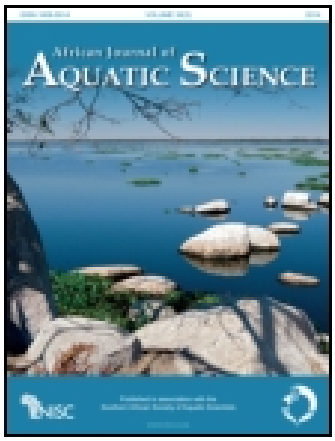

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Genetic diversity and gene flow in Clarias gariepinus from Lakes Victoria and Kanyaboli, Kenya

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Genetic diversity and gene flow in *Clarias gariepinus* from Lakes Victoria and Kanyaboli, Kenya

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The African catfish *Clarias gariepinus* is an important species in the rapidly expanding aquaculture industry in East Africa. Most Kenyan catfish farmers use stocks with unknown genetic characteristics, with uncertified seeds and inter-basin exchange of brood stocks threatening the genetic distinctness of wild populations. Using 346 base pairs of D-loop sequence variation, genetic diversity and gene flow between *C. gariepinus* populations from Lake Victoria and its satellite, Lake Kanyaboli, were explored. A total of 17 haplotypes were identified in 52 individuals sampled, with the two populations sharing four haplotypes, and one haplotype being the most frequent (50%) in both populations. Catfish from Lake Victoria showed marginally higher genetic variation compared to those from Lake Kanyaboli, reflected in the higher number of haplotypes, singletons, polymorphic sites and haplotype and nucleotide diversities. Yet neither population showed signs of significant loss of diversity compared to other wild populations of the species. *Clarias gariepinus* from Lakes Victoria and Kanyaboli clustered into one clade, showing low population structuring and with a between-population F_{ST} value of 0.026, which was not indicative of significant ($p \geq 0.05$) differentiation between the two lakes. Nevertheless, each population contained 60–64% of unique haplotypes. Inter-basin transfer of *Clarias* populations and human impact on Lake Kanyaboli should be controlled to conserve the unique *Clarias* genetic resources in the lake basin of Kenya.

Keywords: African catfish, conservation, genetic variation, haplotype, population differentiation

Introduction

The African catfish *Clarias gariepinus* (Burchell, 1822) is an important food resource for local livelihoods in Kenya. Larvae provide seeding material for pond-based aquaculture, and also serve as bait in the Lake Victoria Nile perch *Lates niloticus* longline fishery. In Kenya, *C. gariepinus* is second only to Nile tilapia *Oreochromis niloticus* as a preferred finfish species in aquaculture. In smallholder production systems, *C. gariepinus* is grown in polyculture with *O. niloticus* to control the prolific recruitment of *O. niloticus* (Musa et al. 2012). The current productivity of catfishes is potentially diminished by uncontrolled crossbreeding, while their future is threatened by overfishing (Aloo 2003), habitat degradation and the introduction of exotic species (Goudswaard and Witte 1997).

Crossbreeding can result from several actions. *Clarias* propagation at major hatcheries in Kenya is based on the indiscriminate collection of males from wild habitats, which are often from different drainage basins (JEB pers. obs.). These males are sacrificed for their pituitary glands for injection into brooders, a practice that leads to a shortage of male brood stock. This could lead to unintended mixing of populations and affect the genetic distinctness of catfish resources in the lake basin of Kenya. This is especially important because from 2011 to 2012 the number of catfish hatcheries in Kenya increased significantly from five to 29, through the government-funded fish farming enterprise productivity programme, to boost food security and incomes among communities. Out-crossing is also done intentionally by many hatcheries to restore genetic variation in stocks after having been maintained at a hatchery for many generations. In this regard, van der Bank et al. (1992) and Wachirachaikarn et al. (2009) confirmed that out-crossing of a hatchery population of *C. gariepinus* with an unrelated population increases genetic variation of the hatchery population. While this is beneficial in the short term, the introduction of new individuals to the hatchery may alter the local catfish gene pool and potentially result in out-breeding depression (Edmands 2006). Consequently, such brood stock may show lowered productivity in aquaculture, as seen for example in the lower survival of larval catfish. The genetic distinctness of wild populations may also be compromised by escapee

farmed catfish, or the human-mediated inter-basin transfer of catfish populations. Introgression of exotic catfish genetic material into native catfish genomes interrupts locally-adapted gene complexes, which compromises the evolutionary potential of the local population (Rhymer and Simberloff 1996).

Overutilisation is evident from the fact that a total of three million catfish baits are required daily by fishermen on the Kenyan side of Lake Victoria (National Frame Surveys Working Group 2006). The attractiveness of *C. gariepinus* fry as baits for *L. niloticus* is because of its higher survival on hooks, enabling the re-use of baits, and its artificial propagation at hatcheries reduces pressure on natural populations. At the price of about US$0.12 per bait, considerable opportunities exist for catfish farmers to improve their livelihoods. However, the large demand for catfish seeds in the lake basin is not met by hatchery or farm propagation of *Clarias*, forcing bait traders to collect larvae from the wild, a practice that is unsustainable.

As a strategy to conserve the native cichlids of the Lake Victoria Basin, Kaufman and Ochumba (1993) suggested the artificial propagation of *C. gariepinus* to provide baits, instead of using cichlids. Low survival of *C. gariepinus* larvae is a common problem in tropical aquaculture (de Graaf et al. 1995; Sulem et al. 2006). This has been attributed to poor diets and predators (Nyina-Wamwiza et al. 2010; Chepkirui-Boit et al. 2011), and poor water quality, occasioning a critical shortage of seeds and the underdevelopment of aquaculture (Sulem et al. 2006; Musa et al. 2012). However, the use of *C. gariepinus* brood stock of admixed ancestry may also be contributing to the lower survival of larvae. Average production of *C. gariepinus* may potentially increase if farmers use brooders of higher genetic diversity. Similarly, higher genetic diversity in *C. gariepinus* may be applied in a genetic improvement programme targeting commercially important traits such as the survival of larvae, growth rate or fecundity, to increase output by farmers.

Competition to *C. gariepinus* arose from the introduction of exotic Nile perch *L. niloticus* into Lake Victoria in the 1950s and 1960s, which caused the decline of indigenous catfish species through intense predation pressure (Goudswaard and Witte 1997). Although the population of the ecologically dominant *C. gariepinus* still exists in the lake, and has even recently shown signs of recovery (Njiru et al. 2002), smaller indigenous clariid species such as *Clarias liocephalus* and *Clarias alluaudi* were extirpated by *L. niloticus* predation (Goudswaard and Witte 1997), and are no longer landed on the Kenyan side of the lake. A reduction in the population size of a species is known to lower genetic variation through the bottleneck effect (Frankham 1996).

The current study investigated genetic variation, population structure and gene flow among conspecific populations of *C. gariepinus* from Lakes Victoria and Kanyaboli, Kenya. In light of the human activities that threaten indigenous fish species in the Lake Victoria Basin (Aloo 2003) and the decimation of clariid catfishes of Lake Victoria by *L. niloticus* predation (Goudswaard and Witte 1997), there is a need to document extant genetic variation in *C. gariepinus* to inform conservation measures and aquaculture ventures. Here, we report on the use of mitochondrial D-loop sequences to study variation in African catfish.

Materials and methods

Study sites and sample collection

Samples of *C. gariepinus* were collected from Lakes Kanyaboli (LKG; 00°04′30″ N, 34°09′36″ E) and Victoria (LVG – Kobala beach, Kendu Bay; 34°38′ E, 0°21′ S) (Figure 1). The sample sizes of the fish collected were 24 and 28 for the LVG and LKG populations, respectively. All the sampled fish were adults, with LVG samples ranging from 15.2 to 56.0 cm in length and 47.3 to 510.6 g in body weight. The LKG samples ranged from 28.5 to 56.7 cm in length, and 141 to 850 g in weight. Lake Kanyaboli (surface area 10.5 km^2) is a satellite of Lake Victoria (69 000 km^2) and is the most remote of that lake's three satellites (Mavuti 1992). Dense papyrus swamps and sand pits inhibit faunal exchange between the two lakes (Abila et al. 2008). No records of *L. niloticus* have been documented in Lake Kanyaboli, supporting the notion that the lake has been completely separated from Lake Victoria at least since the 1950s, when *L. niloticus* was first introduced into Lake Victoria. We also sampled individuals of *C. liocephalus* from

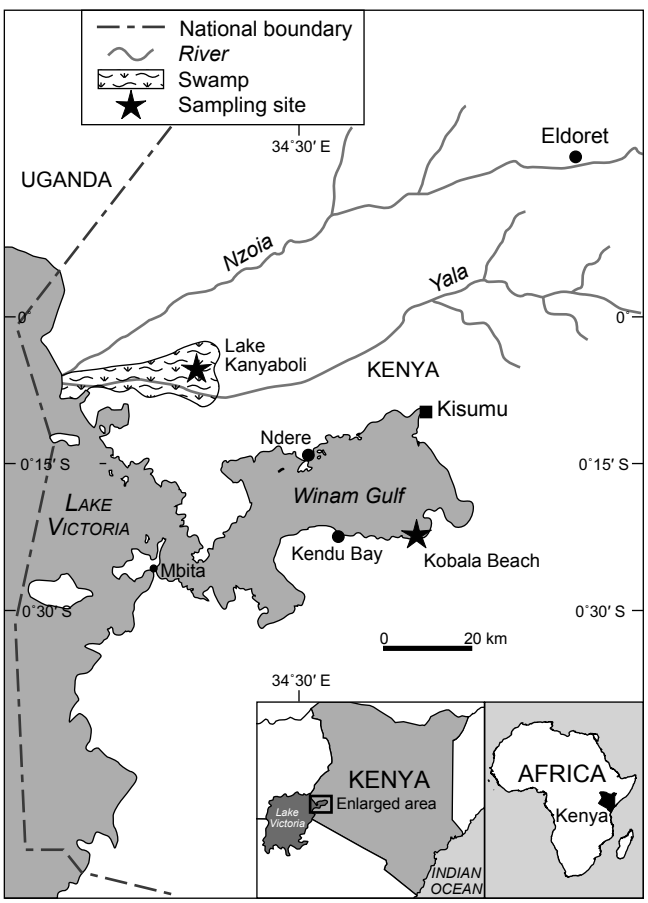

Figure 1: Map of lake basin of Kenya showing sampling sites for *Clarias gariepinus* in Lakes Victoria (Kobala beach) and Kanyaboli

Lake Kanyaboli, to serve as an outgroup for phylogenetic analysis. Fish samples were collected from both lakes by gillnetting. Identification keys for field studies (Witte and van Densen 1995) were used for species identification. Fin clips were collected as sources of DNA, and immediately preserved in 95% ethanol in clean cryovial tubes until laboratory genetic studies were done.

DNA extraction

Genomic DNA was extracted from approximately 25 mg of fin clip tissue, using the Invitrogen PureLink genomic DNA mini kit (cat. no. K1820-02), used according to the manufacturer's instructions. The purity and concentration of eluted DNA was determined by spectrophotometry using a Nanodrop Spectrophotometer 2000. The DNA was stored at −20 °C until required for further analysis.

PCR amplification

The mitochondrial D-loop was PCR amplified in a thermal cycler (ABI 9700) using the following primers: forward primer L16473 (5′-CTAAAAGCATCGGTCTTGTAATCC-3′); reverse primer H355 (5′-CCTGAAATGAGGAGGAACCAGATG-3′) (Nazia et al. 2010). The control region has a high rate of base substitution and changes in the genome are accumulated here faster, making the region suitable for addressing questions of population genetic variation (Meyer 1994). The PCR reactions were done using *AccuPower*® PCR premix (Bioneer Corporation), in a 20 µl volume containing 10 µM each of forward and reverse primers, and 50 ng DNA. The PCR conditions were as described by Nazia et al. (2010) and PCR success was confirmed by 1.6% agarose gel electrophoresis of PCR products. The PCR products were purified by ethanol precipitation (Uthice and Benzie 2003). Precipitated DNA was washed once with 70% ethanol, air-dried for 20 min, resuspended in 20 µl of distilled water and stored at −20 °C. The D-loop forward- and reverse primers yielded sequences of closely comparable quality and length, and the reverse primer H355 was randomly used to sequence the PCR product of the D-loop region. The BigDye terminator premix sequencing kit (cat. no. 4336911; Applied Biosystems | Life Technologies) was used for sequencing reactions, following the manufacturer's protocol. Products of sequence reaction were cleaned by precipitation in absolute alcohol, resuspended in Hi Di™ formamide, and BigDye terminator premix, and run on an Applied Biosystems 3730xl automated sequencer with a capillary length of 50 cm.

Data analysis

The DNA sequences were aligned, assembled and trimmed using BioEdit software v. 7.0.9 (Hall 2005). Duplicate haplotypes were identified using DNASP (version 5) (Librado and Rozas 2009). Genetic diversity within populations was determined as the number of distinct haplotypes, haplotype frequencies and nucleotide diversities, using DNASP and ARLEQUIN (v. 3.5) (Excoffier et al. 2005). The ARLEQUIN software was also used to determine genetic differentiation between groups, expressed as F_{ST} (Wright 1965). A maximum likelihood tree, with *C. liocephalus* as outgroup, was drawn using MEGA v. 6.0.6 (Tamura et al. 2007), with 1 000 bootstrap repeats. Modeltest 3.7 (Posada and Crandall 1998) was used to choose the most likely model of evolution for the *Clarias* mtDNA dataset. A minimum spanning network showing the relationship between haplotypes was drawn using Network 4.56, with a median-joining approach (Bandelt et al. 1999).

Results

After sequence alignment and trimming of ambiguous sequenced areas, a 346 base pair length of the D-loop region was consistently available for statistical analysis. A total of 17 distinct haplotypes based on 25 polymorphic sites were identified in 52 individuals of *C. gariepinus* sampled. These sequences were submitted to the GenBank database (accession numbers KC 594181–594232).

Genetic diversity

Nucleotide diversity was slightly higher in the Lake Victoria population than in the Lake Kanyaboli population (0.008 compared to 0.005) (Table 1). Similarly, LVG had slightly more haplotypes (11) than LKG (10), translating into a marginally higher haplotype diversity of 0.754 in LVG compared to LKG, which had 0.741. Four haplotypes (haplotypes 1, 4, 6 and 9) were shared between the two populations; with a total of 13 singletons out of the 17 haplotypes detected in the two populations of *C. gariepinus* (7 singletons in LVG and 6 in LKG).

Differentiation and phylogenetic relationships between populations

The F_{ST} value between the two *C. gariepinus* populations was 0.026, with an associated *p*-value that was not indicative of significant ($p \geq 0.05$) differentiation. Results from Modeltest showed that variation in the *C. gariepinus* sequences is best described by the Tamura–Nei model of evolution (Tamura and Nei 1993). In the phylogenetic tree constructed using the maximum likelihood approach with an outgroup (*C. liocephalus* [accession number KC 594233]), LKG and LVG haplotypes clustered into a single clade, and the outgroup clustered differently into its own clade (Figure 2). Haplotype 1, the most frequent, with a total of 26 (50%) individuals of LKG (14 samples) and LVG (12 samples), is the most centrally-located in the spanning network, from which all the other haplotypes radiate. This shows that

Table 1: Nucleotide (π) and haplotype (h) diversities and number of haplotypes, singletons and polymorphic sites in populations of *Clarias gariepinus* from Lakes Victoria (LVG) and Kanyaboli (LKG), Kenya. Data based on mitochondrial D-loop region sequence analyses (346 bp) of *C. gariepinus* populations

Population	LVG	LKG
Sample size	24	28
Nucleotide diversity (π)	0.008 ± 0.002	0.005 ± 0.001
Number of haplotypes	11	10
Number of singletons	7	6
Haplotype diversity (h)	0.754 ± 0.093	0.741 ± 0.064
Number of polymorphic sites	14	11

haplotype 1 is the ancestral variant, to which other haplotypes for both populations were connected with one to two substitutions or mutational steps (Figure 3) (Bandelt et al. 1999).

Discussion

Genetic variation

The level of genetic variation in the Lake Victoria population of *C. gariepinus* was marginally higher compared to the level in Lake Kanyaboli, with haplotype diversities of 0.754 and 0.741, respectively, and nucleotide diversities of 0.008 and 0.005, respectively. These haplotype diversity values were slightly lower than values of 0.904–0.941 reported for South African populations of *C. gariepinus* (Roodt-Wilding et al. 2010), but more closely comparable to the nucleotide diversity values of 0.006–0.022 reported by the latter

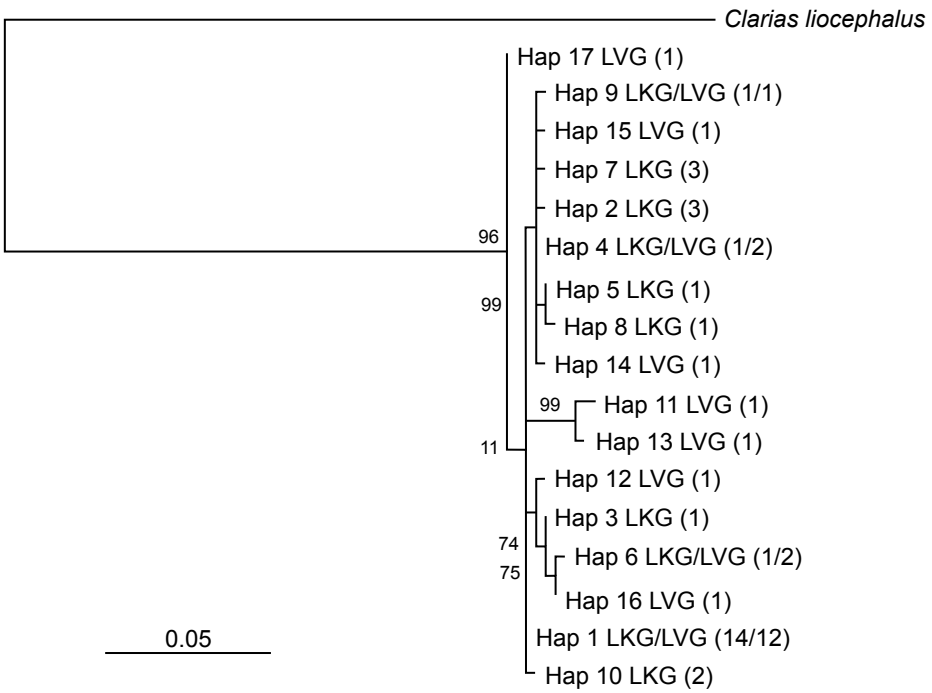

Figure 2: Maximum likelihood tree indicating relationships among mitochondrial D-loop haplotypes of *Clarias gariepinus* from Lakes Victoria (LVG) and Kanyaboli (LKG), with an individual of *C. liocephalus* as an outgroup. Numbers in parentheses represent the frequency of haplotype in samples of LVG and LKG. Numbers at nodes indicate confidence levels, based on 1 000 bootstrap iterations

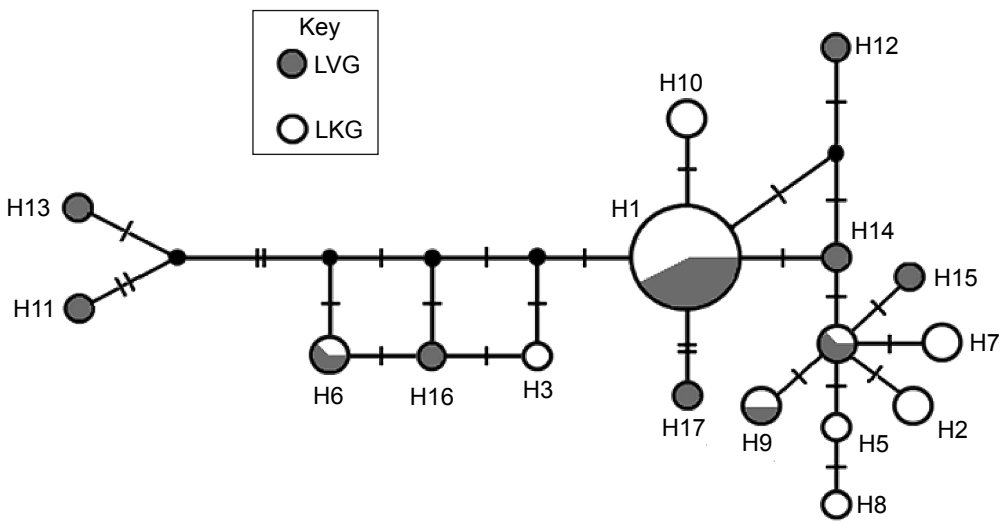

Figure 3: Minimum spanning network showing relationships between haplotypes of *Clarias gariepinus* from Lakes Victoria (LVG) and Kanyaboli (LKG). Circle size proportional to haplotype frequency. Circle fill indicates sampling locations. The shorter cross-lines indicate mutational steps, with a single cross-line denoting one mutational step

authors. Since the values for the South African populations were obtained from extensive river systems with many tributaries, whereas the Kenyan values are from panmictic populations in lakes, the real level of diversity in *C. gariepinus* from the Kenyan lakes and the South African populations are probably very similar. This suggests that representative levels of diversity in Lakes Victoria and Kanyaboli have been largely preserved, despite pressure resulting from exploitation and isolation.

Indigenous clariid catfishes of Lake Victoria, including *C. gariepinus*, suffered dramatic declines in population sizes in the 1980s and early 1990s due to predation from the exotic *L. niloticus* (Goudswaard and Witte 1997). Therefore, the LVG population could be expected to have a reduced level of genetic variation resulting from a possible population bottleneck. However, this study reports representative genetic variation for LVG. Retention of representative levels of high genetic diversity of the LVG population was probably boosted by a number of factors. The large size of the Lake Victoria water mass, estimated at 69 000 km^2 in surface area, implies that the LVG population is large, which would provide a buffer against any bottleneck, despite predation by *L. niloticus*. Furthermore, the temporary demographic dominance of *L. niloticus* in Lake Victoria coincided with substantial changes in ecology of the lake, due to changes in land use and intense human pressure in the catchment. Increased nutrient input favoured the expansion of water hyacinth *Eichhornia crassipes* (Muggide et al. 2005), which created anoxic conditions suitable to *C. gariepinus* but restrictive to *L. niloticus* (Njiru et al. 2002), leading to a decline in biomass of *L. niloticus* in the lake. The growth of exotic water hyacinth mats also provided feeding, breeding and nursery grounds for *C. gariepinus* and also reduced fishing pressure, as beach seining could not be carried out in hyacinth-mat dominated waters, leading to a resurgence of *C. gariepinus*. At the same time, the stock biomass of *L. niloticus* showed signs of decline (LVFRP 2001), due to overfishing (Kayanda et al. 2009) and a market demand for small-sized fish (Odada et al. 2004). This decline in the abundance of *L. niloticus* probably reduced predation pressure on *C. gariepinus* in the lake, leading to its demographic increase.

Although sampling for *C. gariepinus* in Lake Victoria was done from only one part of the lake, the resultant levels of genetic diversity would be representative of the entire population of *C. gariepinus* in the lake, since the larger water mass would harbour a larger population size, with relatively higher levels of genetic diversity. A similar study on cichlids of the Lake Victoria region sampled some cichlid fish species from a single location in the lake (Booton et al. 1999).

Lake Kanyaboli is recognised as an important refugium for the indigenous ichthyofauna of the Lake Victoria Basin (Abila et al. 2004, 2008; Angienda et al. 2011), and has not been invaded by *L. niloticus* (Aloo 2003). *Clarias gariepinus* in this lake has therefore not suffered a decline in population size induced by predation pressure from *L. niloticus*. However, the genetic diversity of *C. gariepinus* in this lake can be expected to be lower than that of Lake Victoria due to fragmentation and population size. At 10.5 km^2, Lake Kanyaboli is a fraction of the size of Lake Victoria, with a catfish population that may be expected to number proportionally less, and to harbour a somewhat lower diversity in *C. gariepinus* haplotypes. This, together with high fishing pressure (Aloo 2003), may have led to slightly lower genetic variation here than in the Lake Victoria population. Fishing pressure is reported to lower genetic variation in fish species (Hauser et al. 2002).

Genetic connectivity

The F_{ST} value between LKG and LVG suggested a lack of significant genetic differentiation between the two populations, with a value of 0.026 compared to F_{ST} values of 0.0786–0.901 reported among pairs of South African *C. gariepinus* (Roodt-Wilding et al. 2010) using the same gene region. High similarity between LKG and LVG was also supported by the maximum likelihood tree for haplotypes (Figure 2), in which haplotypes for LKG and LVG clustered together into a single clade, and the haplotype network. Freshwater fish species often display high levels of geographic structuring because of limited dispersal abilities (Gyllensten 1985) or the presence of barriers to dispersal in freshwater habitats. The absence of significant drift reported in this study could be attributed to the higher historical dispersal ability of the species, through the connection of the two lakes by the Yala swamp, anthropogenic translocation of fish samples across streams and drainage basins for aquaculture, and the trade in catfish baits for use in the *L. niloticus* longline fishery in Lake Victoria (see above). Clariid catfishes usually have high dispersal ability because, in nature in flooded conditions, they move to floodplains to breed during the rainy season. This movement to different habitats is also favoured by their ability to breathe atmospheric oxygen, so the species even survives in habitats with low dissolved oxygen. We hypothesise that this migratory behaviour, together with the connection of the two lakes by the Yala swamp, could be a source of the gene flow between the LKG and LVG populations. Furthermore, the movement of wild live baits from Lake Kanyaboli by traders for use in the Lake Victoria *L. niloticus* longline fishery could also be contributing to gene flow between the LKG and LVG populations. But this hypothesis requires testing. Nazia et al. (2010) reported high genetic diversity and a lack of population structuring in three populations of *C. macrocephalus* in Malaysia, and suggested human-mediated transfer of populations across basins as the possible reason for the lack of structuring.

Despite the apparent similarity between the LVG and LKG populations, based on traditional F_{ST} and various methods of tree-building, there is some evidence to suggest that contemporary gene-flow may be impeded. The presence of six singletons in LKG could be explained by the possibility that LKG has genetic diversity that has arisen *in situ*, or has gone extinct in Lake Victoria. Alternatively, it could represent sampling error, with these haplotypes having simply not been sampled in Lake Victoria. If indeed unique, these haplotypes support the hypothesis that Lake Kanyaboli is an important refugium for indigenous fish species of the Lake Victoria Basin.

The existence of mtDNA haplotypes restricted to the Lake Kanyaboli ichthyofauna, compared to that of Lake Victoria, has been reported in haplochromine cichlids (Abila et al.

2004, 2008) and the African lungfish *Protopterus aethiopicus* (Garner et al. 2006). In their study of population structure and genetic diversity of the haplochromine *Xystichromis phytophagus* from Lake Kanyaboli, Abila et al. (2004) noted the existence of eight private mtDNA control region haplotypes that were absent from the Lake Victoria population. These authors attributed this to the possibility of these haplotypes having either gone extinct from Lake Victoria due to predation pressure by *L. niloticus*, or having arisen *in situ*.

Conclusions

In the current study, various statistical measures support arguments both for and against a hypothesis of significant connectivity between the *C. gariepinus* populations of Lakes Victoria and Kanyaboli. We conclude that there may be temporal differences in the variation measured and that, while F_{ST} reflects historical gene flow between the two lakes (and a core of shared haplotypes), the presence of private haplotypes suggests some more recent genetic diversity among these populations, based on ongoing demographic and evolutionary processes. The presence of singletons may also indicate that the populations are undergoing local adaptations (Nazia et al. 2010), and these singletons could be exploited in selective breeding programmes to improve farmed production of the species in this country. There is a need to regulate the human-mediated transfer of *Clarias* baits or brood stock from these habitats to waterbodies in different basins, to prevent a mixing of populations that could destroy extant genetic diversity. Similarly, the ecological integrity of Lake Kanyaboli should be maintained by avoiding land use changes that reduce the papyrus vegetation on the lake.

Apart from reducing pressure on the exploitation of wild haplochromines as baits, whose artificial breeding techniques are not yet established, baits from the artificial propagation of *C. gariepinus* at hatcheries would also reduce fishing pressure on wild *C. gariepinus*, which is consistent with the need to conserve the indigenous fish species of the Lake Victoria Basin.

The presence of comparatively high levels of genetic diversity in the populations sampled can be exploited in aquaculture in two ways. First, the levels of diversity observed in this study can be used as benchmark to gauge levels of diversity in artificial populations, to prevent inbreeding. Furthermore, knowledge on the existence of diversity in natural populations can be used for future selection programmes, to increase output by farmers. The results of this study are only the first step towards achieving this goal, and more intensive research to link genetic diversity at adaptive loci to growth performance will be needed.

As suggested by Abila et al. (2008), the conservation of Lake Kanyaboli should be community-centred, because local communities derive their livelihood from the lake. However, human activities are currently threatening this important lake through reclamation for settlement and agriculture (Aloo 2003), and through increased fish production by means of cage culture. Therefore, the community should be sensitised to the importance of the lake to their livelihood and to the fish resources, so that they exploit these resources sustainably. It is equally important that the human-mediated introduction of invasive species, especially *L. niloticus*, or the alteration of the ecological conditions of the lake that would otherwise permit a natural invasion of *L. niloticus* into the lake from the neighbouring Lake Sare, should be avoided so as to safeguard the LKG population, as well as other fish species such as *C. lioicephalus* present in the lake.

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