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Genetic structure of Nile tilapia (*Oreochromis niloticus*, L. 1758) in protected and unprotected freshwater lakes in East Africa

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Abstract
There has been a drastic decline in the size of cichlid fishes populations since the beginning of the 20th century. This fish decline is mainly caused by an increase in the size of the human population, increased fishing pressure and fish introductions. This decline results in a reduction in genetic diversity in the surviving populations as a result of genetic drift. The Ecosystem Approach to Fisheries Management agitates for provision of Marine Protected Areas (MPAs) which seem to be effective in developed countries. However, efforts to control artisanal fisheries through protection have not been adequately assessed in East African Freshwater lakes. Assessment of genetic structure in populations is important for their future conservation and management. The population genetic structure of the Nile tilapia was assessed using nucleotide variation of mitochondrial control region sequences and four nuclear microsatellite loci in 128 individuals from seven localities. 43 mitochondrial DNA (mtDNA) haplotypes were observed, fourteen of which were geographically localized. The study revealed a significant genetic differentiation between the populations at the mitochondrial and microsatellite loci. The possible contributions from human activities such as water pollution, overfishing and fish introductions are also discussed.
***Keywords**:* Genetic structure, Nile tilapia, overfishing, freshwater protected areas

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1. Introduction

The freshwater lakes of East Africa contribute to global biodiversity (Beadle, 1981; Fryer and Iles, 1972; Trewavas, 1983; Stiassny and Meyer, 1999). The cichlid family has over 220 recognized genera with approximately 2000 species (Kullander, 1998). Members of this family are found mainly in the freshwaters of Africa. However, the biodiversity in East African freshwater lakes is vulnerable to anthropogenic threats including fishing. Establishing protected areas has been proposed as one of the methods of conserving biodiversity in an ecosystem [Sturmbauer, 2008; Van der Knaap,2013; Vandeperre et al., 2011, Pauly et al., 2002). The use of protected areas ensures that some essentially unmodified ecosystems exist for buffering against uncertainty such as overfishing. It is well documented in marine ecosystems that protected areas harbor more species compared with unprotected areas (Sahyoun et al., 2013). Studies of fresh water ecosystems have reported that fish in protected areas are larger than those in unprotected areas (Cucherousset, et al.,2007). However, the focus of protected areas is on terrestrial ecosystems than aquatic biodiversity, which limits assessment of biodiversity in both protected and unprotected areas (Pressey, et al., 2002). Freshwater protected areas have already been shown to be efficient for conserving bird and fish diversity (Cucherousset, et al.,2007). The East African freshwater lakes studied included Lake Edward which is shared between Uganda (29%) and the Democratic Republic of Congo (71%) which is located in the western Great Rift Valley at an elevation of 920 m above sea level, with its northern shores a few kilometers south of the Equator (0020'S 29036'E).

Lake George is a shallow lake with a mean depth of 2.5 m, a maximum depth of 4 m and an area of 250 km^2. It is situated astride the equator in the western arm of the East African rift valley at an altitude of 914 m. Lake George is shared by Rubirizi, Kasese and Kamwenge districts and three quarters is located in the national park (Fig. 1). The fisheries are an important source of food, livelihood and income to residents in the landing sites and to urban dwellers in western and central Uganda. The fish fauna of the lakes Edward and George is as diverse as its geological history (Bassa et al 2013). The lake shares some fish species with Lake Albert and others with lakes Victoria and Kivu. Geological evidence suggests that Lake Edward has had a connection with Lake Victoria up to probably the early Pleistocene period, approximately one million years ago (Bassa et al 2013). Thus most of the cichlid fishes in the lakes Edward and George are similar to those of Lakes Victoria and Kivu suggesting a common ancestry. Lakes Edward, George and Kazinga channel are home to many fish species with

the commercial fisheries dominated by the Nile Tilapia (Oreochromis niloticus), Bagrus docmac (Cat fish also known locally as Semutundu), and Protopterus aethiopicus (Lungfish) and Clarias gariepinus (Mudfish) and the other fish species include over 50 species of the unexploited haplochromine (Nkejje) that dominate the lakes' fish biomass. Other fauna living in the study area include the chimpanzees, elephants, hippos, crocodiles and lions which are protected by the national parks (Bassa et al 2013).

1.1 Phylogeny of African Cichlids

The Great Lakes of East Africa are home to an exceptionally diverse ichthyofauna (Fryer and Iles, 1972). The most famous elements of the lakes' faunas are the cichlid fishes that have formed species flocks of an unparalleled species-richness and degree of eco-morphological and behavioral complexity (Stiassny and Meyer,1999; Kocher, 2004; Koblmüller *et al*., 2006). It has been estimated that almost 2000 cichlid species inhabit Lakes Tanganyika, Malawi and Victoria and that these lake endemic species are likely to have evolved in the last few million yesrs or as recently as the last thousands of years only (Salzburger, *et al.*, 2005; Salzburger *et al*., 2002). The cichlid species flocks from the East African Great Lakes have received considerable attention as model systems for the study of adaptive radiation and explosive speciation (Salzburger and Meyer, 2004; Kornfield and Smith, 2000). Cichlid fishes are the only freshwater representatives of the suborder Labroidei and are naturally distributed across Africa, Madagascar, South and Central America, the Middle East, and the Indian subcontinent (Fig.1).

The purpose of this study was to assess and compare genetic diversity differences in Nile tilapia populations between protected and unprotected areas. To achieve this, we compared genetic diversity between protected areas and unprotected areas in East African Lakes. This information is important in assessing the extent of human influence in genetic diversity in the ecosystem.

2. Materials and Methods

2.1 Study populations

A total of seven Nile tilapia populations, 5 native (Lakes Albert, Edward, George, Kivu and Tanganyika) and 2 introduced (Lakes Kyoga and Victoria), were investigated in this study. Lakes Albert and Edward are rift valley lakes, found on the western border of Uganda with Democratic Republic of Congo. Edward and George are connected by Kazinga channel, whereas the Victoria Nile connects lakes Victoria, Kyoga and Albert with waterfalls, Owen and Murchison on either side of Lake Kyoga. Lake Kivu is shared by the DRC and Rwanda (Fig. 1). The lake lies in the centre of the axis of the western branch of the East African Rift and is, with an elevation of 1,463 m above sea level, at highest altitude lake within this branch. Lake Kivu has a surface area of 2,370 km^2, a volume of 549 km^3, a catchment area of ~ 7,140 km^2, and reaches a maximum depth of ~ 485 m in its northern basin. All the native populations have zones located in protected areas.

The protected areas of Lake Tanganyika are located at the lake's shores of **Gombe Stream National** Park and Mahale Mountains National Park in Tanzania, Rusizi Natural Reserve in Burundi (which is also a Ramsar Site), and Nsumbu National Park in Zambia**.**

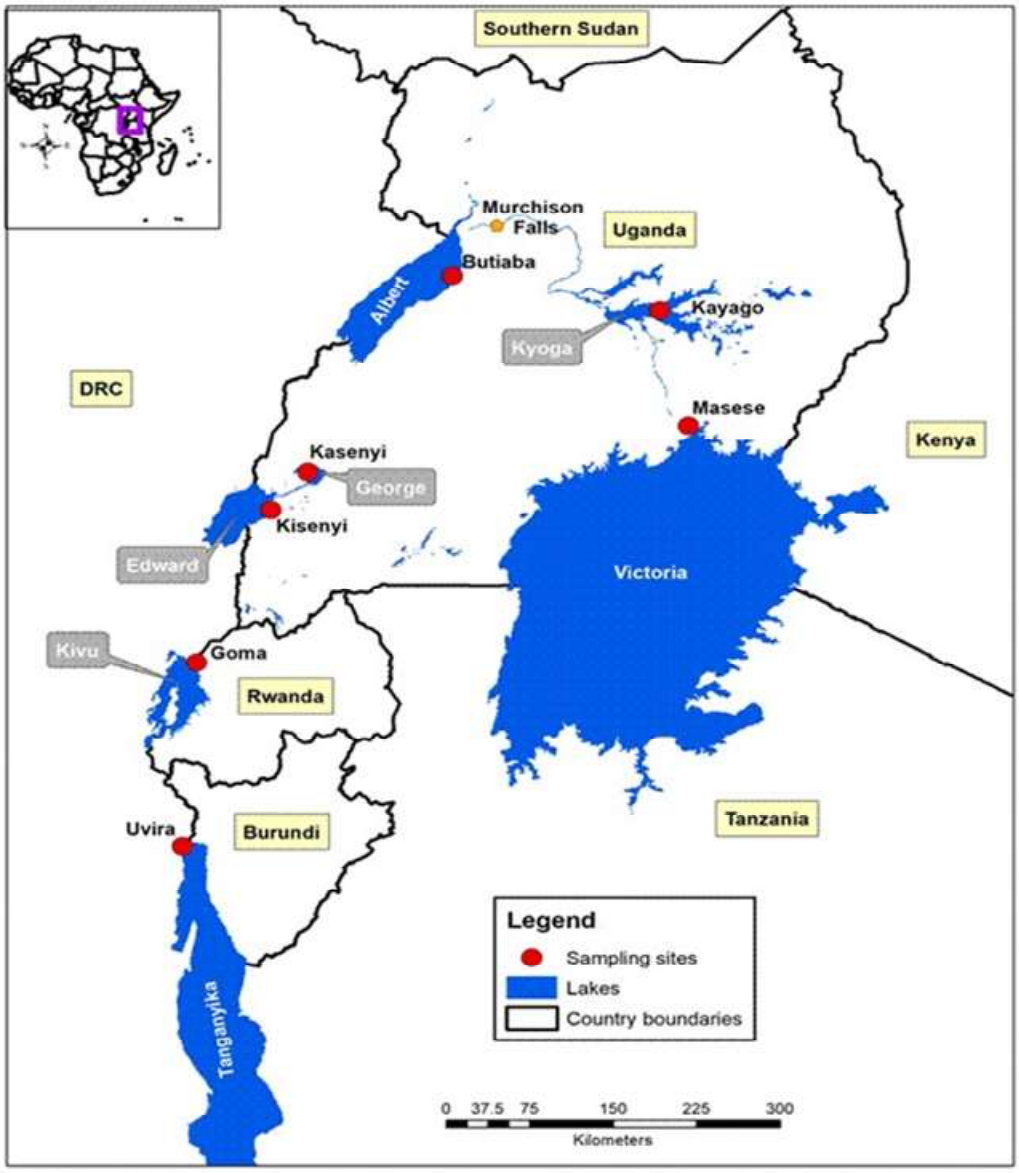

Figure 1: Map of East Africa showing the sampled Nile tilapia populations (Adopted from Twesigye *et al* 2024)

2.2 Protected populations

The protected Nile tilapia populations are located in the Nilotic Lakes of the Western Rift (Figure 1). They include George, Edward and Albert in the valley (Tibihika *et al* 2018). Lake Edward and George are connected by Kazinga Channel. Lake Tanganyika is the largest among the native populations. The Lake is outstanding for its extraordinary north-south extension (670 km) and depth (1,470 m). Lake Kivu is the 5th native population which lies on the border between the Democratic Republic of Congo and Rwanda, and is in the Albertine (western) Rift, a part of the Great Rift Valley. The lake covers a total surface area of some 2,700 km^2 and stands at a height of 1460 m above sea level. Lake Albert is a typical Rift Valley lake lying at an altitude of 615 m between two parallel escarpments on the western side.

2.3 Unprotected populations

Lake Victoria, with a surface area of 68,800 km^2 and an adjoining catchment of 184,000 km^2, is the world's second largest body of fresh water, and the largest in the developing world, second only to Lake Superior in surface area (Ogutu-Ohwayo1990). Lake Victoria touches the Equator in its northern reaches, and is relatively shallow, reaching a maximum depth of about 80 m, and an average depth of about 40 m. Many of the rivers now flowing east into Victoria once flowed west, at least in the Miocene, Pliocene, and part of the Pleistocene eras, possibly eventually into the Nile system, and more recent upthrust of the western side of the basin is thought to have reversed these rivers, and caused Lake Victoria to form by flowing eastwards (Beadle ,1981). Lake Victoria is the youngest of East Africa's Great Lakes that formed between 250,000 and 750,000 years ago (Johnson *et al*., 1996). The second unprotected population of the Nile tilapia is Kyoga which is formed by a complex of earth movement, that began in the Miocene and eventually resulted in the faulting of the Western Rift Valley which caused the reversal of the previous east-west drainage.

2.4 Sampling

Tissue samples were obtained from individual fishes using a pair of forceps and surgical blade from both native and introduced populations of *O. niloticus* (Fig1). The forceps were cleaned with hydrogen peroxide (H_2O_2) and sterilized with 96% ethanol between samples while surgical blades were used only once to prevent cross contamination of subsequent samples. They were collected from Lakes Albert (AL, n = 21); Edward (ED,n =16); George (GE, n = 19); Kivu (KI, n =23); Victoria (VI, n =20); Kyoga (KY, n =09); & Tanganyika (TZ,n =20). In this study each lake was assumed to be comprised of one population. In the field, samples were preserved in sterile microtubes containing 25% dimethylsulphoxide (DMSO) in saturated sodium chloride solution and stored at room temperature in the field and at -80°C in the laboratory. The laboratory methods included three major steps: DNA extraction, amplification and sequencing.

2.5 DNA extraction

In this study, total genomic DNA was extracted using the DNeasy tissue Kit (QIAGEN) according to the manufacturer's instructions. The extraction process involved macerating the sample tissue on a microscope slide using a surgical blade. The macerated material was digested with Proteinase K at 55ºC overnight, followed by binding of the DNA, washing and elution. DNA extracts were stored at -20ºC. The success of the extraction was tested using 5µL of total genomic DNA which was electrophoresed on 2% Neusive Agarose gel stained with Ethidium bromide and visualized using utra violet light.

2.6 DNA amplification and Sequencing

A fragment of the mtDNA control region (D-loop) was PCR amplified using the primer pair *On-fwd (*5'-CCGGATGTCGAAGGTTAAAGTTCCTTCC3') and *On-rvs((*5'CCACGAATAATTGTCCTTGACCTTCAAGAACC 3') specifically designed for this study using *AMPLIFY 1.2* program.The PCR (Polymerase Chain Reaction) was carried out in 50µL reaction volumes containing 10ng of total genomic DNA, 50 pmol of each of the primers, 5XPCR reaction buffer (Boehringer Mannheim GmbH), 50 pmol of deoxynucleotide triphosphates (dNTPs), and 1 unit of *Taq* polymerase. Amplification was performed under the following conditions: one cycle of denaturation at 94ºC for five minutes, followed by 35 cycles denaturation at 94 for one minute, annealing at 55ºC for two minutes and a final extension at 72ºC for three minutes. Negative controls were also run alongside the amplification reactions to check for possible contamination of the reaction cocktails, thus authenticating that the amplified and finally sequenced DNA was from the specimens under study. Single-stranded DNA was dissolved in distilled water and used as template for sequencing by dideoxy chain-termination method (Sanger *et al*. 1977) using sequenase kit version 2.0 (Amersham Pharmacia Biotech, Inc.), [ά-^{35}]-dATP(Amersham Pharmacia Biotech, Inc.) and a primer complemenary to the template. Products of the sequencing reaction were electrophoresed using 6% polyacrylamide/7M-urea gel. The gel was fixed, dried, exposed on a Kodak film for 24-48 hours and read manually.

With the samples which were processed for automated sequencing, the PCR was performed in a 50µL reaction volume cotaining 2-5ng of genomic DNA, 50 pmol of each primer, 10xPCR gold buffer (Applied Biosytems), 50 pmol deoxynucleotide triphosphates (dNTPs),14 µL double distilled water and 1.2 units of *AmpliTaq Gold DNA* polymerase,(Applied Biosytems). PCR control experiments were included in all amplifications to check for any possible contaminations. The double-stranded PCR products were purified using QiaQuick PCR purification kit(Qiagen) and cycle-sequenced using 25 cycles of denaturation at 96ºC for 10 s, annealing at 50ºC for 5 s, and extension at 60ºC for 4 minutes. Both the forward and reverse strands were sequenced following the dideoxy-chain termination method (Sanger *et al*., 1977) with a cycle sequencing kit (Applied Biosystems, USA),

according to the manufacturer's instructions. The cycle-sequenced products were ethanol precipitated using 3M Sodium Acetate (pH 4.6) and 96% Ethanol, followed by 70% and finally dried at 65ºC.The products were electrophoresed using 4% polyacrylamide gels on an ABI 377 prism (Applied Biosystems) and analyzed using the program Sequencher.

2.7 Microsatellite amplification and genotyping

Microsatellite amplification was done using primers developed by Lee and Kocher (1996). Several microsatellite loci originally described were screened for use in the Nile Tilapia. Four of them were chosen on the basis of their polymorphism, clarity of alleles on gels and possibility of multiplexing. The 4 that were chosen and optimized for the Nile tilapia were UNH1009, UNH007, UNH009, and UNH111.Two of the four loci (UNH1009 and UNH111) were dinucleotide repeats while the other two were trinucleotide repeats. The four loci were used for genotyping 78 individuals from 5 populations (Albert, Edward, George, Kyoga, and Victoria). Polymerase chain reaction (PCR) was carried out on all loci using primer labeled with the fluorescent marker for visualization (one primer in each primer set).

2.8 Sequence Data analysis

The mitochondrial DNA control region sequence data was analyzed for three major aspects; genetic diversity, evolutionary relationships between haplotypes, and genetic differentiation between populations. Basic statistics of sequence variation which included haplotype diversity, number of haplotypes and Nucleotide diversity (**π,** equation 10.5, in Nei (1987) were used to estimate genetic variation. Exact tests of population differentiation (based on segregating sites and haploype frequencies, population pairwise comparisons, and analysis of molecular variance (AMOVA: Excoffier *et al.,* 1992) were estimated to infer population genetic structure using the program ARLEQUIN version 2.000 (Schneider *et al.,* 2000).

2.9 Microsatellite data analysis

Microsatellite data was analyzed to assess genetic diversity within populations, population subdivision, and phylogenetic relationships between Nile tilapia populations. Genetic diversity was estimated by calculating mean number of alleles per locus, mean observed and expected heterozygosity per locus (He and Ho) under the Hardy-Weinberg expectations (Nei, 1987).

3. Results

3.1Mitochondrial control region sequence variation patterns

The mitochondrial control region showed significant sequence variation, with 63(15.75%) polymorphic sites from a 400 bp fragment and defining 43 haplotypes out of 128 individuals of Nile tilapia obtained from both native and introduced populations (Fig 2.) The estimated nucleotide diversity for all the populations was 2.6% but it varied from as low as 0.43% in Lake Tanganyika

to 1.2% in Lake Edward and George. Within populations, Lake Tanganyika showed the lowest haplotype diversity (0.46), while the highest was observed in Lake Kivu (0.95). Estimates of genetic diversity for the Nile tilapia populations are summarized in Table 1. In Lake Kyoga 66% (6 out of 9) shared the same haplotype (A886) with Lake Albert, George and Victoria. The other 3 haplotypes (K502; K509 and K511) were encountered once. Three haplotypes were observed in Lake Tanganyika. Seventy five percent (15 out of 20) of all the individuals sampled in Lake Tanganyika had the same haplotype (T1297). Five haplotypes (A886, E937, E940, E944 and E954) occurred in more than one population, with haplotypes E937, E940 and A886 being the most widely distributed. The occurrence of 11 haploypes (2-12) was restricted to Lake Albert while another 11(21 -31) were restricted to Lake Kivu and all the 3 haplotypes (32, 33 and 34) from Lake Tanganyika were not recorded in any other population.

The highest number of hyplotypes were recorded in Lakes Albert, Kivu and George respectively. It should be noted that all the three were native populations and included zones under Protected Areas. Lakes Kyoga and Victoria are introduced and unprotected populations after the decline of the Lake Victoria fishery in the 1950s as a result of overfishing.

The mean nucleotide diversity observed for native populations was 0.89 compared to 0.65 that was observed for introduced populations (Table 1). The native populations recorded a mean haplotype diversity (H) value of 0.77 while the mean value for introduced populations was 0.67. A mean value for the number of haploypes (A) recorded for native populations was 7.6 compared to a mean value of 5.5 for introduced populations. However, both native and introduced populations recorded a mean value of 0.05 for the fraction of segregating sites (***P_S*).**

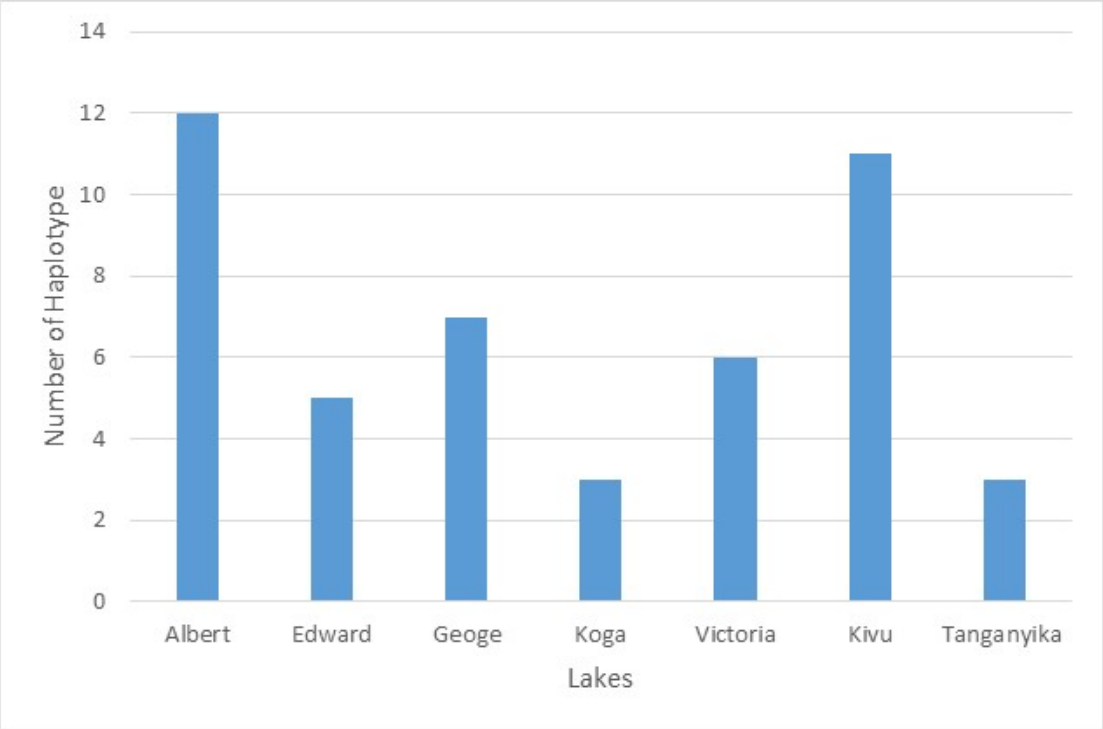

Figure 2. Distribution of 43 haplotypes of Nile tilapia from seven East African Lakes

Table 1. Comparison of means for genetic diversity indices between native and introduced populations of *O.niloticus* based on control region variation

Population	H	***Ps***	**π**	**A**
Native Population	0.77	0.05	93	7.6
Introduced Population	0.67	0.05	0.65	5.5

Key: A= number of haplotypes; H =haplotype diversity; *ps* = fraction of segregating sites; π = nucleotide diversity (in%).

Table 2 AMOVA results of hierarchical genetic subdivision of Nile tilapia populations of native and introduced populations based on control region variation

Source of variation	**% of variance**	**F-statistics**
Among populations within groups	1.17	0.036
Among groups	67.90	0.679
Among populations	30. 93	0.691

According to table 2, 67.90% of variance was due to variation among groups, 30.93% due to variation among populations and 1.17 % due to variation among populations within groups.

3.2 Microsatellite variation

Statistical tests for linkage disequilibrium were computed for all pairs of loci and none was found significant (P>0.05). All 4 loci analyzed in this study exhibited high levels of polymorphism in each of the 5 populations. A total of 156 alleles a cross all loci was found in all the five populations, ranging from 10 for locus UNH111 to 22 for locus UNH007 (Table 4). The most frequent allele in all the five populations at UNH1009 was 168bp while for UNH007 allele 294bp was the only allele shared by the three populations of Albert, Kyoga and Victoria. Three alleles at UNH007 (291bp, 294bp and 297bp) were recorded in Lakes Albert and Victoria. Lakes Albert and George shared two alleles at locus UNH007 (204bp and 210bp). At locus UNH1009, Lakes Albert and George shared the highest number of alleles (11) while Albert and Victoria shared 7 alleles at the same locus. At locus UNH009 the only alleles shared are between Lakes Albert, Kyoga and Victoria (192bp, 195bp, 198bp and 201bp). Alleles 192bp, 195bp, and 198bp occur at high frequencies in both Kyoga and Victoria. The most frequent allele at locus UNH009 was 195bp (0.40) in Kyoga and 0.34 in Victoria. At locus UNH111, four out of the eleven alleles recorded (36.4%) were shared between four populations (Albert, George, Kyoga and Victoria). The most frequent alleles at locus UNH111 were 192bp (0.43) and 178bp (0.29) both in Kyoga. The frequencies of the most common alleles for each of the four loci ranged from 0.05 to 0.50.

The highest number of private alleles was recorded in Albert (9) followed by 2 in George and 2 in Edward. The total number of private alleles recorded was 13. A private allele is one whose occurrence is restricted to only one population. No private alleles were recorded in Lakes Victoria and Kyoga. Two out of the four Loci (UNH 007, UNH 009) had significant differences in allele frequencies between all the five populations while only one locus differentiated Kyoga from Victoria. None of the loci differentiated George from Albert. Mean number of alleles, observed and expected heterozygosity values for each population are presented in Tables 4. All the four loci investigated were highly polymorphic. Observed heterozygosity values ranged from 0.33 to 1.00 on locus UNH007 in Lake Victoria population and on locus UNH1009 in Lake Albert population respectively. The unbiased expected heterozygosities ranged from 0.48 on locus UNH111 in Lake Edward population, to 0.95 on locus UNH009 in Lake Albert. The highest number of alleles was recorded in Lake Albert (45) followed by Lake George (30), Lake Edward and Victoria had 29 alleles each (Table 3). Kyoga recorded the lowest number of alleles (23) from the data set. In general, most of the alleles occurred at low frequencies but with significant differences between the populations.

Table 3 Summary statistics of genetic variation at four microsatellite loci in 5 Nile tilapia populations

Locus	Population					
	AL	ED	GE	KY	VI	Total
UNH1009						
n	20	10	20	05	18	73
A	9	06	8	4	9	36
Ho	1.00	0.86	0.80	1.00	0.78	
He	0.95	0.77	0.94	0.93	0.93	
F_{IS}	-0.08	-0.51	0.13	-2.23	0.14	
P (HW)	0.12	0.04	0.14	0.32	0.08	0.09
UNH007						
n	20	10	20	05	18	73
A	17	07	06	07	08	45
Ho	0.53	0.84	0.66	0.86	0.33	
He	0.90	0.63	0.82	0.53	0.58	
F_{IS}	0.40	-0.04	0.34	0.34	0.40	
P (HW)	0.22	0.32	0.38	0.02	0.10	0.08
UNH009						
n	20	10	20	05	18	73
A	11	09	08	06	4	
Ho	0.40	0.87	0.50	1.00	0.56	
He	0.87	0.85	0.83	0.80	0.74	
F_{IS}	0.54	0.04	0.38	-0.39	0.22	
P (HW)	0.07	0.08	0.04	0.22	0.01	0.06
UNH111						
n	20	10	20	5	18	73
A	8	07	09	06	08	10
Ho	0.68	0.52	1.00	1.00	1.00	
He	0.88	0.48	0.85	0.87	0.85	
F_{IS}	0.20	-0.03	-0.21	-0.38	-0.20	
P_{HW}	0.28	0.67	0.32	0.32	0.32	
A (Total)	45	29	30	23	29	156
He (Ave)	0.90	0.84	0.81	0.85	0.78	
FIS (Ave)	0.24	-0.20	0.34	0.10	0.19	
P (HW Total)	0.28	0.01	0.37	1.00	0.08	<0.01

Key: n = number of individuals genotyped; A = number of alleles detected in each population; A (Total) = total number of alleles summed over all loci; Ho = observed heterozygosity; He = expected heterozygosity; F_{IS} = Weir and Cockerham's (1994) analogue of Wright's fixation index; P(HW) = Single locus P-values

AMOVA analysis based on microsatellites data revealed that 3.85 % of the total genetic variation was explained by population differences within groups while differences among groups explained 5.39 % of the total variance. The remaining 90.77% was explained by differences among populations (Table 4).

Table 4. AMOVA results of hierarchical genetic subdivision of Nile tilapia populations based on microsatellites variation

Source of variation	**% of total variance**	**F-statistics**
Among populations within groups	3.85	0.040
Among groups	5.39	0.054
Among populations	90.77	0.092

According to the microsatellite data analysis 90.77% variation is explained by among population variance, 5.39% by variance among groups and 3.85% by variance among populations within groups.

4. Discussion

Results obtained from the analysis of mtDNA and microsatellite variation showed elements of congruence and discrepancies. Both data sets demonstrated significant genetic partitioning between Nile tilapia populations. The potential stochastic effects of low sample sizes which could be important for mtDNA variation cannot be ignored. Nevertheless, this cannot explain all differences observed. The results show that Nile tilapia sampled from introduced populations (Kyoga and Victoria) showed significant reduction in mtDNA sequence variation compared to those from native populations (Kivu, Albert, George, and Edward) which also have protected zones. These results are in line with (Vandeperre etal 2011) who reported that Marine protected areas (MPAs) are often promoted as tools for biodiversity conservation as well as for fisheries management. Their study in Southern European MPAs showed clear effects on the surrounding fisheries, on the 'catch per unit effort' (CPUE) of target species, but especially on the CPUE of the marketable catch.

4.1 Genetic structure in protected and unprotected of populations of O. niloticus

This study showed clear differences in genetic diversity between protected and unprotected populations of *O.niloticus* in East Africa. The genetic distance between Lakes Tanganyika and Kivu were higher than between the Ugandan populations, indicating a divergence higher than was expected within a species. Lakes Tanganyika and Kivu are isolated from the Lakes in the Rift valley. This might explain the high degree of differentiation of these lakes because of the lack of connectivity and divergent ecological conditions. Contrary, Lakes Edward and George lack a physical barrier between the lakes. The high diversity and number of private alleles found in Lakes Tanganyika, Kivu and Albert can be a consequence of this isolation. The unexpected high genetic diversity in the introduced Nile tilapia populations in Lakes Victoria and Kyoga might be due to introgression from anthropogenic activities. However, this requires further studies using a large number of loci and better sampling strategies. *O. niloticus* populations were clearly structured in two groups: 1) (Lakes George and Edward, 2) Lakes Albert, Kyoga and Victoria system. The Murchison Falls on Victoria Nile[Dumont 2009, Ogutu-Ohwayo 1990], constitutes a strong barrier to gene flow, which keeps these systems apart.

4.2 Effects of fish translocations

It is through increased fishing pressure, environmental degradation and introduction of fish species in water bodies where they did not occur that humans have become a very powerful factor in influencing fish populations that we see today. The number of biological species inhabiting the Great East African Lakes is still a matter of debate, since most still await a proper taxonomic description and a large number of species went extinct due to the recent introduction of the Nile perch and environmental degradation (Ogutu-Ohwayo 1990, Verschuren *et al*,2002). Nevertheless, members of the cichlid fishes have diverged in morphology, ecology, and behavior to such a degree that some authors have allocated them to more than 20 different genera.

Fisheries resources in East Africa are threated through anthropogenic activities which affects the sustainability of the resources (Welcomme 2010). Anthropogenic threats include the change of natural genetic structure of fish stocks through translocations (Todesco 2016, Rhymer& Simberloff 1996).

This study demonstrates the importance of genetic markers in understanding the population genetic structure of *O.niloticus* in East Africa. The generated knowledge is critical in the management and conservation of fisheries resources.

4.3 Effects of barriers on genetic structure of Nile tilapia between water bodies

The main barrier in the Nile Basin is Murchison Falls on the River Nile that acts as a barrier between the systems (Ogutu-Ohwayo 1990, Dumont 2009). The genetic similarity between Lakes Albert, Kyoga, and Victoria populations may have resulted in stocking regimes using Lake Albert as the source (Ogutu-Ohwayo 1990).
Although *O. niloticus* in the seven populations studied, apart from Lakes Edward and George, there are some barriers but there is evidence for shared haplotypes and alleles. It has been reported that introductions into Lake Victoria may have originated from Lake Edward, with other authors suggesting multiple sources (Balirwa 1992, Kaufman, 1992 Pullin 1988), which support results from this study. It is most likely that diverse gene-pool in Lakes Victoria and Kyoga could have originated from the admixture of several lineages due to multiple sources. It is also possible that hybridization of the *introduced O. niloticus* with the indigenous relative species occurred. If admixture or hybridization is responsible for the gene-pool of Lake Victoria, it may have adaptive consequences with a negative impact to the sustainability of *O. niloticus*.

Anthropogenic activities of overfishing in lakes Kyoga and Victoria could have contributed to the low genetic variability and evidence of bottleneck. Given the recent stocking of these water bodies, this pattern may be explained by the founder effects but other anthropogenic activities need to be considered as well. High loss of genetic diversity among populations, particularly, in fresh water fishes has been attributed to overexploitation (Allendorf *et al* 2008). It has been reported that the *O.niloticus* populations in Lakes Victoria and Kyoga following introductions, the species was subsequently overexploited between the 1970s and 80s (Ogutu-Ohwayo *et al* 2013, Njiru *et al* 2008). The planned hydroelectric power dams on Victoria Nile and the oil development in the Albertine Rift is likely to result in low diversity in the affected water systems due to low gene-flow connectivity with other water bodies due to hydroelectric power dams which is expected to increase the effect of genetic drift. However, this needs to be assessed in further studies on samples collected from the affected populations.

4.4 Implications for sustainable management of fisheries resources in East Africa

This study found evidence that anthropogenic activities affected the gene-pool of the Uganda *O.niloticus* poulations. The main consequence might have been admixture and hybridization between different strains and species respectively. It is recommended that management measures and principles be observed to prevent any form of unauthorized fish introductions in the different aquatic ecosystems.

5. Conclusion

Results from this study supported the hypothesis that fish translocation activities affected the genetic structure of *O. niloticus* populations in Uganda freshwater bodies. The genetic variation of populations from Lake Victoria and Lake Kyoga corresponded with possible hybridization. This study demonstrates the role of molecular markers in studying population structure across ecological catchments. Further studies should include *O.niloticus* samples from other regions such as the lower Nile basin, Lake Turkana (Kenya), Tana (Ethiopia) and fresh water bodies from West Africa and Central Africa for a comprehensive picture of cichlid fishes in Africa. Understanding of genetic diversity in both native and introduced populations across the species range could be of great importance for the future development of agricultural strains and for the protection of small-endangered populations. The results of both microsatellite analyses and the sequence dataset clearly reveal population structuring in the populations studied. Differences in genetic variation can generally be explained by (i) mutation rates and selection connected with the evolutionary history of populations, and (ii) genetic drift and migration. Detailed genetic analyses such as that reported here are required for the identification of priority populations for conservation with respect to their uniqueness in terms of genetic divergence from other populations and their genetic diversity.

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