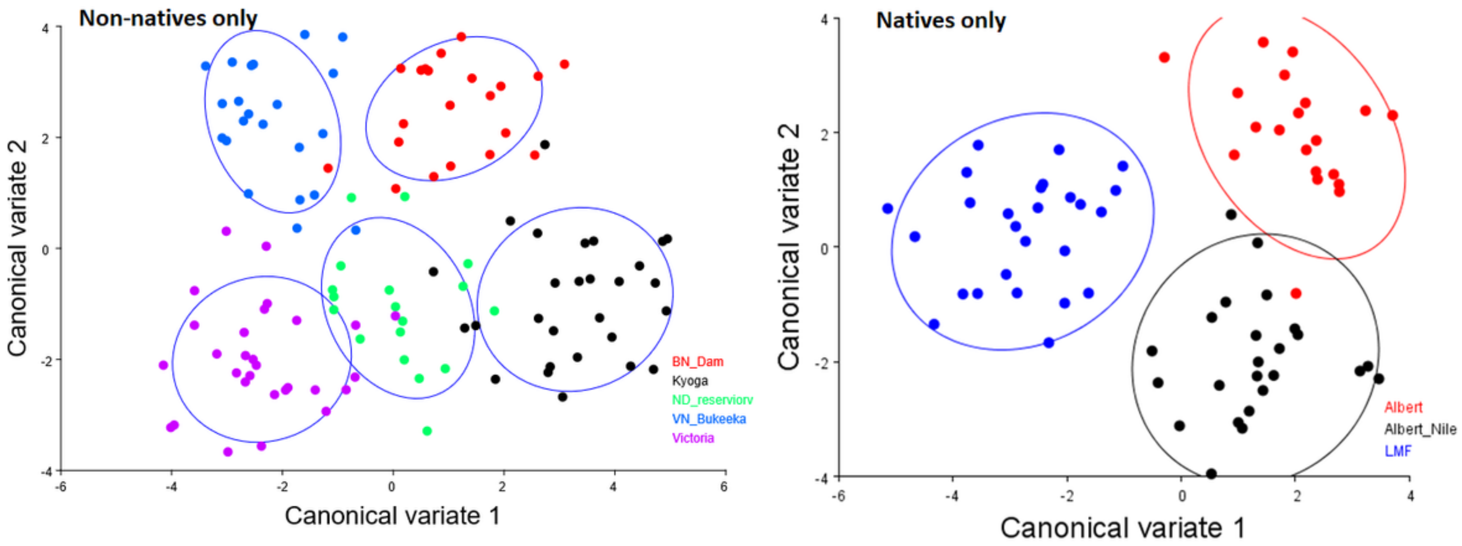

Figure 8

Within CVA results indicate the shape comparisons between Nile tilapia populations in nonnative and native habitats.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarymaterials.docx