The Genetic History of the Introduced Nile Tilapia of Lake Victoria (Uganda - E. Africa): The Population Structure of *Oreochromis niloticus* (Pisces: Cichlidae) Revealed by DNA Microsatellite Markers.

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ABSTRACT

Genetic information was used to partially reconstruct the patterns of introduction of the Nile tilapia into the Lake Victoria region of East Africa. Allele frequencies were determined for ten DNA microsatellite loci in populations of *Oreochromis niloticus* from twelve sampling sites in the Lake Victoria basin and from sites in Lakes Edward, George and Albert. The latter three lakes are probable sources of fish that were introduced into the Lake Victoria basin during the early-mid twentieth century. All populations contained substantial genetic variability. However, as measured by average heterozygosity, the number of alleles and number of private alleles, the derived populations of the Lake Victoria/Lake Kyoga basins show lower genetic variability than variability observed in the three putative source populations (Lakes Edward, George and Albert). Population interrelationships as measured by genetic distances indicate that the populations of the Lake Kyoga basin were most likely derived from initial migrants from Lake Victoria. Populations in the Koki lakes region appear to have been directly derived from source populations in Lake Edward or Lake George. Lake Victoria populations are slightly closer to the Lake George sample, while Lake Kyoga basin samples are equally close to both Lake George and Lake Albert samples. Samples from Lake Edward and Lake George are not closest to each other. Levels of population differentiation, measured by Fst, indicate that migration between introduced populations is influenced by distance, and that current mixing between populations due to migration appears to be limited. This is true between populations from the same basin, or even lake.

INTRODUCTION

The Nile tilapia, *Oreochromis niloticus*, is well known for its wide use in augmenting natural fisheries and for fish farming. It is not a native of the Lake Victoria basin of East Africa. Nevertheless, it has become the most dominant

tilapiine species in the Lake Victoria region and is second only to another introduced species, the Nile perch, *Lates niloticus*, in economic importance in the region (Ogutu-Ohwayo, 1990; Balirwa, 1992; Stiassny, 1996). In the Lake Victoria region, exploitation of the species is still largely from populations in natural waters.

The Nile tilapia invaded Lake Victoria in the early 1900s, with the first recordings of the species in the lake occurring in the 1920s (Trewavas, 1983). Trewavas postulates that *O. niloticus* may have entered the lake through the Kagera River, following introductions into Lake Bunyonyi from Lake Edward. According to Fryer and Iles (1972), intentional introduction of *O. niloticus* into the Lake Victoria basin may first have occurred in the late 1930's, following the repeated failure of attempts to introduce *Tilapia* (*Oreochromis*) *spirulus nigra* into the Koki lakes, a part of the Lake Victoria basin southwest of Lake Victoria. *Tilapia* (*Oreochromis*) *niloticus* was introduced in the Koki lakes, immediately became successfully established, and continues to flourish and dominate the Koki lakes. This success provided a lesson in the versatility of *O. niloticus* for fisheries managers. Subsequently, *O. niloticus* was introduced into virtually all significant water bodies in Uganda (Fryer, 1972; Fryer and Iles, 1972).

Records of the actual pattern of introduction of exotic species into the Lake Victoria region waters are scanty and largely uninformative as recorded in the Reports of the East African Freshwater Fisheries Research Organization from 1947 to 1966. The origin of the brood stock used for an introduction, the number of individuals used for stocking, the number of times stocking was done into a particular water body and the processes of augmentation prior to the introduction are not known. *Oreochromis niloticus* in Lake Victoria is known to have come from multiple sources. Deliberate introductions started in the 1950's, and continued with repeated massive stocking into Lakes Victoria and Kyoga up to mid-1960's (Welcomme, 1965, 1966, 1967). By the late 1960's, *O. niloticus* had become established. The species is the most ecologically and economically dominant tilapiine species in the Lake Victoria region waters in both the main lakes and in most surrounding satellite lakes (Balirwa, 1992). Its dominance, ecological versatility and trophic virtuosity, together with the ability to withstand recent dramatic limnological changes in Lake Victoria, have made *O. niloticus* the mainstay of the regions tilapiine fishery (Balirwa, 1992; Sanderson et al., 1995).

In this study the phylogeography of *Oreochromis niloticus* in the Lake Victoria region was investigated. We attempt to infer historical patterns of establishment by comparing population samples from the Lake Victoria basin with samples of *O. niloticus* populations from lakes representing the native range of the species which are likely sources of the material which was used for stocking (i.e., Lakes Albert, Edward and George). Previous work based on RAPD markers suggested population in Lake Victoria had closer genetic affinities to the native population of Lake Edward, while the Lake Kyoga basin populations were closer to native populations of Lake Albert (Fuerst et al., 1997). However, RAPD markers have several shortcomings, especially a pattern of dominant inheritance, which reduce the reliability of results. Here, we report findings obtained using a set of DNA microsatellite loci to investigate this question. The codominant nature of microsatellite markers allows stronger inference to be made concerning the genetic differences between populations and the patterns of genetic migration. The two types of genetic markers (RAPDs and microsatellites) will be contrasted for their power to identify factors which have molded population structure in the Lake Victoria region.

MATERIALS AND METHODS

Sample Collection.

Fish were sampled using gillnets and seine nets from 15 locations in three lake basins of the Lake Victoria Region (Kyoga, Victoria and Edward/George) (Table 1 and Figure 1) and from Lake Albert. For the purposes of this study, each sample was assumed to represent a single panmictic population in that lake, with the expection of samples from Lake Victoria, where three samples were obtained (Kasensero, Napolean Gulf and Nyanza Gulf). Sample sizes ranged between 8 and 21 individuals (Table 1). For DNA analysis, ~3g of tissue were taken from each individual from the right epaxial muscle of the fish specimen, placed in 95% ethanol for one hour. Ethanol was then replaced by a fresh aliquot, and the sample was labeled and stored until DNA extraction.

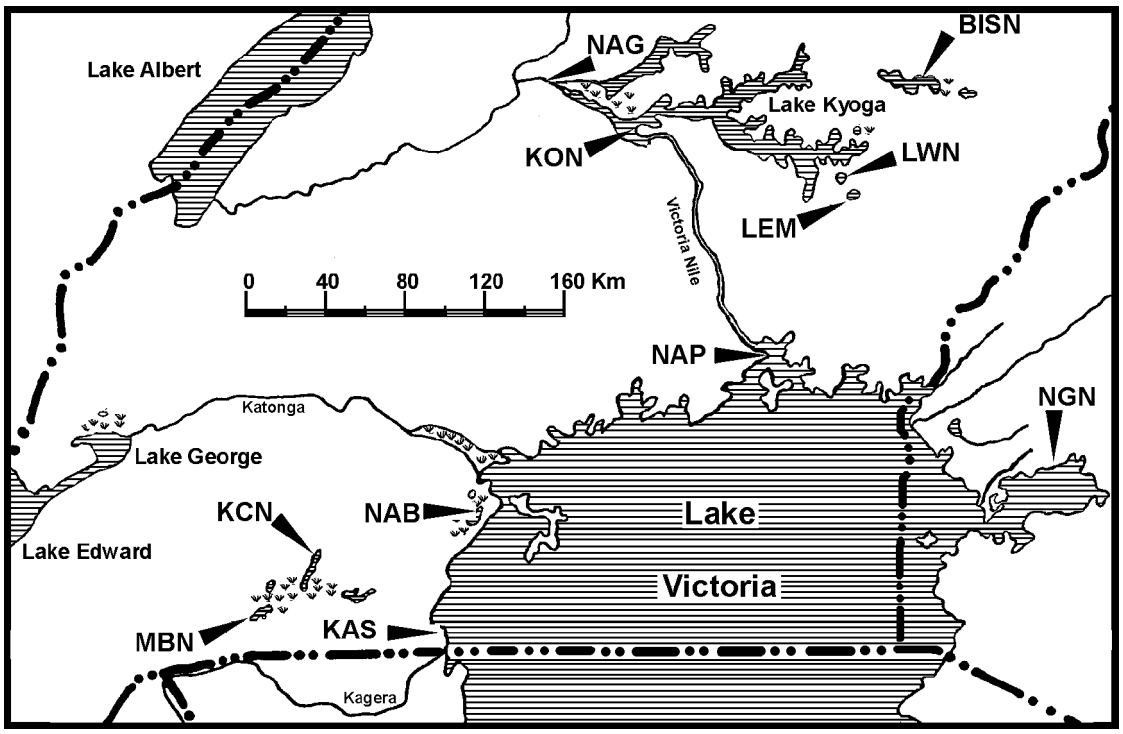

Figure 1. The Lake Victoria Region and Sample Sites. Abbreviations Given in Table 1. (GAG Is Adjacent to LWN and LEM on the Map)

Molecular Analysis.

DNA extraction was performed using either a standard proteinase K, phenol-chloroform protocol (Sambrook et al., 1989), or a NaOH extraction method (Zhang, Tiersch and Cooper, 1994). A set of 10 primer pairs were chosen from an intitial set of 45 pairs of microsatellite primers developed by Lee and Kocher (1996) from *Oreochromis niloticus.* The primers were chosen because they produced scorable amplification products in all species of a multispecies study of all tilapiine species from the Lake Victoria region, to be presented elsewhere. The ten pair of primers produced reproducible amplifications within a size range that could be scored on 6% polyacrylamide gel. The annealing temperatures for PCR for the primer pairs and the identification of the ten pairs which were studied were: 51°C (UNH136); 54°C (UNH104; UNH222); 56°C (UNH118; UNH231); 57°C (UNH169); 58°C (UNH142; UNH149; UNH176; UNH178).

For PCR analysis each forward primer was end-labeled with ^{32}P radioisotope using T4 polynucleotide kinase (GIBCO BRL). PCR reactions were done in a final volume of 10 µl containing 25ng of genomic DNA, 0.3 mM of each primer, 100 mM of deoxynucleotide triphosphate (dATP, dTTP, dCTP, and dGTP), 3 mM of $MgCl_2$, and 0.375 units of *Taq* polymerase (GIBCO BRL). Amplification conditions for the study were: 5 minutes hot start at 95°C, followed by 30 cycles of 45 seconds at 94°C, 30 seconds at the appropriate annealing temperature, and 30 seconds at 72°C. At the end of 30 cycles, a 6 minute extension at 72°C completed the amplification reactions. Amplification products were separated on 6% polyacrylamide sequencing gels with 7M urea. Gels were dried and products visualized using autoradiography. Sizing of the amplification products was based on the sequence ladder of plasmid pUC18, which was run on each gel along with the microsatellite PCR products.

Table 1. Populations Sampled, Basin of Origin and the Sample Sizes.

Lake	Abbreviation	Basin	Sample size
Kasensero (SW)	KAS-LV	Victoria	9
Napoleon Gulf	NAP-LV	Victoria	21
Nyanza (Winam)gulf	NGN-LV	Victoria	10
Nabugabo	NAB	Victoria	20
Kachira	KCN	Victoria/Koki	20
Mburo	MBN	Victoria/Koki	20
Victoria Nile River	NAG	Victoria/Kyoga	18
Kyoga	KON	Kyoga	11
Gigate	GAG	Kyoga	19
Lemwa	LEM	Kyoga	8
Bisina	BISN	Kyoga	10
Nakuwa	LWN	Kyoga	19
Edward	EDN	Edward/George	11
George	GGN	Edward/George	20
Albert	ABN	Albert	18

Data Analysis.

Random mating for microsatellite loci was tested using a chi-square test for the probability of deviation from Hardy-Weinberg expectations as implimented by the program Microsat1.5 developed by E. Minch (http://stanford.edu/microsat). Genetic variability for microsatellite loci was measured by the expected heterozygosity among all individuals at each locus, estimated from allele frequencies in a sample, by the average heterozygosity at all ten loci combined, by the number of alleles for each locus. In addition, the allele size range and distribution within that range, and allele frequency distribution were determined. Population subdivision was estimated based on Wright's F statistics (Weir and Cockham, 1984), on the assumptions of the infinite allele model. Comparisons were also made using the Fst analogue for DNA microsatellite data, Rst, which is based on the stepwise mutation model (Slaktin, 1995). Interpopulation variability was also assessed based on the proportion of private alleles (alleles found in only a single population). Phyletic relationships among populations were estimated by three genetic distance measures. These were based on Fst, Rst, and on the proportion of shared alleles (ps), standardized as 1-ps. Genetic distances were calculated using Microsat1.5 (E. Minch; http://stanford.edu/microsat). Relationships between populations were represented in dendrograms constructed using the neighbor joining method (Saitou and Nei, 1987) as implemented in MEGA (Kumar et al., 1993).

RESULTS

Microsatellite Locus Variability.

Polymorphism was high for all ten loci with an average of 18 alleles per locus among the 15 populations (Table 2). The least polymorphic was locus UNH136 with seven alleles and the most polymorphic was UNH169 with 39 alleles.

Populations averaged over 50 total alleles in the samples considered here. With the exception of UNH178, all loci showed some heterozygote deficiencies, when tested for deviation from Hardy-Weinberg expectations. This suggests that some chromosomes contained "null" alleles, in which PCR primer sites had been changed by mutation, preventing an allele from being amplified. Assuming that all populations were equally likely to have null alleles occur, this would not bias our analysis of population relationships, but would result in a slight underestimate of the levels of genetic variability for this set of loci. The average heterozygosity in the total data set was estimated to be 0.555. Locus UNH136 had significantly lower heterozygosity (0.044) compared to the remaining loci.

Microsatellite Population Variability.

All populations showed high average heterozygosity. Overall mean within population heterozygosity was 0.55. Again, this is likely to be an underestimate of the true heterozygosity because of the presence of null alleles. Populations ranged in average heterozygosity from a low in the Lake Kyoga sample (H = 0.46), to a high in the Kasensero/Lake Victoria population (H = 0.64). Examining populations groups of related samples suggests that the derived populations of the Lake Victoria/Kyoga (LV/LK) basins appear to have lost genetic variability compared to samples from the natural range of *O. niloticus*. Further, this loss seems to have occurred in a sequential pattern, consistent with a series of sequential introduction/invasion events in the recent history of the basin. Samples from the largest populations, those sampled directly from Lake Victoria (KAS, NAP and NGN), where historical records indicate repeated introductions, have mean average heterozygosity (H) = 0.60, compared to H = 0.593 for the three "source" samples (EDN, GGN, ABN). However, smaller populations from the Lake Victoria basin (KCN, MBN, NAB) have lower heterozygosity (H = 0.543). Further, still lower variation (H = 0.512) is seen in the populations from the Lake Kyoga basin (KON, GAG, LM, BISN), which on the basis of our phylogenetic analysis (discussed below) were probably secondarily derived by way of Lake Victoria.

Table 2. Measures of Genetic Variability for the Ten Loci Used in the Study.

Locus	Average Heterozygosity	Total Number Of Alleles	Average Number of Alleles per population
UNH104	0.694	17	5.7
UNH118	0.836	26	10.3
UNH136	0.044	7	1.6
UNH142	0.381	16	3.5
UNH149	0.539	15	4.6
UNH169	0.829	39	10.7
UNH176	0.549	14	4.8
UNH178	0.497	9	3.3
UNH222	0.688	19	6.3
UNH231	0.498	16	5.3
Average	0.555	18	5.6

Genetic variability within populations can also be assessed by examining the number of alleles in a population. Overall, the populations in our study were found to have an average of 5.6 alleles per locus. The "source" populations had more alleles on average (n_a = 6.3) than populations from the LV/LK basins. The six populations from the Lake Victoria/Koki lakes basin had 5.7 alleles per locus, while the five Lake Kyoga populations had 5.0 alleles per locus. Rare alleles are the most likely alleles to be lost through successive invasion/bottleneck events (Fuerst and Maruyama, 1986; Fuerst, 1988). Successive sampling during the invasion process would strip populations of these low frequency alleles, while affecting average heterozygosity only slightly. The pattern of successive allele loss during the invasion of the Lake Victoria region is seen when examining private alleles. Examining all alleles distinguished in our survey, 30% of the alleles observed in the survey can be classified as private alleles (alleles which were observed in only a single population sample). The number of private alleles in all populations is relatively low, with 13 populations having less than five private alleles. The major exception is the Lake Gigate population with 12 private allele. Comparing the three source populations, however, we observe an average of 5.3 private alleles per sample, compared to 2.8 private alleles in six Lake Victoria/Koki lakes populations and 4.2 private alleles per population for the five Lake Kyoga populations. Note that, because of its location and possible migrational effects, the Victoria Nile population could be considered either a Lake Victoria associated or a Lake Kyoga associated population. Variability in this population is more similar to that seen the Lake Kyoga basin populations (lower heterozygosity, number of alleles and private alleles).

Table 3. Number of Loci, Allele Number, Private Alleles, and Genic Heterozygosity for Populations of *Oreochromis Niloticus* in the Lake Victoria Region Populations.

Population	Code	Loci	Allele number	Alleles per locus	Private Alleles	Observed Heterozygosity
Kasensero	(KAS)	10	56	5.6	3	0.64
Napoleon gulf	(NAP)	10	63	6.3	5	0.60
Nyanza G ulf	(NGN)	10	42	4.2	1	0.56
Kachira	(KCN)	10	74	7.4	4	0.59
Mburo	(MBN)	8	50	6.2	3	0.53
Nabugabo	(NAB)	10	47	4.7	1	0.51
Victoria Nile	(NAG)	10	51	5.1	0	0.52
Kyoga	(KON)	9	43	4.9	1	0.46
Gigate	(GAG)	10	76	7.6	12	0.59
Lemwa	(LEM)	10	42	4.2	1	0.49
Bisina	(BISN)	10	47	4.7	4	0.54
Nakuwa	(LWN)	10	38	3.8	3	0.48
Edward	(EDN)	10	54	5.4	4	0.60
George	(GGN)	10	74	7.4	8	0.58
Albert	(ABN)	10	62	6.2	4	0.60

Population Differentiation.

Table 4 shows the pairwise Fst values among populations. In general, and as expected, populations showed more differentiation between lake basins than within lake basins. For instance, the three samples from Lake Victoria show an

average pairwise Fst of 0.061, suggesting substantial genetic migrations and only slight differentiation. Differentiation between the three Lake Victoria samples and Lake Nabugabo is almost twice as great (average Fst = 0.119), while differentiation is more than twice as great between the three Lake Victoria samples and the two samples from the Koki Lakes (KCN, MBN; average Fst = 0.133).

There is little differentiation seen between the Lake Kyoga sample and the sample from the connected portion of the Victoria Nile (Fst = 0.037). Within the cluster of populations from the Lake Kyoga basin, Lake Gigate shows substantial differences from other samples. This sample also shows a high number of private alleles, and we have accumulated some evidence that some of these alleles may represent alleles from congeneric species, entering the Lake Gigate population by hybridization (Mwanja, 2000). The other satellite lakes of Lake Kyoga show only moderate differentiation from the Lake Kyoga/Victoria Nile pair of samples, and less difference (average Fst = 0.083) than that seen between the Lake Victoria samples and the Lake Nabugabo population. This would be consistent with migration occurring during periodic connections between Lake Kyoga and its satellite lakes as water levels fluctuate, whereas migration would be restricted for Lake Nabugabo, which is never directly connected with Lake Victoria.

Table 4. Pairwise Fst Values Between Population Samples of *O. niloticus*

Pop	KAS	NAP	NGN	KCN	MBN	NAB	NAG	KON	GAG	LEM	BIS	LWN	EDN	GGN	ABN
KAS	-	0.073	0.012	0.075	0.134	0.115	0.046	0.111	0.107	0.079	0.054	0.136	0.098	0.072	0.088
NAP	-	-	0.097	0.121	0.166	0.110	0.134	0.172	0.138	0.147	0.131	0.181	0.085	0.084	0.044
NGN	-	-	-	0.134	0.169	0.131	0.059	0.064	0.132	0.082	0.064	0.120	0.131	0.120	0.118
KCN	-	-	-	-	0.179	0.215	0.156	0.243	0.099	0.174	0.167	0.249	0.104	0.024	0.085
MBN	-	-	-	-	-	0.258	0.203	0.281	0.220	0.215	0.199	0.276	0.082	0.156	0.142
NAB	-	-	-	-	-	-	0.154	0.201	0.206	0.197	0.194	0.196	0.195	0.181	0.167
NAG	-	-	-	-	-	-	-	0.037	0.188	0.058	0.078	0.103	0.197	0.147	0.139
KON	-	-	-	-	-	-	-	-	0.253	0.071	0.097	0.098	0.258	0.224	0.193
GAG	-	-	-	-	-	-	-	-	-	0.212	0.180	0.273	0.150	0.115	0.113
LEM	-	-	-	-	-	-	-	-	-	-	0.105	0.101	0.199	0.177	0.143
BIS	-	-	-	-	-	-	-	-	-	-	-	0.143	0.168	0.146	0.146
LWN	-	-	-	-	-	-	-	-	-	-	-	-	0.231	0.230	0.204
EDN	-	-	-	-	-	-	-	-	-	-	-	-	-	0.074	0.079
ABN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.063
GGN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Of note, genetic differentiation between the three "source" population samples is fairly low, but no pair of the three (Lakes Edward, George or Albert) shows particular affinities. The Fst value between Lake George and Lake Edward populations which are physically connected is 0.074, while that between the Lake George and Lake Albert populations is 0.063, and the Lake Edward/Albert comparison yields an Fst of 0.079.

Phyletic Relationships among Populations.

Genetic distances between the various populations are given in Table 5. Figure 2 shows the dendrogram based on a neighbor joining analysis of Nei's standard genetic distance, as calculated in Microsat- 1.5. Similar relationships among populations were obtained using a distance based on (1 - the proportion of shared alleles). The dendrogram in Figure 2 is unrooted. A central point was arbitrarily placed between the putative source populations (Lakes, Edward, George and Albert) and populations which were not grouped with the source populations.

Table 5. Pairwise Genetic Distance Values Between Population Samples of *O. niloticus*

	NAP	NGN	KCN	MBN	NAB	NAG	KON	GAG	LEM	BIS	LWN	EDN	GGN	ABN
KAS	0.146	0.030	0.144	0.249	0.191	0.056	0.145	0.239	0.131	0.082	0.209	0.217	0.139	0.234
NAP		0.181	0.239	0.286	0.174	0.236	0.285	0.299	0.274	0.245	0.319	0.161	0.151	0.109
NGN			0.262	0.270	0.200	0.083	0.072	0.264	0.126	0.094	0.163	0.261	0.228	0.276
KCN				0.286	0.439	0.281	0.500	0.189	0.344	0.328	0.515	0.201	0.041	0.173
MBN					0.450	0.326	0.459	0.425	0.347	0.317	0.439	0.114	0.241	0.227
NAB						0.233	0.281	0.414	0.315	0.328	0.291	0.370	0.336	0.330
NAG							0.041	0.378	0.075	0.104	0.133	0.395	0.258	0.279
KON								0.506	0.078	0.111	0.107	0.505	0.445	0.373
GAG									0.472	0.384	0.617	0.339	0.231	0.251
LEM										0.144	0.120	0.410	0.346	0.307
BIS											0.193	0.338	0.275	0.337
LWN												0.444	0.442	0.399
EDN													0.133	0.160
GGN														0.124

In the dendrogram, populations of the Kyoga basin (KON, GAG,LEM, BIS. LWN) are the most distant from putative source populations. The majority of the Kyoga region populations (including the Lake Kyoga sample and three of the four satellite lake populations) formed the most derived group. This cluster also includes the Victoria Nile sample population. This site has a direct connection with Lake Kyoga, but has been semi-isolated from Lake Victoria since the completion of the Owen Falls' hydroelectric plant in 1954. The Kyoga group diverges out of a succession of populations which represent the central Lake Victoria samples. The three Lake Victoria samples (KAS, NAP, NGN) diverge from one another at the base of the main cluster of introduced populations, clearly associated with the Lake Nabugabo sample. Thus, nine of the twelve "introduced" population samples forms a distinct grouping which has seemingly diverged from the source populations as a monophyletic group.

The remaining three "introduced" populations show affinities to the source population cluster. One of the Kyoga satellite lakes, Lake Gigate, is phyletically associated with the source clade. However, this sample is quite unusual. We have already noted that the Lake Gigate sample had the highest number of private alleles (actually more than twice as many as any other sample), and it shows a very long branch linking it to the "source" clade. Other analyses, which we will present elsewhere (full results in Mwanja, 2000) suggest that the Lake Gigate sample of *O. niloticus* may represent a sample which has been affected by hybridization with other congeners which occur in this satellite lake. The two Koki lakes populations (Lakes Mburo and Kachira) were placed closer to the Lake Edward and Lake George samples, respectively, than to the rest of the Lake Victoria populations. This is consistent with their geographic proximity to the Lake Edward/George system in Western Uganda. Interestingly, despite the fact that the Mburo and Kachira samples are geographically closer to each other than they are to Lakes Edward or George, they do not cluster with each other (nor do Lakes Edward and George). The Kachira sample has a smaller distance to the sample from Lake George than to any other population, while the same is true of the distance relationship between the Mburo sample and that from Lake Edward.

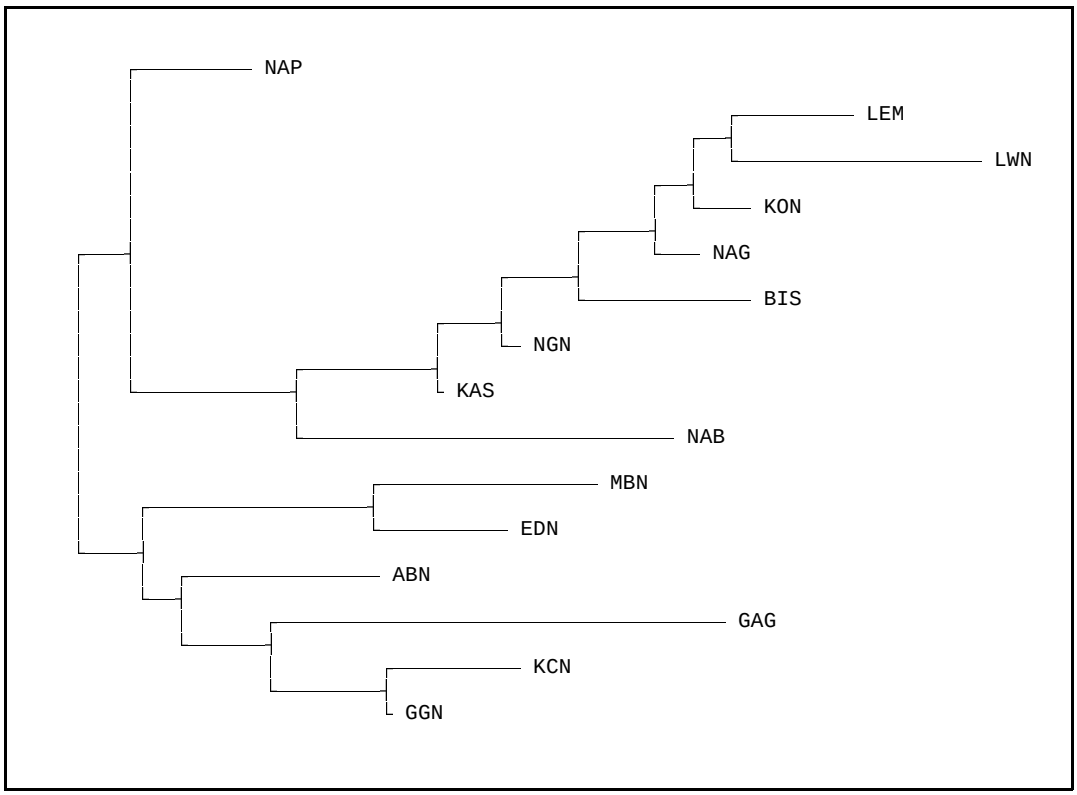

Figure 2. Unrooted Phenogram Based on Nei's Genetic Distance Calculated from Microsatellite Allele Frequencies Showing Relationships among Fifteen Populations of *Oreochromis Niloticus* from the Lake Victoria Region

Several aspects of genetic relationships between the three source populations are notable. First, the samples from Lake Edward and Lake George do not cluster with one another, even though they are physically linked. Rather, the sample from Lake Albert is placed between the Lake George and the Lake Edward sample. In fact, the sample from Lake George is closer to Lake Albert, as shown by a smaller genetic distance, than it is to Lake Edward. Similar results were seen in our earlier analysis using RAPDs (Fuerst et al., 1997).

DISCUSSION

Unfortunately, this study is only the second to examine genetic population structural changes in the course of evolution of the Lake Victoria region fishery. We first studied this using RAPD analysis of genetic variability of LVR tilapiine species (Fuerst et al., 1997). The earlier ecological work in the region (Fryer and Iles, 1972; Lowe-McConnell, 1987; Ogutu-Ohwayo, 1990; Balirwa, 1992) assumed the dominance of *Oreochromis niloticus*, giving hypothetical reasons as to why the species did so well despite the limnological changes, and heightened fishing pressure, especially in waters where other introduced congeners had failed. But comparison of the population structure of the species was not considered in any detail and the role of genetic diversity in the success of *O. niloticus* was only hypothesized. Certainly high genetic diversity is one component of the ecological dominance of *O. niloticus* in Lake Victoria region waters. Nevertheless, studies that we will present elsewhere indicate that introduced populations of *O. niloticus* do not have greater genetic variability than native congeners. However, the genetic structures of populations are different for the various species. The relationship between ecological dominance and genetic variability will become more evident when we compare and contrast the genetic population structures of all tilapiine species in the region.

This study bears on the various theories that have been put forward for the ecological dominance of *Oreochromis niloticus* in Lake Victoria region (Ogutu-Ohwayo, 1990; Balirwa, 1992; Sanderson et al., 1995; Stiassny, 1996; Batjakas, 1997). All the theories have some plausibility and may explain the dominance of *O. niloticus* in Lake Victoria region waters. Most of the theories cited have been developed essentially from the ecological, and especially the trophic, point of view. Here we extend considerations to include genetic variability within and among populations of *O. niloticus* in the Lake Victoria region's waters. Initially we postulated that (1) the higher genetic variability due to repeated and multiple sources of seed, (2) rapid population expansion, and (3) genetic interaction with the native congeners, provided *O. niloticus* with the evolutionary flexibility to become successfully established where congeners have failed. The higher genetic variability, together with the ecological versatility, are attributes which are not shared with any other introduced tilapiine species in the region (data in Mwanja, 2000). It is consistent that the combination of higher genetic variability and ecological versatility were main factors that led to the ecological dominance of *O. niloticus* in LVR waters. It is hard in any population genetics study to directly link the success of a species to its genetic diversity, but ecological success of a species in such a diverse aquatic system may be reflected in the genetic variability of its populations in the system. So in this study comparison of diversity within and among populations should reflect the ecological performance of *O. niloticus*. Higher genetic variability, low population subdivision and high rate of gene flow between populations, are some of the attributes that may be directly linked to the ecological dominance of a species.

We looked at 15 populations of *Oreochromis niloticus* in the Lake Victoria region using microsatellite markers at 10 loci. All loci were found to be polymorphic among all populations save for locus UNH136 which, although having seven alleles over the entire sample, was largely monomorphic within populations. The populations also had a significant proportion of private alleles. There was a decrease in levels of genetic variability between the introduced populations and the populations from Lakes Albert, George and Edward. Comparison between the populations from the main lakes (Victoria, Kyoga, Albert, George and Edward) to the populations from their satellite lakes showed nearly similar level of heterozygosity but the satellite lakes had significantly lower diversity compared to the main lakes. Only Lake Gigate deviated substantially from this pattern, and represents a region in which we found the highest incidence of intermediate morphs between tilapiine species (unpublished data). The higher allelic diversity found in this satellite lake was thought to be a result of introgressive hybridization between *Oreochromis niloticus* and native species.

Changes in genetic diversity immediately following introduction will be most noticeable in allelic diversity. Normally it takes several generations before noticeable differences in heterozygosity levels occur between the source and the introduced populations (Fuerst and Maruyma, 1986). In the case of the Lake Victoria region *O. niloticus* populations, allele diversity decreased in introduced populations, as the case would have to be if small founder populations were involved. Genetic interaction between *O. niloticus* and native tilapiine species may be an important factor responsible for the current population genetic structure exhibited by *O. niloticus*.

Comparison of the putative source populations showed differences between the Lake Albert and Lake Edward/George populations, though Lake George had a lower pairwise value of Fst with the Lake Albert population than with that from Lake Edward. This peculiarity was also observed in our past studies using RAPD markers (Fuerst, et al., 1997), and we believe that it is a result of the introduction fervor of the 1950s when *Oreochromis niloticus* was transplanted from Lakes Albert, George and Edward to nearly every water body in the region. The closer similarity between the Lake George and Lake Albert populations may be due to Lake Albert fish being introduced into Lake George.

In this analysis, examination of various distance measures indicated that there were consistent patterns in overall phyletic relationship among the various groups of samples: Lake Kyoga basin populations, Lake Victoria basin populations, Lake Edward/George populations and Lake Albert population. Using Lake Albert population as an outgroup, for all distance measures the Lake Kyoga populations were the most derived, while the Koki lakes' populations were phyletically closer to the Lake Edward/George populations than they were to the Lake Albert population. Differences between Lake Kyoga and Lake Kyoga satellite lakes is probably a reflection of the accelerated differentiation as a result of isolation and of some degree of introgressive hybridization in the satellite lakes. Hybridization is no longer a factor in Lake Kyoga, since native tilapiine species were displaced from the the lake following the establishment of *O. niloticus* and the Nile perch.

Among the Lake Victoria basin populations, the populations of Lake Kyoga, Victoria Nile and Napoleon gulf were closer to the Lake Albert population than to Lake Edward/George populations. Both the Koki lakes' populations were closer to Lake Edward/George populations than to the Lake Albert population. The same is true for the population from the Southwest part of

Lake Victoria (Kansenero population) but not so for Napoleon Gulf, which shows some affinities for being closer to Lake Albert. The differences in the number of different brood stock introduced into the respective waters could be reflected by the allelic diversity. Multiple sources of the brood stock would result in populations with higher allelic diversity in the short term before equilibrium is established.

Our results represent one of the first widescale attempts to characterize population structure of introduced populations of the Nile tilapia. Comparison of our results with those obtained for other species, both native and introduced, in the same system (Mwanja, 2000 and papers in preparation), and with results from the Nile tilapia in other water systems where introductions have occurred, will be important for a better understanding of how genetic factors contribute to the versatility of this fish.

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