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Full Length Research Paper

Preliminary results of the analysis of the population structure of the Nile perch (*Lates niloticus* linnaeus, 1758) of Lake Victoria using microsatellite markers

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Preliminary results are provided of a study instituted to analyze the genetic population structure of the Nile perch in Lake Victoria since 2002. 293 individuals from six geographically distinct locations within the lake were analyzed using two polymorphic microsatellite DNA markers. Tests for differentiation with an overall F_{ST} = 0.03 (P < 0.05) suggested that populations were genetically differentiated, with the closet population pairs Nyaburu-Rubafu and Mirunda-Maboko as the most differentiated populations. There was an extensive gene flow between the populations (*Nm* = 20.77). The overall gene diversity (0.17) was low. All the results point to the fact that Nile perch was only recently introduced species in the lake based on a small founder population, which though slow in establishing later exploded to become the most dominant species in the lake. On the whole the two loci indicate some level of differentiation between locations; however, the levels of genetic differentiation shown by the two loci were not enough to define the structure of Nile perch stocks, and assess the level of exchange between locations. Further work is underway using bigger number of microsatellite markers.

Key words: Nile perch, Lake Victoria, microsatellite DNA, population structure.

INTRODUCTION

Fishing pressure on the wild stocks in the Lakes Victoria and Kyoga with the inception and establishment of the commercial fishing prompted the resource managers to transplant fish species into Lake Victoria Region waters starting as early as the 1920s (Lowe-McConnell, 1959; 1987; Fryer and Iles, 1972). Nile perch from Lake Albert and Lake Turkana was introduced in Lake Victoria and surrounding lakes starting in the 1950s in attempt to fill the gap left by declining tilapia fishery, turn the small cichlids (haplochromines) into table size fish, and allow for a sport fishery on these waters (Hamblyn, 1961; Eaffro, 1967; Welcomme, 1988). During the first 20 to 30 years of its introduction Nile perch formed only a minor component of the fisheries which at that time were dominated by the haplochromine cichlids (Kudhongania and Chitamweba, 1995). The Nile perch fishery exploded and began to dominate the fisheries of Lakes Victoria and Kyoga only in the early 1980s (Arunga, 1981; Okaronon et al., 1985; Goudswaard and Ligtvoet, 1988; FAO, 1993). As the Nile perch rapidly increased and flourished, the stocks of the native species greatly declined notably the endemic haplochromine cichlids (Ribbink, 1987; Witte et al., 1992). Nile perch became cast as the ecological villain believing that it was the major cause of the decline in number of native species in Lake Victoria (Barel et al., 1985). Further studies in the different regions of the lake (Okaronon et al., 1985; Ogari, 1985; Witte and Goudswaard, 1985) reinforced this observation, although to others factors like eutrophication (Hecky, 1993) and over-fishing (Bundy and Pitcher, 1995) may have been the major contributors to the decline of the native species

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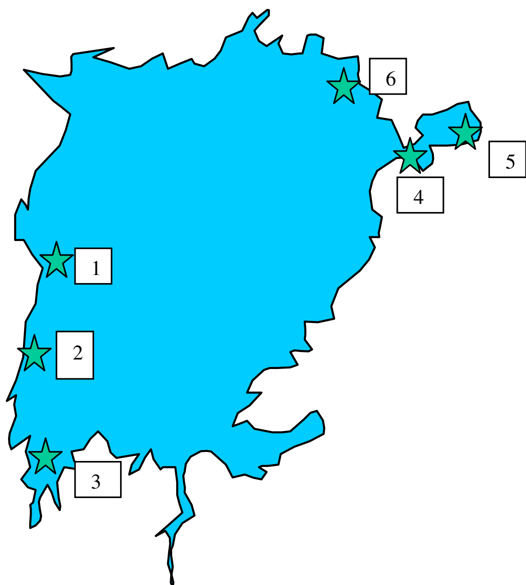

Figure 1. Map of lake Victoria showing the sampled sites. **Site 1 =** Rubafu Tanzania (RUB), **Site 2 =** Nyaburu Tanzania (NYR), **Site 3 =** Kabiga Tanzania (KAB), **Site 4 =** Maboko Kenya (MKO), **Site 5 =** Nyanza Mirunda Kenya (NYA),; **Site 6 =** Sigulu, Uganda (SIG).

and not necessarily the Nile perch. Today the Nile perch dominates the fishery of Lake Victoria (DFR, 2004). Nile perch has a lake wide distribution, occurring throughout the lake (Witte et al., 1992), and together with the introduced Nile tilapia and native *Rastreneobola argenta,* currently form the mainstay of the commercial fisheries of Lake Victoria.

Despite being fronted as the one responsible for the diminishing number of the native fish species and/or their stocks in Lake Victoria, Nile perch has now established as key fishery species on which the three Lake Victoria riparian countries' 300 million dollar annual fish process-sing and export industry depends (MFPED, 1999). Hence the sustain-ability of the Nile perch fishery in Lake Victoria has become a high priority management concern, and most of the key fisheries management decisions and measures on the lake are geared toward the sustainable and productive exploitation of the Nile perch. One area of interest to fisheries managers on the lake has been the population structure of the Nile perch (IFMP, 2003) for its effective management and sustain-ability. Questions as to whether we dealing with one panmictic population or a geographically subdivided population units/stocks need answers for the equitable and sustainable exploitation of the Nile perch. This study was conducted by the Lake Victoria Research Project funded by EU (2001 - 2004) in attempt to answer these very questions using molecular tools.

Due to behavioural and physical restrictions on dis-persal, and the increased localised fishing pressure on the Nile perch, variation in limnolgical conditions over the lake width and depth with time, the explosion of water hyacinth, the uneven distribution of the Nile perch prey, and the sheer size of the lake we believe the Nile perch exists as several distinct stocks or subunits with limited genetic exchange between units/stocks. Some limited studies using allozyme markers by Hauser et al. (1998) in agreement that the Nile perch of Lake Victoria is subdivided within the lake. This is so despite its migratory nature pointed out by Ligtvoet and Mkumbo (1990). The object of this study therefore was establish the genetic population structure of the Nile perch in Lake Victoria, define and map the extant stocks of this fishery.

The small founder population during introduction of which only a portion may have survived to reproduce in the new environment (Anderson, 1961; Gee, 1964), the slow rate of population increase after establishment (Carvalho and Hauser, 1995), and the population explosion in just 20 years (Arunga, 1981; Okaranon et al., 1985; Goudswaard and Witte, 1985; Goudswaard and Ligtvoet, 1988), must have greatly reduced the genetic variability of Nile perch. This makes it necessary to establish and quantify the genetic variability of the Nile perch of Lake Victoria as one attempt to define the geographic subdivisions of this species. Managers have recognized that the prudent harvest of a wild species requires the knowledge of intraspecific structuring, be-cause of differences in abundance and demography from one area to another (Sinclair, 1988).

Since the Nile perch was transplanted into Lake Victoria from Lakes Albert and Turkana a total of 374 individuals were obtained from Lake Albert and eight individuals from Lake Turkana as reference points for the study. Taxonomical use of morphological characters to differentiate Nile perch subspecies by Harrison (1991) and Hauser et al. (unpublished data) failed to identify these fishes unambiguously as *L. niloticus*, however, Hauser et al. (1998) findings indicated that the introduced Nile perch were mainly *L. niloticus* from Lake Albert. Unfortunately these studies (Hauser et al., 1998) did not rule out *Lates macrophthalmus* a subspecies more suited to the open waters (Hunter, 1970) like those of Lake Victoria. However, Holden (1967) study of the taxonomy of this species finds existence of two subspecies of Lates niloticus in Lake Albert.

This study was based on microsatellite marker analysis, and though two loci have been studied so far the intention is to developed more markers now that preliminary results below have shown great promise in delineating the stocks of Nile perch. This study was part of the Lake Victoria Research Project (LVRP 2002) funded by the European Union.

METHODS AND MATERIALS

Study area

Lake Victoria is the world's largest tropical lake and the second largest in the world. It is situated between longitude 31° 40¹ E to 34°

50¹ E and latitude 3° 40¹ S and 0° 30¹ N (Figure 1). It has a total surface area of 68,680 km^2. Its average depth is 40 m and maximum depth 80 m with the cichlid fishes as the endemic species (Graham, 1929; Worthington, 1929). Nile perch samples were taken from six different locations within Lake Victoria, three locations from the Tanzanian waters of the lake, two locations from the Kenyan waters, one location from the Ugandan waters of the lake (Figure 1). The transects used in sampling were pre-determined with the guide of hydro-acoustics after considering factors such as the traditional fishing grounds of the Nile perch, previous knowledge of Nile perch distribution, tagging studies and the lake topography. The fish were caught using the bottom trawling with the guide of the hydroccoustics.

Sampling targeted the spawning fish, which minimized collecting non-spawning migrants from other areas together with the local population. In addition, at least 10 immature individuals were randomly sampled from each location. Whenever possible a minimum 50 individuals was sampled from each single geographical location depending on amount of fish caught at given location. A fin clip cut out of the pectoral fin was taken from each sampled fish and put into a labeled vial pre-filled with 95% ethanol. The tissue to ethanol ratio was kept to approximately 1:5. In the laboratory the samples were kept under refrigeration at –20°C prior to genetic analysis.

Extraction of DNA

Total genomic DNA was extracted using the Dneasy™ tissue kit (QIAGEN) following the manufacturer's instructions. In the laboratory the sample tissue was macerated and together with the lysing solution, digested with proteinase K at 55°C for 2 - 3 h, and followed by cleaning/washing and eluting. A negative control that did not contain the tissue was used. The DNA extracts were dissolved in 300 µl of elution buffer and stored at -20°C. To test for success of the DNA extracts, 4 µl of the total genomic DNA was electrophoresed on 2% agarose gel stained with ethidium bromide (EtBr) and then visualized under ultra violet (U.V) light for clear DNA bands.

Amplification of microsatellites

PCR amplifications were carried out on an Eppendorf mastercycler gradient in 10 µl reaction volumes containing 1 µl of genomic DNA, 1 µl Taq buffer, 4 µl dNTPs, 1 µl reverse primer, 0.6 µl forward primer cocktail, 3.4 µl double distilled water, 0.05 µl Taq polymerase. The PCR conditions included an initial denaturation step at 94°C for 5 min, followed by 34 cycles of 30 s comprising of denaturation at 94°C, annealing at 55°C for 1 min and final extension at 72°C for 3 min. The forward primer for each locus was labeled with $\gamma^{32}P$ on the 5' end for detecting the microsatellite alleles. The PCR products were mixed with an equal volume of formamide loading dye, heated to 90 - 100°C for 3 min and then run on a 6% denaturing polyacrylamide/7M urea sequencing gel for 2 - 3 h.

An M13 control sequencing reaction was run adjacent to the samples to provide an absolute size marker for the microsatellite alleles. The gel was then fixed in acetic acid solution to remove the urea, washed in water dried and exposed on a Kodak film for overnight autoradiography. The film was fixed and developed in a dark room. Scoring of the microsatellite alleles was done manually. The two loci Lno27 and Lno28 amplified successfully and genotypes at the two loci were determined for the majority of individuals.

Data analysis

Tests for linkage disequilibrium, conformity to Hardy-Weinberg expectations and the pairwise tests for population differentiation using both allele and genotype frequencies, were conducted using GENEPOP (Raymond and Rousset, 1995) Version 3.1c. Genetic variation was measured as mean number of alleles per locus (A), observed heterozygosity (H_o), expected heterozygosity from Hardy-Weinberg expectations (H_e), using the program POPGENE Version 1.31 (Yeh et al., 1999). Since GENEPOP provides only estimates of the F-statistics (Newman and Squire, 2001), to quantify the extent of genetic differentiation among the samples, the Weir and Cockerham (1984) analogues of Wright's *F*-statistics F_{ST}, F_{IS} and F_{IT} were calculated using the program ARLEQUIN 2.0 (Schneider et al., 2000) and their significance determined by Fisher's method (Manly, 1985; Raymond and Rousset, 1995a). Analysis of molecular variance (AMOVA) was performed as in Michalakis and Excoffier (1996), in order to partition the genetic diversity based on allele frequency into: (i) variance between populations; (ii) variance between individuals within populations; and (iii) variance within the individuals. The significance of the variance components was tested using nonparametric permutation procedures as implementted in ARLEQUIN 2.000. The relationships between the six populations were assessed by computing Nei's (1978) unbiased measures of Genetic Identity and Genetic distances using POPGENE Version 1.31. The matrix of pairwise distances obtained was used to construct a population phenogram using the neighbour-joining algorithm available in PHYLIP (Felsenstein, 1995). Multilocus estimates of the effective number of migrants (Nm) per generation over all locations were calculated using the private-allele method of Slatkin (1985) and were corrected for sample size as given in Barton and Slatkin (1986).

RESULTS

Gene diversity

The two loci showed genetic diversity, they were polymorphic, with three alleles detected at each of the loci, but low levels of expected heterozygosity (0.058 < H_E < 0.323). All populations contained the three alleles 1, 2 and 3 detected at locus Lno27. For locus Lno28, all populations contained only allele 1 and 2, except the KAB population which in addition also contained allele 3 (Table 4). The most common allele (Figure 2) for all populations at both loci was the same resulting in the low levels of expected heterozygosity. At locus Lno27 most common allele was number 1 with frequencies ranging from 0.820 to 0.909 and at locus Lno28 most common allele was number 2 with frequencies ranging from 0.800 to 1.00 (Table 3). The mean overall gene diversity was 0.17 and the mean gene diversity per population was 0.09 (Table 3). Three genotypes were detected at the locus Lno27 and four genotypes at locus Lno28 (Figure 2). All populations contained the three genotypes (1,1), (1,2), and (1,3) detected at locus Lno27 (Table 1). All populations contained genotypes (1,1), (1,2) and (2,2); the KAB population also contained another genotype (2,3) all detected at locus Lno28 (Table 2).

The single population linkage disequilibria were determined as in Weir and Cockerham (1979), using POPGENE version 1.31, the number of significant ($P < 0.05$) linkage disequilibria (LD) was equal to zero (LD = 0, df = 1) for each of the six populations, indicating that the two loci were independent. The genotypic disequilibrium P-values calculated using GENEPOP (Raymond and

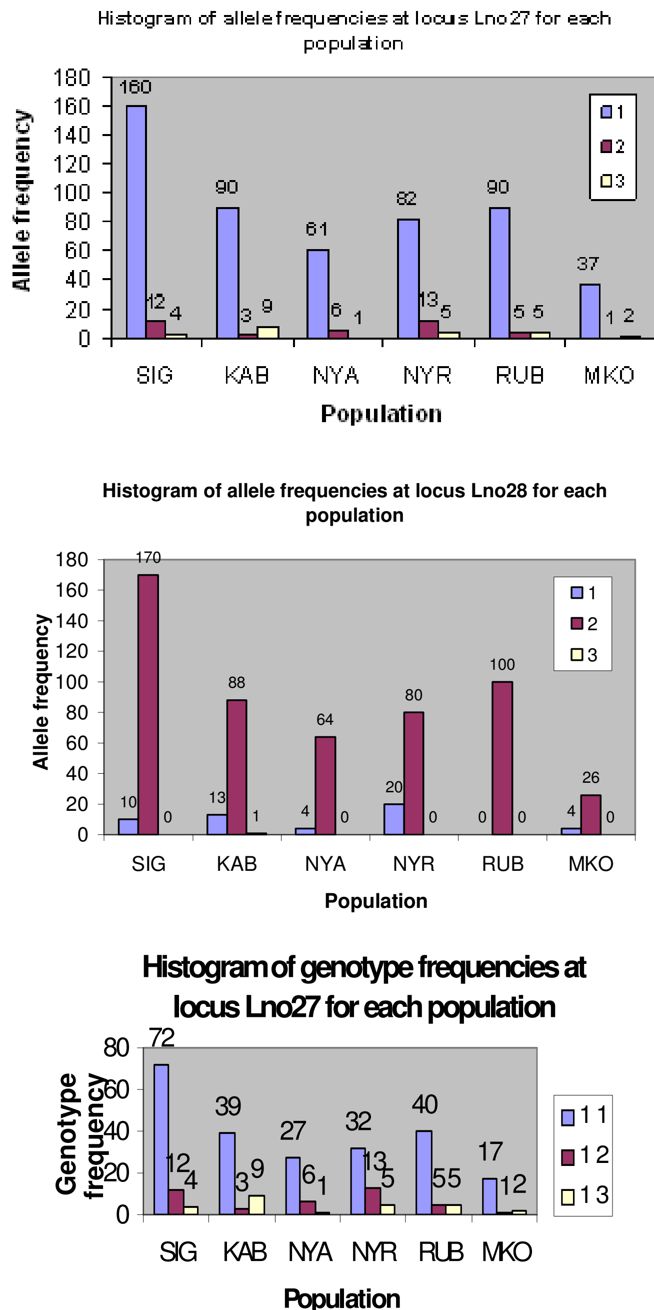

Figure 2. Allelic and genotypic frequencies at the two loci studied for the 6 locations.

Table 1. Genic and genotypic differentiation for each population pair at locus Lno27. Bald figures above diagonal are P-values for genic differentiation and figures below diagonal are P-values for genotypic differentiation.

	SIG	KAB	NYA	NYR	RUB	MKO
SIG	---	0.02*	0.85	0.87	0.42	0.31
KAB	0.02*	---	0.04*	0.02*	0.50	0.89
NYA	0.85	0.03*	---	0.34	0.34	0.30
NYR	0.89	0.01*	0.26	---	0.16	0.16
RUB	0.38	0.49	0.35	0.16	---	0.89
MKO	0.51	0.78	0.39	0.15	0.86	---

*Significantly differentiated.

Rousset, 1995) for the two loci for all populations (0.47 < P < 1.00), were not significant (P < 0.05) (Table 4). The P-value for the locus pair across all populations, calculated using Fisher's method, was not significant (P = 0.91), indicating that the two loci assort independently.

The expected and observed genotype frequencies at the two loci for all populations differed only slightly (Table 1 and 2), suggesting conformity with Hardy-Weinberg expectations. The P-values (0.09 < P < 1.00) at all loci and 0.36 across all loci and all populations for Hardy-Weinberg test calculated using GENEPOP (Raymond and Rousset, 1995), were significant (P > 0.05) further suggesting that the populations were in Hardy-Weiberg proportions. The expected heterozygosity (H_E) values and the single locus P-values (P_{HW}) for the Hardy-Weinberg probability test (Table 4) were determined using POPGENE (Yeh et al., 1999) version 1.31c. At locus Lno27 all populations showed heterozygosity excess and at locus Lno28, the KAB population showed heterozygosity deficiency though the difference was small, while the other populations all showed heterozygosity excess. The difference (H_O - H_E), between observed and expected heterozygosity in all populations was not much. The corresponding P- values ($0.38 < P_{HW} < 0.98$) computed using the Markov chain method with 1000 dememorisations and 100 batches of 1000 iterations for all populations were highly significant (P> 0.05) also indicating conformity with the Hardy-Weinberg expectations. The fixation indice F_{IS} (Weir and Cockerham, 1984) values at locus Lno27 ($–0.149 < F_{IS} < –0.062$) are all negative values, and for locus Lno28 ($–0.125 < F_{IS} < 0.181$) there is one positive and small value for the KAB population suggesting levels of nonrandom mating within populations were small (Table 4).

Population differentiation

The P-value for genotypic and allelic differentiation for all loci and all populations (P= 0.00, χ^2 = infinity, df = 4) were both highly significant (P<0.05) suggesting the Nile perch populations within Lake Victoria are differentiated. At locus Lno27 it were only three population pairs, SIG-KAB, KAB-NYA, and KAB-NYR (Table 1), of the fifteen population pairs, that were significantly (P< 0.05) differentiated. The most differentiated population pair at this locus was KAB-NYR (P = 0.019), and the least differentiated population pair was RUB-MKO (P = 0.89). At locus Lno28 eight population pairs, SIG-KAB, SIG-NYR, SIG-RUB, KAB-RUB, NYA-NYR, NYA-RUB, NYR-RUB and RUB-MKO (Table 2), were significantly differentiated. The most differentiated population pair at this locus was NYR-RUB (P = 0.00), and the least differentiated population pair was

Table 2. Genic and genotypic differentiation for each population pair at locus Lno28. Bald figures above diagonal are P-values for genic differentiation and figures below diagonal are P-values for genotypic differentiation.

	SIG	KAB	NYA	NYR	RUB	MKO
SIG	---	0.02*	1.00	0.00*	0.02*	0.12
KAB	0.04*	---	0.24	0.19	0.00*	1.00
NYA	1.00	0.26	---	0.01*	0.02*	0.24
NYR	0.00*	0.18	0.01*	---	0.00*	0.57
RUB	0.01*	0.00*	0.06	0.00*	---	0.00*
MKO	0.21	1.00	0.45	0.42	0.00*	---

*Significantly differentiated.

Table 3. Overall genetic diversity at the two loci over the six populations. A is the overall number of alleles, H_E is the overall gene diversity, H_E/pop is the mean gene diversity per population and H_O/pop the mean observed heterozygosity per population. Allelic size range is also indicated.

Locus	A	H_E	H_E/pop	H_O/pop	Allelic size range
Lno27	3	0.19	0.17	0.21	138-146
Lno28	3	0.16	0.02	0.15	246-254
Mean	3	0.17	0.09	0.18	

KAB-MKO (P = 1.00). The F_{ST}s determined using ARLEQUIN 2.0 by the distance method, that uses the number of different alleles as in Weir and Cockerham (1984), ranged from 0.003 < F_{ST} < 0.138, and most of them (70%) were not significantly different from zero (Table 5). The correspondding P-values ranged from 0.00 < P < 0.99 with over 60% significant (P < 0.05), sugges-ting further that most of the populations were different-tiated. The hierarchical analysis of molecular variance (AMOVA) computed as in Excoffier et al. (1992) and Weir and Cockerham (1979) revealed that 3.05% of the total variance was attributable to variation between popula-tions, -6.16% to variation between individuals within populations and 103.10% to variation within individuals (Table 5).

Gene flow

The multilocus estimate of the effective number of mi-grants (Nm) per generation based on private alleles (Barton and Slatkin, 1986) was 20.77 indicating extensive amount of gene flow within the Nile perch populations of Lake Victoria.

Population relationship

Nei's (1978) genetic identity between populations was high ranging from 0.98 between RUB and NYR – 1.00 between MKO and KAB populations, indicating that the six populations shared 98-100% common alleles. The genetic distance between populations was low, varied between –0.002 (KAB vs. MKO) and 0.018 (NYR vs. RUB).

DISCUSSION

The genetic diversity levels at the two microsatellite loci were generally low, with the overall genetic diversity only at 0.17 and genetic diversity per population even lower at 0.09. The results also indicated low levels of expected heterozygosity (H_E) ranging from 0.058< H_E <0.323, a small number of mean observed alleles per locus, na = 3.00 (Table 3). The fact that the most common alleles (Figure 1) were the same for all populations could have caused the low levels of expected heterozygosity, and or the fact that you need more loci to fully answer questions on genetic diversity. But this could be also explained by the small founder population, the rapid population explo-sion in just twenty years and the slow colonization after introduction factors all known to drastically reduce species genetic variability (Nei et al., 1975; Carvalho and Hauser, 1995). The results for both the single population disequilibria and the genic and genotypic disequilibrium indicated that the two loci Lno27 and Lno28 were independent.

Most of the populations save for the Kabiga (KAB) population all showed excess heterozygosity (Table 4), although the difference between the observed and exp-ected heterozygosity were not much, the corresponding P-values were highly significant (P>0.05) suggesting that

Table 4. Summary statistics of genetic variation at two microsatellite loci in six populations of Nile perch of L.Victoria. N is number of individuals scored; A is total number of alleles detected in each population; H_O is observed heterozygosity; H_E is expected heterozygosity; F_{IS} is the Weir and Cockerham's (1984) analogue of Wright's fixation index F_{IS} and P(*HW*) the single locus P-values for Hardy-Wienberg tests

Population	Lno27						Lno28					
	N	A	H_O	H_E	F_{IS}	P (H_W)	N	A	H_O	H_E	F_{IS}	P (*HW*)
SIG	90	3	0.144	0.137	-0.063	0.82	90	2	0.111	0.106	-0.059	0.47
KAB	51	3	0.235	0.215	-0.106	0.69	34	3	0.196	0.242	+0.181	0.54
NYA	34	3	0.206	0.190	-0.099	0.86	51	2	0.059	0.058	-0.030	0.86
NYR	50	3	0.320	0.281	-0.149	0.41	50	2	0.360	0.323	-0.125	0.38
RUB	50	3	0.200	0.187	-0.081	0.80	50	1	-	-	-	-
MKO	20	3	0.150	0.145	-0.062	0.98	16	2	0.268	0.239	-0.154	0.50
Mean		3	0.209	0.193	-0.093	0.76		2	0.166	0.161	-0.187	0.46

Table 5. Analysis of Molecular variance (AMOVA) by the distance method using number of alleles as in Weir and Cockerham (1984).

Source of variation	d.f	Sum of squares	Variance components	Percentage of variation
Among populations	5	3.308	0.00532 Va	3.05
Among Individuals Within populations	289	45.721	-0.01073 Vb	-6.16
Within Individuals	295	53.000	0.17966 Vc	103.10
Total	589	102.029	0.17425	

d.f is the degrees of freedom.
Fixation Indices: FIS = -0.06361, FST = 0.03054, FIT = -0.03103.

populations were in conformity with the Hardy-Weinberg expectations. This could be probably be due to low levels of nonrandom mating within the Nile perch populations as suggested by the values of the Wright's fixation index F_{IS} (Table 4), which almost all negative and significantly different from zero. The low levels of nonrandom mating and the consequent agreement with Hardy – Weinberg expectations could be probably due to little or lack of mating choice (Caroline et al., 1999) in Nile perch populations as the females just shade their eggs in the open waters (Okedi, 1971).

The overall G-like test P-value for genotypic differenttiation for both loci and all populations computed using GENEPOP (Raymond and Rousset, 1995) was 0.00, which was highly significant, ($P < 0.05$) suggesting that the Nile perch populations were differentiated, that is, there is genetic variation of the *Lates* spp. within Lake Victoria. This is in agreement with Hauser et al. (1998) using allozyme variation of Nile perch within the lake. At the individual loci, for locus Lno27 the P-value was 0.06 indicating the populations were not differentiated at this locus, though the difference was not much. At locus Lno28 the P-value was 0.00 indicating the populations were highly differentiated at this locus. The pairwise comparison at locus Lno27 showed that it were only three population pairs out of the possible fifteen vis SIG and KAB, KAB and NYA, and KAB and NYR (Table 1) that were significantly differentiated. At locus Lno28 seven out of fifteen population pairs were significantly differentiated, vis KAB and SIG, NYR and SIG, NYR and NYA, RUB and SIG, RUB and KAB, RUB and NYR, and RUB and MKO (Table 2). These results suggest that there was higher variation at locus Lno28 which has a trinucleotide repeat motif than there was at locus Lno27 with dinucleotide motif, contrary to what is expected that trinucleotide loci may have lower rates of mutation than dinuncleotide loci in a variety of taxa (Robert and Tina, 2001). Results from AMOVA showed that the contribution to total variation (Table 5) from the between population component (3.05%) was more than the contribution from within the populations (-6.16%), with that from between individuals within populations being the biggest (103.10%). This suggests that there is genetic variation between the different Nile perch populations within Lake Victoria. Though the level of variation between different populations is low, the results have indicated that there is a high possibility of isolated Nile populations within Lake Victoria that may have limited genetic exchange between them.

The results indicated an extensive amount of gene flow between the populations, this is probably accounted for probably by the high mobility and migratory nature of the Nile perch (Ligtvoet and Mkumbo, 1990) and mode of reproduction where the female sheds the eggs in open water (Okedi, 1971), lack of parental care which makes it

possible for the eggs and larvae to be carried away by the water currents. But the effects to genetic variation may be limited by the eggs and larvae being preyed upon and eventual mortality as they are carried along by the water currents.

Conclusion

The overall genetic diversity at the two loci of the Nile perch of Lake Victoria is low. The Nile perch in this lake is probably differentiated by stocks although the level of differentiation is still low, probably due to the nature of the *Lates* spp. being an open water species and highly mobile and migratory (Ligtvoet and Mkumbo, 1990), and or limited analysis given the low number of loci used. Also, because Nile perch has been in this lake only for a short time getting established since only about 25 years ago, is a very short time on the evolutionary scale. Nonetheless, since differentiation has been indicated to be able to define the different stocks, there is need to further study the Nile perch using more microsatellite loci and a higher number of samples in spawning condition (100 - 200 samples from each different location). For meaningful estimates of F-statistics Goudet (1995) suggested use of at least 5 microsatellite loci. The collection of non-spawning migrants from other areas together with the local populations may mask the existing genetic variation. In addition the seasonal or even annual aspect should be included in the sampling by repeating surveys. Consistent patterns of differentiation will unlikely be due to sampling artifacts (Waples, 1998) and will confirm the true population structuring. To assess microgeographical differentiation, it is recommended that repeat sampling is done in same area. Microgeographical differentiation reveals clearer boundaries between populations. In addition to genetic analysis, there is need to study the geographical variability in behaviour, reproduction, recruitment patterns, morphology, elemental composition, parasite load, physiology, migration, life history differences, to complement the genetic analysis, and may be to reveal structuring that may be not be genetically based (Grant et al., 1999). It's also important to note that genetically this work is not definitive, and it is only preliminary to a larger study planned in the near future using more microsatellite loci, and more fine sampling structuring geographically.

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REFERENCES

Anderson AM (1961). Further observations concerning the proposed introduction of Nile perch into lake Victoria. E. Afr. Agric. J. 26: 195-201.

Arunga JO (1981). A case study of lake Victoria Nile perch *Lates niloticus* (Mbuta) Fishery, 165-184. In: Proceedings of the workshop of the Kenya Marine and Fisheries Research Institute on aquatic resources of Kenya, 13-19 July 1981, Mombasa. Kenya Marine and Fisheries Research Institute and Kenya National Academy for Advancement of Arts and Sciences.

Barel CDN, Dorit R, Greenwood PH, Fryer G, Hughes NF, Jackson PBN, Kawanabe H, Lowe-McConnell RH, Nagoshi M, Ribbink AJ, Trewavas E, Witte F, Yamaoka K (1985). Destruction of fisheries in Africa's Lakes. Nature. 315: 19-20.

Barton NH, Slatkin M (1986). A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. Heredity, 56: 409-415.

Bundy A, Pitcher TJ (1995). An analysis of species changes in Lake Victoria: did the Nile perch act alone? In: The Impact of species Changes in African Lakes. (eds Pitcher TJ, Har PJB), pp. 111-136. Chapman and Hall, London.

Carvalho GR, Hauser L (1995). Genetic impacts of fish introductions: a perspective on African lakes. In: Species Changes in African Lakes (eds Pitcher, T.J; Hart PJB), pp. 457-494.

Chapman, Hall, London. DFR (2004). Fisheries Production and Fish Processing and Export Data 1999 to 2004. Department of Fisheries Resources, Ministry of Agriculture, Animal Industry and Fisheries. Entebbe Uganda.

EAFFRO (1967). East Africa Freshwater Fisheries Organization annual reports 1961-1967. Entebbe, Uganda.

Excoffier L, Smouse PE, Quattro JM (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes-application to human mitochondrial DNA restriction data. Genetics, 131: 479-491.

FAO (1993). Review of the State of Marine Fisheries Resources. FAO Technical paper No. 335. FAO, Rome, Italy, p. 136.

Felsenstein J (1995). PHYLIP – Phylogeny Inference Package, Version 3.572c. Universty of Washington Seattle. In: Proceedings of the workshop of the Kenya Marine and Fisheries, pp. 165-184

Fryer G, Illes TD (1972). The cichlid fishes of the Great Lakes of Africa: their Biology and Evolution. Oliver and Boyd, Edinbutgh, UK.

Gee JM (1964). Nile perch investigations. Ann. Rep. E. Africa Freshwat. Res. Org. (1962/63): 14-24.

Goudet J (1995). F-STAT (1. 2), a computer program to calculate F-statistics. J. Hered., 86: 485-486.

Goudswaard PC, Ligtvoet W (1988). Recent developments the fishery of Haplochromines (Pisces: Cichlidae) and the Nile perch *Lates niloticus*(L.) (Pisces: Centropomidae) in lake Victoria. pp. 101-112. In: CIFA. Report of the fourth session of the subcommittee for development and management of the fisheries of lake Victoria, 6-10 April 1987, Kisumu, Kenya. FAO Fish. Rep.388. FAO, Rome.

Goudswaard PC, Witte F (1985). Observations on Nile perch - *Lates niloticus* (L. 1758) in the Tanzanian waters of lake Victoria. pp. 62-67. In: CIFA. Report of the third session of the subcommittee for the development and management of the fisheries of lake Victoria, 4-5th October 1984, Jinja, Uganda. FAO Fish. Rep. 335. FAO, Rome.

Graham M (1929). The Victoria Nyanza and it's fisheries. A report on the fishing surveys of lake Victoria (1927-28). Crown Agents Colonies, London.

Grant WS, Garcia-Marin JL, Utter FM (1999). Defining population boundaries for Fishery management. In: S. Mustafa (ed.) Genetics in sustainable fisheries management. Blackwell Science, Malden, MA.

Hamblyn EL (1961). The Nile perch project. EAFRO Ann. Rep. (1960): 26-32.
Harrison K (1991). The taxonomy of East African Nile perch, *Lates* spp. (Perciformes, Centropomidae). J. Fish. Biol. 38: 175-186.
Hauser LG, Carvalho GR, Pitcher TJ, Ogutu-Ohwayo R (1998). Genetic affinities of an introduced predator: Nile perch in Lake Victoria, East Africa. Mol. Ecol. 7: 849-857.
Hecky RE (1993). The eutrophication of Lake Victoria. *Verhandlungen Vereinigung fir Limnologie,* 25: 39-48.
Holden MJ (1967). The systematics of the genus *Lates* (Teleostei: Centropomidae) in Lake Albert, East Africa. J. Zool. London, 151: 329-342.
Hunter JB (1970). Observations on the taxonomy and biology of *Lates* (Cuvier 1828) in Lake Albert. Game and Fisheries Uganda Occasional papers, 3: 1-7.
IFMP (2003). The Implementation of a Fisheries Management Plan (IFMP) project 2003 -2008. Lake Victoria Fisheries Organization, Jinja Uganda
Kudhongania AW, Chitamweba DBR (1995). Impact of environmental change, species introductions and ecological interactions on the fish stocks of Lake Victoria. In Pitcher TJ, Hart P (eds.), Species Changes in African lakes, Chapman and Hall, London pp. 20-44.
Ligtvoet W, Mkumbo OC (1990). Synopsis of ecological and fishery research on Nile perch (*Lates niloticus*) in lake Victoria, conducted by HEST/AFIRI. Pp. 35-74. In: CIFA. Report on the fifth session on the development and management of the fisheries of Lake Victoria, 12-14 September 1989, Mwanza, Tanzania. FAO Fish. Rep. 430. FAO, Rome.
Linnaeus C (1758). Systema Naturae, Ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.) Holmiae. Systema Nat. ed. 10 i-ii + 1-824.
Lowe-McConnell RH (1959). Breeding behaviour patterns and ecological differences between species and their significance for evolution within the genus Tilapia (Pisces, Cichlidae). Proc. Zool. Soc. London, 132(1): 1-30.
Lowe-McConnell RH (1987) Ecological studies in tropical fish communities. Cambridge University Press, Cambridge.
LVRP (2002). Lake Victoria Fisheries Research Project (LVFRP) 1997 – 2002. Lake Victoria Fisheries Organization, Jinja Uganda.
Michalakis Y, Excoffier L (1996). A genetic estimation of population subdivision using distances between alleles with special reference to microsatellite loci. Genetics, 142: 1061-1064.
Ministry of Finance, Planning and Economic Development Government of Uganda (MFPED), (1999). Policy Statement for fiscal year 1999/2000. MFPED, Kampala.
Nei M (1978). Estimation of average heterozygisity and genetic distance from a small number of individuals. *Genetics*, 89, 583-590.
Nei M, Maruyama T, Chakraborty R (1975). The bottle neck effect and genetic variability in populations.Evolution, 29: 1-10.
Newman RA, Squire T (2001). Microsatellite variation and fine-scale population structure in the wood frog (*Rana Sylvatica*). Mol. Ecol. 10: 1087-1100.
Ogari J (1985). Distribution, food and feeding habits of *Lates niloticus* in Nyanza Gulf of Lake Victoria (Kenya). pp. 68-80. In : CIFA. Report of the third session of the sub-committee for the development and management of the fisheries of Lake Victoria, 4 -5 October 1984, Jinja, Uganda. FAO Fish. Rep. 335. FAO Rome.
Okaranon JO, Acere TO, Ocenodongo DL (1985). The current state of the fisheries in the northern portion of lake Victoria. pp. 89-98. In: CIFA. Report of the third session of the subcommittee for development and management of the fisheries of lake Victoria, 4-5th October 1984, Jinja, Uganda. FAO Fish. Rep. 335. FAO, Rome.
Okedi J (1971). Further observations on the ecology of the Nile perch (*Lates niloticus* Linnaeus, 1758) in lake Victoria and Kyoga. EAFFRO Ann. Rep. (1970): 42-55.
Raymond M, Rousset F (1995). GENEPOP (version 3) population genetics software for exact tests and ecumenism. J. Heredity, 86: 248-249.
Ribbink AJ (1987). African lakes and their fishes: conservation scenarios and suggestions. Env. Biol. Fishes, 19: 3-26.
Schneider S, Rossli D, Excoffier L (2000). ARLEQUIN, version 2.000: a software for population Genetic Data Analysis. Genetics and Biometry Laboratory, University of Geneva Switzerland.
Sinclair M (1988). Marine populations an essay on population Regulation and Speciation. University of Washington Press, Seatle.
Slatkin M (1985). Rare alleles as indicators of gene flow. Evolution, 39: 53-65.
Waples RS (1998). Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J. Hered., 89: 438-450.
Weir BS, Cockerham CC (1979). Estimation of linkage disequilibrium in randomly mating populations. Heredity, 42: 105-111.
Weir BS, Cockerham CC (1984). Estimating *F-statistics* for the analysis of population structure. Evolution, 38: 1358-1370.
Welcomme RL (1988). International introductions of inland aquatic species. FAO Fish. Tech. Pap. 249. FAO, Rome.
Witte F, Goldschmidt T, Wanink JH, Oijen MJP, van Goudswaard PC, Wtte-Maas ELM, Bouton N, (1992). The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of lake Victoria. Environ. Biol. Fish. 34: 1-28.
Yeh FC, Boyle T, Rongcai Y, Zhihonge Y, Xiyan JM (1999). POPGENE version 1.31. A microsoft Window-based Freeware for population Genetic Analysis. Department of Renewable resources University of Alberta, Edmonton, Canada.