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Research Article

Delineating African Catfish (*Clarias gariepinus* Burchell, 1822) Populations Through Molecular Genetic Approaches to Contribute to Aquaculture Performance in Uganda

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Aquaculture in Uganda is mainly anchored on two fish species: Nile tilapia (*Oreochromis niloticus*) and the Ugandan African catfish (*Clarias gariepinus*). The Ugandan *C. gariepinus* is popular among farmers nationwide because of its desirable traits, such as high growth rates, a broad array of trophic levels, and resistance to diseases and parasites. Nevertheless, the species' productivity is limited by insufficient molecular genetic data that can be used to inform selective breeding efforts. We fill this gap by sequencing the mtDNA D-loop of 192 *C. gariepinus* individuals from five major water bodies of Uganda. The results show that the Western Rift Valley lakes (Edward, George, and Albert) are more genetically diverse, with the least being the Central region lakes, particularly the Kyoga basin lakes. *Fst* values and the haplotype network group the *C. gariepinus* populations into two genetic clusters: the Western Rift Valley lakes (Albert, Edward, and George systems) and the Lakes Victoria and Kyoga systems. In particular, the current study reveals that Lakes Edward and George are likely a panmictic population. However, we noted genetic heterogeneity in L. Victoria, relatively indicating within-lake genetic structure. These results present the initial steps for genetically characterizing the Ugandan *C. gariepinus* populations and are key to guiding the use of the wild stocks in aquaculture for selective breeding programs to propel fish farming in Uganda.

Keywords: aquaculture; broodstocks; *Clarias gariepinus*; genetic diversity; mtDNA

1. Introduction

Aquaculture in Uganda began with the introduction of carp by the British in 1941 but faced huge challenges related to policy vagaries coupled with brutal government shifts [1]. Because of the past political insurgencies in the country, especially from the late 1970s to the 1980s, many economic sectors dwindled, including aquaculture as a subsector of agriculture [2]. As a consequence, aquaculture, which had begun with a vigorous extension of the farming system, faced reduced support and suffered particularly from a lack of quality and quantity of seed supply or limited technical guidance [3, 4].

With the current government's strategic interventions and support from development partners [5], the aquaculture subsector in Uganda has picked up gradually, with a present production rate of 138,558 metric tons [6]. This economic shift was propelled mainly by the Government of Uganda's specific interventions, such as the Plan for the Modernisation of Agriculture (PMA) and the Fisheries and Aquaculture Policy [4]. Presently, two freshwater fish species dominate the aquaculture industry in the country: Nile tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus;* Burchell, 1822) [5]. Nile tilapia's high growth rates, ease of fish seed production, and good taste make the species dominate aquaculture production systems across the country [1]. However, the major drawback of the Nile tilapia culture is its prolific breeding nature, resulting in strong size dimorphism with subsequent low performance under culture conditions. This increases management intensity and makes the culture less cost-effective [1, 7]. In this context, the *C. gariepinus* is sometimes a better option for farmers and is now the common fish species under aquaculture in Uganda [8].

The *C. gariepinus* is indigenous to Uganda and is distributed virtually in most of the country's water bodies, especially those associated with the wetlands [5]. The surge in the popularity of aquaculture activities involving *C. gariepinus* was propelled by market demand and the fish's attributes, including high growth rates, withstanding adverse environmental/water conditions, disease tolerance, and acceptance of a wide array of trophic levels (omnivorous) [8, 9]. Despite the promising cultivation of *C. gariepinus* in Uganda, the species is still constrained by various challenges, mainly the lack of quality fish seed [8, 10]. Although the seed quality is currently being addressed by pertinent research institutions and commercial farmers in Uganda, little or no data are available on the wild broodstock genetics in the country, which are usually the guiding principles for breeding programs. This is key, as it exposes the farmers to culture-unknown seed sources and exacerbates the subsequent poor performance of the culture systems, mostly reflected by poor growth rates coupled with fry and fingerling mortalities.

Previous studies in Uganda have indicated very low performance of the *C. gariepinus* culture, with fish often showing deformed fingerlings [8]. In captivity, this may be linked to a combination of different factors, including poor husbandry practices, diseases, unknown fish genetics, and parasites [11]. While many of these constraints can be counteracted by improving management practices, using genetically unknown broodstocks as a base for culture may contribute greatly to the poor performance of the species in captivity [12, 13]. The use of populations with low genetic diversity or even closely related individuals as the foundation for breeding may result in inbreeding depression and greatly compromise performance [14]. Furthermore, aquaculture practices are associated with founder effects that reduce genetic diversity [8], and this confounds further production and productivity as a function of poor seed. The challenge of low-quality seed coupled with high mortalities still prevails among many farmers, which may be attributed to poor genotypes (possibility of outbred or inbred individuals) associated with limited knowledge of the base populations.

It appears that most commercial farmers source their parental stocks from already genetically degenerated broodstocks of other farms/hatcheries or from natural water bodies without knowledge of the genetic traits [15]. Such practices, coupled with unregulated fish translocations, can result in a rapid reduction of the genetic quality of farmed fish [16]. Until recently, most studies on the *C. gariepinus* aquaculture in Uganda have focused on nutrition [10, 17, 18], health [19], and culture systems [20], with little information on the population genetics of the wild and cultured forms of this species, as well as differentiation patterns within and between populations and regions in the country [21]. Considering reports of the poor, uneven, and unpredictable performance of the species, in particular, at the fingerling stage, coupled with high farm-level losses [21], DNA-level stock characterization may play a pivotal role in improving the breeding and culture success of the *C. gariepinus* in Uganda.

Most efficient breeding technologies (both in plants and animals) entirely rely on molecular genetic tools [13]. This is because the most economically important traits, such as growth rates, disease resistance, and sex, among others, have a genetic component [13]. While in some countries, the idea of utilizing genetic markers in fish breeding has been in practice for decades (since the 1960s), in Uganda, the genetic approaches are generally limited. Recent genetic data on the Kenyan *C. gariepinus* populations indicate high extant genetic variation in natural populations compared to the farmed ones [14]. A similar or different situation could be in the Ugandan *C. gariepinus* populations, but the species traits based on molecular genetic studies are limited [8]. For example, the extent of fish performance below the farmers' expectations may be attributed to cryptic genetic differentiation of the species cultured.

In this study, we investigate the haplotypes of the mitochondrial DNA (mtDNA) D-loop control region as initial steps in characterizing the stock structure of *C. gariepinus* from the major lake sources for breeding in Uganda. We take advantage of mtDNA's high mutation rate, copy number, and supposed virtually neutral mode of evolution to evaluate intraspecific variation patterns in a fast and inexpensive way. Furthermore, mtDNA can demonstrate demographic effects such as variation in population size differentiation between species or populations [22]. The choice of D-loop, being the only noncoding region of the mitogenome, is associated with high variability, ensuring the retrieval of variation patterns at the population level [23]. Specifically, we determine genetic diversity within populations, investigate potential genetic structure, and use haplotype divergence to outline a hypothesis for potential taxonomic units to explain strain incompatibilities. The data in the current study, together with the previous attempt on the Ugandan *C. gariepinus* [24], form the first step to characterize the species population structure and the extent of genetic variability among the catfish populations in the country.

2. Materials and Methods

2.1. Sampling Strategy. The *C. gariepinus* fin clips were collected from the five major Ugandan Lakes: Edward, George, Albert, Victoria, and Kyoga, as well as the fish under captivity

at the Aquaculture Research and Development Centre, Kajjansi (ARDC) (Table 1; Figure 1). Lakes Albert, Edward, and George are located in the Western Rift Valley, while the Lake Kyoga basin and the studied part of Lake Victoria lie in central Uganda [25]. Depending on water body size, multiple locations were sampled to account for possible genetic heterogeneity within the ecosystems (Table 1; Figure 1). For instance, because of the complex nature of the Lake Kyoga basin, we sampled different satellite lakes, including the main Lake Kyoga, Kyoga Nile (also referred to as Victoria Nile as it stretches from L. Victoria to upper Murchison Falls through L. Kyoga), L. Kyoga Kwania, as well as L. Kyoga Nakuwa (Kwania and Nakuwa are satellite lakes in the Lake Kyoga basin). A single location of the sample collection represents Lake George, given its relatively smaller size (Figure 1). During the fieldwork, local fishermen were employed to collect samples using the recommended gillnets of mesh size 127 mm. The fieldwork was conducted between 2019 and 2021, and in total, 200 fin clips were collected and preserved in absolute ethanol contained in 2.0 mL tubes. The samples were later stored in a freezer at −21°C until genotyping at the Institute for Integrative Nature Conservation Research (INF)–BOKU University, Vienna, Austria. Sampling was conducted in collaboration and with authorization from the respective Ugandan authorities, and, therefore, no special permission or permits were required. Additionally, no special animal rights/welfare were observed during the fieldwork, as the fish were already dead when obtained from the local fishermen.

2.2. Genomic DNA Extraction and mtDNA Amplification. Genomic DNA was extracted with standard protocols using SDS-buffer magnetic beads (MagSi-DNA-MagnaMedics, Geleen, Netherlands) and a magnetic separator, SL-MagSep96 (Steinbrenner, Germany), as described in Tibihika et al. [26]. We amplified around 350 bp of the mtDNA D-loop control region using the primers 33_15,870 F 5′-AACTCCCAAAGCTAGGATTC and 33_16,382 R 5′-GAACCAGATGCCAGGAATA as described in [27]. The purified PCR products were then submitted for sequencing using the Sanger platform at the Genomics Service Unit at Ludwig Maximilian Universität, München, Germany. The raw reads were submitted to the Sequence Read Archive (SRA) database with the reference number PRJNA1162749.

2.3. Genetic Statistical Analysis. Sequence reads were visually inspected using the BioEdit program [28] and aligned/trimmed using the Geneious software Version 10.3 [29]. Sequence uncertainties were resolved through the visual inspection of chromatogram plots. The taxonomic identity of the sequences was confirmed using BLAST searches at the NCBI database (https://www.ncbi.nlm.nih.gov/BLAST/cgi). Genetic diversity depicted by haplotype diversity (Hd), Tajima's *D*, and nucleotide diversity across populations was determined using the DNASP program Version 5.10.01 [30]. Tajima's *D* test was key to investigating deviations to neutrality that might represent demographic changes such as population contraction (reduced) or expansion [31]. Population haplotype frequencies, number of shared haplotypes between the populations, and population differentiation (Fst) were calculated using the Arlequin program Version 3.11 [32]. To investigate the relationships between haplotypes that might reflect population structure, a median-joining network was constructed using the PopArt program Version 1.7 [33]. To estimate the evolutionary history and relationships between the *C. gariepinus* populations, a phylogeny was constructed using PhyML Version 3.0 based on maximum likelihood [34] using the online platform at https://www.atgc-montpellier.fr/. A published dataset of *C. gariepinus* from the Kenyan natural population [35] available in the GenBank (MF150204 to MF150238) was also included to evaluate further structure patterns. The optimal substitution model was chosen using AIC, and branch support was calculated based on 1000 bootstrap replicates. Up to two individuals per taxon of the other *Clarias* species with data publicly available were included as outgroups. The pairwise distance among the haplotype sequences was calculated using the HKY distance in PAUP* V4.0 [36].

3. Results

3.1. Sequence Success. Almost all samples produced a sequence resulting in a dataset of between 9 and 50 individuals per population: L. Albert (50), L. Edward (26), L. George (10), ARDC (10), L. Victoria (38), Kyoga (17), L. Kyoga–Nk (16), L. Kyoga–Nl, and L. Kyoga–Kw (9) (Table 2). The resulting alignment was composed of 347 bp and contained a total of 192 sequences, condensed to a total of 49 haplotypes and 346 sites.

3.2. Genetic Diversity. The number of haplotypes varied between 4 and 15, with L. Victoria indicating the highest value (15), followed by Lakes Edward and Albert, each with 14. In L. Kyoga, 13 haplotypes were recorded, while the lowest number was detected in Kyoga Nile and Kyoga Kwania, each with 4. The Hd ranged from 0.583 to 0.933, with the highest values indicated in L. George and ARDC, each with 0.9330, followed by L. Edward (0.920), and the least observed in Kyoga Kwania (Table 2). Similarly, the nucleotide diversity values were consistent with the Hd across the populations (Table 2). Despite not being significant ($p > 0.05$), Tajima's D was negative for lakes Albert, Edward, Victoria, Kyoga, Kyoga Nile, Kyoga Kwania, and Kyoga Nakuwa and positive for George and ARDC (Table 2).

3.3. Genetic Differentiation Between Populations. Fst values reflect the existence of two major groups (Table 3), separating the western Rift Valley lakes (George, Edward, and Albert) from the remaining populations of central Uganda (Victoria, Kyoga, and ARDC). Within each of these groups, Fst values were low (≤ 0.116) with the exception of Kyoga–Nl and ARDC (Fst = 0.314), as well as Kyoga–Nl and Victoria (Fst = 0.273), presenting high Fst values (Table 3). Higher Fst values (≥ 0.453) are found among water bodies of western and central Uganda. When we compared the *Fst* values between subpopulations or within populations, consistent results supporting a division between western and central

Table 1: Sample collection sources of different *Clarias gariepinus* populations in Uganda.

S. code	District	Landing site	Lake	Longitude	Latitude	Elevation (m)
VBK	Masaka	Bukakata	Victoria	S00 2730.4	E032 02663	1109
VNJ	Jinja	Njeru	V. Nile	N00 2622.0	E033 1125.5	1142
VMD	Busia	Maduwa	Victoria	N00 1300.5	E033 5707.7	1140
KNO	Palisa	Opeta	Kyoga–Nk	N01 1408.3	E033 2853.1	1023
KKN	Kiryandongo	Kabonyi	Kyoga–Nl	N01 4755.4	E032 1340.7	1042
KKD	Dokolo	Dalaja	Kyoga–Kw	N01 5238.3	E032 5758.8	1026
KNS	Amolator	Namasale	Kyoga	N01 2908.1	E032 3710.4	1038
ABC	Bulisa	Butiaba	Albert	N01 5024.5	E031 1937.7	1056
ABK	Kikuube	Buhuka	Albert	NO1 14 11.2	E030 4236.3	621
AN0	Kikuube	Ntoroko	Albert	N01 0435.6	E030 3404.5	640
AS0	Kikuube	Sebagaro	Albert	N01 3311.2	E030 5813.3	618
AWE	Bulisa	Wanseko	Albert	N02 1104.9	E031 2157.4	623
EKW	Kasese	Katwe	Edward	S00 1028.7	E029 4948.4	786
EKY	Kasese	Kayanja	Edward	S00 0446.1	E029 4443.9	787
ERS	Rukungiri	Rwenshama	Edward	S00 2109.3	E029 4917.2	932
GKH	Kasese	Kahendero	George	N00 0214.2	E030 0633.8	914
ARDC	Wakiso	ARDC	Fish ponds	N001319.3	E0323203.7	1142

Note: S = sample; V = Victoria; Nk = Nakuwa; Kw = Kwania; Nl = Nile; ARDC = Aquaculture Research and Development Centre Kajjansi; ABC = L. Albert Butiaba; ABK = L. Albert Buhuka; ANO = L. Albert Ntoroko; ASO = L. Albert Sebagaro; AWE = L. Albert Wanseko; EKW = Lake Edward Katwe; EKY = Lake Edward Kayanja; ERS = Lake Edward Rwenshama; GKH = L. George Kahendero; ARDC = Aquaculture Research and Development Centre, Kajjansi; VNJ = L. Victoria Njeru; VMD = L. Victoria Maduwa; VBK = L. Victoria Bukakata; KNS = L. Kyoga Namasale; KNO = L. Kyoga Opeta–Nakuwa; KKN = L. Kyoga Kabonyi–Nile; KKD = L. Kyoga Dalaja–Kwania.

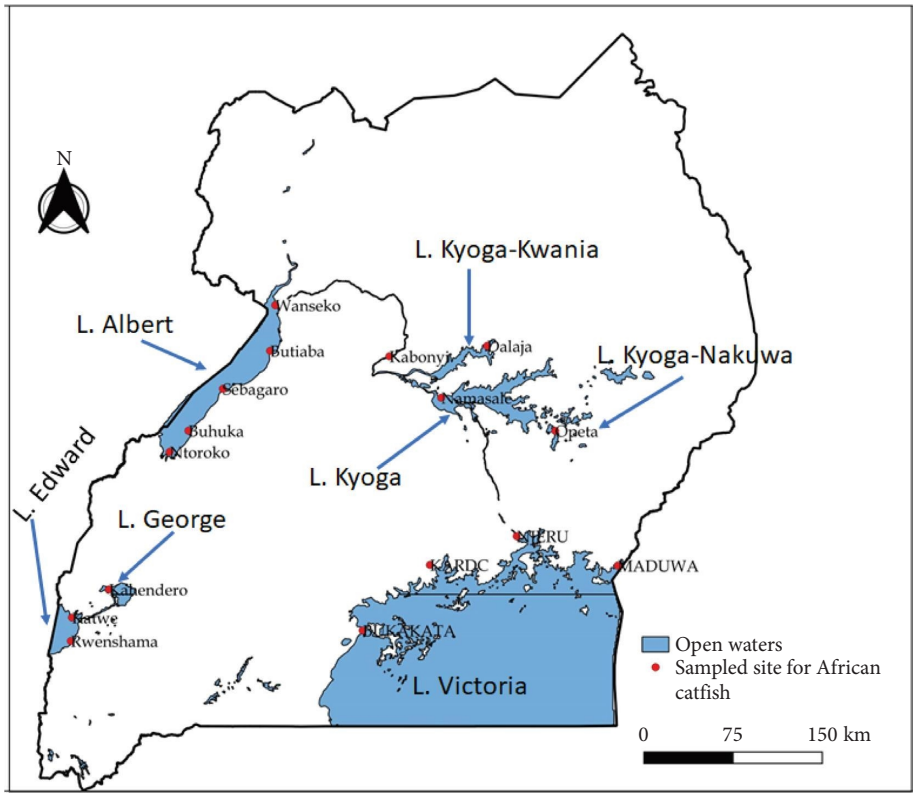

Figure 1: Locations of sample collection from the major lakes of Uganda.

populations were observed (Table 4). Within the Western Rift Valley Lakes, Edward's ERS population was the most differentiated, with values above 0.2 against Lake Albert's ABK, ANO, and AWE populations. Amongst the central lakes, genetic differentiation between the L. Kyoga subpopulations (KNS, KNO, KKN, and KKD) yielded very low *Fst* figures. Conversely, Lake Victoria's populations, VMD and VBK, showed relatively high Fst values, both between them and to other lakes in central Uganda. This contrasts with the L. Victoria subpopulation (VNJ) that revealed very low *Fst* values, especially to all L. Kyoga subpopulations (0.016; 0.032; 0.081; 0.009) (Table 4).

Table 2: Genetic diversity indices between *Clarias gariepinus* populations.

Genetic indices	Populations								
	Albert	Edward	George	ARDC	Victoria	Kyoga	Kyoga–Nk	Kyoga–Nl	Kyoga–Kw
No. of sequences	50	26	10	10	38	17	16	16	9
No. of haplotypes (h)	14	14	7	7	15	13	9	4	4
Haplotype diversity (Hd)	0.846	0.920	0.933	0.933	0.846	0.696	0.817	0.617	0.583
Nucleotide diversity (Pi)	0.019	0.014	0.021	0.013	0.011	0.007	0.010	0.004	0.004
Tajima's D	−0.479	−1.268	0.136	0.820	−0.449	−0.039	−0.509	−0.741	−0.341
Tajima's D *p* value	0.349	0.08	0.585	0.825	0.389	0.519	0.351	0.261	0.372

Table 3: Genetic differentiation between the *Clarias gariepinus* populations based on the heatmap of the *Fst* values on a red (low)/green (high) scale.

	Albert	Edward	George	ARDC	Victoria	Kyoga	Kyoga–Nk	Kyoga–Nl	Kyoga–Kw
Albert	—								
Edward	0.116	—							
George	0.108	0.046	—						
ARDC	0.555	0.652	0.453	—					
Victoria	0.61	0.683	0.525	0.119	—				
Kyoga	0.569	0.679	0.509	0.101	0.183	—			
Kyoga–Nk	0.564	0.668	0.484	0.09	0.091	−0.019	—		
Kyoga–Nl	0.585	0.716	0.578	0.314	0.273	0.047	0.05	—	
Kyoga–Kw	0.554	0.674	0.477	0.114	0.151	−0.068	−0.062	0.02	

Note: Nk = Nakuwa; Nl = Nile; Kw = Kwania.

Table 4: Genetic differentiation between the *C. gariepinus* subpopulations/within populations based on the heatmap of the *Fst* values.

	ABC	ABK	ANO	ASO	AWE	EKW	EKY	ERS	GKH	ARDC	VNJ	VMD	VBK	KNS	KNO	KKN	KKD
ABC	—																
ABK	−0.017	—															
ANO	−0.097	−0.042	—														
ASO	0.018	−0.007	−0.014	—													
AWE	0.034	0.196	0.181	0.030	—												
EKW	0.010	0.142	0.176	0.033	0.173	—											
EKY	0.121	0.171	0.175	−0.002	0.100	−0.060	—										
ERS	0.057	0.292	0.323	0.129	0.238	−0.009	0.071	—									
GKH	0.570	0.169	0.191	0.059	0.132	−0.021	−0.055	0.123	—								
ARDC	0.625	0.739	0.731	0.570	0.409	0.634	0.539	0.723	0.453	—							
VNJ	0.640	0.776	0.769	0.626	0.480	0.678	0.605	0.765	0.493	0.061	—						
VMD	0.672	0.776	0.771	0.638	0.499	0.677	0.608	0.759	0.500	0.176	0.230	—					
VBK	0.630	0.867	0.856	0.671	0.491	0.727	0.650	0.820	0.521	0.284	0.286	−0.005	—				
KNS	0.619	0.774	0.768	0.630	0.486	0.685	0.620	0.769	0.509	0.101	0.016	0.324	0.401	—			
KNO	0.698	0.765	0.759	0.619	0.476	0.670	0.598	0.757	0.484	0.090	−0.032	0.231	0.286	−0.019	—		
KKN	0.612	0.870	0.861	0.698	0.541	0.762	0.711	0.846	0.578	0.314	0.081	0.481	0.621	0.047	0.050	—	
KKD		0.821	0.809	0.613	0.430	0.688	0.604	0.790	0.477	0.114	−0.009	0.310	0.435	−0.068	−0.062	0.020	—

Note: ABC = L. Albert Butiaba; ABK = L. Albert Buhuka; ANO = L. Albert Ntoroko; ASO = L. Albert Sebagaro; AWE = L. Albert Wanseko; EKW = L. Edward Katwe; EKY = L. Edward Kayanja; ERS = L. Edward Rwenshama; GKH = L. George Kahendero; ARDC = Aquaculture Research and Development Centre, Kajjansi; VNJ = L. Victoria Njeru; VMD = L. Victoria Maduwa; VBK = L. Victoria Bukakata; KNS = L. Kyoga Namasale; KNO = L. Kyoga Opeta–Nakuwa; KKN = L. Kyoga Kabonyi–Nile; KKD = L. Kyoga Dalaja– Kwania.

3.4. Haplotype Network and Phylogeny Structure. The median-joining network was generally consistent with the genetic differentiation between western and central Uganda populations (Figure 2; Table S1). In the Western Rift Valley Lakes, most haplotypes are shared between George and Edward (Tables S1 and S2). Similarly, Lakes Kyoga and Victoria, as well as ARDC, demonstrated many shared haplotypes (Figures 2 and 3; Table S1). On the other hand, despite some haplotypes of *C. gariepinus* in L. Albert being shared with Edward and George, most haplotypes in the former lake appear conserved (Figures 2 and 3; Table S1). Additionally, of the two groups, only one haplotype found in Lake Albert proved to be highly divergent from all remaining catfish populations.

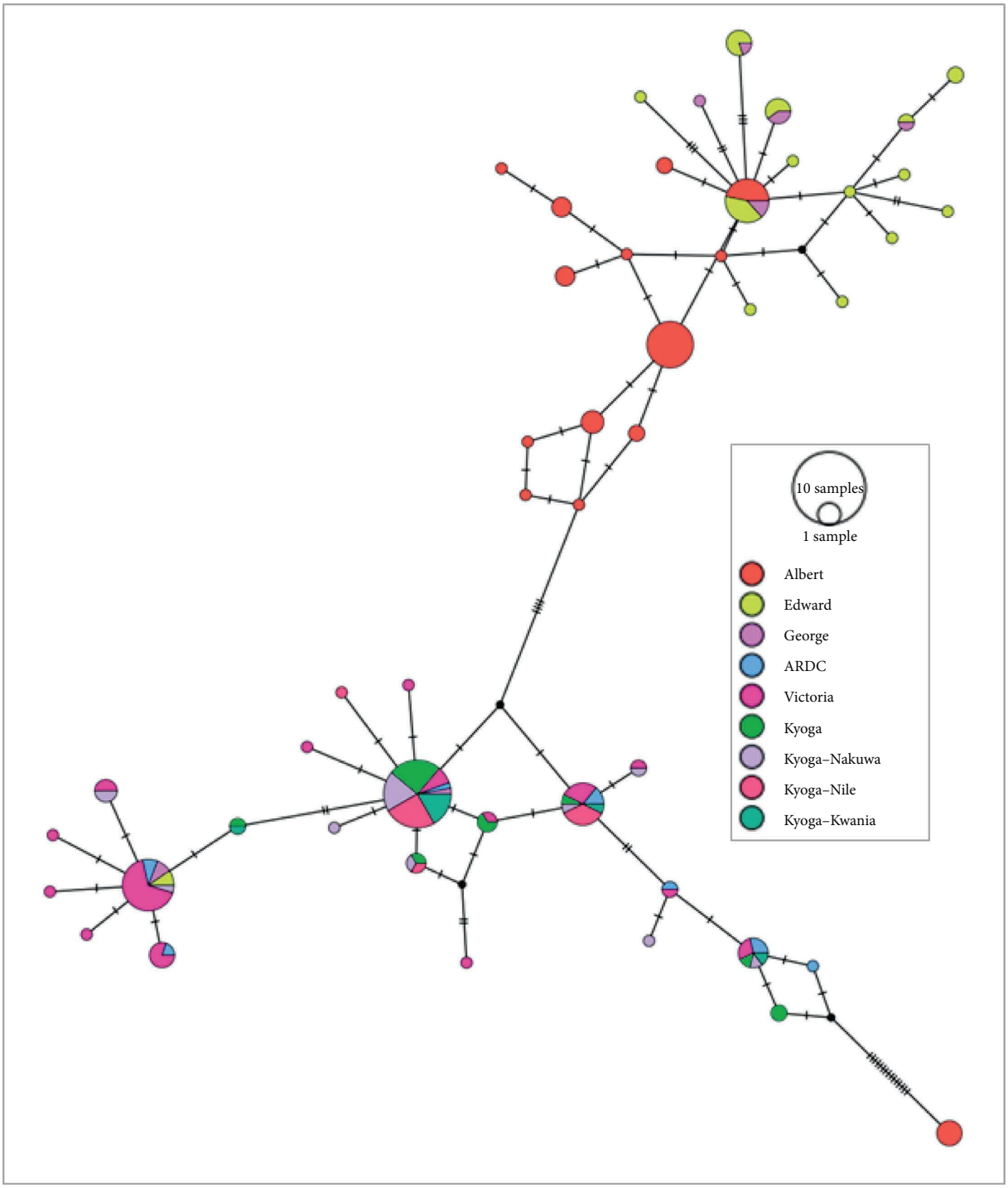

FIGURE 2: The median joining network depicting the haplotype relationships between the *Clarias gariepinus* populations. Each circle/ball represents a haplotype. The size of each circle is proportional to the number of individuals presenting the corresponding haplotype. The different colors represent the specific lakes/populations of *C. gariepinus*. The bars indicate mutational steps between haplotypes.

When the haplotype network was visualized per subpopulation, a consistent trend was observed (Figure 3; Table S2). However, under this approach, more intricate patterns were obtained. For instance, we noted that within L. Albert, subpopulation ABC shares fewer haplotypes with ABK and ANO than with the remaining subpopulations from this lake (Figure 3; Table S2). Within L. Edward, the subpopulations EKW and ERS shared more haplotypes (5 and 3, respectively) with L. George than with other subpopulations of the same lake (Figure 3; Table S2). We also noted that the *C. gariepinus* at ARDC (experimental fish farm) shares many haplotypes with samples from Lakes

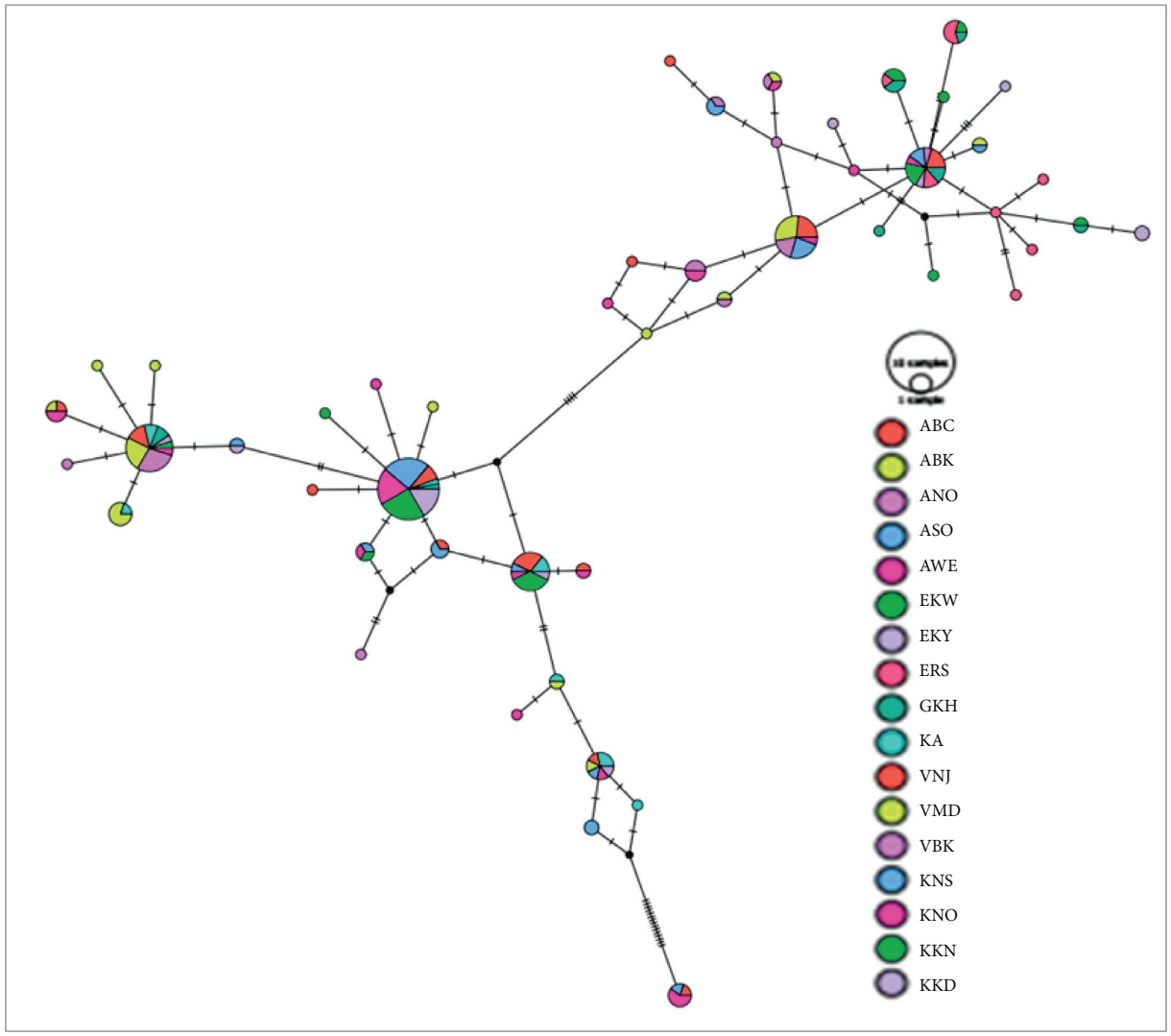

FIGURE 3: The median joining network depicting the haplotype relationships between the Clarias gariepinus sub-populations corresponding to Figure 2. The sub-populations are defined as landing sites/specific locations within the lakes.

Victoria and Kyoga, particularly VNJ, VMD (sub-populations of L. Victoria), and KNS, KNO, and KKD (populations of Kyoga lakes). While some subpopulations in L. Victoria share many haplotypes with the Kyoga Lakes (e.g., VNJ and KNS 4, VNJ and KNO 6, VNJ and KKD 3, as well as VMD and KNO 3), it was revealed that the other within L. Victoria subpopulations share an insignificant number of haplotypes (Figure 3; Table S2). On the other hand, all the Kyoga basin lakes appear to share haplotypes. Overall, the pairwise distance among haplotypes is low with a mean of 0.027 (Table 5). Nevertheless, one haplotype (hap 5) in L. Albert shows a higher level of divergence than all other haplotypes, with distances ranging between 0.057 and 0.101. This is only found in five individuals from Lake Albert.

The phylogenetic tree showed consistent results with the haplotype network in which a clear monophyletic group was composed of the Western Rift Valley Lakes (bootstrap = 93%), while the remaining lakes appeared paraphyletic (Figure 4). The Kenyan population is grouped mostly together with the individuals from the Victoria and Kyoga basins. The separation between the Western Rift Valley Lakes and the remaining water bodies was contradicted by the placement of a few individuals of Lakes George and Edward within the lineages that dominate in the Victoria and Kyoga drainage. Of note is the existence of a highly supported (98%) and divergent clade composed of four individuals from Lake Albert placed in the remaining populations' basal position. A similar pattern was found in some individuals from the Sagana and Athi River in Kenya that form sister groups to the remaining East African populations. These do not group with any of the other *Clarias* species included in the analysis.

They correspond to the phylogenetic analysis, with samples from Lake Albert forming the neighbor group of all remaining haplotypes. These stem from different sub-populations within Lake Albert, indicating the sympatric occurrence of differentiated groups or taxonomic units.

Table 5: Minimum and maximum pairwise distances (HKY model) between all the haplotypes.

Haplotype	Albert	Edward	George	V. Nile	Victoria	Kyoga	Kyoga–Nk	Kyoga–Nl	Kyoga–Kw	Minimum distance	Maximum distance
1	1									0.00339195	0.08469763
2	17									0.00339211	0.08474015
3	7	6	2							0.00339206	0.08882339
4	1									0.00339229	0.07668458
5	5									0.05711912	0.10140495
6	3									0.00339217	0.08883885
7	2									0.00339206	0.0929443
8	1									0.00339198	0.07663978
9	2									0.00339206	0.08066888
10	4									0.00339203	0.08066888
11	1									0.00339217	0.08475446
12	3									0.00339226	0.08072034
13	1									0.00339211	0.08883885
14	1									0.00339195	0.08063149
15		1	1							0.0033922	0.08887171
16		3	2							0.00339206	0.08471291
17		1								0.00339211	0.0929781
18		4	1							0.0102604	0.10140495
19		1								0.00679122	0.08440637
20		2	2	2	11		1			0.00339204	0.06872446
21		2								0.00339232	0.08479969
22		1								0.00339217	0.09299586
23		1								0.01025985	0.10135943
24		1								0.00681189	0.08471291
25		1								0.00339211	0.08066888
26		1								0.00339211	0.08882339
27		1								0.00339211	0.08474015
28			1							0.00679314	0.09631018
29			1		3	9	6	9	6	0.00339212	0.06482493
30				1	1	1	1		1	0.0033922	0.06096808
32					4					0.00339212	0.07267523
33				4		1	1	5	1	0.00339228	0.07270487
34					1		1			0.00339228	0.06484749
35				1			1			0.00339233	0.06876547
36				1						0.00339216	0.0609599
37				1		2				0.0033922	0.06875008
38				1	1		2			0.00339208	0.06481262
39					1					0.00339216	0.06873917
40					1					0.00339212	0.06482493
41					1					0.00339204	0.0726465
42					1					0.01026051	0.08067552
43					1					0.00339204	0.0726465
44						2				0.0033922	0.05711912
45						1			1	0.00339208	0.06481262
46						1	1	1		0.00339216	0.06873917
47							1			0.00339212	0.06872446
48								1		0.00339216	0.06873917

Note: Information on how many individuals per population share each haplotype is also added.

4. Discussion

As one of the main farmed species contributing to the rapidly growing aquaculture industry, there is a strong demand for improved brood stock and fish seed for the *C. gariepinus* in Uganda. The current poor performance of the species under captivity may result from unknown broodstocks for seed production and selective breeding programs. The data presented here form a first step in characterizing the Ugandan *C. gariepinus* to generate insights for the precise recruitment of the species into aquaculture for breeding, with efforts focused on enhancing the production and productivity of the sector.

4.1. Genetic Diversity. The current investigation revealed higher genetic diversity in the Western Rift Valley lakes of Albert, Edward, and George, and the least in the Kyoga basin lakes. Although L. Victoria indicated a relatively higher number of haplotypes, the other genetic indices generally

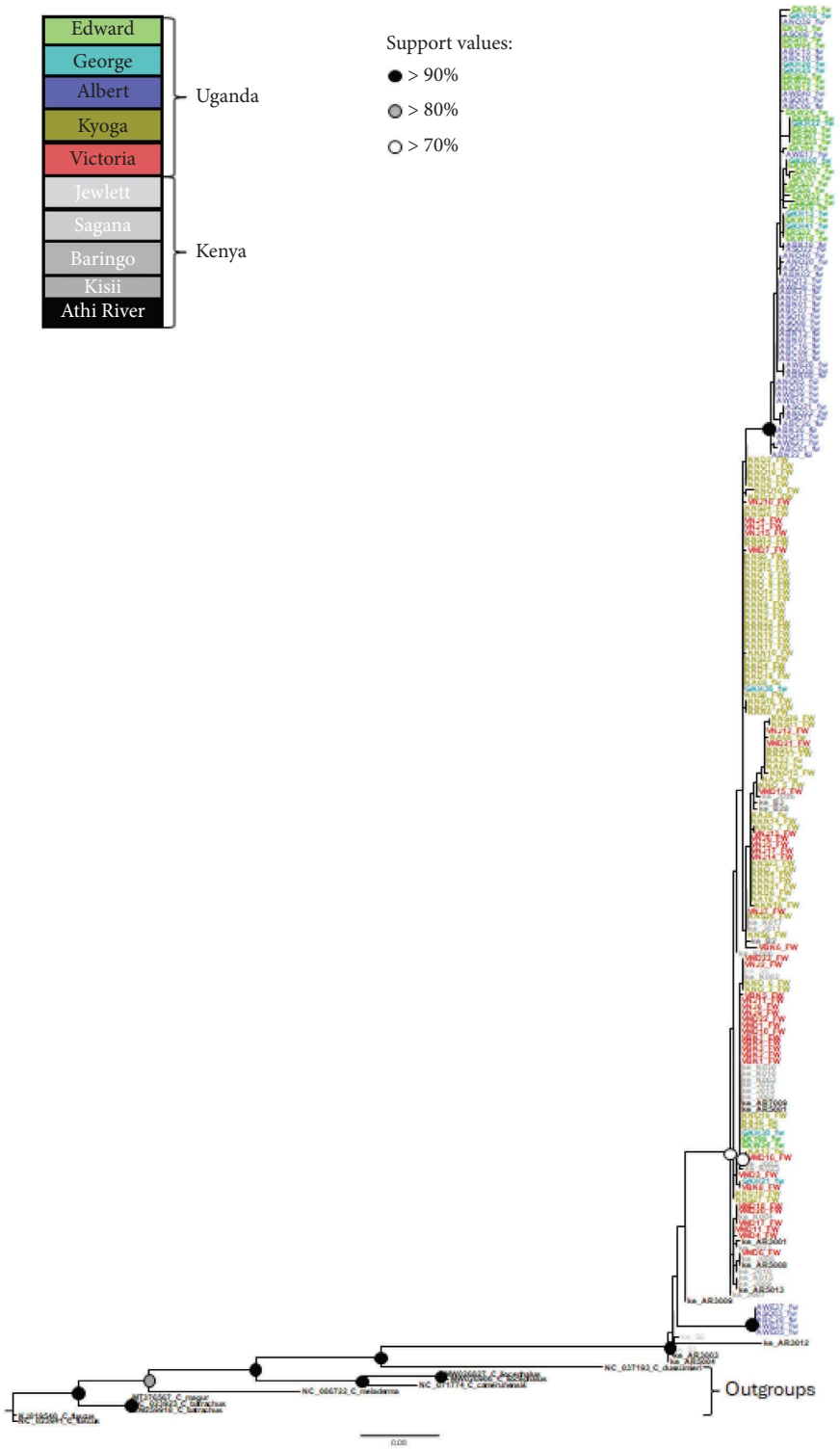

FIGURE 4: Maximum likelihood tree of the *Clarias gariepinus* populations. Sample labels are color-coded based on the water body of origin, while circles correspond to bootstrap branch support values above 70%.

showed low values. Interestingly, although L. George and ARDC are presented as among the genetically diverse populations, on the contrary, these groups indicated higher values of Tajima's D (but not significant), which may suggest indicators of recently contracted populations. On the other hand, the low genetically diverse populations of the Kyoga basin indicated lower Tajima's D values ($D < 0$), suggesting recent expansion. However, it is important to note that Tajima's D results were all insignificant despite varying values among the populations. The Tajima's D results show

indicators of recent population contraction and expansion among the Uganda *C. gariepinus* populations. These indicators, specifically the population contraction, may suggest some underlying pressures such as anthropogenic threats (e.g., overfishing) or even natural phenomena such as climate change. Climate change may influence a rise in water temperatures with a subsequent decline in fish biodiversity and related population contraction [37].

The relatively low genetic diversity observed in some *C. gariepinus* populations, particularly the Kyoga basin lakes, might be associated with anthropogenic activities and other ecological factors. Anthropogenic activities such as overfishing have been widely reported in the L. Victoria basin, including the Kyoga systems [38–40]. Usually, as the fishing effort intensifies, the fish stocks may be reduced with subsequent loss of alleles and the effective population size [41, 42]. Despite the prevalence of several other factors that can be detrimental to fish stocks, such as habitat loss, climate change, water pollution, predation pressure from Nile perch, and so on, the low genetic diversity in the Kyoga basin lakes may be a function of overexploitation with potential subsequent bottlenecks of the species, which would support the positive Tajima's D values. Fish stocks, particularly the native species in Lakes Victoria and Kyoga, have reduced significantly over the last 3 decades due to the combined effects of fish introductions and overfishing [40]. Most importantly, the stocks of *C. gariepinus* reduced dramatically during the surge of the introduced voracious predator, Nile perch (*Lates niloticus*), in the 1980s [43]. For instance, in the deeper water bodies where Nile perch densities were dominant, *C. gariepinus* and other catfish, especially the juveniles, vanished as a consequence of Nile perch predation [43]. On the other hand, the observed high genetic diversity of the ARDC population, which is expected, may be elucidated from the potential effects of multiple stockings for breeding purposes at the institution. This corresponds to other reports that show higher genetic variation among the farmed fish than in the natural populations [44, 45] and attribute this to the regular introduction of individuals from natural populations into the farms or from other farms [46]. Since ARDC handles different aspects of fish breeding, it is expected that multiple introductions of individuals from natural populations could be prevalent, and this brings together various alleles from different sources into one gene pool, which may elucidate the current results. On the other hand, the observed high genetic diversity in Lakes George and Edward may be linked to generally less overexploited fish stocks in these systems compared to the other lakes. Lakes George and Edward are located in the highly protected wildlife area, Queen Elizabeth National Park, by the Uganda Wildlife Authority (UWA). It is thus likely that the observed high genetic diversity of the *C. gariepinus* populations in these water bodies may be associated with minimal perturbations from destructive anthropogenic activities such as overfishing. This explanation can be supported by recent studies that have reported high fish yields from the protected areas of the Lakes Edward–George system compared to the unprotected areas [47, 48].

4.2. Genetic Differentiation and Haplotype Network/Phylogeny Structure Between Populations. The genetic differentiation results generally revealed significant population isolation congruent with the geographical distribution of the *C. gariepinus* species in Uganda. One group is composed of the western Rift Valley Lakes, while the second is the water bodies located in the central part of the country. These results are consistent with the findings of Ojiambo [24], who indicates two phylogenetic groups between the western Rift Valley Lakes (Albertine lakes) and the central part of the country (Victoria basin). Overall, within each group, there is a water flow interconnectivity, so these results are not surprising. Evidence of this is the high genetic analogies found between the *C. gariepinus* populations in Lakes George and Edward. This genetic similarity may be the function of the geographically close interconnection between these systems that allows easy and continuous gene flow in the species [49]. These results are consistent with the findings of Tibihika et al. [50] and Tibihika et al. [51], who equally found no genetic structure of Nile tilapia (*O. niloticus*) populations in Lakes George and Edward and attributed this to the continuous gene flow between the populations as a consequence of adjacent water interconnectivity. Lakes George and Edward are interlinked via a river-like large mass of water body called the Kazinga Channel [49, 52, 53]. The fact that the channel covers a short distance (less than 7 km) and the water is slow-moving makes it easy for fish movement and thus enhances genetic contact. The high genetic interface among the *C. gariepinus* stocks in the Edward–George systems is particularly likely to be more intense in the rainy season when *C. gariepinus* are breeding in inundated areas [54]. Contrary to what was found in *O. niloticus* populations [50, 51], the *C. gariepinus* population of L. Albert seems to be more similar to the L. Edward–George system than to the remaining water bodies in Uganda. This result may be attributed to the water interconnectivity through the Semliki River. The Edward–George basin receives a significant influx of water from the Rwenzori mountains, from which the outflow from these lakes forms the Semliki River that discharges into L. Albert [25]. Here, this water interchange may propel the continuous gene flow of the *C. gariepinus* populations between these systems, particularly during the rainy seasons/floods, when the fish is breeding. These findings further show the importance of the Rift Valley in shaping the genetic structure of the Ugandan *C. gariepinus* populations.

Similarly, water connectivity and interchange may explain the genetic similarity between the L. Kyoga basin and L. Victoria. Over several decades, the water levels in the L. Kyoga Basin and L. Victoria have been on the rise concomitantly with surging temperatures [55]. The Victoria Nile River, which connects these water bodies (Victoria to Kyoga Basin), coupled with floodplains, may trigger the interbreeding of the *C. gariepinus* populations in these systems, which expounds the genetic similarity through gene flow. It is important to note that the reproduction and fecundity of *C. gariepinus* are triggered seasonally, with peak spawning coinciding with rainy periods [56]. Being a shallow lake, the Kyoga basin and its neighbor, L. Victoria, through

the Victoria Nile, are generally vulnerable to floods, and this may continuously stimulate the gene flow between the *C. gariepinus* stocks in these systems. In general, the observed two genetic clusters of the Lakes Edward–George–Albert and Victoria–Kyoga systems are a result of shared ancestry resulting from current and historical connectivity of the rivers. On the other hand, the genetic similarity between ARDC and some populations in L. Victoria and Kyoga may be associated with the breeding programs at the institution. In this context, the L. Victoria and Kyoga basins may suggest the origin of the *C. gariepinus* broodstocks for breeding at ARDC. Our results further indicated genetic heterogeneity of *C. gariepinus* in L. Victoria, with one subpopulation (VNJ) genetically divergent but closely related to the L. Kyoga subpopulations. It appears that the genetic divergence of the *C. gariepinus* in L. Victoria may be linked to multiple introductions into the lake through anthropogenic activities. This may, particularly, be through indirect aspects such as escapees from the various hatcheries and farms around the lake, as reported by Mwanja et al. [15]. Several hatcheries are either located within the periphery or near river bodies draining into the lakes [57]. With poor management practices among these fish farms, it is likely that at some point the fish fingerlings may find their way into the natural water bodies, thus propelling gene flow between populations. Additionally, the use of live *C. gariepinus* fingerlings as bait for Nile perch in Lakes Victoria and Kyoga may also result in some escapees into the lakes. The establishment of the alien stocks in L. Victoria may delineate the observed genetic heterogeneity. On the other hand, the fact that L. Victoria is a vast water body implies that the gene flow between fish populations within the system might be limited, which can subsequently induce genetic structure. Therefore, the lack of shared haplotypes in some subpopulations of L. Victoria may be an indicator of barriers to, such as rocky islands and aquatic weeds, within the same lake. The presence of population-specific haplotypes indicates that this phenomenon might not be restricted to Lake Victoria.

Our data suggest the existence of an independent species in Lake Albert, opening the discussion of insufficient taxonomic circumscription of *C. gariepinus*. This conclusion is supported by five individuals from this lake showing a highly divergent haplotype with genetic distances ranging from 5% to 10% to the remaining haplotypes. This haplotype forms a sister lineage to all remaining Ugandan haplotypes in the phylogenetic analysis. The observed degree of nucleotide divergence is in line with the reported interspecific comparisons in the D-loop (8.3%–14.3%). Being a widely distributed species, the genetic divergence patterns of the *C. gariepinus* have not been comprehensively studied across its distribution ranges; thus, it is not surprising about the cryptic speciation pattern indicators. Specifically for L. Albert, if the haplotypes are not part of the same gene pool, this can be interpreted as the sympatric distribution of different cryptic species. The occurrence of the western Rift Valley haplotypes in L. Victoria would, in this case, be explainable by translocation events, effected by anthropogenic activities through aquaculture practices [58]. Regardless of the taxonomic status of individuals characterized by the two haplotype groups, the strong divergence between them might have led to some extent of reproductive isolation, also below the species level.

The high number of diverged haplotypes indicates that the strategy to maximize diversity by including different localities in breeding by farmers may rather increase the probability of incompatible, ecologically or geographically differentiated strains. If the base populations derived from such material are further used for breeding or fry production, chances of deformations at farms can be explained by the segregation and accumulation of maladapted alleles due to recombination. A closer investigation of the material using codominant nuclear markers is ongoing to determine the level of differentiation and to define compatible strains.

5. Conclusions and Recommendations

The current study presents novel molecular genetic results of *C. gariepinus* in Uganda. The findings show that the *C. gariepinus* in the major water bodies of Uganda are divided into two groups: the western Rift Valley group and the central Uganda major lakes, the Albert–Edward–George system, and the Victoria–Kyoga basin system, respectively. These genetic clusters might have been propelled by water body connectivity and anthropogenic activities. Ideally, all the populations may be included in the selective breeding programs. In this context, two sources for the *C. gariepinus* broodstocks may be the Edward–George–Albert and Victoria–Kyoga lakes. More separate populations for breeding may be sourced from within L. Victoria, as indicated by the genetic heterogeneity in the system. Studying many subpopulations in L. Victoria might yield vital information required for management and aquaculture practices. We recommend further extensive studies using more polymorphic nuclear genetic markers such as single sequence repeats (SSRs) to gain more insights into the genetic structure of *C. gariepinus* in Uganda. Furthermore, the existence of a potential cryptic species within L. Albert stresses the need for the implementation of molecular tools able to differentiate them in monitoring programs for better guiding farmers' breeding practices.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. *(Supporting Information)*

Table S1: Illustration of shared haplotypes between African catfish populations.

Table S2: Illustration of shared haplotypes between African catfish subpopulations.

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