

Comparison of the genetic and ecological diversity of the native to the introduced tilapiines (Pisces: Cichlidae), and their population structures in the Lake Victoria region, East Africa

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The impact of introduced tilapiines in Lake Victoria Region (LVR) was studied using experimental fishing survey methods and microsatellite DNA marker analysis. The experiments were carried out between 1993 and 2000. Oreochromis esculentus and O. variabilis, the two native forms of the LVR and original principals of the fisheries of these waters, were found to be completely displaced from the major lakes and were only occasionally found in a few minor satellite lakes surrounding Lakes Kyoga and Victoria. Nile tilapia, O. niloticus, is now the dominant tilapiine, and one of the three key fisheries species of LVR along with Nile perch, Lates niloticus, and the minnow-like Rastrineobola argentea. Oreochromis leucostictus, also introduced to the LVR from the nilotic system, was largely restricted to swampy fringes of LVR water bodies. Tilapia zillii, also introduced from nilotic waters and earlier recorded to have been the most prevalent introduced tilapiine in LVR, occurred only sparsely and was very restricted in distribution. Genetic studies showed Nile tilapia having the highest genetic diversity, and being the least subdivided among LVR tilapiines. O. leucostictus was next in variability, but had the greatest gene flow, probably due to its ability to traverse low oxygen waters such as swamps which separate most LVR water bodies. The native forms were genetically the least variable, except where they coexist with introduced congeners. 'Uncontaminated' native forms were observed only in satellite Lakes of Kanyanja, Kayugi, Manywa, Kawi and Kanyaboli. The population structure of native forms of LVR suggest they are being genetically swamped, especially for O. variabilis by Nile tilapia alleles, due to genetic exchange with introduced forms, resulting in highly localized differentiation of native species. T. zillii was equally highly subdivided, but has higher genetic variation within subpopulations, a situation linked to monogamous breeding behaviour which allows most individuals of its population to participate in breeding. Hybridization with T. rendalli, which was only occasionally encountered and previously mistaken for dwarf Nile tilapia, may also contribute to high within population variation in small T. zillii populations. On a macro-evolutionary level, the sister relationship between O. niloticus and O. esculentus is questionable and in need of further phylogenetic analysis. Overall the study showed a changed fishery, and the need to manage satellite lakes in a manner that will preserve the previous premier elements of the region's fishery (O. esculentus and O. variabilis) within natural refugia.

Keywords: *Oreochromis*, *Tilapia*, ecological displacement, introgression, *O. esculentus*, *O. variabilis*

Introduction

The Lake Victoria region is a remarkable zoogeographical area with water bodies containing repeatedly similar cichlid faunal groups that have evolved throughout the region. These groups are known for their relatively recent ‘explosive radiation’ (Fryer and Iles, 1972). The region includes Lakes Victoria, Kyoga, Edward, George, Kivu and surrounding minor water bodies known as satellite lakes (Kaufman and Ochumba, 1993). The story of the evolution of cichlid fishes in the LVR has changed to one of outcry and call for conservation (Kaufman, 1992) following drastic changes (both natural and human induced) that resulted in hundreds of the haplochromine species disappearing (Barel et al., 1985; Trewavas et al., 1985; Goldschmidt and Witte, 1992). Among human induced changes was the introduction of alien species into the LVR, including Nile perch, *Lates niloticus*, and several Tilapia species (Welcomme, 1967; Lowe-McConnell, 1987; Balirwa, 1992), starting around the 1930s, in response to the collapse of the native tilapiine fishery of the region (Lowe-McConnell, 1958, 1959; Welcomme, 1967; Mwanja, 2006). Following introductions, a new commercial fishery was established with Nile perch and Nile tilapia becoming the ecologically dominant species and the mainstay of the remade fishery, along with the native minnow-like species, *Rastrineobola argentea* (Balirwa, 1992). The success of the two alien species had detrimental effects on the region’s native species, as well as the other introduced species in the LVR. Effects included a curtailed recovery of the two native tilapiine species which formed the original commercial fishery and marginalization of earlier introduced focuses of the fishery such as *Tilapia zillii* (Welcomme, 1967; Ogutu-Ohwayo, 1990; Lowe-McConnell, 1987; Balirwa, 1992; Staissny, 1996).

A single species, the introduced *Oreochromis niloticus* (Nile tilapia), has come to dominate the tilapiine fauna in the region over the last four decades. Three other introduced species, *T. zillii*, *T. rendalli*, and *O. leucostictus*, together with the two native tilapiine species, *O. esculentus* and *O. variabilis*, remain but as minor components in most waters (Mwanja et al., 1997). Other introduced forms such as *O. spirulus nigra* and *O. hornorum*, have not been recorded in collections since the earlier records of introduction (Fryer and Iles, 1972; Mwanja, 2006). Earlier studies (Balirwa, 1992; Sanderson et

al., 1996; Batjakas et al., 1997; Mwanja and Kaufman, 1995; Mwanja, 1996; Mwanja et al., 1997) argued that the differences in success of different tilapiines in the LVR may have been due to genetic variation and genetic interaction (hybridization) among the regional tilapiines species. *Oreochromis spirulus nigra*, is now believed to have been lost due to genetic swamping by hybridization with both the Nile tilapia (*O. niloticus*) and another introduced species, *O. leucostictus* (Fryer and Iles, 1972; Leveque, 1997).

This paper examines the postulate (Mwanja and Kaufman, 1995; Mwanja, 1996) that genetic swamping of marginalized forms by ecologically dominant forms where they coexist may play a major role in the demise of remnant populations of the native tilapiine species, as evidenced by existence of intermediate morphs between species in such water bodies. This work was part of the cichlid conservation genetics project on the LVR cichlids assessing the ecological and evolutionary impact of introduced species on the natives. Also of interest was establishing reasons for differential ecological success among introduced tilapiine species, and determining if ecological success was driven by greater genetic variability among the introduced forms. This was undertaken by comparing the species’ ecological status through fisheries and ecological surveys, and by comparing their genetic variability and population genetic structures using molecular analysis based on microsatellite markers.

Materials and Methods

Fishing survey

Fisheries surveys using experimental fishing and fishermen’s catch analysis were conducted for Lakes Victoria, Kyoga, Nabugabo, Edward, George, Albert and their surrounding minor satellite lakes (Figure 1; Table 1). Occurrence and ecological dominance of the species in each lake was established through catch composition analysis in both the experimental fishing and fishermen’s fish catches monthly from year 1992 to 1997. Experimental fishing was conducted in different habitats following differences in bottom substrates, vegetation types, onshore versus offshore, around suds and islands within large lakes, and swampy shores versus clear shores. Fishing was done using multiple fleets of nets with mesh sizes ranging from 1 inch to 7 inches at mesh size intervals of 0.5 inch.

Table 1. Fishing surveys of LVR tilapiine species, 1992 to 1997. Relative qualitative abundance shown by number of positive signs; absence of a species indicated by dashes. (ON = *Oreochromis niloticus*; O.E = *O. esculentus*; OL = *O. leucostictus*; OV = *O. variabilis*; SG = *Sarathorodon galileus*; TZ = *Tilapia zillii*; and TR = *T. rendalli*).

Species	ON	OE	OL	OV	SG	TZ	TR
Lake Victoria Basin							
Lake Victoria (main lake)	+++	—	++	+	—	++	+
Wamala (isolated)	+++	—	++	—	—	—	—
Nabugabo Lakes							
Nabugabo	+++	—	—	—	—	++—	+++
Kayanja	—	+++	—	—	—	—	—
Kayugl	—	+++	—	—	—	—	—
Manywa	—	+++	—	—	—	—	—
Kooki Lakes							
Mburo	++	++	+	—	—	—	—
Kachera	+++	++	++	—	—	—	—
Kijanebalola	++	++	+	—	—	—	—
Yala system							
Lake Kanyaboli	+	+++	—	—	—	—	—
Lake Sare	+++	—	++	—	—	+	—
Kyoga Lakes							
Kyoga (main lakes)	+++	—	++	—	—	++	—
Nawampasa	+	++	+	++	—	+	—
Nakuwa	++	—	+	—	—	—	—
Kasudho	+	++	+	+	—	+	+
Nabusejere	++	++	+	+	—	—	—
Muwuru	++	++	+	+	—	+	—
Namumbya	++	++	++	++	—	—	—
Lemwa	+	+++	—	—	—	—	—
Dalaja	++	+	+	+	—	—	—
Nyaguo	++	+++	+	+	—	+	—
Bisina	++	++	+	++	—	++	—
Ameito	++	—	—	+	—	—	—
Victoria Nile River System							
Namasagali	+++	—	++	—	—	++	—
Bugondo (Mbulamuti)	+++	—	++	+	—	+	—
Nababirye (Kizoi)	+++	—	++	++	—	++	—
Buwendha	+++	—	++	+	—	+	—

Molecular analysis

For each identifiable form, based on descriptions of LVR fishes (Greenwood, 1966), a minimum of 20 individuals was sampled and tissue taken from each for molecular analysis. Molecular analysis included 10 microsatellite loci, visualized using PCR primers developed from an *O. niloticus* DNA library (Lee and Kocher, 1996). Analysis of data was performed using Microsat1.5 (Minch, 1996) and Genepop3.1 (Raymond and Rousset, 1995). Means of statistics used in analysis of population genetic

structure were summarized for comparison of the species' structures in the region. Population comparisons used Nei's standard genetic distance, Dst (Nei, 1972). Phyletic relationships among selected populations of species thought to be hybridized were estimated using the proportion of shared alleles (ps), standardized as $[-\ln(ps)]$. Genetic distance measures based on proportion of shared alleles reflects the exchange of alleles between species in a manner not compounded by consideration of allele frequency. Change in allele frequency may occur with hybridization, but estimating the degree of

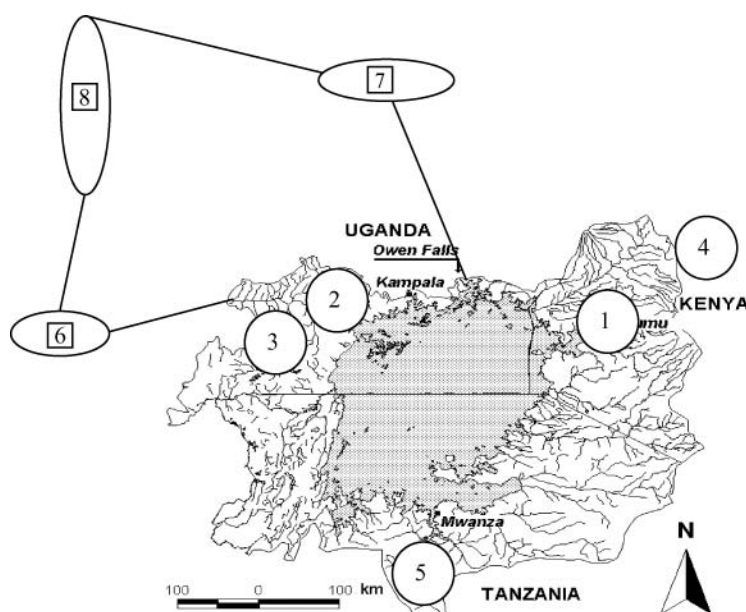


Figure 1. Lake Victoria Basin Systems: 1. Yala Basin; 2. Nabugabo lakes; 3. Kooki lakes; 4. Eastern Rift Valley lakes; 5. Northern Tanzania lakes; 6. Lakes Edward and George systems; 7. Lake Kyoga complex; and 8. Lake Albert system.

hybridization from allele frequency is sensitive to the starting allele frequencies in the original populations, and may be less appropriate as an indicator of hybridization.

Results

The distribution of species is presented in Table 1. The survey revealed four species of *Oreochromis*: Nile tilapia being the most dominant, two of *Tilapia*, and one species of *Sarotherodon* found only in Lake Albert. Intermediate morphs, especially between congeners, were a common occurrence in many lakes in which species coexisted. Genetic indices of population variability and phyletic relationships are given in Tables 2 and 3. All species showed high levels of genic heterozygosity. Mea-

sures of inbreeding, F_{is} and F_{st} , both functions of observed and expected heterozygosity expressed in terms of gene (alleles) and genotype frequencies (Nei, 1977), showed that native species were more subdivided and had relatively higher levels of population inbreeding, compared to that of the introduced species which are shown in Table 4. *Oreochromis niloticus* had the lowest values among the species of *Oreochromis*, while *Tilapia zillii* had a negative value for F_{is} (suggesting preferential outbreeding/hybridization with closely related *T. rendalli*). *O. niloticus* had the biggest proportion of loci with negative F_{is} and F_{st} values. Using F_{st} as a measure for population subdivision, *T. zillii* and *O. esculentus* were found to be the most subdivided while *O. niloticus*, *O. leucostictus* and *O. variabilis* were the least. Table 2 shows estimates of migration

Table 2. Genetic indices for key LVR tilapiine species, including number of migrants estimated from private alleles (after Barton and Slatkin, 1986). Values corrected for sample sizes.

Species	No. Popns.	Mean sample	Alleles/ locus	Avg. Het/ locus	Frequency private alls	% Private alleles	Number of migrants
<i>O. esculentus</i>	11	15	27	0.583	0.06	39.1	2.13
<i>O. variabilis</i>	06	10	20	0.712	0.11	41.2	1.17
<i>O. leucostictus</i>	10	15	22	0.614	0.05	51.0	3.46
<i>O. niloticus</i>	15	15	18	0.555	0.06	30.0	2.34
<i>T. zillii</i>	06	15	13	0.541	0.08	55.0	1.50

Table 3. Genetic variation at microsatellite loci for LVR Tilapiine populations, including F-statistics estimations (F_{we}) following Weir and Cockerham (1984).

Species	No. Popns.	No. Loci	Alleles/ locus	Avg. Het./ locus	F _{we(is)}	F _{we(st)}	F _{we(it)}	Negative F _{is} Values
<i>O. esculentus</i>	11	10	7.3	0.596	0.054	0.216	0.258	3/10
<i>O. variabilis</i>	06	10	7.6	0.711	0.116	0.133	0.234	2/10
<i>O. leucostictus</i>	10	10	7.2	0.610	0.130	0.156	0.266	1/10
<i>O. niloticus</i>	15	10	5.6	0.552	0.002	0.150	0.152	5/10
<i>T. zillii</i>	06	07	4.9	0.548	−0.123	0.215	0.119	2/07

within species for the four *Oreochromis* species and for *Tilapia zillii*. There were no significant differences in the mean frequency of private alleles, tested pairwise among *O. niloticus*, *O. leucostictus*, *O. esculentus* and *T. zillii*, but each showed slight significant differences compared to *O. variabilis* (Table 2). Figure 2 shows phyletic relationships among populations of *Oreochromis* species from the LVR, while Figure 3 shows the phyletic relationship between populations of *Tilapia*.

Discussion

Fisheries Ecology

The introduced tilapiines in the LVR have supplanted native species in the large lakes and relegated them to minor water bodies surrounding the larger systems, where they continue to face increased ecological competition from introduced species, in combination with fishing pressure from

Table 4. Relational occurrence and status of tilapiine species in LVR: *O. esculentus* (OE), *O. variabilis* (OV), *O. niloticus* (ON), *O. leucostictus* (OL), *T. zillii* (TZ) and *T. rendalli* (TR).

Reference species	Location/lake	Congeners present	Most dominant tilapiine
<i>Oreochromis esculentus</i>	Nabugabo lakes		
	Kayanja	none	<i>O. esculentus</i>
	Manywa	none	<i>O. esculentus</i>
	Kayugi	none	<i>O. esculentus</i>
	Koki lakes		
	Mburo	ON and OL	<i>O. niloticus</i>
	Kachera	ON and OL	<i>O. niloticus</i>
	Yala basin		
	Kanyaboli	OL	<i>O. esculentus</i>
	Kyoga lakes		
	Nawampasa	ON, OV, OL	equally abundant
	Lemwa	ON	<i>O. niloticus</i>
	Kawi	ON	<i>O. esculentus</i>
	Nyaguo	ON, OV	Not clear
<i>Oreochromis variabilis</i>	Bisina	ON, OL, OV	<i>O. niloticus</i>
	Lake Victoria	ON, OL	<i>O. niloticus</i>
	Kyoga lakes		
	Nawampasa	ON, OE, OL	equally abundant
	Gigat	ON, OL	
	Victoria Nile	ON, OL	<i>O. niloticus</i>
<i>Tilapia rendalli</i>	Bisina	ON, OL, OE	<i>O. niloticus</i>
	Lake Nabugabo	TZ	<i>T. zillii</i>
	Lake Victoria	TZ	<i>T. zillii</i>
	Lake Kyoga	TZ	<i>T. zillii</i>
Kyoga lakes	TZ	<i>T. zillii</i>	

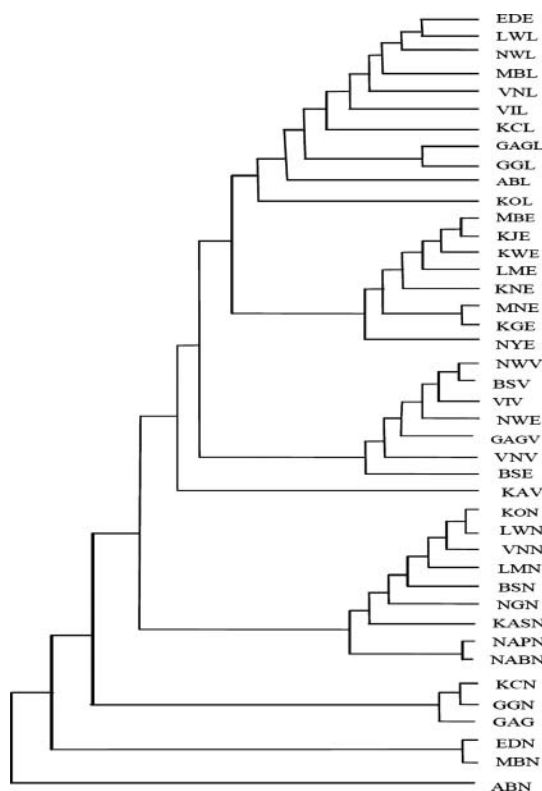


Figure 2. Phylogram of populations of *Oreochromis* species from Lake Victoria Region and conspecifics from their putative origin of Lake Albert Tilapiine populations based on Nei's genetic distance. Lake site designated by first letters, species by last letter. Localities: AB = L. Albert; BS = L. Bisina; ED = L. Edward; GG = L. George; GAG = L. Gigate; KAS = South-west of Lake Victoria at Kasensero; KC = L. Kachera; KG = L. Kayugi; KJ = L. Kayanja; KN = L. Kanyaboli; KO = L. Kyoga; KW = L. Kawi; LM = L. Lemwa; LW = L. Nakuwa; MB = L. Mburo; MN = L. Manywa; NAB = Lake Nabugabo NAP = L. Victoria (Napoleon Gulf); NG = Lake Victoria (Winam Gulf); NW = L. Nawampasa; NY = L. Nyaguo; VI = L. Victoria; VNL = Victoria Nile; Species: E = *O. esculentus*; L = *O. leucostictus*; N = *O. niloticus*; V = *O. variabilis*.

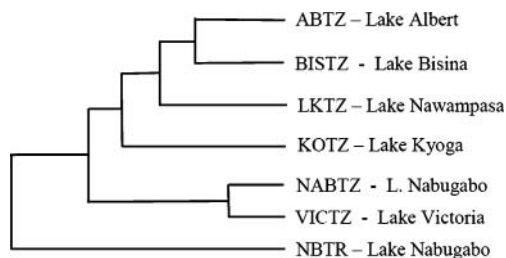


Figure 3. Phylogram of populations of *Tilapia zillii* (Z) from Lake Victoria region and from their putative origin of Lake Albert in relation to *Tilapia rendalli* (R) from Lake Nabugabo. Genetic distances based on standardized proportion of shared alleles (ps).

the attendant communities. The minor surrounding bodies, the satellite lakes as described by Kaufman and Ochumba (1983) serve as the only natural refugia for species that were the previous focus of the fishery – the native species. In the majority of satellite lakes, native species coexisted with non-indigenous forms, but are dominated in numbers by one or a combination of non-indigenous species, although *O. variabilis* was still found within Lake Victoria as small isolated pockets of individuals but which were inconsequential in terms of fisheries. *O. esculentus* was completely displaced from the main lakes, but retained sizeable populations in a few satellite lakes. Among non indigenous species, *O. niloticus* was the most abundant and most widely distributed, occurring in nearly all water bodies in the LVR. *O. leucostictus* was widely distributed, but far less abundant than *O. niloticus*. *T. zillii* was widespread, occurring in the majority of the water bodies but in relatively smaller population sizes. *T. rendalli* also was widely distributed, though with very low numbers.

Genetic analysis

Ecological lability, behavioural versatility, and relatively higher genetic variation have ensured the continued dominance of *O. niloticus* (Mwanja et al., 1995; Mwanja, 1996) in LVR despite immense and growing fishing pressure factors that led to the collapse of native tilapiine fisheries (Mwanja, 1996). The native forms, *O. esculentus* and *O. variabilis*, showed the highest subdivision, arguably because of isolated and marginalized remnant populations. *O. leucostictus* was less subdivided than *O. niloticus*, possibly due to an ability to use lagoons and swamps adjacent to lake edges that effectively allow exchange between populations in such vast swampy areas as the Kyoga lakes that present a naturally hypoxic barrier to genetic exchange. However, Chapman et al. (1995) showed that all tilapiine species in the LVR show similar tolerance to hypoxia. Other factors must contribute to the ability of *O. leucostictus* to use swamps more effectively than its congeners.

Phyletic relationships

Notable in Figure 2 was the lack of a clear sister relationship between *O. esculentus* and *O. niloticus*, as proposed by Trewavas (1983). Among the species studied *O. esculentus* appears closer to

O. leucostictus than to *O. niloticus*. *O. variabilis*, which has been placed in a distinct subgenus and appears closer to *O. niloticus* than to other congeners. Tilapiine populations could be identified without ambiguity with the exception of some populations of native species. *O. variabilis* populations were small and appear to have undergone hybridization with *O. niloticus*, as earlier reported by Fryer and Iles (1972). This may have contributed to the highly derived position of the *O. niloticus* Kyoga population. Populations of *O. niloticus* from the Koki lakes were found to be closer to one putative source, the population of Lake Edward, than to an alternative source of introduction, Lake Albert. As previously observed in Fuerst et al. (1997) the Lake George population was phylogenetically more distinct from the geographically proximate population of Lake Edward than it was from the geographically more distant Lake Albert population. This could best be explained by the vagaries of intermittent stocking of the tilapiines practiced in the last century in Uganda.

Genetic interaction

All populations of *Oreochromis* from sampling sites where coexistence occurs between populations of congeners were found to be phylogenetically more differentiated and more derived compared to 'pure' representatives of either species. Samples that clustered as 'pure' representatives of a species were associated with collecting sites where they did not coexist with congeners, or where they were clearly the overwhelmingly dominant species in abundance among congeners. This pattern of phylogenetically intermediate 'mixed' populations was observed for the native tilapiine species, providing strong evidence for the occurrence of hybridization, and indicating the direction of introgression. Further, the Lake Kyoga populations of all the tilapiine species, both native and non-indigenous, were highly derived, arguably due to genetic exchanges between all the species in this ecosystem.

O. esculentus from the Nabugabo lakes was found to be the only extant near 'pure' representatives of this species. A danger to continued preservation of the *O. esculentus* genotype exists since, in Lake Nabugabo itself, *O. niloticus* and *O. leucostictus* are abundant. Fortunately some of the Nabugabo lakes such as L. Kayanga and L. Manywa still have sizeable populations of *O. esculentus* that could be augmented through artificial nursery propagation to bolster the species' ecological status. Tradi-

tional practices by the fishing community of the area have managed to protect and conserve these populations, but since these practices are not backed by law or gazetted regulations we cannot continue to rely on these alone. Elsewhere, *O. esculentus* populations, especially those of Lake Kyoga and the Lake Edward/George system have been genetically swamped and are in danger of disappearing. Among samples from the Kyoga lakes, only the sample from Lake Kawi (KWE) resembles the genotypes seen in the populations of the Nabugabo lakes. Lake Kawi was dominated by *O. esculentus*, with *O. niloticus* as a very minor component, providing an explanation for the survival of an *O. esculentus* population in this lake in more or less 'pure' form.

Of the two Tilapia species, *T. zillii* was more abundant and by far the most frequently encountered species. The sporadic occurrence of *T. rendalli* in the LVR makes its continued survival precarious, given that our genetic data and observations on morphology suggest that it readily hybridizes with *T. zillii*. In Lake Nabugabo, hybrids were more frequent than either pure species. This would be the final phase in eliminating one of the parent species, the species that constitutes the minor component. As mentioned previously, such a phenomenon has been reported for *Oreochromis spirulus nigra* in Lake Naivasha (Leveque, 1997), the Koki lakes (Fryer and Iles, 1972) and in Lake Bunyonyi (Lowe-McConnell, 1958), where hybridization occurred with *Oreochromis niloticus* and/or *O. leucostictus*.

Management Options

Evolutionary questions regarding the diversity and management of multispecies fisheries are critical to understanding and guiding the options for management of the fisheries resources (Fuerst and Mwanja, 2000), and are critical for monitoring the ecological trends in fisheries (Kaufman, 1992), and for the successful implementation of management approaches that, at minimum, can ensure the continued existence of most species within such systems. In this study, it is clear that where native tilapiine species do not share the waters, and or when natives are dominant, they appear much more likely to survive as distinct gene pools. It is vitally important that lakes with populations of native species that are considered 'pure' forms be managed in ways to prevent movement of alien Tilapiines into these waters.

It is also plausible that the deterioration of native Tilapia where co-existence occurs could be reversed through selective augmentation of the native species populations, using such means as bolstering the survival of young collected from the wild in artificial nurseries adjacent to the native lakes, with eventual release back to these waters. This will hopefully increase recruitment and eventually lead to local ecological dominance over other tilapia species, an ecological requirement needed to stem genetic swamping from introduced forms.

Conclusions

Nile tilapia, *Oreochromis niloticus*, has become the mainstay of the tilapia fisheries in LVR and is currently found in most of the water bodies in this region. Its labile ecology and aggressive behavior is already being used in displacing of the native tilapiines which are at increasing risk of introgression with Nile tilapia and other introduced conspecifics. The native tilapiines of the LVR have sizeable stocks in a few of the satellite lakes around Lake Victoria and Kyoga but are faced with competition from Nile tilapia, fishing pressure and environmental degradation as attendant human communities seek to reclaim the surrounding and protective marshes/swamps for agriculture production.

Management of the satellite lakes as refugia for the native tilapiines will not only offer chance of continued existence to the native forms but will also give protection to tens if not hundreds of key ecological and evolutionary cichlid species usually referred to as haplochromines. This study has revealed the continued danger faced by cichlid fishes in the LVR and calls for concerted efforts to map out and work with communities to manage these important resources for current and future use as well as for preservation of important evolutionary resource of the region.

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