Genetic viability of Nabugabo lakes (LVR satellite lakes) fish species

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GENETIC VIABILITY OF NABUGABO LAKES (LVR SATELLITE LAKES) FISH SPECIES

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Abstract

Natural populations of fish species in Lake Victoria Region (LVR) have under gone dramatic changes including severe reduction in sizes, division of original stocks into disjunct subunits, and segregation into several isolated population units either within a single water body or even worse into separate waters. In addition, these changes have been either preceded or precipitated by introductions of non-indigenous species that outcompeted the native forms and in case of closely related species genetically swamped them through hybridisation. The latter is especially the case in Nabugabo lakes. Such events lead to fragmentation of populations, which results in reduction in genetic diversity due to genetic drift, inbreeding and reduced or lack of gene flow among independent units. Such phenomena make the continued existence of fisheries stocks in the wild precarious, more so in the face of the competition from exotic species. Species introductions coupled with growing exploitation pressure of the fisheries of these lakes have put the native stocks at risk. Nabugabo lakes harbour cichlid species that are unique to these lakes more so species of the cichlid complex. In this paper the ecological status and genetic viability of key Nabugabo lakes fish species is examined and management options are discussed.

Key words: Nabugabo lakes, fishes, species introductions, genetic viability

Introduction

Nabugabo lakes comprise Lakes Nabugabo, Kayanja, Manywa and Kayugi lying in the northwest part of Lake Victoria Basin and separated from Lake Victoria by two to three kilometre wide sand dune. Nabugabo lakes are known to have become separated from Lake Victoria about 4000 years ago and is recorded to have contained six endemic haplochromine species of which one is thought to have gone extinct following the introduction of Nile perch in Lake Nabugabo (Greenwood, 1974, 1981). Among the tilapiine species, Lake Nabugabo and Lake Kayanja were recorded to have contained only *Oreochromis esculentus* as native form (Greenwood, 1966). *O. esculentus* has since been completely displaced out of Lake Nabugabo, and exists as isolated and marginal populations in the other three Nabugabo lakes. In Lake Nabugabo three other tilapiine species were introduced in effort to bolster the lake's fisheries. These species include *Oreochromis niloticus*, *Oreochromis leucostictus*, *Tilapia zilli* and *Tilapia rendalli* (Mwanja *et al.*, 1995).

The effect of the species introductions and movements has been the displacement of the native tilapiine and loss of one endemic haplochromine species, and the marginalization of other native forms in population sizes (Mwanja, 1996). These ecological changes are certain to have been followed by reduction in genetic diversity, and ecological and evolutionary viability through genetic drift and due to little or no genetic exchange between isolated remnant units. In examining the viability of key species in Nabugabo lakes the following questions have to be asked:

1. What is the extent of population structuring of native fishery species relative to the non-indigenous forms?
2. What is relationship between population size, spread/distribution and genetic diversity of tilapiines?
3. Does segregation into separate subunits play a major role in maintaining genetic variability in native species, and/or what is the role of satellite lakes in maintaining genetic diversity?
4. How evolutionarily viable are key ecological species in Nabugabo lakes?

The change in structure from a continuous single population into disjunct units, with little or no gene flow among units, or as completely isolated units in independent water bodies puts the native species at a situation of accelerated intrapopulation differentiation among subunits and at loss of genetic variability within units through increased genetic drift and inbreeding. There are two typical resultant structures, the shrunk and disjunct, and the shrunk and isolated. Its expected that the intrapopulation differentiation and loss of genetic variability within units would be more extreme in the latter given that there is no chance of genetic interaction among populations in this case. In case where closely related species coexist we expect hybridization between such species. The result of this will be genetic exchange that may signal elevated genetic variability in populations that would have otherwise been predicted to be low in variability. Typically such units would be genetically distant from the 'pure' forms of that species. Among the introduced non-indigenous species we expect to see a reflection of the genetic variation from their introduction histories as well as a representation of the genetic structure of their putative origins into the Nabugabo lakes.

On the evolutionary scale it is especially important to establish and understand the linkage between the speciation history and hydrological processes that shaped the LVR fish faunal system. It is essential that we determine whether the fish species of these small water bodies are of recent origin or reflect longer historical changes in the LVR. The efforts to conserve the contained fish biodiversity depend largely on our knowledge of the extant species and their evolutionary relationships to the volatile geological and hydrological history of the region. This requires that we have evolutionary markers that are universal, versatile, and inherent, and can reflect the enormous diversity yet reveal the deep evolutionary trends that have shaped the individual species and lineages. Earlier molecular studies revealed no marked genetic differences between various Lake Victoria haplochromine species (Sage *et al.*, 1982, Meyer *et al.*, 1990). However, the newly developed types of molecular markers (in this case microsatellite DNA markers), produced specifically for LVR haplochromine cichlid species in Prof. Paul Fuerst laboratory (Wu *et al.*, 1999), can differentiate populations and species even at a very fine scale. The developed markers are currently being used in investigating several phylogenetic and macroevolutionary questions in the region's haplochromine species assemblage. Similar markers were employed in the very laboratory in attempting to look at genetic viability of fishes of Nabugabo lakes, and details of their usage are described below.

Methods

Fieldwork involved establishment of the ecological status of the remnant populations of the native species, and the level of establishment of the non-indigenous species. All lakes were surveyed for existing fish species and relative abundance. Molecular analysis in the laboratory was designed to study individual populations then compare these to conspecifics. As comparison among species was the overall aim, molecular tools were standardized to allow comparison of data across species. Two molecular methods, the RAPDs and the microsatellite techniques, were used as defined in Mwanja, 2000. RAPD technique generated adequate number of population markers (bands) that enabled comparison populations phylogenetically but did not provide the genetic population statistics since there are inherent deficiencies in the method to allow for proper genetic statistical analysis (Lynch and Milligan, 1994). RAPD population markers also allowed for use of cladistics analysis using individual's profiles given the highly variable and numerous band patterns generated by the technique. The microsatellite technique generated markers appropriate for population statistics for all populations where the number of individuals was sufficient and also allowed for the phenetic estimation of the phylogenies based on population genetic distances.

Results

As part of the overall LVR project we carried out fishing survey that revealed taxa ecologically similar and/or taxonomically close to many species known to be extinct from the main lakes, as still extant in several of the satellite lakes in the LVR. Examples of the extant species/genera obtained in surveys of the satellite lakes are shown in Table 1. Relative numbers of fish species found extant in the various water bodies in LVR are shown as well as the introduced tilapiine species and the Nile perch are shown in Table 2. Some of the satellite lakes, such as the Nabugabo lakes contained only a small number of species. Others, such as the satellite lakes around Lake Kyoga had a wide variety of taxa, which included both known species, as well as several undescribed species that were equivalent to species or genera reminiscent of the main lakes before the establishment of the Nile perch (Greenwood, 1981; Kaufman and Wandera, *unpublished*). A few groups, such as *Astatoreochromis allaudi*, *Pseudocrenilabrus victoriae*, and species of the genera *Astatotilapia* and *Paralabidochromis*, were widely distributed both in the main lakes and in the satellite lakes. Most of the piscivorous cichlids, such as species of *Harpogochromis*, *Psammochromis* and *Prognathochromis*, were restricted to only a few satellite lakes, though some of the species in these groups were indeed wide spread among the satellite lakes. Among the native tilapiine cichlids of the LVR, we found significant populations of the two native forms, *Oreochromis esculentus* and *Oreochromis variabilis*, in several of the satellite lakes. The former has been displaced completely out of the main lakes.

Table 1. List of examples of genera extinct from the main Lakes Victoria and Kyoga but still extant in satellite lakes.

Taxa	Occurrence	
	Main lakes	Satelite lakes
Allochromis	Extinct	present (Kyoga lakes)
Harpogochromis	Extinct	present (Nabugabo, Kyoga, and Kooki lakes)
Astatotilapia latafisciata	Extinct	present (Kyoga lakes)
Prognathromis	Extinct	present (Nabugabo, Kyoga and Kooki lakes)
Lipochromis	Extinct	present (Kyoga lakes)
Piscichromis	Extinct	present (Kyoga lakes)
Haplochromis annectendens	Absent	rare (Nabugabo lakes)
Haplochromis obliquidens	Extinct	*absent
Haplochromis lividis	Extinct	*absent
Tridontochromis	Extinct	only one extant species (Kyoga lakes)
Prognathochromis perrieri	Extinct	*absent

* In case where the species has never been found or recorded its marked as 'absent'.

Preliminary Genetic Analysis

Molecular analyses of the haplochromine cichlid species of the LVR revealed that there is strong population structuring, with differentiation between the remnant populations within the main lakes and between the main lakes and associated satellite lakes for the haplochromine species assemblage (Wu, 1999). All species, both the widespread and restricted forms, were found to be highly subdivided. Migration was estimated to be highest within lakes and least between the totally isolated satellite lakes. Genetic diversity though has not been depleted in these species. The majority of species exhibited high within population heterozygosity and allelic diversity (Table 3). Among the tilapiine species of the Nabugabo lakes, we found evidence of genetic interaction between the native and introduced species as was the case with Kyoga satellite lakes (Mwanja *et al.*, 1995; Mwanja, 1996; Mwanja, 2000). Tilapiine swamp forms such as *Oreochromis leucostictus* were less differentiated than strict lacustrine species like *Oreochromis esculentus*.

Table 2. Estimates of the number of cichlid fishes contained in Nabugabo lakes as compared to other LVR satellite lakes based on our field survey data from1990 to1997.

Haplocromines		Tilapiines		Nile perch
Lake Victoria Basin				
Main lake		Native	Introduced	
Lake Victoria	>200	1	4	Dominant
Nabugabo lakes				
Lake Nabugabo	<5	0	4	Dominant
Lake Manywa	<5	1	0	Absent
Lake Kayanja	<5	1	2	Absent
Kooki lakes				
Lake Kachera	>20	1	4	Absent
Lake Kijanebalola	>20	1	4	Absent
Lake Mburo	>20	1	4	Absent
Lake Kyoga Basin				
Main lake				
Lake Kyoga	<50	0	4	Dominant
Satellite lakes				
Lake Nawampasa	>60	2	3	Absent
Lake Lemwa	>50	2	2	Absent
Lake Bisina	>30	2	4	Rare
Lake Nyaguo	>50	2	2	Absent
Lake Nakuwa	<5	0	4	Dominant
Lake Nyasala	<30	1	4	Dominant
Lake Edward-George System				
Lake Edward		3	2	Absent
Lake George		3	1	Absent
Satellite lakes				
Lake Saka		0	1	Absent
Lake Kabaleka		3	1	Absent

* The table also shows the occurrence of the Nile perch, *Lates niloticus*, in the LVR lakes

Table 3. Preliminary genetic analysis of cichlid fishes of satellite lakes species in comparison to similar species of the main lakes based on RAPD (for tilapiine species) and microsatellite markers (for haplochromine species). Results are extracted from Mwanja, 1996, Wu *et al.*, 1999 and Wu, 1999.

Species	Polymorphism	Heterozygosity	Allelic diversity	Population subdivision
1. Native Tilapiinehs				
◆ *O. esculentus*	Higher	Higher	Higher	Higher
◆ *O. variabilis*	Equivalent	Equivalent	Higher	Higher
2. Non-native Tilapiines				
◆ *O. leucostictus*	Higher	Higher	Higher	Lower
◆ *O. niloticus*	Lower	Lower	Higher	Higher
◆ *T. rendalli*	Equivalent	Lower	Higher	Higher
◆ *T. zilli*	Equivalent	Higher	Higher	Equivalent
3. Haplochromine Complex				
◆ *Haplochromis spp*	Higher	Higher	Higher	Higher
◆ *A. alluadi*	Lower	Equivalent	Equivalent	Higher
◆ *Astatotilapia spp*	Higher	Higher	Higher	Higher

Discussion

Although previous studies (Sage *et al.*, 1984; Meyer *et al.*, 1990) revealed very limited genetic differences between various Lake Victoria haplochromine species, new sets of molecular markers (microsatellite DNA markers) developed in Professor Paul Fuerst's laboratory can differentiate populations and species even at a very fine scale. These molecular markers are currently being used to examine and analyse a series of phylogenetic and macro evolutionary questions in the haplochromine cichlids (Wu *et al.*, 1999; Wu 1999). Whether the species that were found in the small water bodies are of recent origin, or reflect long-term historical patterns in LVR, is of great importance in elucidating evolutionary and hydrological processes that have shaped the LVR system. Among the tilapiine cichlids, which form a sister group to the haplochromine species, significant populations of the two native forms remain in satellite lakes, even though they have been displaced completely from the main lakes of the region. Nabugabo lakes in particular contain the most 'genetically pure' reserves of the region's native tilapiine species *O. esculentus* (Mwanja, 1996). Batjakas *et al.*, 1997 postulated that limnological changes in the main lakes, from a diatom-dominated ecosystem to one dominated by blue green algae, may account for the displacement of the originally most important commercial species of the

LVR, the "Ngege" , *Oreochromis esculentus*, from the main lakes and its current relegation to the minor satellite lakes which tend to be less eutrophic, and less dominated by cyanobacterial phytoplankton.

Of no doubt is the role these minor lakes, such as Nabugabo lakes, are currently playing as refugia for endemic species ravaged by the dramatic human impact on the LVR since the turn of the 20th century. The satellite lakes present the only manageable natural refuge that can guarantee the continued existence of the most vulnerable forms or species. Molecular analysis results show that the resident populations of satellite lakes are highly differentiated among lakes. Thus, it would be highly advisable to maintain and manage various satellite lakes as independent evolutionary units. Movement of individuals between satellite lakes should only be done after a careful analysis of the genetic and ecological implications of such actions. Such conservative management practices will ensure the integrity of the isolated populations and give them a chance to continue to evolve without anthropogenic pressures.

Our recent discovery in satellite lakes in the LVR of cichlid fauna equivalent to portions of the extinct species of the large Lakes Kyoga and Victoria, has led us into speculation of a broader, and rather different role for satellite lakes than Greenwood, 1974 had envisioned. Minor satellite lakes act not only as nursery beds of prototypes for the big lakes, but also as critical refugia for diverse ecological types and genetic lineages. Satellite lakes may generate species through allopatric isolation and local selection regimes at the same pace, but on a smaller scale, as the large lakes. Meanwhile, their sheltered habitats offer protection to species equivalent to those in the greater lakes systems from the anthropogenic changes that the big lakes have been experiencing. The evolutionary findings so far point to the fact small lakes have often been part of the ontogenetic speciation cycles of big lakes (Kaufman, 1997). Given such a fact Nabugabo lakes and other similar lakes in the region evolutionarily important zones for the continued existence and conservation of the LVR fish species.

Introduction of Nile perch and non-indigenous tilapiine fishes into the LVR left little room for refuge by the native species, especially in the big lakes. However, in only a few of the minor lakes, such as Lake Nabugabo in the Lake Victoria basin and Lake Nyasala in the Lake Kyoga basin, has the Nile perch been able to become established, take over and exert its 'extinction machinery' on the endemic fauna. In some of the minor lakes, such as Lake Bisina in the Lake Kyoga Basin, the Nile perch flourished early following introduction, but since has been reported to undergo population declines due to selective fishing mortality. When this has occurred, there appears to be a possible resurgence by the original native cichlid species. Such situations provide us with a set of natural experiments on the effect of the Nile perch and/or other factors that have been thought to lead to the decimation of fish species in the LVR.

Several factors have had a severe negative impact upon both the aquatic species diversity and overall genetic diversity within the inland fisheries. Environmental degradation has often resulted in reductions of population sizes and local or even widespread extirpation of populations. Populations have often become fragmented and the pieces become isolated because of alterations in the habitats. Introduction of exotic species have been poorly conceived and often have resulted in unforeseen ecosystem-wide problems. Appreciation of the historical importance of the regional native food fishes suggests that the development, nurturing and improvement of native strains is a promising approach which should be considered as an important part of management strategies to maintain sustainable fisheries. This can only occur if efforts are made now to conserve the genetic diversity of these local endemic fish species.

In most cases in fisheries management efforts have been put on maintaining high species numbers and boosting population sizes. Little or no emphasis at all is put on the genetic or evolutionary viability of wild fisheries. Most genetics work that has been done to date for Nabugabo lakes fishes has been for characterization of species for taxonomic or macroevolutionary purposes (Mwanja 1996, 2000; Wu, 1999) rather than maintaining or managing populations in the wild. However, the new technology and effort to conserve biodiversity have put renewed hope in increase of population genetics studies especially in key areas of aquatic biodiversity such as the satellite lakes of the LVR. In the preliminary findings for example Nabugabo lakes species have been found to be of equivalent or higher genetic variability when compared to similar forms in other lakes in the LVR. Even though there is no historical population genetic information on the LVR fishes as whole including those of Nabugabo lakes, it can be assumed that levels of genetic variation were at least at current levels, and possibly higher in many species. Given the continued marginalization of native species it can with a good degree of certainty be implied that the genetic and evolutionary viability of native forms has been declining. This and ongoing studies using nucleic acid markers, provide data baselines with which to compare future studies and follow changes with the evolution of the fisheries. Such information is very important, since the most likely scenario involves loss of genetic variation in the future in many species.

To establish the genetic and evolutionary viability of Nabugabo lakes fishes, there is need to understand the ecological (ecosystem) forces which shaped these at least since the mid of the 20th Century – when direct human interference in these lakes started to manifest. A number of interacting elements affect the levels and preservation of genetic biodiversity in the species of a fisheries system. In the pre-20th Century, natural selection and adaptation to local environmental conditions probably occurred over hundreds or thousands of years in relatively far slower changing environment. As the environmental changes accelerate into the 21st Century, factors conspire to reduce diversity. Among the elements which reduce genetic diversity are: (1) the factors which can cause loss of genetic diversity within a population, including inbreeding and random genetic drift because of restricted small population size, (2) the ecological effects of the introduction of alien species, including direct competition or predation, and indirect effects caused by alterations in the environment, (3) the biological and physical factors which can hinder genetic exchange between populations of species, potentially leading to the subdivision of large continuous populations into small disjunct units, (4) the possibility of hybridization and introgression in species leading likely to 'genetic swamping' of the marginalized species, and (5) the consequences of monoculture resulting from argumentation in species which are being used to boost the fisheries stocks and for aquaculture or fish farming.

Although a consideration of the list of factors affecting genetic variation suggests that we should first focus directly on inbreeding and population size, it makes more sense to first consider how human pressures and management decisions lead to population subdivision and reduction of size. For such factors indirectly result in changes in the genetic composition of populations by encouraging inbreeding and small population sizes. Most notable for lakes has been use of alien species for boosting the lakes' fisheries, and pollution. These in most cases have led to small, disjunct and/or isolated units and/or ultimately total loss of the affected species. An example includes the haplochromine species of Lake Nabugabo that have vanished since the introduction of Nile perch and tilapiine species in the lake (Kaufman and Wandera, *unpublished data*). This species is no longer seen and has not been recorded in the lake since Greenwood's studies, 1974.

On one hand is the opening up of systems that have been closed naturally by geographic barriers allows accelerated gene flow among independent population units, while on the other hand we erect physical barriers to the natural gene flow among population units which have historically been mixing. In the first scenario has resulted in disruption of evolutionary and geographically coadapted and/or the locally adapted gene pools/complexes. Co-adaptation is viewed as individuals of a population that have evolved a well internally balanced gene pool with respect to reproductive fitness. Opening up such populations to hybridization by conspecifics disrupts the genetic balance and leads to decline in fitness due to reproductive dysfunction and genetic aberrations. Local adaptation on the other hand results from populations over a long time evolving a gene pool that best suits the habitat conditions. Such a match between gene pool and habitat can be easily disrupted by entry of foreign alleles and their incorporation into the local gene pools. On the other hand erecting barriers in the way of natural flow of water has the effect of blocking gene flow between populations, and most times subdividing naturally single populations into independent population units. This has the genetic effect of blocking the source for new variation through exchange of alleles between adjacent population units.

The subdivision of originally mixing populations renders the several units vulnerable to increased inbreeding and genetic drift effects, a combination that usually is detrimental to the genetic diversity and ultimately survival of any population unit. Markedly so, is the danger of exposing deleterious recessive alleles and loss of vital but originally rare alleles, situations both of which lead to decline in species fitness. The quest for 'economic development' and the pressures of ever increasing human population in the LVR has made lakes very susceptible to disruption and abuse by human activities, and thus in process affecting the adaptations of the occupant fauna. There is urgent need to drum beat the campaign to incorporate into any developmental or exploitative design those factors that promote and allow for the process of evolution of the fisheries so as to ensure continued survival of these resources.

A general fear is that economic and developmental activities will outpace our ability to discover, study and protect aquatic biodiversity. The bodies of water that are affected by development may have species that might have been economically unimportant prior to the planning of 'development projects' on such waters. The economic potential of such populations can never be known as often they are lost following the implementation of the planned activities. The negative effects of rampant damming of rivers and of increased agriculture adjacent to the water bodies, activities that have been detrimental to aquatic life, have been overlooked for the "economic good". This arithmetic may be good in short term but may not yield positive returns when long-term negative effects are accounted for. Even the short term gains may seem positive because the evaluation is narrowly focused to direct economic benefits neglecting the demise that may be already happening to the system overall.

Worldwide, introduced exotic species have menaced native forms of life, often out-competing ecologically similar local forms for the same niches, or acting as direct predators of the native species. The failure of past management policies to protect genetic diversity was in part due the policy of abandoning the local strains in rush to fix economic 'short falls' by introducing versatile and ecologically labile non indigenous species/strains. Such policies, though economically sound sometimes, have wrecked ecological havoc on the systems leading to displacement of the native forms, and most times resulting in permanent alteration of the ecosystems. In the LVR use of the Nile perch and non indigenous tilapiines to boost the original native tilapiine and labeine fisheries that formed the mainstay of the commercial fisheries then, did not boost the original fishery but supplanted it and completely transformed the ecosystem with hundreds of native species feared extinct while many more are at the peril of extinction as a result (Barel *et al.*, 1985; Kaufman, 1992).

When the exotic forms are closely related to and hybridise with the native species, such genetic interaction may lead to introgression which may result in 'swamping out' one of the species involved. Usually the more ecologically labile and aggressive species' attributes normally used as a basis for the choice in introduction, swamps out the marginalized species through repeated hybridization and backcrossing to the dominant type. Effects of introductions are not immediate, and establishment of the alien species in most cases takes place long after the act of introduction and the collapse of the native species. Thus effectively monitoring introduction of alien species on local strains is usually hard without the keen interest on part of the managers on the continued survival of the native species. Mechanisms that would naturally guard against genetic interaction between closely related species tend to breakdown with increased disturbance of the environment.

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