

The role of the Yala swamp lakes in the conservation of Lake Victoria region haplochromine cichlids: Evidence from genetic and trophic ecology studies

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Abstract

Lake Kanyaboli, an isolated satellite lake of Lake Victoria, has been suggested as a potential refugium for haplochromine cichlids that have gone extinct in the main basin of Lake Victoria. Mitochondrial DNA (mtDNA) molecular markers, as well as feeding ecology studies, were employed in this study to re-evaluate the evolutionary and ecological significance of six common Lake Kanyaboli haplochromines. The mtDNA marker revealed high genetic variability within four of the six haplochromine cichlids. Five haplotypes were discerned in *Astatoreochromis alluaudi* ($n = 27$), seven in *Lipochromis maxillaris* ($n = 29$), five in *Astatotilapia nubila* ($n = 12$) and 11 in the endangered *Xystichromis phytophagus* ($n = 205$). A haplotype genealogy suggests that Lake Kanyaboli harbours mtDNA haplotypes that could have been lost or not sampled in Lake Victoria, or could have arisen *in situ*. *Lipochromis maxillaris* appears to have undergone a recent demographic expansion. The pairwise F_{ST} s indicated that only the comparison between *X. phytophagus* and *A. nubila* led to a non-significant F_{ST} value. All other comparisons were significant at the 0.01 level, indicating the genetic distinctiveness of the haplochromines in the satellite lake. This could suggest that the lake harbours 'pure' relict populations of the haplochromines and therefore that Lake Kanyaboli can be considered a 'genetic reservoir'. Gut content analysis of the six haplochromine species revealed that eight different food items were consumed. No single species fed exclusively on a single food item, but certain food items contributed higher proportions of the fish diet for each fish species. Resource partitioning therefore could be discerned within this haplochromine community. Thus, Lake Kanyaboli and similar satellite lakes provide an opportunity for conservation of both genetic and trophic diversity threatened by introduction of exotics in the Lake Victoria basin. Lake Kanyaboli should be recognized and conserved as important evolutionary significant units for Lake Victoria region haplochromine species.

Key words

cichlids, conservation genetics, Lake Victoria region, mitochondrial DNA, trophic ecology, Yala swamp.

INTRODUCTION

The adaptive radiation of haplochromine cichlid fishes in Lake Victoria, East Africa, has one of the highest rates of speciation among living vertebrates (Seehausen 2002). This extraordinary adaptive radiation has an age of not > 200 000 years (Verheyen *et al.* 2003; Genner *et al.* 2007),

and has been attributed to both sexual selection and trophic specializations. Feeding specializations of the haplochromine cichlids have been instrumental in resource partitioning and therefore in shaping the cichlid community structure and maintaining its high diversity (Bouton *et al.* 1999). This trophic differentiation contributed to the evolution and adaptive radiation of the cichlid species flock of Lake Victoria. Previous genetic work has illustrated that the cichlid fishes of Lake Victoria form a superflock with the representatives from other lakes in the area, such as Lakes Albert, Edward, George and Kivu (Verheyen *et al.* 2003).

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The cichlid fauna of Lake Victoria formed an important component of the fisheries of the lake, thereby playing a critical role in the provision of protein requirements to the riparian communities (Sumaila *et al.* 2000). In the 1980s, however, the haplochromine cichlid fauna of Lake Victoria experienced an unprecedented rate of extinction. The loss of the haplochromines has been attributed to pollution that hinders colour-based mate choice (Seehausen *et al.* 1997), as well as predation from the exotic Nile perch (*Lates niloticus*, L.) (Ogutu-Ohwayo 1990). Thus, the conservation of the remaining cichlid species is of utmost importance. To protect the remaining populations, it is important not only to study their ecology, but also to characterize them genetically. One goal of conservation biology is to preserve genetic diversity. Quantification of levels of genetic biodiversity in extant endangered species is important in the recognition of taxonomic units in need of protection (Moritz 1994; Avise 1994). An understanding of the genetic structure of a population also is key to our understanding of the importance of genetic resources, and the importance of genes for conserving species and biodiversity. In the broadest sense, conservation of the genetic diversity and integrity of a species depends on identifying the critical genetic units and then managing the units in a coordinated manner (Lesica & Allendorf 1995). Not surprisingly, therefore, the maintenance of genetic variation has been a central theme in most long-term programmes for populations under conservation concern (Lande & Barrowclough 1987;

Soule 1987). Recent advances in molecular genetics have provided a valuable means of identifying population structure, especially with regard to identifying units of conservation, management and evolutionary significance (Frankham *et al.* 2004). Genetic information can be used as a basis for future re-stocking or aquaculture and management of different waterbodies as distinct genetic units.

Some cichlid species that have been virtually lost from Lake Victoria still thrive in small isolated waterbodies (commonly referred to as satellite lakes) scattered around the Lake Victoria basin (Loiselle 1996; Aloo 2003; Abila *et al.* 2004). These satellite lakes range from small lakes to dams and reservoirs. They have been recognized as having special significance in the conservation and future survival of these cichlids, and can be considered as functional refugia (Kaufman & Ochumba 1993; Maithya 1998; Mwanja *et al.* 2001; Mbabazi *et al.* 2004). Comprehensive studies on the genetic status of the haplochromine cichlid faunae in such lakes, however, are absent. As a result, they have not yet been incorporated into management practices.

The goal of this study was to evaluate the conservation significance of Lake Kanyaboli, the largest Yala wetland lake in Kenya (Fig. 1), by studying the trophic ecology of the six common haplochromine cichlid species, using gut content analyses and sequences of mitochondrial DNA (mtDNA). Because of their high rate of evolution and neutral nature, mtDNA is an ideal marker for studying

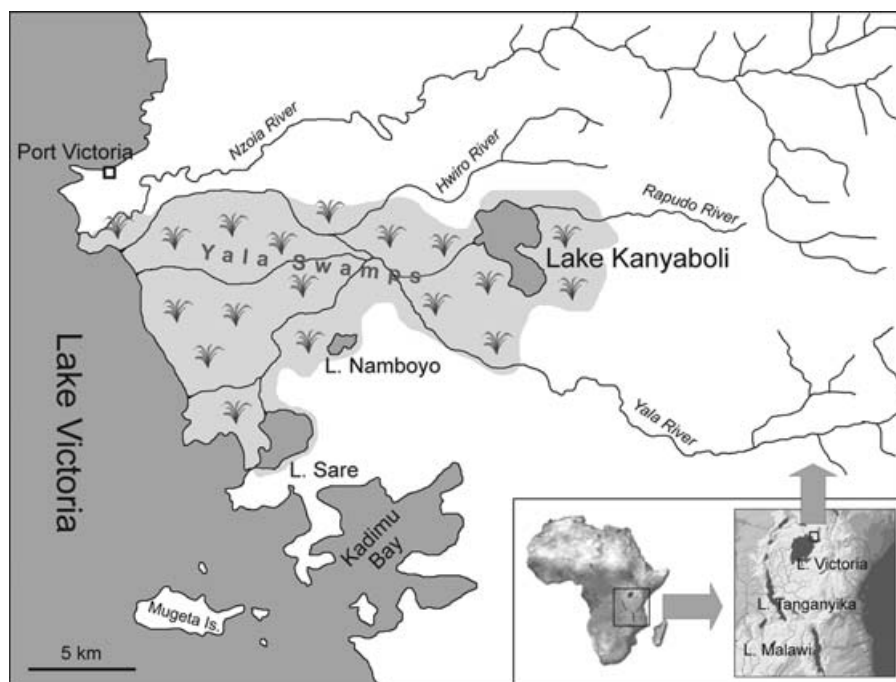


Fig. 1. Map of Yala swamp region, East Africa.

population genetics in evolutionarily young clades, such as the Lake Victoria haplochromines (Mwanja *et al.* 2001; Abila *et al.* 2004; Strecker 2006).

METHODS

Study area

The study was carried out in Lake Kanyaboli, a small (surface area = 10.5 km²), shallow (average depth = 2.5 m; maximum depth = 4.5 m) freshwater lake situated in the Yala wetlands in Western Kenya (Fig. 1). The Yala swamp is Kenya's largest freshwater wetland, covering ≈ 175 km² along the northern shore of Lake Victoria, Kenya. It is bordered in the North by the Nzoia River, and in the South by the Yala River. Three main lakes (Kanyaboli, Namboyo and Sare), of which Lake Kanyaboli is the largest and farthest from Lake Victoria, are found within the Yala swamps. Lake Kanyaboli is separated from Lake Victoria by massive papyrus swamps that presently inhibit faunal exchanges between the two lakes. No Nile perch has ever been observed in Lake Kanyaboli, corroborating the belief that it has been isolated from Lake Victoria since at least the 1950s. The fish fauna of Lake Kanyaboli is dominated by cichlids, including three species of tilapia (*Oreochromis esculentus*, (Graham 1929), *Oreochromis variabilis* (Boulenger 1904), and *Oreochromis leucostictus* (Trewavas 1983)), and about eight haplochromine cichlid species (Kaufman & Ochumba 1993; Aloo 2003). In addition to its cichlid fauna, the Yala swamp is home to a rich, complex community of animals, including the endangered Sitatunga antelope (*Tragecephalus spekeii*), and eight papyrus endemic birds (Birdlife International 2005).

Sampling of Lake Kanyaboli haplochromine cichlid fishes

Six species of haplochromines were collected from Lake Kanyaboli using a 3.81-cm monofilament gill net, including *Astatoreochromis alluaudi* (Pellegrin 1903), *Lipochromis maxillaris* (Greenwood 1980), *Astatotilapia nubila* (Boulenger 1906), *Xystichromis phytophagus* (Greenwood 1965), *Pseudocranilabrus multicolor victoriae* (Seegers 1990) and *Astatotilapia* sp. 'big eye' (Kaufman 1996). Additional *P. m. victoriae* samples were obtained by angling along the papyrus fringing swamps.

Trophic analysis

The stomachs and guts from 260 fishes were dissected, and preserved in 90% ethanol. The characterization and contribution of each food item to the fish diet were estimated by determining the relative abundance, percentage of occurrence, and prominence values, as described in Hyslop (1980), utilizing a stereomicroscope.

DNA extraction, PCR amplification and sequencing of mitochondrial DNA

Muscle tissue from specimens preserved in 90% ethanol was used as a DNA source. The total DNA was extracted by sodium chloride extraction and ethanol precipitation, after initial proteinase K digestion (Bruford *et al.* 1998).

For polymerase chain reaction (PCR) amplification of the first section of the mitochondrial control region, the fastest evolving segment of the mitochondrial genome (the published primers L-Pro-F (Meyer *et al.* 1994), and TDK-D (Lee *et al.* 1995)) was used. The sequences of *X. phytophagus* were included in a previous study (Abila *et al.* 2004). PCR amplification was performed in a reaction volume of 21.1 µL (9.9 µL high performance liquid chromatography (HPLC) water; 2 µL buffer; 1.6 µL 10 mmol L⁻¹ dNTPs; 1.4 µL 10 mmol L⁻¹ MgCl₂; 2 µL of each primer/2 nmol L⁻¹; 0.2 µL *Taq* DNA polymerase; 2 µL of diluted DNA) under the following conditions: (i) 35 cycles with a denaturation phase at 94°C for 30 s; (ii) an annealing phase at 52°C for 30 s; and (iii) an extension phase at 72°C for 90 s. PCR products were visualized by minigel electrophoresis, using ethidium-bromide staining and 1% agarose gels.

Two microlitres of purified PCR product was used as a template in the cycle sequencing reaction. The reaction mixture for cycle sequencing was made up of 1 µL of 10 µmol L⁻¹ L-Pro-F primer, 1.5 µL of the BigDye termination reaction mix (Applied Biosystems, Foster City, CA, USA), and 5.5 µL of HPLC water. The annealing temperature for cycle sequencing was adjusted to 50°C. The cycle-sequenced products were purified with an ethanol-sodium acetate precipitation, resuspended in 15 µL of HPLC water, and analysed on an ABI 3100 capillary DNA sequencer (Applied Biosystems).

Data analysis

The newly generated mtDNA data were first combined with previously published sequences (Verheyen *et al.* 2003; Abila *et al.* 2004). As only the first part of the mitochondrial control region was sequenced, DNA sequences obtained from other studies were brought to the same length. COLLAPSE (Posada 1999) was then used to cluster together identical control region sequences, so that each mitochondrial haplotype was represented only by a single sequence. The frequency of each haplotype was obtained from the original studies (Verheyen *et al.* 2003; Abila *et al.* 2004) or, in the case of the new sequences, from the COLLAPSE results.

The mtDNA sequence data were then used to construct a haplotype genealogy. To this end, a maximum likelihood analysis was performed in PAUP* (Swofford 2003), using

the model of molecular evolution, and the model parameters as indicated by ModelTest (Posada & Crandall 1998). The optimal maximum likelihood topology was then used, being translated into a phylogram on the basis of maximum-parsimony branch lengths, and a haplotype genealogy was constructed (see Abila *et al.* 2004). *Astatoreochromis alluaudi* and *P. m. victoriae* belong to two ancestral and widely distributed, though species-poor, lineages of haplochromines (Salzburger *et al.* 2005). As such, they do not belong to the superflock of cichlid fishes in the Lake Victoria region (Verheyen *et al.* 2003) and have, consequently, not been included in the construction of the haplotype genealogy. To reconstruct the demographic history of populations of haplochromine cichlid fishes in Lake Kanyaboli, a mismatch-analysis was performed with ARLEQUIN 2.000 (Schneider *et al.* 2000).

Genetic variability was estimated by calculating the haplotype diversity in each population. The genetic differentiation between the sampled populations was tested with F-statistics (the fixation index) (Weir & Cockerham 1984; Raymond & Rousset 1995), as calculated by ARLEQUIN. The fixation index (F_{ST}) serves as a convenient, widely used measure of genetic differences between populations (Wright 1978). Theoretically, F_{ST} has a minimum value of 0, indicating no genetic difference, and a theoretical maximum value of 1, indicating fixation for alternative alleles/haplotypes in the subpopulations. As only two individuals were genotyped, *Astatotilapia* sp. 'big eye' was not included in this analysis.

RESULTS

Feeding and trophic relationships of the haplochromine cichlids

The fish gut content analysis revealed that diet of the six haplochromine species comprised a total of eight food items, including algae (blue-green algae; diatoms), chironomid and *Chaoborus* larvae, other unidentified insects, molluscs, fish embryos, fish eggs, plant remains and detritus. Based on the frequency of occurrence, chironomid and *Chaoborus* larvae were the main food item, being observed in 64.3% of the guts examined, followed by plant remains (43.8%), detritus (37.5%) and other insects (33.5%). All the six examined haplochromine species fed on chironomid/*Chaoborus* larvae. Molluscivory and paedophagy (egg and embryo feeding) were restricted to *A. alluaudi* and *L. maxillaris*, respectively. Thus, these latter two food items contributed less to the total quantity of food items taken by the haplochromines. Only 15.2% of the examined guts contained molluscs, and 16.1% and 6.25%, respectively, contained fish embryos and eggs.

Based on relative abundance, chironomid and *Chaoborus* larvae constituted the largest quantity (29.3%) of taken food. The low values of relative abundance indicate that each type of food was taken only in low quantities. The overall diets of the six haplochromine species, expressed as frequency of occurrence and relative abundance, are summarized in Table 1. *Astatotilapia nubila* can be classified as an insectivore, *Astatotilapia* 'big eye' as an algivore, *L. maxillaris* as a paedophage, *X. phytophagus* as a plant

Table 1. Dietary composition of Lake Kanyaboli haplochromines, expressed as percentage frequency of occurrence and relative abundance

Species	Food		Type		Consumed			
	Algae	Chironomid/ Chaoborus larvae	Other insects	Molluscs	Fish embryos	Fish eggs	Plant remains	Detritus
<i>Xystichromis</i>	FO: 23.8	9.5	52.4	–	–	–	85.7	4.8
<i>phytophagus</i> (50)	RA: 2.5	5.7	36.9	–	–	–	56.1	0.6
<i>Pseudocranilabrus</i>	FO: 100.0	70.0	10.0	–	–	–	10.0	80.0
<i>multicolor</i> (47)	RA: 49.0	26.9	0.9	–	–	–	0.9	19.4
<i>Lipochromis</i>	FO: –	71.0	38.7	–	58.0	22.6	6.5	6.5
<i>maxillaris</i> (44)	RA: –	44.9	15.9	–	28.0	8.1	0.9	1.2
<i>Astatoreochromis</i>	FO: 12.5	70.8	41.7	70.0	–	–	37.5	87.5
<i>alluaudi</i> (56)	RA: 3.8	21.5	11.6	55.0	–	–	3.0	6.0
<i>Astatotilapia</i>	FO: 68.8	93.8	25.0	–	–	–	43.8	62.5
<i>nubila</i> (37)	RA: 25.3	39.0	5.7	–	–	–	11.5	20.7
<i>Astatotilapia</i>	FO: 98.0	80.0	–	–	–	–	20.0	–
'big eye' (26)	RA: 64.7	29.4	–	–	–	–	5.9	–

FO, frequency of occurrence; RA, relative abundance; number in parentheses indicates number sampled; dash (–) indicates food type not found.

feeder, *A. alluaudi* as a molluscivore, and *P. m. victoriae* as an algivore.

Population genetic structure inferred from mitochondrial DNA sequences

DNA sequences of the 359 base-pair segment of the mtDNA control region revealed five haplotypes for the 27 individuals of *A. alluaudi*, seven haplotypes for the 29 individuals of *L. maxillaris*, five haplotypes for *Astatot. nubila* ($n = 12$), 11 haplotypes for *X. phytophagus* ($n = 205$) (see Abila *et al.* 2004 for population genetic structure of *X. phytophagus*, based on microsatellite DNA), and one haplotype each for *P. m. victoriae* ($n = 14$), and *Astatotilapia* sp. 'big eye' ($n = 2$). Several haplotypes clustered together with each other, or with haplotypes that have so far only been known for the main body of Lake Victoria.

The haplotype genealogy (Fig. 2; *A. alluaudi* and *P. m. victoriae* are not included) clearly indicates the haplotypes

found in *A. nubila*, *Astatotilapia* sp. 'big eye', *L. maxillaris*, and *X. phytophagus* belong to the superflock of cichlid fishes from the Lake Victoria region (*sensu* Verheyen *et al.* 2003). As already reported by Abila *et al.* (2004) for *X. phytophagus*, there is a surprisingly high genetic diversity in cichlids from Lake Kanyaboli, as compared to Lake Victoria. For the six species from Lake Kanyaboli, 14 distinct mitochondrial haplotypes were found, compared to 41 for Lake Victoria (including some tributaries in the Lake Victoria region). Of the 14 Lake Kanyaboli haplotypes, eight were private (i.e. not found in the available sample of Lake Victoria cichlids).

The mismatch analysis (Fig. 3) revealed different demographic scenarios for different species. Lake Kanyaboli's two most common species, also belonging to the Lake Victoria region superflock (*X. phytophagus* and *A. nubila*), exhibit a relatively similar pattern, with high frequencies of pairwise comparisons in the categories of 0, 3 and 4 (in

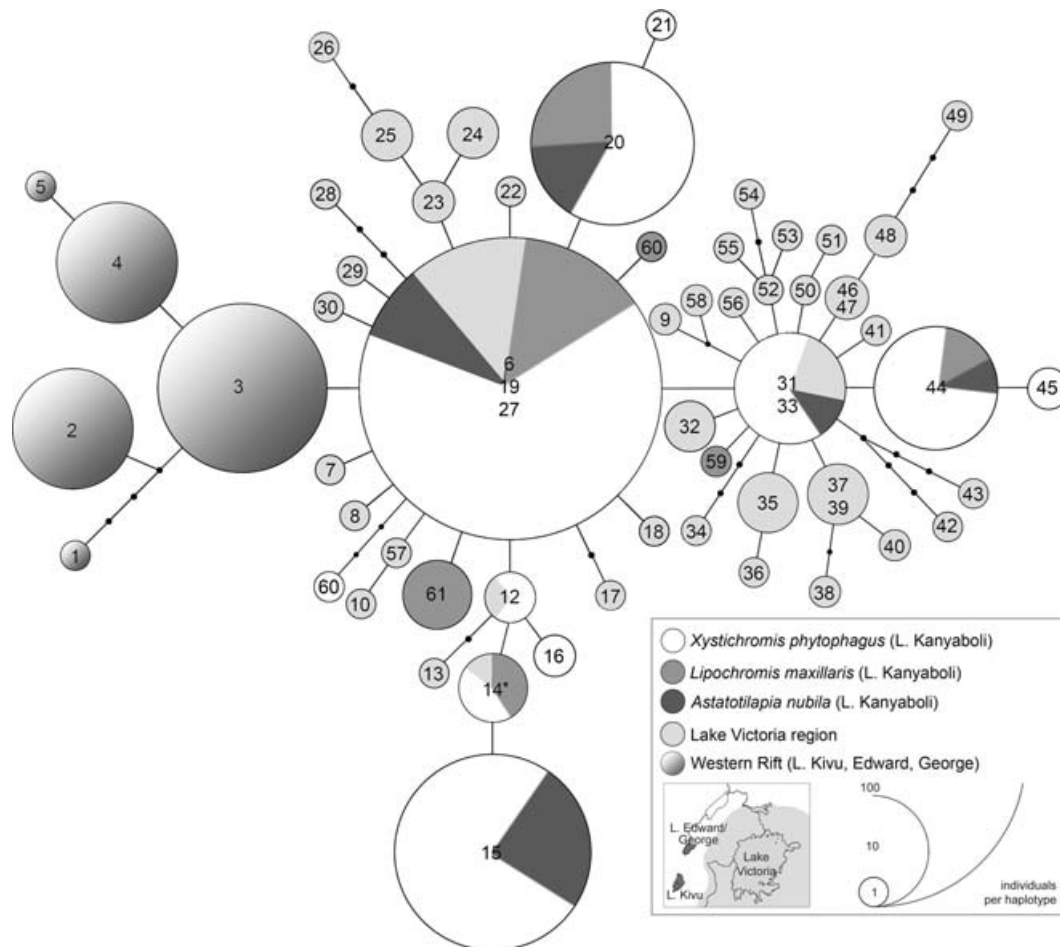


Fig. 2. Mitochondrial haplotype genealogy (each mitochondrial haplotype is represented by a circle; the size of the circle reflects the number of individuals sharing that haplotype; the colour-coding refers to the different species. Five haplotypes observed in the Western Rift region (1–5; Verheyen *et al.* 2003) were included. Haplotype numbers are taken from Abila *et al.* (2004). Because of the shorter sequences used in the present study, some mitochondrial haplotypes collapsed).

A. nubila) mutations and a τ (moment estimator of the time to the expansion) of 3.44 and 3.96, respectively. Both mismatch distributions exhibit two modes, with the older one being similar to that found when plotting the control region haplotypes of the entire species assemblage of Lake Victoria (Verheyen *et al.* 2003). *Lipochromis maxillaris* appears to have more recently undergone a demographic expansion ($\tau = 1.65$); a single haplotype was found in *Astatotilapia* sp. 'big-eye'. Very different demographic histories became evident for the two representatives of basal haplochromine lineages. While only a single haplotype was detected in the 14 specimens of *P. m. victoriae*, suggesting a rather recent colonization and/or expansion, a much greater diversity of haplotypes was found for *A.*

alluaudi, also being reflected in the mismatch distribution ($\tau = 2.50$).

The pairwise F_{ST} s (Table 2) indicated that only the comparison between *X. phytophagus* and *A. nubila* led to a non-significant F_{ST} value. All other comparisons were significant at the 0.01 level, indicating their genetic distinctiveness. The high F_{ST} s in the pairwise comparisons involving *A. alluaudi* and *P. m. victoriae* are explained by the existence of relatively distinct and private haplotypes only in these species.

DISCUSSION

A relatively high number of trophic groups, compared to what has been reported in the area/in Lake Victoria, were

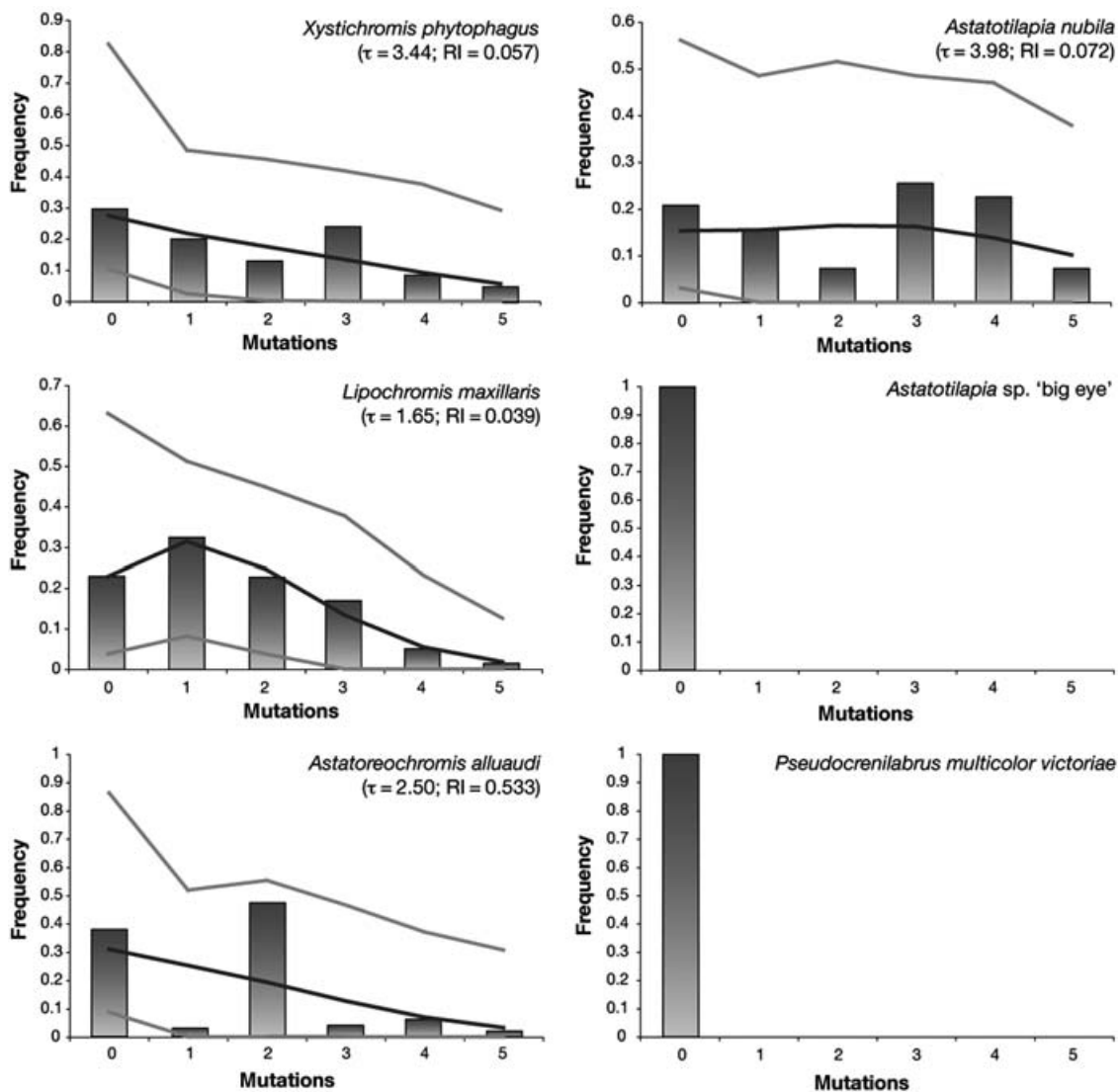


Fig. 3. Mismatch distributions (the mismatch distribution based on the pairwise comparison of all individuals is shown for each species; bars indicate observed frequencies, dark-grey lines show the modelled frequencies; light-grey lines indicate the 95% interval; RI Harpending's raggedness index).

observed in this study on Lake Kanyaboli. The absence of Nile perch in Lake Kanyaboli can be attributed to the presence of the massive swamp that separates it from Lake Victoria. Similarly, higher trophic diversities also have been determined for the satellite lakes Nawampasa, Gigati and Agu in Uganda that were not adversely impacted by Nile perch (Mbabazi *et al.* 2004). Greenwood (1981) and van Oijen (1982) reported that the pre-Nile perch haplochromines in Lake Victoria exhibited diverse feeding habits, including detritivory, insectivory, higher plant feeding, zooplanktivory, molluscivory, paedophagy and piscivory. The presence of Nile perch, however, simplified the trophic structure of the haplochromines from the above diverse trophic groups, to only two that belong to a single trophic level (Namulemo 1998). Most of the pre-Nile perch trophic groups, however, are still represented among the six Lake Kanyaboli haplochromines, where they occupy three trophic levels (i.e. primary, secondary and tertiary levels). Thus, Lake Kanyaboli has a more direct energy flow from primary to tertiary consumers through the haplochromines and, as such, the haplochromines play an important role in the energy flow and overall ecological efficiency of the lake system. Thus, ensuring the overall habitat integrity of the Lake Kanyaboli ecosystem should be a top management priority. Loss of the fringing papyrus swamp would lead to the loss of the main habitat of the haplochromines and loss of this trophic diversity. Unfortunately, current land-use changes involving swamp conversion threaten the future of the fringing swamp. The continued papyrus habitat loss and degradation have recently been suggested to represent a significant threat to biodiversity conservation, not only for fish, but also for papyrus-specialist birds (Owino & Ryan 2007).

The mtDNA molecular marker employed in this study revealed relatively high genetic variability in the haplochromine species. From a genetic point of view, high genetic diversity enhances an organism's ability to respond to selective pressures, and could contribute to its long-term survival. There is evidence that populations with low genetic diversity tend to be less fit (e.g. wolf, Northern

elephant seal, humpback whale, Florida panther, cheetah; O'Brien 1994; also see Caro & Laurenson 1994). Seventy-seven percent of threatened species have been shown to exhibit lower genetic diversity than related non-endangered species (Frankham *et al.* 2004). Thus, it can be argued that the relatively high genetic variability exhibited in haplochromine species portends well for the species, and implies that genetic variability has been conserved in the Lake Kanyaboli assemblage.

The relatively high number of haplotypes private to Lake Kanyaboli (Fig. 2) suggests that, while Lake Kanyaboli haplochromines essentially belong to the Lake Victoria species flock, the lake harbours genetic diversity that has either (i) arisen *in situ*; (ii) gone extinct in Lake Victoria; or (iii) not been detected within the Lake Victoria haplochromines, despite the extensive study of Verheyen *et al.* (2003). Relatively high genetic variation, and the presence of mtDNA haplotypes restricted to Lake Kanyaboli, has also been found in the marbled lungfish *Protopterus aethiopicus* (Garner *et al.* 2006). Such observations support the hypothesis that peripheral waterbodies could have been important refugia during the late Pleistocene desiccation and therefore that such peripheral waterbodies could have played a role in the evolution and conservation of the genetic diversity of the ichthyofauna in the Lake Victoria region.

The significant F_{ST} values between pairs of species indicate high levels of genetic distinctiveness. This is significant from an evolutionary point of view. Seehausen *et al.* (1997) have hypothesized that, because of anthropogenic effects, eutrophication of Lake Victoria has led to the erosion of the mate recognition capability of the haplochromines, thereby reducing colour-based mate choice. The results of such a phenomenon would have been random mating, and the loss of genetic and species distinctiveness. That the genetic distinctiveness can be discerned among the Lake Kanyaboli haplochromines could be evidence of strong reproductive isolation among the species. Thus, Lake Kanyaboli haplochromines can be considered to represent 'pure' forms of the haplochromines.

Table 2. Population pairwise F_{ST} s (F_{ST} s = measure of the genetic distinctiveness between pairs of species)

	<i>X. phytophagus</i>	<i>A. nubila</i>	<i>L. maxillaris</i>	<i>A. alluaudi</i>	<i>P. m. victoriae</i>
<i>X. phytophagus</i>	–				
<i>A. nubila</i>	0.025 ^{ns}	–			
<i>L. maxillaris</i>	0.060*	0.12*	–		
<i>A. alluaudi</i>	0.96*	0.96*	0.97*	–	
<i>P. m. victoriae</i>	0.97*	0.98*	0.98*	0.97*	–

ns, not significant; * $P < 0.01$.

One proposed strategy to restore the cichlid populations in the Lake Victoria basin has been aquaculture and captive breeding (J. Maithya and J. Okeyo-Owuor, undated abstract). The success of such aquaculture ventures relies on identifying genetically pure and robust populations as a source. The finding of genetically robust haplochromine populations in Lake Kanyaboli indicates that the Lake Kanyaboli populations can be used as a source to restock other genetically depauperate lakes in the Lake Victoria region (Loiselle 1996). Genome-based studies are increasingly being considered as fundamental in aquaculture and conservation, if selective breeders can build on basic genetic research into mechanisms of disease resistance, and the control of growth (Kocher *et al.* 2005). The present study provides the first attempt to genetically characterize the haplochromine cichlids of Lake Kanyaboli. Thus, there is a need to genetically characterize other cichlid populations within the Lake Victoria satellite lakes, and to test their suitability for aquaculture. Among the tilapiines, populations of *O. esculentus* (Graham 1929), *O. leucostictus* (Trewavas 1983) and *O. variabilis* (Boulenger 1904) still thrive in Lake Kanyaboli and other Yala swamp lakes. One management implication of this study is that, in order to sustain and exploit this unique genetic resource, it is necessary to manage each Yala swamp lakes as distinct ecological entities, and to restrict any introduction of species, and human-induced interlake species movements. Tilapia (*O. niloticus*) cage farming is currently being attempted in Lake Kanyaboli. Such activities, which could be justifiable from another perspective, could adversely affect the genetic integrity of the naturally occurring tilapias through hybridization (G.F. Turner, pers. comm., 2007).

This study has indicated that Lake Kanyaboli could provide an opportunity not only for the conservation of species, but also of trophic and genetic diversity threatened by introductions of exotics, and other anthropogenic impacts in Lake Victoria. In this regard, Lake Kanyaboli is an important refugium to Lake Victoria haplochromines, and probably other cichlids. Lake Kanyaboli and similar satellite lakes should be accorded active management to minimize habitat loss and degradation, and species introduction which could compromise their genetic and ecological integrity. Because of the critical socioeconomic role that Lake Kanyaboli and the adjoining Yala swamps play in the lives of the local community (Abila 2002, 2005), it is strongly recommended that any conservation initiatives be community-based. Unfortunately, however, ongoing land-use changes, being done ostensibly to improve food security in this area, have greatly altered this wetland, and also is a major threat to the future survival of its biodiversity (Mwakubo *et al.* 2007).

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REFERENCES

- Abila R. (2002) Utilization and economic valuation of the Yala swamp wetland, Kenya. In: *Best Practices in Participatory Management* (ed. M. Gawler) pp. 96–104. Workshop Proceedings, 2nd International Conference on Wetlands and Development, Dakar, Senegal. Wetlands International. IUCN – WWF Publications no. 65 Wageningen, The Netherlands.
- Abila R. (2005) Biodiversity and sustainable management of a tropical wetland lake ecosystem: A case study of Lake Kanyaboli, Kenya. *FWU – Water Resour. Pub.* **3**, 1–11.
- Abila R., Barluenga M., Engelken J., Meyer A. & Salzburger W. (2004) Population structure and genetic diversity in a haplochromine cichlid of a satellite lake of Lake Victoria. *Mol. Ecol.* **13**, 2589–602.
- Aloo P. O. (2003) Biological diversity of the Yala Swamp lakes, with special emphasis on fish species composition, in relation to changes in the Lake Victoria Basin (Kenya): Threats and conservation measures. *Biodiversity Conservation* **12**, 905–20.
- Avise J. C. (1994) *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York.
- Birdlife International (2005) *Birdlife's Online World Bird Database: The Site for Bird Conservation*, Version 2.0. BirdLife International, Cambridge, UK.
- Bouton N., Witte F., van Alphen J. J. M., Schenk A. & Seehausen O. (1999) Local adaptations in populations of rock – Dwelling haplochromines (Pisces: Cichlidae) from southern Lake Victoria. *Proc. R. Soc. Lond.* **266**, 355–60.
- Bruford M. W., Hanotte O., Brookfield J. F. Y. & Burke T. (1998) Multilocus and single locus DNA fingerprinting. In: *Molecular Genetics Analysis of Populations: A Practical Approach* (ed. A. R. Hoelzel) pp. 287–336. Oxford University Press, Oxford, UK.

- Caro T. M. & Laurenson M. K. (1994) Ecological and genetic factors in conservation: A cautionary tale. *Science* **263**, 485–6.
- Frankham R., Ballou J. D. & Briscoe D. A. (2004) *A Primer of Conservation Genetics*. Cambridge University Press, New York.
- Garner S., Birt T. P., Mlewa C. M., Green J. M., Seifert A. & Friesen V. L. (2006) Genetic variation in the marbled lungfish *Protopterus aethiopicus* in Lake Victoria and introduction to Lake Baringo, Kenya. *J. Fish Biol.* **69** (Suppl. B), 189–99.
- Genner M. J., Nichols P., Carvalho G. R., Robinson R. L., Shaw P. W. & Turner G. F. (2007) Reproductive isolation among deep-water cichlid fishes of Lake Malawi. Differing in monochromatic male breeding dress. *Mol. Ecol.* **16**, 651–62.
- Greenwood P. H. (1981) *The Haplochromine Fishes of the East African Lakes*. Kraus International Publications, München, Germany.
- Hyslop E. J. (1980) Stomach contents analysis – A review of methods and their application. *J. Fish Biol.* **17**, 411–29.
- Kaufman L. S. & Ochumba P. (1993) Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in Northern Lake Victoria. *Conservation Biol.* **7**, 719–30.
- Kocher T. D., Fernald R., Hoffmann H. *et al.* (2005) Genome sequence of a cichlid fish: The Nile tilapia (*Oreochromis niloticus*, L.). Proposal to the JGI Community Sequencing Program. Genome Sequencing Consortium, University of New Hampshire. Available from URL: <http://hcg.unh.edu/cichlid/TilapiaCSP2005.pdf>
- Lande R. & Barrowclough G. F. (1987) Effective population size, genetic variation and their use in population management. In: *Viable Populations for Conservation* (ed. M. E. Soule) pp. 87–123. Cambridge University Press, New York.
- Lee W. J., Conroy J., Howell W. H. & Kocher T. D. (1995) Structure and evolution of teleost mitochondrial control regions. *J. Mol. Biol.* **40**, 1–13.
- Lesica P. & Allendorf F. W. (1995) When are peripheral populations viable for conservation? *Conserv. Biol.* **9**, 753–60.
- Loiselle P. V. (1996) 'Fulu' of the Yala Swamp. *Cichlid News* **5**, 3, 11–18.
- Maithya J. (1998) A survey of ichthyofauna of Lake Kanyaboli and other small water bodies in Kenya: Alternative refugia for endangered fish species. *Naga, The ICLARM Quarterly* **1**, 54–56.
- Mbabazi D., Ogutu-Ohwayo R., Wandera S. B. & Kizito Y. (2004) Fish species and trophic diversity of haplochromine cichlids in the Kyoga satellite lakes (Uganda). *Afr. J. Ecol.* **42**, 59–68.
- Meyer A., Morrissey J. M. & Scharl M. (1994) Recurrent origin of a sexually selected trait in Xiphophorus fishes inferred from a molecular phylogeny. *Nature* **368**, 539–42.
- Moritz C. (1994) Application of mtDNA analysis in conservation: A critical review. *Mol. Ecol.* **3**, 401–11.
- Mwakubo M. S., Ikiara M. M. & Abila R. (2007) Socio-economic and ecological determinants in wetland fisheries in the Yala Swamp. *Wetlands Ecol. Manage.* **15**, 521–8.
- Mwanja W. W., Armoudlian A. S., Wandera S. B. *et al.* (2001) The bounty of minor lakes: The role of small water bodies in evolution and conservation of fishes in the Lake Victoria Region, East Africa. *Hydrobiologia* **458**, 55–62.
- Namulemo G. (1998) Distribution, relative abundance, population structure and food of surviving haplochromine cichlids in littoral areas of Napoleon Gulf (Lake Victoria). MSc Thesis, Makerere University, Kampala, Uganda.
- O'Brien S. J. (1994) A role for molecular genetics in biological conservation. *Proc. Natl Acad. Sci. USA* **91**, 5748–55.
- Ogutu-Ohwayo R. (1990) The decline of the native fishes of Lakes Victoria and Kyoga (E. Africa) and the impact of introduced species, especially the Nile Perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Env. Biol. Fish* **27**, 81–96.
- van Oijen M. J. P. (1982) Ecological differentiation among the piscivorous haplochromine cichlids of Lake Victoria (East Africa). *Neth. J. Zool.* **32**, 336–63.
- Owino A. & Ryan P. (2007) Recent papyrus swamp habitat loss and conservation implications in western Kenya. *Wetlands Ecol. Manage* **15**, 1–12.
- Posada D. (1999) *COLLAPSE*, Version 1.1. Department of Zoology, Brigham Young University, Provo, Utah.
- Posada D. & Crandall K. A. (1998) Modeltest: Testing the model of DNA substitution. *Bioinformatics* **14**, 817–8.
- Raymond M. & Rousset F. (1995) GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. *J. Heredity* **86**, 248–9.
- Schneider S., Roessli D. & Excoffier L. (2000) *ARLEQUIN, Version 2.000: A Software for Population Genetic Data Analysis*. Genetics and Biometry Laboratory, University of Geneva, Switzerland. Available from URL: <http://www.anthro.unige.ch/arlequin>. Accessed 15 June 2006.
- Seehausen O. (2002) Explosive speciation rates and unusual species richness in haplochromine cichlid fishes: Effects of sexual selection. *Adv. Ecol. Res.* **31**, 237–74.

- Seehausen O., Alphen J. J. M. & Witte F. (1997) Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–11.
- Soule M. E. (1987) *Viable Populations for Conservation*. Cambridge University Press, New York.
- Strecker U. (2006) Characterization and cross-species amplification of microsatellite loci in a *Cyprinodon* species flock. *Mol. Ecol. Notes* **6**, 843–6.
- Sumaila U. R., Chuenpagdee R. & Vasconcellos M., eds. (2000) Proceedings of the INCO–DC International Workshop on Markets, Global Fisheries and Local Development. *ACP-EU Fish. Res. Rep.* **7**, 86–7.
- Swofford D. L. (2003) *PAUP** — *Phylogenetic Analyses Using Parsimony and Other Methods*, Version 4.0. Sinauer, Sunderland, Massachusetts.
- Verheyen E., Salzburger W., Snoeks J. & Meyer A. (2003) Origin of the superflock of cichlid fishes from lake Victoria, East Africa. *Science* **300**, 325–9.
- Weir B. S. & Cockerham C. C. (1984) Estimating F-statistics for the analysis of population structure. *Evolution* **38**, 1358–70.
- Wright S. (1978) *Evolution and the Genetics of Population, Vol. 4: Variability Within and Among Natural Populations*. University of Chicago Press, Chicago, Illinois.