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Assessment of genetic variations of Nile Tilapia (*Oreochromis niloticus* L.) in the Volta Lake of Ghana using microsatellite markers

Mireku, K. K.[1]*, Kassam, D.[1], Changadeya, W.[2], Attipoe, F. Y. K.[3] and Adinortey, C. A.[4]

[1]Department of Aquaculture and Fisheries, Lilongwe University of Agriculture and Natural Resources (LUANAR), P. O. Box 219, Lilongwe, Malawi.
[2]Molecular Biology and Ecology Research Unit (MBERU) DNA Laboratory Chancellor College, University of Malawi, P. O. Box 280, Zomba, Malawi.
[3]Aquaculture Research and Development Center, Water Research Institute, P. O. Box AB139 Akosombo, Ghana.
[4]Department of Molecular Biology and Biotechnology, University of Cape Coast, Ghana.

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A study was conducted to investigate genetic diversity and population structure among populations of Nile tilapia *Oreochromis niloticus* (*Cichlidae*) in the Volta Lake of Ghana using microsatellite markers. Four hundred (400) fish specimens were obtained from nine naturally occurring subpopulations and one selectively bred strain, 'Akosombo strain'. These were characterized using 15 microsatellite loci. Twelve of the loci were multi-allelic, producing 2 to 11 alleles per locus while the effective number of expected alleles (Ne) ranged from 2.030 to 2.855. The observed heterozygosity (Ho) and expected heterozygosity (He) were high ranging between 0.488 - 0.594 and 0.424 – 0.502, respectively. The Kpando-Toko populations had the highest variability (He = 0.502) whilst the Buipe population had the least variability (He = 0.424). Gene diversity based on locus ranged between 0.1638 and 0.8673 whilst the genetic differentiation between populations (F_{ST}) was 0.074 indicating moderate differentiation between the populations. However, there was very high genetic variation (93%) within individuals. Nei's distance between the populations ranged between 0.011.and 0.133, whilst estimated overall gene flow (Nm) and Shannon Information Index were 8.265 and 0.822 respectively. The 10 populations studied formed two main clusters with the longest pairwise Nei's genetic distance of 0.133 between the Dzemeni and Kete-Krachi populations.

Key words: *Oreochromis niloticus*, microsatellite, Akosombo strain, gene diversity.

INTRODUCTION

Oreochromis niloticus (Nile tilapia) is an economically and nutritionally important fish found in the Volta Lake of Ghana (Ofori-Danson, 2000; FAO, 2005). It is the most farmed species in the country, contributing to more than

*Corresponding author. E-mail: kmireku@ucc.edu.gh.

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80% of the total yield (Ghana Fisheries Commission, 2011). Globally, this species is the second most extensively farmed fish in freshwater aquaculture (FAO, 2014). Due to its excellent culture features, Nile tilapia has been introduced to other freshwater bodies where it has increased landings. Given its unique culture characteristics, it is predicted that the global production of the species would exceed carp production in the future (Fitzsimmons, 2013).

Nile tilapia has a number of important characteristics which makes it a key species for aquaculture. It has a relatively short generation time (approximately 8 months) relative to other species such as carp and trout, which ensures that the production cycle is completed within a single year. The species is also both planktivorous and omnivorous, making it an excellent fit for low-cost aquaculture (Abdelghany, 1993; Getabu, 1994). They also survive in water conditions that normally would not support the most of the other aquaculture species (Fitzsimmons, 2000). The ability of the species to adapt to various environmental conditions has led to its widespread production.

With the success story of the Genetic Improvement of Farmed Tilapia (GIFT) programme, there has been production of different strains of tilapia. The Akosombo strain, produced by reciprocal crosses of four populations *viz* Nawuni, Yeji, Kpando and a farmed stock from Nsawam, is a product resulting from the application of selective breeding to tilapia in Ghana. These fish genetic resources have economic, ecological and social value and need to be characterized. The proper identification of breeding stock has potential benefits regarding the characterization, conservation and sustainable use of resources (Carvalho and Pitcher, 1994). Characterization of species and strains in culture therefore continues to be an important aspect for the efficiency and success of any breeding programme, especially given that most aquatic genetic resources are poorly documented.

Traditional methods using both morphometric and meristic characters have not yielded concrete results (Pante et al., 1988). However, with the advent of the PCR machine, further enhanced molecular studies involving new approaches to genetic marker acquisition have been achieved. These include the use of random amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLPs) and microsatellites (Bardakci and Skibinski, 1999; Hassanien and Gilbey, 2005; Bezault et al., 2011; Chi et al., 2014). Falk and Abban (2004) used RAPD to assess the genetic diversity of *O. niloticus* in the Volta Lake and tributaries of the Volta system. However, RAPDs are dominant markers and hence difficult to differentiate between homozygotes and heterozygotes. This calls for further studies and use of co-dominant markers which gives further insight on the genetic diversity of the species.

With the current surge in floating cages in the Volta Lake, escapes are inevitable from this technology (McCrary et al., 2001). As a result, the characterization of the available fish populations of the Nile tilapia in the country is necessary so as to ascertain the nature and structure of available genetic diversity of the wild stocks. Characterization of individual populations will help to determine which ones will be selected so as to be included in a strain comparison trial, genetic improvement programs as well as providing baseline information for the management of the species within the Volta Lake system.

Knowledge of genetic variation within and between populations is essential for the establishment of effective and efficient conservation practices for indigenous species. In addition, such information is significant in breeding for heterosis and proper management of fish stocks (Lee and Kocher, 1998; Bo-Young et al., 2005). This research therefore sought to assess genetic diversity of wild populations of Nile tilapia in the Volta Lake, Ghana as well as the newly developed Akosombo strain of tilapia using microsatellite markers. Information resulting from this study will provide a database essential for devising strategy on monitoring, planning future genetic improvement programs and conserving genetic diversity.

MATERIALS AND METHODS

Study area

Ghana lies north of equator with latitudes between 4.5°N and 11.5°N, and longitudes between 3.5°W and 1.3°E. The Volta Lake, is the most important inland water body in the country with a surface area of 8480 km² and 5200 km of shoreline (Figure 1). The lake contributes approximately 90% (90 000 mt) of the total inland fishery production in Ghana (Abban, 1999).

Collection of fish samples and extraction of DNA

The geographical locations and sample sizes of the examined *O. niloticus* populations are presented in Table 1. Forty (40) fish of similar size ranges were sampled from each of the eight strata of the Volta Lake from December 2014–February 2015. In addition, an improved strain of the same species, Akosombo strain, was also included in the sample. A piece of caudal fin (about 50 mg) was obtained from each individual, kept in 95% ethyl alcohol and sent to the laboratories of the Department of Molecular Biology and Biotechnology, University of Cape Coast. Extraction of genomic DNA was undertaken by using the Bioneer Genomic Extraction Kit™ after which the DNA samples were stored in TE buffer at -20°C. The DNA concentration as well as purity was estimated by determining the ratio of absorbance at 260 and 280 nm respectively using a Jenway Genova Life Science Nano Micro-Volume spectrophotometer. DNA quality was then checked by gel electrophoresis on 0.8% agarose gel. The brightness and integrity of the band produced was used as a basis to estimate the quality of DNA produced.

Microsatellite primer selection and polymerase chain reaction conditions

A single locus PCR for each of 15 primers (Table 2) based on

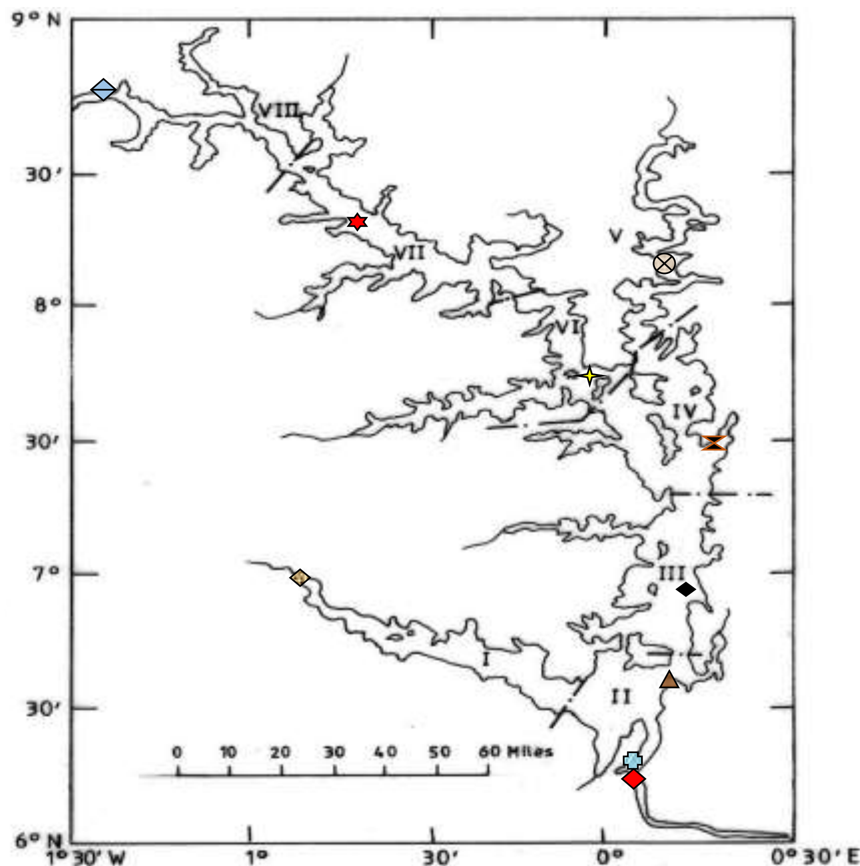

Figure 1. The Volta Lake indicating its sampling sites management strata. I = (Kotoso); II = (Akosombo-Marine and Dzemeni); III = Kpando-Toko ; IV = (Tapa Abotoase); V = (Dambai); VI = lower Volta riverine body (Kete-Krachi); VII = (Yeji); and VIII = (Buipe).

Table 1. Sampling sites and sample size of *Oreochromis niloticus* population.

Population	Code	Latitude (y)	Longitude (x)
Kwahu-Kotoso	KOT	6°45'06.91"N	0°38'31.77"W
Akosombo Strain	AKO	6°16'08.1"N	0°03'2.5"E
Akosombo-Marine	AKM	6°18'30.40"N	0°03'29.62"E
Dzemeni	DZE	6°35'19.12"N	0°12'43.50"E
Kpando-Toko	KPA	6°59'46.8"N	0°17'28.5"E
Tapa-Abotoase	ATB	7°29'05.21"N	0°17'20.83"E
Dambai	DAM	8°04'0.4"N	0°10'28.5"E
Kete-Krachi	KET	7°47'42.5"N	0°03'29.62"E
Yeji	YEJ	8°13'21.8"N	0°39'36.7"W
Buipe	BUI	8°45'18.2"N	1°27'12.3"W

previous studies (Rutten et al., 2004; Sukmanomon et al., 2012; Trọng, 2013) was undertaken. Each reaction mixture of 15 µl contained 1 µl of 10 pmol of forward and 1 µl of 1 pmol of reverse primers of the microsatellite, as well as Bioneer master mix (Bioneer Corporation, South Korea), 2 µl sterile molecular biology grade water and 2 µl of 100 ng/µl DNA. PCR was performed using a Techne TC-512 thermal cycler (Bibby Scientific, UK). This involved 35 cycles of initial denaturation at 94°C for 30 s, an elongation at 48°C for 30 s (depending on annealing temperature of primer), an extension at 72°C 1min and held at 10°C after completion.

Amplified products were electrophoretically separated on 2.0% agarose gels buffered with 0.5X TBE. A DNA ladder was included as a size marker (100 to 2000 bp). After staining with ethidium bromide for 30 min, DNA fragments were identified by viewing the gel under a UV trans-illuminator. Digital images of the products

Table 2. List of primers used in the polymerase chain reaction.

Locus ID	Forward Primer	Reverse Primer
UNH106	CCTTCAGCATCCGTATAT	GTCTCTTTCTCTCTGTCACAAG
UNH123	CATCATCACAGACAGATTAGA	GATTGAGATTTCATTCAAG
UNH132	ATATAAGAAACTGAGTCGGTGAG	TGGAAATAGAGGGTGGGTGAG
UNH136	TGTGAGAATTCACATATCACTA	TACTCCAGTGACTCCTGA
UNH138	T TCAGCTTCATCTCTTG	CCATTTTAACCTCTCCATCT
UNH140	GAGAGCTCTTTAGTCTGTGAG	TCCAGCAGTGTAGTCATC
UNH142	CTTTACGTTGACGCAGT	GTGACATGCAGCAGATA
UNH146	CCACTCTGCCTGCCCTCTAT	AGCTGCGTCAAACTCTCAAAAG
UNH153	TCTGCTTTGCTTTTTCTCATTCT	TACGGCACACTCCCTCCAT
UNH159	TTGTTTTAGGAGCTTCTTTTGTC	ATATTCATCTGGATTTGGCTCTAA
UNH211	GGGAGGTGCTAGTCATA	CAAGGAAAACAATGGTGATA
UNH222	CTCTAGCACACGTGCAT	TAACAGGTGGGAACTCA
GM211	GCAAGTTGAGAGGCTACTGT	AAACAACCCACAACCTTAGTT
GM531	AAAGCCAACGGTCTGAATTG	AGCAGAGGACACCCCTCAT
GM538	CAGCATGTTGTCTGGATCTTG	TTTGTTGCTGTGGTCTGTTCTT

were taken and the bands were later scored.

Analysis of microsatellite data

Genetic polymorphism for each population was estimated as mean number of alleles per locus (Na), number of effective alleles (Ne), observed heterozygosity (Ho), expected heterozygosity (He) and percentage of polymorphic bands (PPBs) using POPGENE Version 1.31 freeware (Yeh et al., 1999) and GenAlEx 6.502 software (Peakall and Smouse, 2012). The polymorphism information content (PIC) for each primer was analyzed based on allelic frequencies using the PowerMarker Software v 3.6 (Lui and Muse, 2005). The Genepop on the web (Raymond and Rousset, 1995) was then used to estimate Wright's F-statistics (F_{IS}, F_{IT} and F_{ST}). The pairwise F_{ST} values were used to generate a matrix on the number of migrants exchanged per generation (N*m*).

A test for conformation to the Hardy-Weinberg equilibrium (HWE) by a Markov chain approximation of the exact test (Guo and Thompson, 1992) was undertaken by the Genepop on the web (Raymond and Rousset, 1995). The test for linkage disequilibrium based on the chi-square test was performed, wherein the disequilibrium coefficient was provided. To assess genetic differentiation among populations, the GenAlEx 6.502 software was used to determine molecular variance (AMOVA) and Shannon's information index (I). The proportion of private alleles in each subpopulation was also used to assess inter-population variability. Genetic differentiation indices such as Nei's genetic distance (D) and Nei's genetic identity were was also calculated using the GenAlEx 6.502 software. A standardized version of Mantel test (Mantel, 1967) was then performed to assess the correlation between the genetic distance and the geographic distance using 999 permutations. Nei's genetic distance (D) matrix was exported to Mega 4 (Tamura et al., 2007) from which a phenetic tree was constructed using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA).

RESULTS

In the present study, 15 microsatellite markers were used to characterize the *O. niloticus* populations in the Volta Lake of Ghana (Table 3). Twelve (12) of these markers showed variable level of polymorphism whilst three (UNH132, UNH136 and UNH153) were monomorphic.

Intra-population diversity

The number of alleles ranged from 2 to 11 per locus whereas the mean number of different alleles (Na) and the effective number of alleles (Ne) per locus was 3.275 and 2.254, respectively (Table 4). Further analysis of alleles revealed that the Akosombo strain, Kotoso and Kpando-Toko populations had 33.3, 8.3 and 16.7% private alleles respectively. The mean expected heterozygosity within populations (He) was 0.459 whilst the mean observed heterozygosity (Ho) was 0.526 (Table 4). Among the 10 populations that were assessed, the Kpando-Toko population had the highest expected heterozygosity of 0.502 whilst the Buipe population had the least expected heterozygosity (0.424). Kete-Krachi population had the highest observed heterozygosity of 0.594 whilst the Dzemeni population recorded the least observed heterozygosity (0.488). The Akosombo strain (AKO) had the highest Shannon diversity index (I) of 0.973 whilst BUI had the least diversity (0.731). Fixation index (F_{IS}) ranged between -0.207 and 0.144 with a mean of -0.060. With the exception of the Kpando-Toko and Abotoase populations, all the other sub-populations had negative F_{IS} values indicating excess of heterozygosity.

Locus variability

Of the 12 polymorphic loci that were assessed, locus UNH211 produced the highest total observed

Table 3. Annealing temperature (T_A) and size range of SSR.

Serial number	Primer	T_A/°C	Size range/bp
1	UNH106	40.6	135-160
2	UNH123	37.45	160-290
3	UNH132	46.95	550
4	UNH136	37.58	175
5	UNH138	38.25	175-190
6	UNH140	38.30	150 -175
7	UNH142	36.80	150 - 175
8	UNH146	50.30	120 -150
9	UNH153	49.45	200
10	UNH159	47.20	240 -270
11	UNH211	39.25	140 - 410
12	UNH222	37.85	190 - 210
13	GM211	43.90	150 - 390
14	GM531	48.45	220 - 350
15	GM538	48.20	160 - 240

Table 4. Some genetic parameters of the ten populations.

Population	Statistical parameters	N	Na	Ne	Np	I	Ho	He	F_{IS}
AKO	Mean	40.000	4.083	2.855	0.333	0.973	0.567	0.501	-0.074
	SE	0.000	0.783	0.600	0.256	0.180	0.101	0.075	0.080
KOT	Mean	40.000	3.333	2.142	0.083	0.806	0.508	0.447	-0.065
	SE	0.000	0.414	0.267	0.083	0.131	0.103	0.066	0.108
AKM	Mean	40.000	3.000	2.158	0.000	0.768	0.490	0.439	-0.011
	SE	0.000	0.426	0.335	0.000	0.129	0.104	0.063	0.128
DZE	Mean	40.000	3.250	2.064	0.000	0.777	0.488	0.438	-0.020
	SE	0.000	0.392	0.273	0.000	0.117	0.102	0.058	0.131
KPA	Mean	40.000	3.667	2.446	0.167	0.925	0.488	0.502	0.079
	SE	0.000	0.595	0.383	0.112	0.139	0.090	0.056	0.108
ABO	Mean	40.000	3.083	2.154	0.000	0.830	0.504	0.479	0.020
	SE	0.000	0.336	0.242	0.000	0.102	0.105	0.048	0.144
DAM	Mean	40.000	3.333	2.281	0.000	0.828	0.504	0.461	-0.003
	SE	0.000	0.620	0.344	0.000	0.151	0.112	0.069	0.139
KET	Mean	40.000	3.083	2.290	0.000	0.814	0.594	0.461	-0.207
	SE	0.000	0.468	0.304	0.000	0.147	0.113	0.075	0.126
YEJ	Mean	40.000	3.000	2.116	0.000	0.766	0.558	0.441	-0.146
	SE	0.000	0.461	0.269	0.000	0.132	0.116	0.067	0.165
BUI	Mean	40.000	2.917	2.030	0.000	0.731	0.558	0.424	-0.196
	SE	0.000	0.358	0.237	0.000	0.126	0.118	0.069	0.155
Total	Mean	40.000	3.275	2.254		0.822	0.526	0.459	-0.060
	SE	0.000	0.156	0.106		0.042	0.033	0.020	0.040

Na = number of different alleles; Ne = number of effective alleles; Np = number of private alleles; I = Shannon's Information Index; He = expected heterozygosity or gene diversity; Ho = observed heterozygosity; F_{IS} = fixation index (F_{IS}).

Table 5. The total heterozygosity, gene diversity, polymorphism information content, and Hardy–Weinberg genetic deviation probabilities.

Locus	Gene diversity	Ht (obs)	Ht (ave)	PIC	Allele No.	Exact p-value
UNH106	0.1638	0.0700	0.1546	0.1504	2.00	0.0000
UNH123	0.8246	0.8325	0.7543	0.8016	10.00	0.0000
UNH138	0.3361	0.4075	0.3258	0.2796	2.00	0.0000
UNH140	0.3617	0.4150	0.3332	0.3163	3.00	0.0004
UNH142	0.4128	0.3075	0.4443	0.3336	3.00	0.0000
UNH146	0.2119	0.1250	0.1942	0.2009	3.00	0.0000
UNH159	0.3347	0.1900	0.2597	0.3096	3.00	0.0000
UNH211	0.8673	0.9825	0.7264	0.8531	11.00	0.0000
UNH222	0.4747	0.4800	0.4567	0.3620	2.00	0.9265
GM211	0.7196	0.5725	0.5964	0.6775	8.00	0.0000
GM531	0.6053	0.9900	0.5992	0.5244	4.00	0.0000
GM538	0.7268	0.9025	0.6397	0.6789	5.00	0.0000
Means	0.503	0.523	0.4570	0.457	4.667	

Table 6. F-Statistics and estimates of Nm over all pops for each locus.

Locus	F_{IS}	F_{IT}	F_{ST}	Nm
UNH106	0.518	0.545	0.058	4.074
UNH123	-0.108	-0.009	0.089	2.552
UNH138	-0.249	-0.210	0.031	7.815
UNH140	-0.174	-0.122	0.044	5.426
UNH142	0.183	0.220	0.045	5.323
UNH146	0.400	0.451	0.084	2.731
UNH159	0.253	0.392	0.186	1.097
UNH211	-0.333	-0.183	0.113	1.971
UNH222	-0.057	-0.013	0.042	5.722
GM211	0.041	0.205	0.171	1.209
GM531	-0.663	-0.655	0.005	51.042
GM538	-0.411	-0.377	0.024	10.219
Mean	-0.050	0.020	0.074	8.265
SE	0.100	0.103	0.016	3.968

heterozygosity with a value of 0.9825 and a polymorphism information content of 0.8531, whilst UNH106 had the least observed heterozygosity (0.070) (Table 5). With respect to the mean expected heterozygosity, UNH123 had the highest value of 0.754 whilst UNH106 had the least value of 0.155. With the exception of UNH222, all the other loci deviated significantly from the HWE (P<0.05) as shown in Table 5.

Inter-population diversity

The mean F_{IS} ranged between -0.0.663 (GM531) and 0.518 (UNH106) with an average of -0.050 (Table 6). The F_{IT} values ranged between -0.655 (GM531) and 0.545 (UNH106) with a mean of 0.222 whilst the F_{ST} values ranged between 0.058 and 0.186 (UNH159) with a mean of 0.074. The mean number of migrants per generation was 8.265 whilst the least genetic distance of 0.011 was found between the YEJ and BUI populations as shown in Table 7. The furthest distance of 0.133 as found between DZE and KET populations. Nei's genetic identity matrix produced values ranging from 0.876 (DZE vrs KET) and 0.989 (YEJ vrs BUI) (Table 7).

Generally, genetic differentiation between subpopulation in the Volta Lake was moderate. The pairwise F_{ST} indicates the relative closeness between the BUI and YEJ population. The AKO strain also shows more closeness to the KPA rather than to the KET subpopulation. The inter-population differentiation (Gst) was 0.068 indicating that about 6.8% of the variance existed among populations whilst within population variance was about 93.2%. This result was similar to those from the analysis of molecular variance which indicates that 93% of the observed variance was as a result of variation within individuals, whilst 7% of the variation was shared between subpopulations.

Population clustering

The UPGMA tree for the ten populations generated from Nei genetic distance clearly shows two main clusters (Figure 2). The first main cluster includes: AKM, DZE, YEJ, BUI, KPA, ATB, AKO, DMB and KET population. In the second main cluster in the lower portion of the dendrogram contained the KOT population. Among the populations in the first cluster, KET and DAM formed a different cluster whilst AKO strain also formed a different cluster. The results from the Mantel test showed a weak correlation between the genetic distance (Nei) and the geographic distance (r = 0.014; p= 0.200) indicating that

Table 7. A matrix of pairwise Nei genetic distance (below diagonal) and Nei genetic identity (above diagonal) among the ten populations of *Orechromis niloticus.*

Matrix	AKO	KOT	AKM	DZE	KPA	ABO	DAM	KET	YEJ	BUI
AKO	**	0.906	0.909	0.913	0.924	0.921	0.924	0.888	0.905	0.912
KOT	0.099	**	0.897	0.912	0.913	0.915	0.911	0.885	0.898	0.890
AKM	0.095	0.108	**	0.948	0.914	0.928	0.934	0.878	0.925	0.931
DZE	0.091	0.092	0.054	**	0.937	0.942	0.936	0.876	0.942	0.955
KPA	0.079	0.091	0.089	0.065	**	0.978	0.919	0.906	0.931	0.928
ABO	0.082	0.089	0.074	0.059	0.023	**	0.942	0.917	0.921	0.922
DAM	0.079	0.093	0.068	0.066	0.084	0.059	**	0.938	0.918	0.915
KET	0.118	0.122	0.130	0.133	0.099	0.087	0.064	**	0.908	0.891
YEJ	0.100	0.107	0.078	0.060	0.071	0.082	0.085	0.096	**	0.989
BUI	0.093	0.116	0.072	0.046	0.074	0.082	0.088	0.115	0.011	**

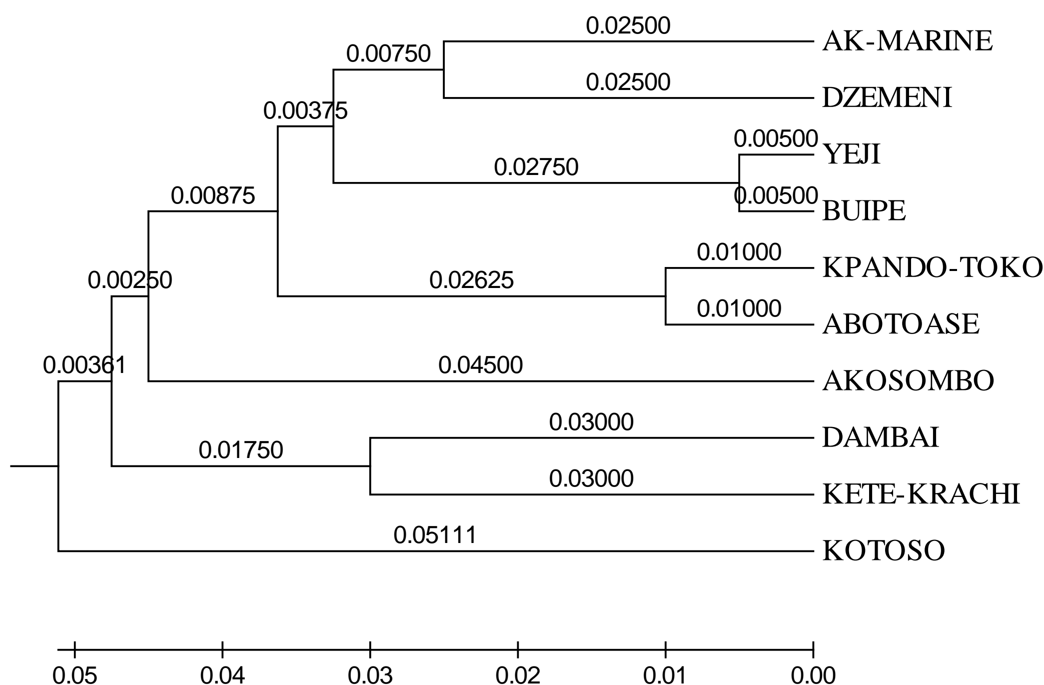

Figure 2. UPGMA trees of the ten populations of *Oreochromis niloticus* from the Volta Lake constructed using Nei's genetic distance matrix (values attached are branch length).

the population structure is not a result of isolation due to geographic distances.

DISCUSSION

Genetic variation within populations

Genetic variation is one of the fundamental subjects of investigation in population genetics. Characterizing the genetic structure of populations is of major importance in studies such as evolutionary biology. It describes naturally occurring genetic differences among individuals of the same species. Generally, natural populations are subdivided into a number of subpopulations or demes, which are characterized by significant genetic differentiation (Bezault et al., 2011). High Shannon diversity and heterozygosity of the Akosombo strain (AKO) population suggests proper genetic management of the strain. Although this strain has undergone selection for more than nine generations, selection pressure for characters such as growth has not affected the gene pool of the strain. The strain has not lost alleles through random genetic drift. Breeding pattern in this artificial

population is non-random; selection for specific trait is evident and hence most of the assumptions underlining the HWE are violated. This is also reflected in the negative F_{IS} value (-0.074) which indicates excess of heterozygotes in that population. In contrast to what is expected in a production system where intensive selection for growth traits lead to increased homozygosity, the results of the present study for the Akosombo strain showed an opposite trend. This indicates that the effective population size (Ne) used for the breeding was high enough and led to the increase in heterozygosity of the improved strain. This is similar to results obtained from the GIFT strain (Rutten et al., 2004).

Deviations from Hardy-Weinberg equilibrium in the total population (F_{IT}) and averaged deviation from Hardy-Weinberg within subdivisions (F_{IS}) have been used in population genetics to assess the levels of heterozygosities in natural population (Çiftci and Okumu, 2002). Crow and Kimura (1970) noted that there is an excess of heterozygosity especially when there are alleles with low frequencies. The negative values obtained in the current research indicate presence of excess heterozygotes in the population due to outcrossing and the presence of different genotypes which occurred in very low proportions. This suggests that sexual selection, mutation or migration, the allele frequencies and the genotype frequencies are not constant from generation to generation as expected under Hardy-Weinberg equilibrium (HWE). This feature is very common in natural populations which do not always comply with Wright's (1951) island model (Briñez et al., 2011). However, it is noteworthy that the result of Mantel's test indicates that structuring within the population is not due to isolation by geographic distances.

The high genetic variation within populations suggests a very high genetic diversity within populations. This characteristic feature is key in selecting individual for any breeding programme. The current results confirm those of Falk and Abban (2004) who noted the presence of an essential genetic structure within the Ghana population of *O. niloticus.* The high diversity could be due to abundance of niches, mating system and lifespan of the species. Conversely, results from the analysis of molecular variance indicated a moderate genetic differentiation (F_{ST} = 0.074) among subpopulations which could be due to effective gene exchange between individuals of the species. Gene flow has been noted to be effective in changing the spatial distributions of genes (Slatkin, 1985). This phenomenon homogenizes gene frequencies and also reduces local adaptation by preventing divergence resulting in the formation of a weak population structure (Barton and Hewitt, 1985; Balloux and Lugon-Moulin, 2002; Cristescu et al., 2012).

Population genetic structure of living organisms is largely shaped by both historical and contemporary gene flow in the species range (Holsinger and Weir, 2009). The interplay of these factors characterizes the structure of populations. The high genetic variation within individual in the population (92.8%) indicates high genetic diversity. These values were high compared with 54.12% obtained from six populations of red hybrid tilapia (Briñez et al., 2011). Low levels of differentiation (Fst < 0.05) have been reported in some improved strains of Nile tilapia (Sukmanomon et al., 2012). However, the high differentiation of the Ghanaian population provides a basis for further improvement of the already available Akosombo strain. The presence of private alleles among three of the populations did not affect the F_{ST}. Jost (2008) showed that as heterozygosity becomes large, F_{ST} will naturally approach 0 - indicating low differentiation - even if all alleles at a locus are private.

Genetic differentiation between populations

Assessment of genetic diversity and population structure is an important feature in population and quantitative genetics. The total heterozygosity of the alleles was 0.523 while the mean observed and expected heterozygosity were 0.526 and 0.459, respectively, indicating that the gene pool of the species was effectively maintained leading to a high genetic variability. The high diversity of the population was further confirmed, since gene diversity and Shannon information index were significantly greater than zero (P>0.05). Bezault et al. (2011) reported similar ranges of heterozygosity for the species obtained in the Kpando and Nyinuto portions of the Volta Lake. This is consistent with the known fact that large naturally outbreeding species have high genetic diversity (Nei and Kumar, 2000).

The genetic differentiation among populations is affected by mutation, migration, drift and selection (Gall, 1987; Holsinger and Weir, 2009; Whitlock, 2011). Other extrinsic factors (for example habitat heterogeneity), and intrinsic factors (e.g. dispersal capability, mating system and habitat preference) have an impact on gene pool composition at intra-population level (Bezault et al., 2011). Given the vast nature of the lake, the possibility of different niches cannot be underestimated. Habitat preference and high gene flow per generation are two important factors resulting in the high gene diversity. Generally, population subdivision results in the loss of genetic variation within subpopulations due to their small size and genetic drift acting within each one of them. High genetic variation theoretically promotes better adaptability of the populations to changing environmental conditions (Allendorf and Phelps, 1980).

The very low genetic differentiation in the Buipe and Yeji subpopulations could be the result of great mixing of genetic materials between these two populations. This is further supported by the very high number of migrant

(51.7) shared by the two population per generation and the phylogenetic tree which clustered BUI and YEJ subpopulations together indicating that these two populations were the most genetically relevant. Falk and Abban (2004) who used RAPDs to the characterize Nile tilapia populations in Ghana noted that the norther portion of the Volta system had the least variability while the central portions (lacustrine regions) had high diversity. High levels of migration and gene flow between populations increases their similarity (Neigel, 1997).

The clustering of the Akosombo strain (AKO) with the other subpopulations also confirms the presence of alleles from these subpopulations in the development of the strain (Attipoe, 2006; Attipoe et al., 2013). The separate cluster formed by KOT, KET and DAM subpopulation confirms that these were not used as parent material in the production of the strain. Generally, there was a reduction in the number of migrant downstream possibly due to a reduction in the effective number of migrants (Nm) from the riverine to the lacustrine portion. This observation could be due to the availability of more niches and presence of different microhabitats. The riverine portions of the lake are generally narrow while the lacustrine portions are broader. Hence the lacustrine section of the lake exhibited more variation in allele frequency (genetic differentiation) than the riverine portion.

Conclusion

The Nile tilapia population in the Volta exhibits high within population variability and low among population variability. There is high gene flow within most of the populations which suggests the Ghanaian population are evolving toward homogeneity. However, due to the high within population variation, management of each of the examined populations is necessary for selection of population for breeding purposes. The Akosombo strain and the Kpando-Toko population exhibited the highest diversity.

Conflict of Interests

The authors have not declared any conflict of interests.

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