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Research Article

Genetic diversity of Nile tilapia (*Oreochromis niloticus*, L. 1758) in native and introduced populations in East Africa

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Abstract

Freshwater fish in East African Lakes are under severe threat due to the recently discovered oil and gas in the Albertine Region and overfishing across the entire East African Region. The threats, primarily caused by overfishing, are a matter of declining fish populations and a potential reduction in genetic diversity in the surviving populations due to genetic drift. This study, therefore, is of utmost importance as it assessed genetic diversity in seven populations, including five from native and two from introduced populations. The assessment of genetic diversity in *Oreochromis niloticus* was conducted using molecular markers in 128 samples. The results showed a moderate genetic variation between native and introduced populations at mitochondrial and microsatellite loci. The potential effects of overfishing, fish introductions, and new threats from cage farming on the genetic diversity and ecological integrity of wildlife species are discussed, highlighting the need for immediate action.

Keywords: Aquaculture, Cage farming, Gene flow, Nile tilapia, Overfishing

Introduction

This study is of immense practical significance to biodiversity Conservation and Natural Resources Management in East Africa. The Albertine Rift and the Lake Victoria Basin stand as biodiversity hotspots of Global importance, boasting a high level of endemism in the regions (Trewavas, 1983; Balirwa, 1992; Beadle, 1981; Kocher.,2004). The Lake Victoria Basin, a part of the Nile system, is unique in its ichthyofauna, which differs substantially from most of the downstream Nile basin (Greenwood, 1983; Johnson et al., 1996; Roberts, 1975; Snoeks et al., 1997; Witte et al., 2009). Recent biogeographic and genetic studies have unveiled a mosaic ichthyofauna in Lake Victoria and the smaller lakes in the region, predominantly composed of Nilotic and Congolese elements with quite balanced contributions from the two (Meier et al., 2017; Seehausen, 2002; Fryer et al.,1972). The large endemic cichlid species radiation evolved from a population of hybrid origins between cichlids from the Nile and the Congo (Meier et al., 2017). Cichlids, the major component of the fish fauna of the Lake Victoria Basin and the Albertine Region, are under threat due to the rapid human population growth, environmental degradation and increased demand for fish (Hecky *et al*.,2010; Salerno et al., 2017; Darwall et al*.,* 2011; Njiru et al*.,* 2012).

A big increase in fish consumption led to overharvesting after the discovery of oil in 2006 in the Albertine Rift. Overfishing is a major driver to fish genetic diversity loss. The capture fishery on Lake Victoria makes a very big contribution to the East African community and is a major source of fish protein in East Africa and beyond. However, the capture fishery declined after being very successful between the 1970s and 1990s. The Red List assessments indicate that freshwater fishes of the Lake Victoria Basin are under high threat levels. Of the 234 species assessed, 86 species are classified as threatened.

Fish Introductions

The decline of the fishery had a very significant impact on the genetic diversity of all affected species. This decline was largely attributed to *Oreochrimis niloticus* and *Lates niloticus.* However, the other key drivers for the decline of the Lake Victoria fishery were increased demand for fish in the region, leading to overfishing, eutrophication, pollution, climate change, and environmental changes associated with anthropogenic activities in the Lake Victoria watershed (Fig.1).

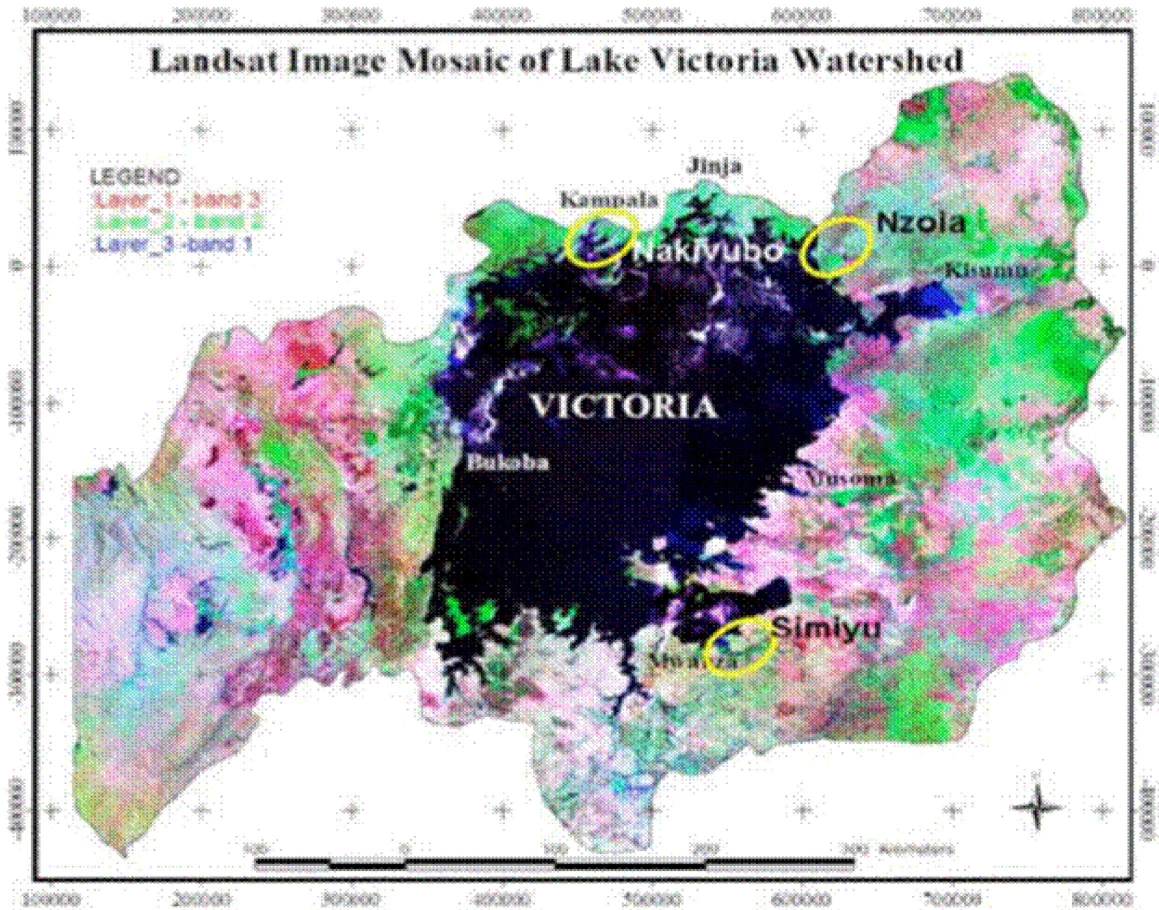

Figure 1. Map of the Lake Victoria watershed showing sites of heavy pollution (**Source**: Twesigye et al.,2011)

Threats to genetic diversity in freshwater fishes

The freshwater fishes of East African Lakes support continental inland fisheries. Overharvesting is a major threat to genetic diversity among freshwater fishes of livelihood value. Nile tilapia is the most important aquaculture species in the world, and this factor puts its genetic diversity under extreme threat due to hybridization and admixture. A new threat associated with Cage fish farming with potential threats to fish biodiversity. A few studies have been conducted in this area but with no clear conclusive results. Fish cages should be installed in deep waters, but farmers prefer shallow waters. This causes a real threat to many endemic fish species. Fish species used in cage farming are normally not native, and escapees from cages may impact native species negatively, leading to genetic erosion (Table 1).

Table 1. East African Lakes installed with fish cages

Lake	Year	Farm/ Main actors	Country
1.Albert	2020	Bafa (Buhuka Albert Fishers Association	DRC, Uganda
2. Edward	2014	Local Fish Farmers Group	DRC, Uganda,
3. George	NA	None (Lake is shallow)	Uganda
4. Kivu	2013	DRC	DRC, Rwanda, Burundi, Tanzania
5. Kyoga	2011	Pilot Family Project	Uganda
6. Tanzania	2010	July 2023	Zambia
7. Victoria	2005 (Ke) 2010 (Ug)	Victory Farms UgaChick SUN	Uganda, Kenya, Tanzania Belgium, China

Material and methods

Populations

The populations included five lakes in the Albertine Rift, Victoria, and Kyogo from the Lake Victoria Basin (Fig. 2). The two regions included in this study are among the most biodiversity hotspots globally. Cage fish farming has been introduced in all East African Freshwater lakes apart from Lake George, which is too shallow for installing fish cages.

Fish samples

A total of 128 Nile tilapia (*O. niloticus*) tissue samples were collected from seven freshwater lakes (Fig. 2).

Table 2. Study sites with GPS Coordinates, species and number of samples

Lake	**Sampling Site**	**GPS Coordinates**	***Species***	**No. of samples**
1.Albert	Butiaba	1.8152°N 31.3243° E	*O. niloticus*	20
2.Edward	Kisenyi	0.3095°S 29.8618° E	*O. niloticus*	17
3.George	Kasenyi	0.03194°S 30.1486° E	*O. niloticus*	20
4.Kyoga	Kayago	1.2959°N 33°00'0.0°E	*O. niloticus*	22
5.Victoria	Masese	0.4500°N, 33.2333°E	*O. niloticus*	19
6.Kivu	Goma	1.7044° S , 29.2598°*E*	*O. niloticus*	19
7.Tanganyika	Uvira	3.3729° S, 29.1449°E	*O. niloticus*	11

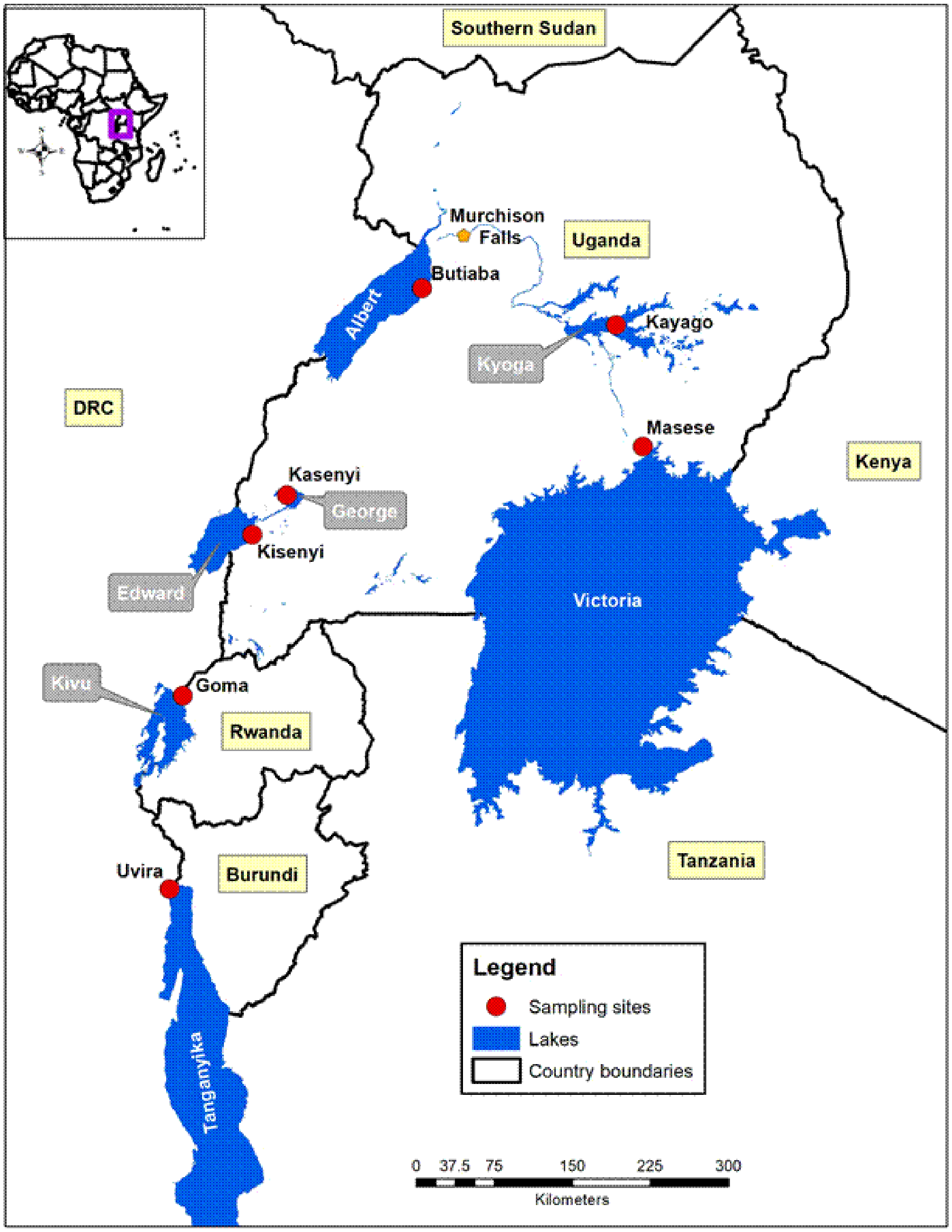

Figure 2: Sampling sites on East African Lakes

Table 3. Sample locations, including coordinates and the numbers of samples screened for both mtDNA and microsatellite variation

Population	Pop code	Lat. (N) Long.(E)	Sample size	Altitude(m)	Mean Depth(m)	Surface Area(km^2)	Volume(km^3)
Albert*	AL	1.6833°N, 30.91, 67° E	21	615	25	5,300	280
Edward*	ED	0.3256° S, 29.6963° E	16	912	17	2,325	39.5
George*	GE	0.0161° N, 30.1820° E	19	914	2.4	250	0.8
Kivu*	KI	2.0448° S, 29.1856° E	23	1463	485	2,370	550
Tanganyika*	TA	6.2556° S, 29.5108° E	20	773	572	32,000	17,800
Kyogo #	KY	1.5047° N, 32.9438° E	20	914	5.7	1,720	~8
Victoria #	VI	0.7558° S, 33.4384° E	20	1134	40	68,800	2,750

Pop. Code=population code; Lat. =latitude; Long. =Longitude; * =Native population; # = Introduced population

Table 4. Detailed information on primers used to amplify 4 microsatellite loci in *O.nilotics* from 5 locations in East Africa (Kocher, 2004; Lee, and Kocher., 1996).

Assession No.	Primer Name	Repeat sequence	Primer Sequence (5' to 3'	A. Temp.	No. Cycles
G68285	UNHI1009	(CA)n	A: CCATCTGCATGCTGTAAGACA B: TCCCATTTGTCAGGTTCAGG	58^{0}C	34
G68283	UNH007	(AAC)n	A: CAACAAAATGAGCAGAATAAG B: AAGAACGAAAAACGACGGAAAGT	58^{0}C	34
G68324	UNH009	(AAC)n	A: TGAAAAGAAGGTGATGGCTAA B: AAAAGTAATGTAACCTGGAATAAC	54^{0}C	34
G12264	UNH111	(AAC)n	A:TGCTGTTCTTATTTTCGC B: ATAAGAGTGTATGCATTACTGG	54	34

Four primers in table 4 were used in genotyping 78 samples from 5 populations of Nile tilapia. Primers used for amplification, annealing temperatures and number of cycles are listed in table 5.

DNA Analysis

After sample collection and DNA extraction, further analysis was conducted as described in Twesigye et al.,2009 using a

commercially available DNA Purification Kit) as per the manufacturer's instructions.

D-loop Sequence Data

The mtDNA data was analyzed to determine population genetic structure (**Excoffier, L., Smouse, P. and Quattro, J. (1992**). The level of differentiation among Nile tilapia populations was also determined. Genetic variation was evaluated following Hardy-Weinberg Principles (Nei, 1987).

Results

Genetic diversity in Nile tilapia from native populations in the Albertine Region and introduced

Results from native populations showed moderate differences in genetic diversity from introduced populations (Table 6) compared to previous studies of freshwater fish (Tibihika *et al*., 2020)

Table 5. Genetic diversity in selected Nile tilapia populations

	Albertine Rift					Lake Victoria Basin		
	Albert	Edward	George	Kivu	Tanganyika	Victoria	Kyoga	Total
N	20	17	20	22	19	19	11	128
A	12	05	08	11	03	06	03	43
H	0.83	0.77	0.88	0.85	0.55	0.76	0.58	0.85
P_s	0.09	0.04	0.04	0.06	0.03	0.05	0.03	0.22
π	0.9	0.8	0.8	0.62	0.63	0.73	0.56	5.04

Table 6. Segregating sites in Nile tilapia De-loop sequences

		SEGREGATING SITES															
		10	20	30	40	50	60										
			1111111111	1111111111	1111111122	2222222223	3333333333	333									
		2245566778	0023333444	5555555567	7788888901	2233447890	0111112333	445									
		5950939480	3540268489	0123457894	5712456476	4525287774	5123486567	098	ALBERT	EDWARD	GEORGE	KYOGA	VICTORIA	KIVU	TANGANYIKA	TOTAL
1	A886	CCCCCCAAAA	TCATCTTATA	CACTGTTTTT	CACTTAAGTT	CAATGTATCC	CTTCTTTAGC	ATT	7	-	1	6	9	-	-	23
2	A887	....	....	....	.....G....	.CG.......	....	...	1	-	-	-	-	-	-	1
3	A888	....	....	....	....	.....G....	....	...	2	-	-	-	-	-	-	2
4	A891	....	....	....	....	....A.....	....	...	1	-	-	-	-	-	-	1
5	A892	....	....	....	....	....	.......C..	...	1	-	-	-	-	-	-	1
6	A893	.........G	....	....	....	....	....	...	2	-	-	-	-	-	-	2
7	A896	........G.	....	....	....	....	....	...	1	-	-	-	-	-	-	1
8	A897	........G.	....	.......C..	..T.......	T........T	....	...	2	-	-	-	-	-	-	2
9	A904	....	....	..T.......	....	....	....	...	1	-	-	-	-	-	-	1
10	A906	....	..T.......	....	....	....	....	...	1	-	-	-	-	-	-	1
11	A907	...T..GG..	........C.	T.........	..T.C..A.C	..A.....T.	.C........	.CC	1	-	-	-	-	-	-	1
12	A908	..G.......	....	....	....	....C.....	....	...	1	-	-	-	-	-	-	1
13	E937	....	.......G..	.......C..	..T.......	T........T	....	...	-	8	9	-	-	-	-	17
14	E940	......G...	....	..T.....C.	........C.	....	....C.....	...	-	5	3	-	-	-	-	8
15	E941	....	.......G..	.....CC...	..T.......	T........T	....	...	-	1	-	-	-	-	-	1
16	E944	......G...	.......G..	.......C..	..T.......	.........T	....	...	-	1	1	-	-	-	-	2
17	E954	....	.......G..	.......C..	..T.......	.........T	....	...	-	1	2	-	-	-	-	3
18	G923	....	.......G..	.......C..	..T.....A.	T........T	....	...	-	-	1	-	-	-	-	1
19	G928	......G...	....	C	........C.	....	....C.....	...	-	-	1	-	-	-	-	1
20	G933	....	.......G..	..T....C..	..T.......	T........T	....	...	-	-	1	-	-	-	-	1
21	K502	T.........	....	....	....	....	....	...	-	-	-	1	-	-	-	1
22	K509	....	....	....	..C.......	....	....	...	-	-	-	1	-	-	-	1
23	K511	.......G..	....	....	..T.C..C..	......G...	..CT......	G..	-	-	-	1	-	-	-	1
24	V461	....	....	....	.....G....	....	.....A...G	...	-	-	-	-	1	-	-	1
25	V464	....	....	.......C..	..T.C.....	.........T	....	...	-	-	-	-	1	-	-	1
26	V468	.......G..	....	..T.......	........C.	....	....C.....	...	-	-	-	-	4	-	-	4
27	V469	....	....	..T.......	........C.	....	....C.....	...	-	-	-	-	3	-	-	3
28	V475	....	....	..T.......	....	....	....	...	-	-	-	-	1	-	-	1
29	V476	..T....G..	....	..T....G..	.C......C.	....	....C.....	...	-	-	-	-	1	-	-	1
30	KV001	.......G.G	....	..T.....C.	........C.	....	....C.....	...	-	-	-	-	-	4	-	4
31	KV005	.......G.G	....	..T.....C.	.......AC.	....	....C.....	...	-	-	-	-	-	1	-	1
32	KV1283	.......G..	....	..T.......	........C.	.......G..	.......G..	...	-	-	-	-	-	4	-	4
33	KV1284	.......G..	...C......	..T.......	........C.	.......G..	......AG..	...	-	-	-	-	-	1	-	1
34	KV1285	.......G..	....	..T.......	........C.	....	....	...	-	-	-	-	-	2	-	2
35	KV1286	.......G..	....	..T.......	........C.	....	.......G..	...	-	-	-	-	-	3	-	3
36	KV1289	.......G..	....	..T.......	........C.	.........T	T.........	...	-	-	-	-	-	2	-	2
37	KV1293	.......G..	...C......	..T.......	........C.	.......G..	......G...	...	-	-	-	-	-	2	-	2
38	KV1318	.......G..	....	.GT.....C.	A.......C.	.......G..	......G...	...	-	-	-	-	-	1	-	1
39	KV1319	.......G..	....	.GT.......	........C.	.......G..	......G...	...	-	-	-	-	-	2	-	2
40	KV1321	.T....GG..	.C........	.G...CCC..	........C.	.......G..	......G...	...	-	-	-	-	-	1	-	1
41	T1297	.T..TTGG..	.T.CTCC..C	....	........C.	.......G..	......G...	...	-	-	-	-	-	-	15	15
42	T1312	.T..TTGG..	.T.CTCC..C	...CACC...	........C.	.......G..	......G...	...	-	-	-	-	-	-	1	1
43	T1313	.T..TTGG..	.T.CTCC..C	...CACC...	.T......C.	.......G..	......G...	...	-	-	-	-	-	-	4	4
N0 of basaes		2222222222	2222222222	2222222222	2222222222	2222222222	2222222222	222	21	16	19	9	20	23	20	128

Genetic diversity

The genetic diversity in native *O. niloticus* was similar, though higher in Lakes Albert and Lake Kivu than Lakes Edward, George and Tanganyika. *O. niloticus* from Lake Tanganyika had the least genetic diversity among all seven populations sampled, followed by introduced populations in Lakes Victoria and Kyoga (Table 5 & 6). Recent studies in Lake Tanganyika have confirmed catches of *O. niloticus* though rare. *O. tanganicae* is the most common in the lake and the indigenous in the oldest lake in Africa. There are global concerns for the genetic purity of *O. tanganicae* which would affect the genetic integrity of *O. tanganicae.* Native *O. niloticus* has always been known to exist in the Albertine Lakes (Kivu, Edward, George and Albert). The haplotype tree (Fig.3) revealed four haplotype clades including Lakes from Uganda, Lake Tanganyika, Lake Kivu and for Edward and George. These clades coincide with the drainage systems and there is a weak structuring of haplotypes reflecting geographic origin. However, with the rapidly increasing introduction of fish species into new ecosystems for Aquaculture, there is urgent need for conservation measures to protect indigenous fish species. Our recent field studies in the Albertine region provided evidence for current threats for biodiversity in both aquatic and terrestrial ecosystems (Twesigye et al., 2024). There is urgent need for assessing genetic diversity in both native and introduced populations using recent advances in high-throughput sequencing (Allen et al.2018, D'Aloia et al., 220, Lemopoulos et al.,2019, Righi et al., 2020, Timm et al.,2020 and Therkildsen *et al*., 2019; Sadler *et al.,* 2023).

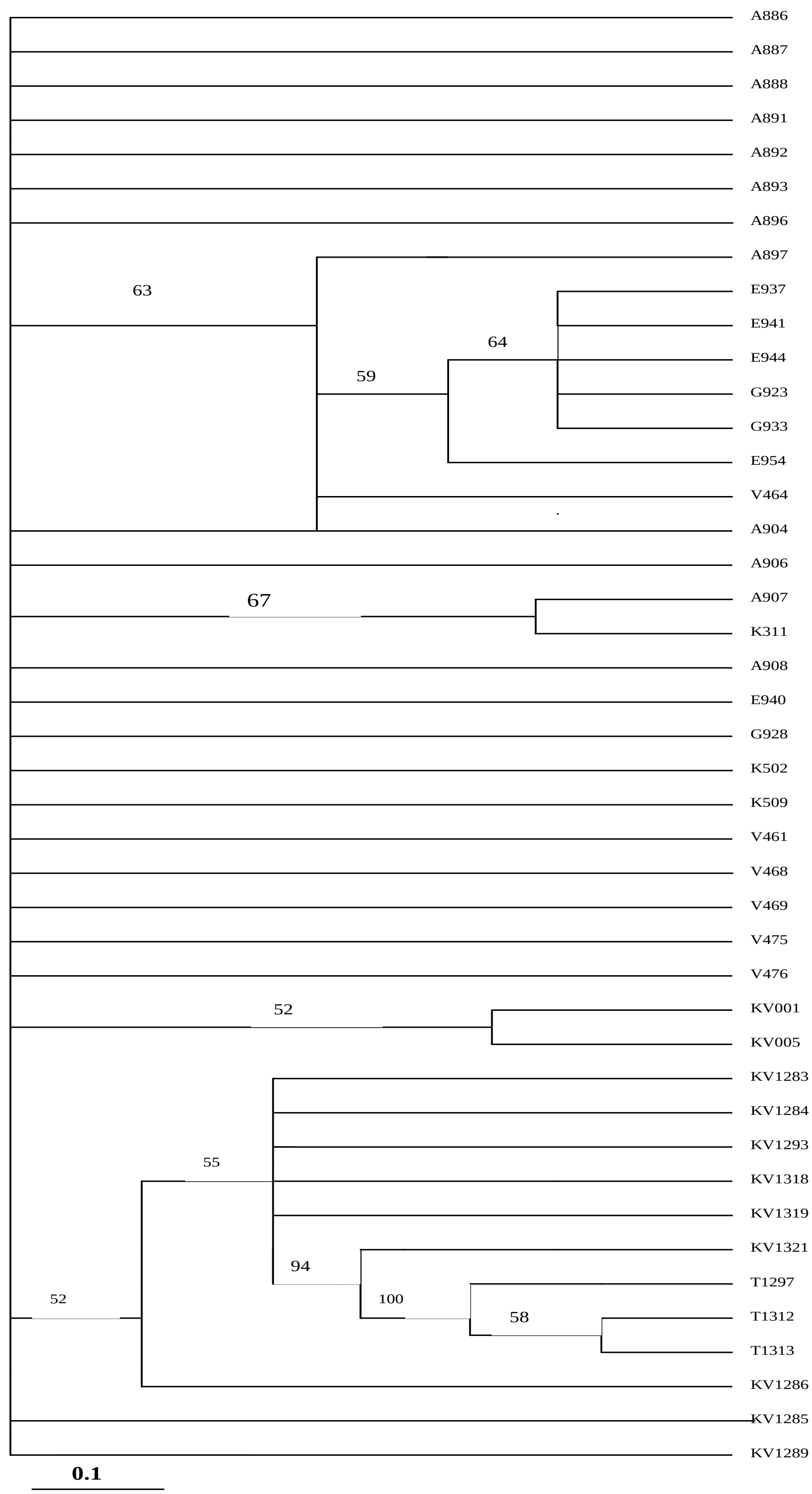

Figure 3. A 43 haplotype tree for 128 *O.niloticus* fish individuals from East African Lakes

Microsatellite variation

All four loci investigated showed moderate levels of variation. The frequencies of all the alleles were between 0.03 and 0.4 (Tables 4 and 7). Protected areas had the highest private alleles in all the landscapes studied. In all the populations investigated, Lakes Edward and George had the most similar alleles and sequences. This finding confirms that there is no barrier between Lakes Edward and George (Fig. 2).

Over all the highest number alleles were recorded in lake Albert (44) followed by George (31), Edward and Victoria recorded similar numbers of (29) and Kyoga (20). A total 153 alleles were recorded across all the four loci and five populations. Allele (174) under locus UNH009 (Table 4) had the highest frequency at 0.4 in Lake Kyoga, while alleles (172 and 174) were the most common in all the 5 populations studied. The allele frequency across the 5 populations ranged from 0.03 to 0.4(Table 4). Due to a delay in acquiring fish samples from lakes Kivu and Tanganyika, their samples were not included in the microsatellite loci analysis (Table 7). According to the results in Table 7, locus UNH1009 produced the largest number of alleles, UNH007 (20), UNH009 (10), and UNH111 (8), giving a total of 60 alleles (Table 7).

Table 7. Allele frequency in five Nile tilapia populations sampled from Uganda

UNH 1009							UNH 007						UNH009						UNH111					
		AL	ED	GE	KY	VI		AL	ED	GE	KYU	VI		AL	ED	GE	KY	VI		AL	ED	GE	KY	VI
	N	20	10	20	05	18		20	10	20	05	18		20	10	20	05	18		20	10	20	05	18
170		0.15	0.5	0.05		0.1	**201**		0.15	0.03			**192**				0.10	0.28	**176**	1.15			1.0	
172		0.2	0.1	0.05	0.25		**204**	0.03	0.05	0.03		0.05	**195**	0.03			0.40	0.31	**178**	0.27	0.10	0.15	0.30	0.05
174		0.2	0.1	0.15	0.4	0.22	**207**			013			**198**	0.03			0.10	0.28	**180**			0.05		0.11
176				0.25	0.1	0.05	**210**	0.05	0.10	0.27	0.10		**201**					0.13	**182**	0.05	0.05	0.07		
178		0.05		0.1	0.25	0.1	**213**		0.15	0.20			**204**	0.05			0.2							
180		0.15					**219**	0.05	0.40	0.35	0.20	0.03	**213**	0.10			0.10		**186**	0.07	0.15	0.07		0.08
182		0.05	0.1				**222**		0.10				**219**				0.10		**188**		0.20	0.10	0.10	0.19
184		0.05					**228**		0.05				**222**						**190**	0.13	0.05	0.05	0.10	1.14
186		0.05		0.2			**234**	0.03					**228**		0.05	0.05			**192**	0.13	0.35	0.25	0,30	0.25
188			0.1				**237**	0.03			0.10		**234**		0.20	0.14			**194**	0.13		0.20	0.10	014
190							**246**	0.03				0.03	**240**		0.15	0.36			**196**	0.07	1.10	0.05		0,03
192				0.05			**258**	0.05					**243**		0.10	0.14								
194						0.03	**261**	0.05					**246**		0.05	0.11								
196		0.15				0.03	**267**	0.03					**249**	0.03	0.05									
198			0.1				**273**	0.05					**252**	0.18	0.15	0.11								
							276	0.03					**256**	0.03	0.15	0.14								
							282	0.05				0.03	**258**		0.10	0,05								
							285	0.05					**264**	0.3										
							288	0.08				0.03	**273**	0.10										
							291	.20				0.33	**276**	0.15										
							294	0.13				0.30												
							297	0.10				0.19												
15							**22**						**20**						**10**					
A		9	6	8	4	9		17	07	06	04	08		10	9	08	06	04		8	7	9	6	8

Discussion

Genetic differentiation

The genetic distance between Lakes Tanganyika and Kivu were higher than between the Ugandan populations because of a river barrier between the two lakes. Contrary, Lakes Edward and George are similar. The moderate levels in Lakes Victoria and Kyoga might be due to hybridization and admixture (Agnèse *et al*.1997). However, this requires further studies using a large number of loci and better sampling strategies. Our results show that genetic diversity observed in this study is a result of habitat type, fish introductions, intensity harvesting and sensitivity of genetic markers used in the study

Genetic variation

Our results show moderate genetic variation but less than that reported in earlier studies (Agnèse 1997, Mwanja 1996, Allendorf, 2017; Tibihika *et al*., 2020). The possible causes of decline in genetic diversity in the Nile tilapia populations studied could be overfishing, environmental degradation and increasing pollution in East African Freshwater lakes and the newly introduced cage farming (Allendorf,2008, Allen *et al*., 2018). In terms of habitat, the Albertine Lakes are more salty than the Lake Victoria Basin. The Murchison –Semliki Landscape is characterized by a number of river falls and rapids which serve as a strong force for isolating mechanism in the evolution of fish in East Africa. Along the shores of Lake Albert are a number isolated lagoons from each other and from the main lake. In the Albertine Rift lakes it is only Lakes Edward and George which lack a physical barrier between them.

Fish Introductions

The overfishing in Lake Victoria was due to increased fish demand, which resulted in the introduction of new fish species in the 1950s in Lake Victoria and Kyogo to support the capture fisheries. There was also high demand for fish in Lake Albert after the discovery of oil in 2006. Fisheries resources in East Africa are threatened by high fishing pressure and environmental degradation (Welcomme, 2010; Kaufman L. (1992, Todesco, 2016; Rhymer& Simberloff, 1996; Pinsky *et al*.,2014).

Effects of Barriers on the Genetic structure of Nile Tilapia between Water bodies

The main barrier in the Nile Basin is Murchison Falls, which separates it from the Lake Victoria Basin (Ogutu-Ohwayo, 1990; Dumont, 2009; Allendorf, 2017). The native fish species in Lakes

Albert and Edward are isolated from each other due to rapids on the Semliki River, while native fish in Lakes Kivu and Tanganyika are isolated by Panzi Falls on the River Ruzizi. The fish of Lake Kivu are isolated from the fish of Lake Edward due to volcanic activity that reversed the water flow towards Lake Tanganyika.

Sustainable management of fisheries resources in East Africa

It is recommended that management measures and principles be observed to prevent any form of unauthorized fish introductions in different water bodies. It is very important to study these isolated fish populations before too much damage has been done due to fish introductions associated with aquaculture. Genetic differentiation is due to barriers in the form of falls and rapids, which influence the direction of gene flow amongst populations. Our study revealed isolated populations on Lake Albert that have not been documented. The shoreline for Lake Albert is characterized by lagoons isolated from the main lake main lake and contain fish species not common in the main lake. Further isolation on the shoreline is due to very steep lake shores unsuitable for tilapia species such as O.niloticus, which prefer shallow waters. Lower genetic diversity in Lakes Victoria and Kyoga is consistent with patterns of introduced populations.

Impacts of fish Cages on Freshwater ecosystems

This study noted that all East African Great lakes have been installed with fish cages (Lubembe *et al., 2024*; FAO, 2020; Okechi *et al.,*2022; FAO, 2020). Only Lake George has not been installed with fish cages because it is very shallow. The potential effects of cage farming on ecological integrity of the lakes is not yet known. This calls for constant monitoring of all lakes installed with fish cages. Despite growing concerns about the potential impacts of cage fish farming on capture fisheries and livelihoods, no current studies have been conducted on Lake Victoria.

Conclusion

Our results show moderate genetic variation in all populations studied. Further research is recommended in all the landscapes of the Albertine Rift and other regions such as Lake Turkana (Kenya), Tana (Ethiopia), West Africa, and Central Africa for a comprehensive picture of cichlid fishes in Africa. These genetic diversity studies should be extended to aquatic and terrestrial ecosystems in protected and unprotected environments to monitor ecological integrity. The level of genetic diversity reported in this study is moderate but less than that reported in earlier studies. The possible causes of the decline in genetic diversity in the Nile tilapia populations studied could be overfishing, environmental degradation, increasing pollution in East African Freshwater lakes, and the newly introduced cage farming.

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