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Demographic history, genetic connectivity, and conservation implications for the African bonytongue, *Heterotis niloticus p*opulations in West Africa

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Demographic History, Genetic Connectivity, and Conservation Implications for the African Bonytongue, *Heterotis niloticus* Populations in West Africa

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Abstract

The African bonytongue*, Heterotis niloticus,* is a commercially important freshwater fish that occurs naturally in the major rivers and basins of West Africa. In this study, we examined the demographic history of *H. niloticus* from inland waters in West Africa, four in Nigeria and 11 in Benin. The aim was to identify the genetic groups (populations) within these locations, assess their genetic connectivity, and infer ancestral lineages within these groups. Our findings showed that the fifteen locations sampled represent four genetic groups, as revealed by multivariate and Bayesian genetic clustering methods. These groups are Kainji Lake, Malanville, Southern Benin, and Southern Nigeria. Based on this grouping, we observed a north-to-south divergence pattern among these populations based on evolutionary model selection with Approximate Bayesian Computation (ABC). The northern groups (Kainji and Malanville) were ancestral lineages, whereas the southern groups, from Nigeria and Benin, are genetically closer with a more recent divergence. Also, we found that the population from Kainji Lake had the largest effective population size and genetic diversity estimate, while Malanville had the lowest effective population size and genetic diversity estimate. The study concluded that populations from Southern Nigeria and Southern Benin represent more connected populations, while the northern populations are genetically distinct. Evidence of bottlenecks and genetic contraction was indicated in some of the populations. These findings point to the need for management and conservation efforts that both acknowledge such demographic and genetic divergence to improve the chances of long-term use and conservation of this economically important species.

Keywords

Divergence time, Effective population size, Arapaimidae, West Africa

Introduction

Freshwater ecosystems in West Africa are among the most biodiverse but also the most threatened globally (Darwall *et al.,* 2011). Anthropogenic pressures such as habitat modification, overfishing, and pollution, combined with natural processes like river fragmentation and climatic fluctuations, have changed the connectivity of aquatic habitats (Darwall *et al.,* 2011; Chen *et al.*, 2023). Over the past few decades, these anthropogenic pressures have significantly impacted river systems, leading to a decline in migratory fish populations (Ferreira *et al.*, 2016). Additionally, threats to migratory fish populations in Nigeria, as in other parts of the world, include agricultural and industrial activities, deforestation, river flow obstructions, introduced species, and overfishing (Ikomi *et al.*, 2014; Arojojoye *et al.*, 2018; Adelakun *et al.*, 2019). Notably, the damming of rivers for hydroelectric power and other uses disrupts the natural migration pathways of fish, resulting in restricted gene flow and population isolation (Vrijenhoek, 1998). Such restrictions in gene flow promote inbreeding and reduce genetic diversity, thereby threatening fishery productivity and the long-term sustainability of populations (Agostinho *et al.*, 2003; Hoeinghaus *et al.*, 2009)**.** Understanding the historical demographic processes and genetic connectivity of fish populations is critical for determining population units, which is relevant for making management and conservation plans. This plays a significant role in local and regional fisheries and livelihoods.

Heterotis niloticus is a freshwater fish of the family Arapaimidae (Ferraris, 2003). It is native to Africa with a geographic distribution that includes the large rivers and lakes of the Nilo Sudanese region, Nile, Niger, Gambia, Oueme, Benoue, Senegal, and Lake Chad (Levêque *et al*., 1990; Li and Wilson, 1996; Mbega, 2004; Adite *et al.,* 2005). This species has been successfully introduced as a fisheries resource in many rivers in Africa, such as the Nyong and Sanaga in South Cameroon, the Ubangui River in the Central African Republic, Ogowe (Gabon), Madagascar, Lake Kossou and Ayame in the Ivory Coast and Congo basins. Commonly called the African bonytongue, the species is widely exploited by fisheries in several parts of Africa, with the greatest harvest occurring in Nigeria (FAO, 2020). Previous genetic research on *H. niloticus* has revealed significant differentiation patterns among populations across different river basins in West Africa, reflecting the influence of geographic isolation and environmental heterogeneity (Hurtado *et al*., 2013; Oladimeji *et al.,* 2022; Wikondi *et al*., 2023). Nonetheless, questions regarding the factors driving genetic divergence, especially among distinct and isolated populations, remain. Information on the divergence times, effective population size, and historical demographic changes, such as bottlenecks or expansions, is critical for understanding the evolutionary history of the species and its potential adaptability to environmental changes, which is critical for long-term conservation and management efforts.

Objective

In this study, we explore the demographic history of *H. niloticus* populations in Nigeria and Benin to elucidate their genetic connectivity, which will aid in identifying management units for conserving this species in West Africa.

Material and methods

Study Area

The study area includes natural populations of *H. niloticus* from four inland waters in Nigeria and three river basins in Benin, representing major fishing areas of this species in both countries. The Nigerian locations of study include Kainji Lake, a reservoir on the Niger River created by the Kainji Dam in North-central Nigeria, and three inland waters in Southern Nigeria, namely the Epe Lagoon, Ethiope River, and the Igbokoda River. The Benin locations include nine localities in the Oueme´-So River floodplain system, one locality in the Mono River, and one in the Niger River (Malanvile) (Table 1) (Figure 1).

Table 1: Locations sampled, country, their geographic coordinates, and the sample size.

S/N	Location	Country	Geographic Coordinate	Sample size
1	Kainji Lake	Nigeria	09°83'36"N; 004°61'69"E	23
2	Epe Lagoon	Nigeria	06°56'69"N; 003°98'36"E	20
3	Ethiope River	Nigeria	05°88'36"N; 005°71'69"E	19
4	Igbokoda River	Nigeria	06°28'36"N; 004°81'69"E	15
5	Niger River at Malanville	Benin	11°52'34"N; 003°24'29"E	12
6	Mono River	Benin	06°18'14"N; 001°50'24"E	15
7	Lake Codo	Benin	07°07'30"N; 002°20'46"E	20
8	Lake Cele	Benin	07°09'18"N; 002°26'10"E	9
9	Lake Azilli	Benin	07°15'23"N; 002°27'36"E	32
10	Lake Nakava	Benin	07°12'25"N; 002°17'40"E	17
11	Lake Hlan	Benin	06°57'07"N; 002°19'33"E	36
12	Ouemé River channel	Benin	06°44'47"N; 002°28'41"E	6
13	Ouemé River floodplain	Benin	06°40'21"N; 002°28'22"E	34
14	Sô River channel	Benin	06°34'54"N; 002°23'48"E	10
15	Sô River floodplain	Benin	06°35'43"N; 002°23'15"E	20

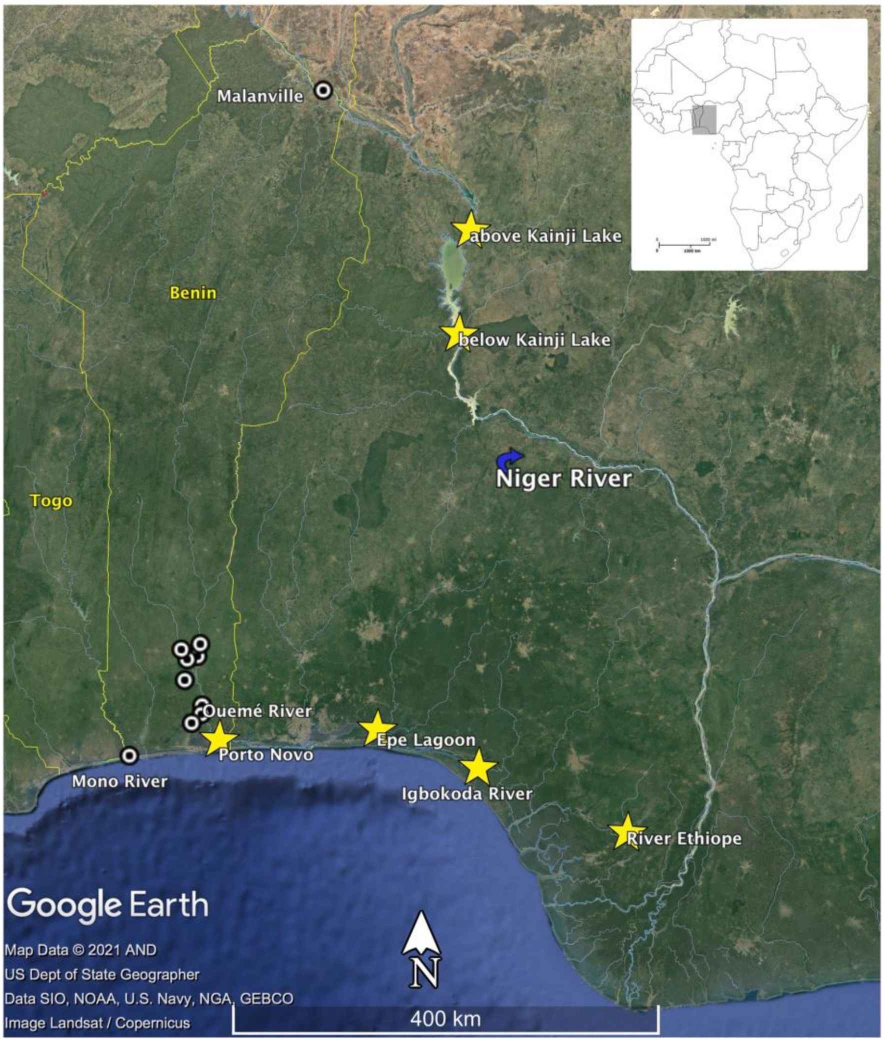


Fig. 1: Map of the study area showing the sampling sites of *Heterostis niloticus*. Yellow stars indicate the sampling sites in Nigeria, while the

Kainji Lake was formed by the impoundment of the River Niger on the border between Niger State and Kebbi State in the North-central region of Nigeria, about 700 km upstream from the expansive Niger River delta, which spans approximately 240 km before the river flows into the Atlantic Ocean (Balogun and Ibeun, 1995). Within the delta, the Niger River splits into a complex network of waterways, bordered by vast floodplains that extend approximately 320 km along the coast and encompass an area of about 36,000 km. The Ethiope and Igbokoda rivers are situated in the western part of the Delta, while Epe Lagoon lies further west of the Delta.

The study employed published datasets from two previous studies (Hurtado *et al.,* 2013; Oladimeji *et al*., 2022). Genotypes from seven microsatellite loci common to both datasets were normalized using allelogram software (Morin *et al*., 2009). This was done to validate the congruence of genotypes from the two different datasets and overcome problems emerging from allele size shifts as data were generated at different times. The normalized datasets were used for further analysis. The datasets were converted into different formats used as input files for the various analyses using PGDSpider v. 2.1.1.3 (Lischer & Excoffier, 2012).

Population Differentiation Analysis

Two different approaches were used to determine the genetic structure of the populations. First, a Bayesian clustering method, STRUCTURE (Falush *et al*., 2003; Pritchard *et al*., 2000), was employed using resources from the CIPRES Science Gateway (Miller *et al.,* 2010). We assumed an admixture model with correlated allele frequencies and considered a pre-determined number of groups (K) varying from 1 to 11. We performed 20 independent runs, with 500,000 steps and a burn-in of 125,000 steps, while all other settings were set to default. The STRUCTURESELECTOR program (Li and Liu, 2018) was used to determine the optimal number of genetic clusters using the *ad hoc* ΔK metric (Evanno *et al*., 2005) and to assign individuals to groups. Additionally, postprocessing of the outputs was carried out in CLUMPAK program (Kopelman *et al*., 2015) to deal with the multimodality of runs across different K. The bar plots derived from the output files of STRUCTURESELECTOR were customised directly in StructuRly (Criscuol and Angelini, 2020). A multivariate approach was also applied with Discriminant analysis of principal component (DAPC) implemented in the adegenet v.2.1.3 (Jombart, 2008; 2011) R package to complement the model-based approach. Genetic clusters indicating the variation between groups were identified using k-means, a clustering algorithm that identifies genetic groups by prioritising the variation between groups above the variation within groups. The *optim.a.score* function was employed to avoid overfitting, and K was determined using the Bayesian Information Criterion (BIC).

Genetic Diversity Analysis

The populations identified by STRUCTURE and DAPC analysis were subjected to genetic diversity statistics: average number of alleles (Na), average number of effective alleles (Ne), Shannon's information index (I), mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), unbiased expected heterozygosity (uH_E), and inbreeding coefficient (F_{IS}) using GenAIEx v. 6.5 (Peakall & Smouse 2006; 2012)

Demographic history inference

The demographic history of the populations identified by both STRUCTURE and DAPC (see results) was determined using a coalescent-based Approximate Bayesian Computation (ABC) in the software DIYABC v.2.1.0 (Cornuet *et al*., 2014). Different evolutionary scenarios were developed and tested assuming a mean mutation rate of 0.0005 and a mean coefficient (p) of 0.22. We performed 1,000,000 simulations for five scenarios ($5x10^6$) to select the model closest to the observed data, having the highest posterior probability via both direct and logistic regression, following Cornuet *et al.* (2014). The analyses were repeated three times to ensure consistency in results. False positive and false negative errors were further assessed to validate the selected scenario. The demographic parameters used for the DIYABC are summarized in Table 2. A generation time of two years was assumed because it is the estimated reproductive maturity period for the species (Ofori-Darkwah, 2024).

We tested five different scenarios for the four Populations (Kainji Lake, Southern Nigeria, Southern Benin, and Malanville) of *H. niloticus* identified by the STRUCTURE and DAPC (see Results) as follows: Scenario 1 assumes that the Southern Nigeria and Southern Benin populations share a common lineage more recently, while Kainji Lake and Malanville share another lineage, and both groups diverged in parallel at the same time (t2). Scenario 2 suggests a hierarchical divergence as Malanville splits earlier (t3), then Kainji diverges (t2), and finally Southern Nigeria and Southern Benin are most recently divergent (t1). The assumption of Scenario 3 is that Southern Nigeria and Southern Benin are sister populations, diverging most recently, while Kainji Lake and Malanville diverged independently earlier (t2). Scenario 4 assumes that Kainji Lake and Malanville diverged most recently from a common ancestor, while Southern Nigeria and Southern Benin also diverged from a common ancestor at an earlier time (t2). Finally, scenario 5 considers that Kainji Lake, Southern Nigeria, Southern Benin, and Malanville all diverged simultaneously from a single ancestral population at time t1, with no hierarchical branching (Figure 2). Goodness of fit of the selected model was assessed using Principal Component Analysis (PCA).

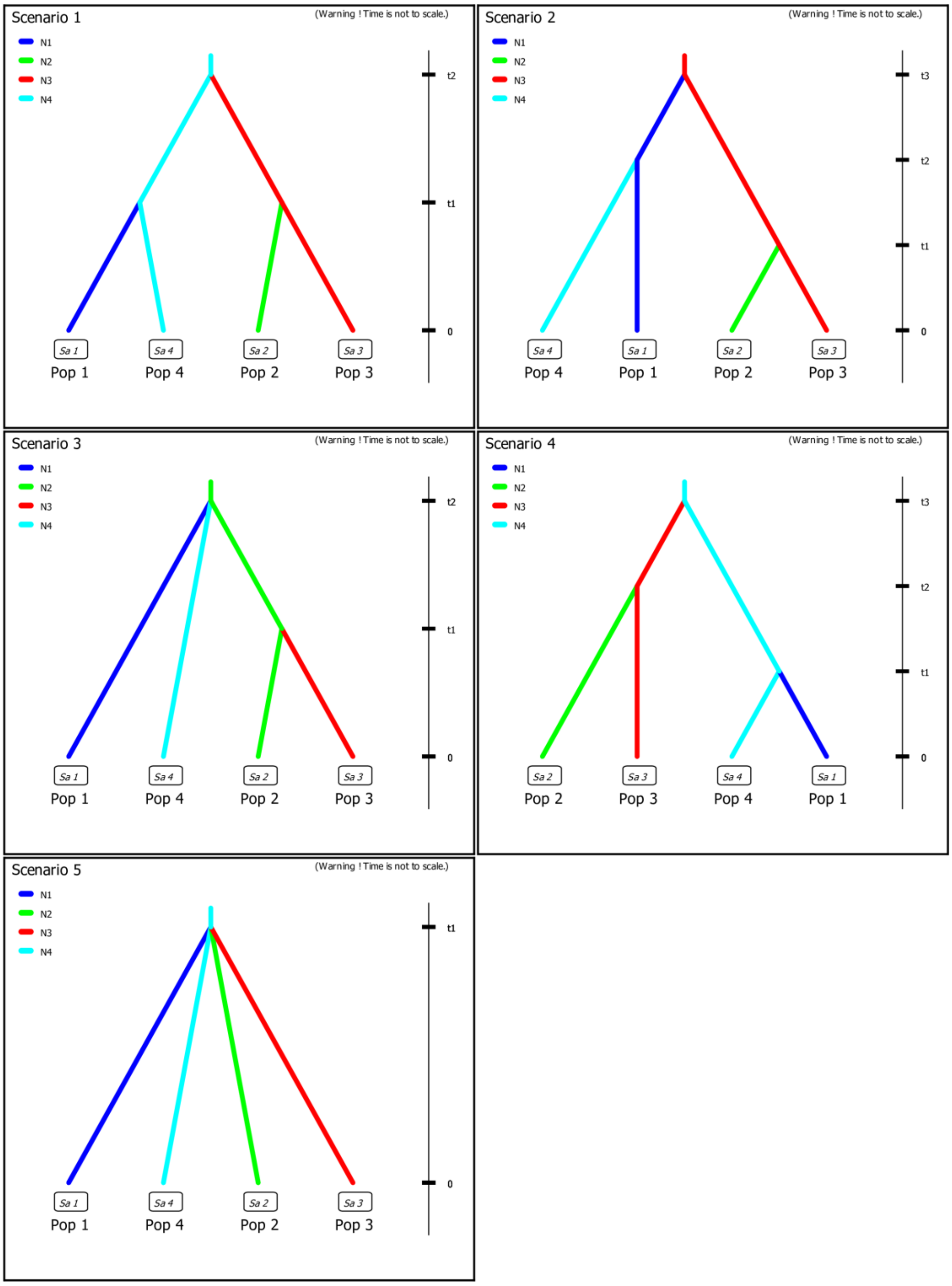


Fig. 2. Schematic representation of the different evolutionary scenarios tested for the *H. niloticus* populations with DIYABC. Pop1, Kainji Lake; Pop2, Southern Nigeria; Pop3, Southern Benin; Pop4, Malanville. Time events were set to 0 (present), t1 (early event), t2 (old event), and t3 (older event).

Table 2: Demographic parameters for estimating the demographic history of *H. niloticus* populations

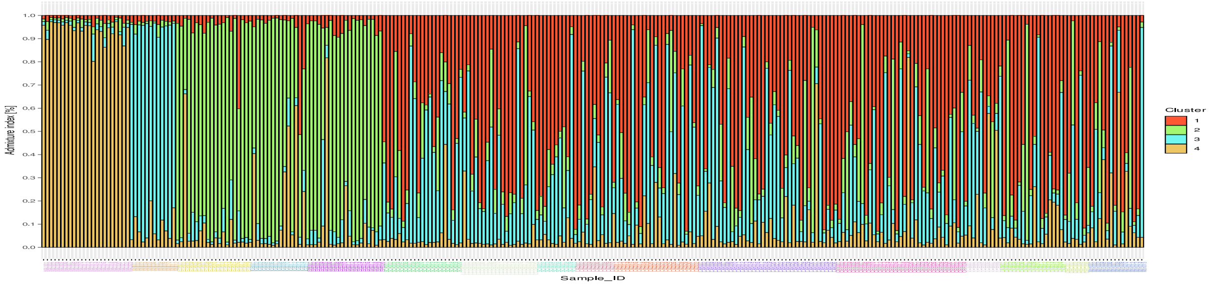
Demographic Parameter	Description	Prior Distribution	Prior Condition
N1	Effective population size of Kaiji Lake	10^1-10^4	uniform
N2	Effective Population size of	10^1-10^4	uniform
N3	Effective Population size of	10^1-10^4	uniform
N4	Effective Population size of	10^1-10^4	uniform
t1	Divergence time at the first population event	10-1000 generations	
t2	Divergence time at the second population event	500-5000 generations	t2>t1
t3	Divergence time at the third population event	5000-50000 generations	t3>t2

Results

We observed two evolutionary scenarios as outputs of the Bayesian clustering method implemented in STRUCTURE that best represented our data: K = 5 and K = 7, according to the Δ*K ad hoc* metric. However, regardless of the model with K ranging from 4 to 7, the *H. niloticus* populations were consistently separated into four groups (Fig. 3), namely Kainji Lake, Malanville, Southern Benin (Oueme-So floodplain System and Mono River), and Southern Nigeria (Ethiope River, Igbokoda River, and Epe Lagoon). In DAPC analysis, we retained 12 PC's, and the K that represents our genetic data ranged from seven to 10, according to the BIC, while K=8 was selected as the optimal. The

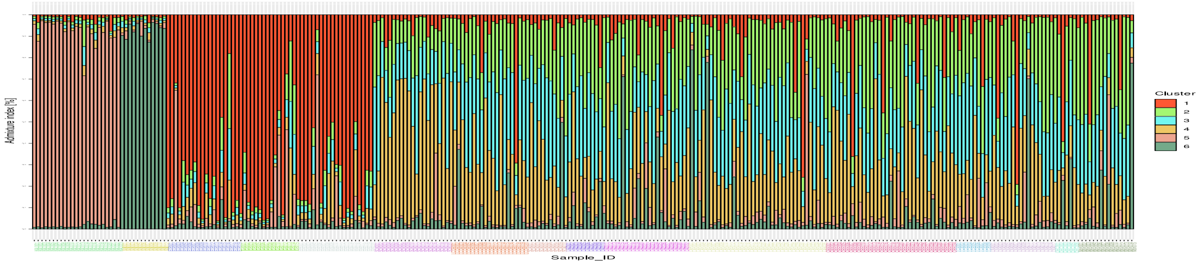
DAPC scatter plot revealed four genetic groups (Fig. 4) similar to the output of the STRUCTURE.

K=4



K=5

K=6



K=7

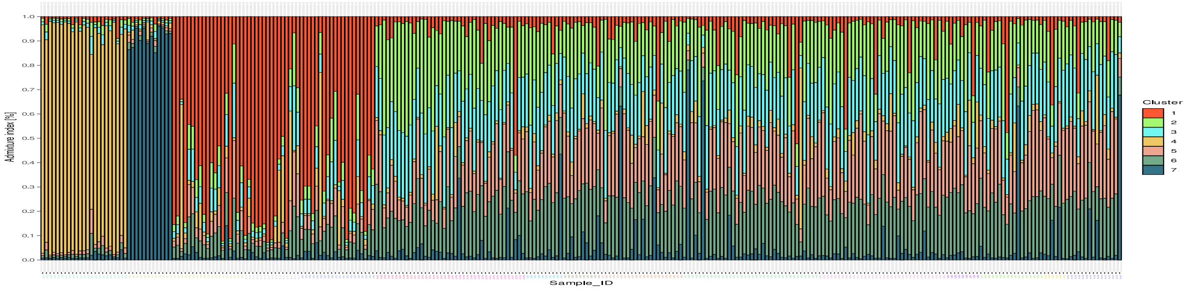


Fig. 3. Population structure inference for *H. niloticus* in West Africa using the Bayesian method STRUCTURE for *K* = 4, 5, 6, and 7. Vertical lines represent *H. niloticus* individuals, and colors denote inferred ancestry from K ancestral populations (Cluster) for each individual.

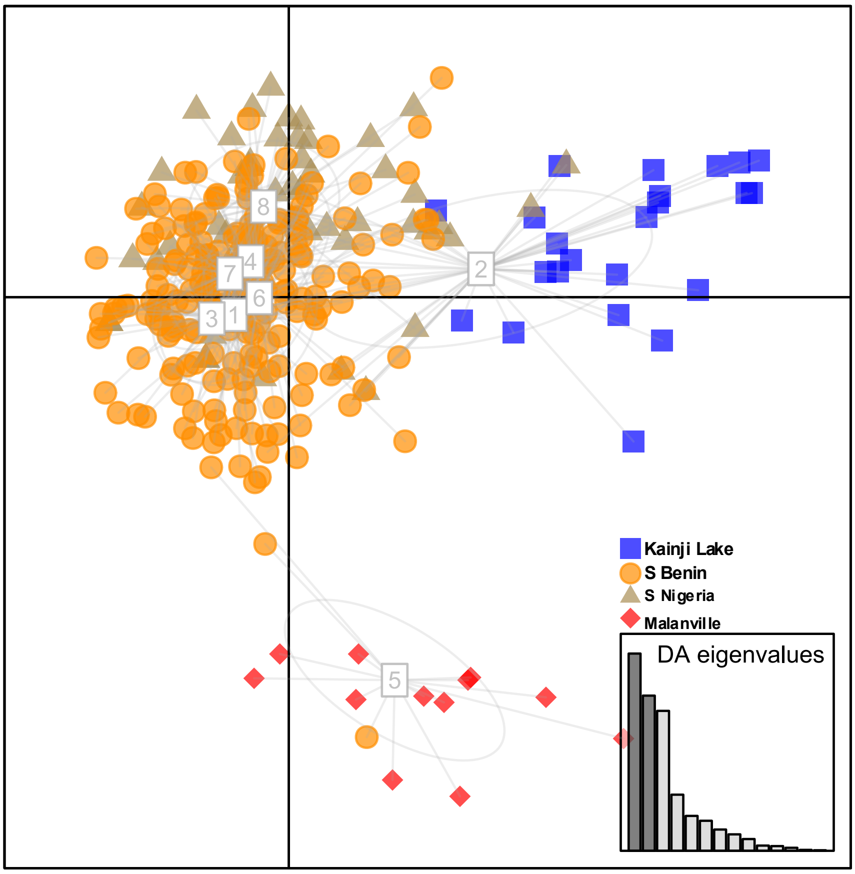


Fig. 4. Population structure inference for *H. niloticus* in West Africa using Discriminant Analysis of Principal Components. Dots represent individuals which were clustered into four groups, with their geographic origin represented by different colors. The inset shows the relative magnitude of eigenvalues for the discriminants used.

Genetic Diversity Estimates

We observed a substantial variation in the distribution of genetic diversity across inferred populations (Table 2). The Kainji Lake population of *H. niloticus* had the highest genetic diversity estimate among the four populations examined with average number of alleles (*Na*) = 8.33; average number of effective alleles (*Ne*) = 4.35; Shannon's information index (*I*) = 1.589; observed heterozygosity (H_O) = 0.714; expected heterozygosity ($\mathrm{H_E}$) = 0.704; and unbiased expected heterozygosity (uH_E) = 0.72. The inbreeding coefficient (F_{IS}) was very low in this population (-0.012). Genetic diversity was considerably lower in the three other populations (Southern Nigeria, Southern Benin, and Malanville). *Ne* ranged between 2.081 (Malanville) and 3.409 (Southern Benin); *I* between 0.752 and 1.436; H_O between 0.333 and 0.606; $\mathrm{H_E}$ between 0.401 and 0.674;

uH_E between 0.418 and 0.676. *H. niloticus* samples from Malanville had the lowest estimates across all the indices of genetic diversity (Table 3).

Table 3: Genetic diversity estimates for *H. niloticus* from four populations in Nigeria and Benin.

Population	***N***	***Na***	***Ne***	***I***	H_O	H_E	uH_E	F_{IS}
Kainji Lake	23.000	8.000	4.346	1.589	0.714	0.704	0.720	-0.012
Southern Nigeria	54.000	7.143	2.472	1.126	0.479	0.540	0.546	0.117
Southern Benin	199.000	8.857	3.409	1.436	0.606	0.674	0.676	0.093
Malanville	12.000	3.429	2.081	0.752	0.333	0.401	0.418	0.230

N, number of individuals; *Na*, average number of alleles per locus; *Ne*, average number of effective alleles per locus; *I*, Shannon's information index; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; uH_E, mean unbiased expected heterozygosity; F_{IS}, inbreeding coefficient.

Demographic history inference

The five evolutionary scenarios we simulated revealed different posterior probability, but scenario 3 best fit our data (Figure 5) and presented the highest posterior probability of 0.9147 (95% CI 0.8868 - 0.9425) as revealed by both direct (Figure 6) and logistic regression models (Figure 7). The PCA model check between the prior and posterior distribution also confirmed scenario 3 as the best model fit, as the simulated data grossly overlapped with the observed data (Figure 8). False positive error for the most likely scenario (3) was 0.148, whereas false negative error ranged from 0.004 to 0.075, while the posterior predictive error (the proportion of scenarios identified incorrectly over 1000 test data sets by the logistic approach) computed over all scenarios is 0.115. Scenario 3 revealed that Southern Nigeria and Southern Benin are likely sister populations, sharing a common origin and with a more recent divergence about 1,550 years ago, while Kainji Lake and Malanville diverged earlier independently and simultaneously, ~ 4380 years ago (Table 4).

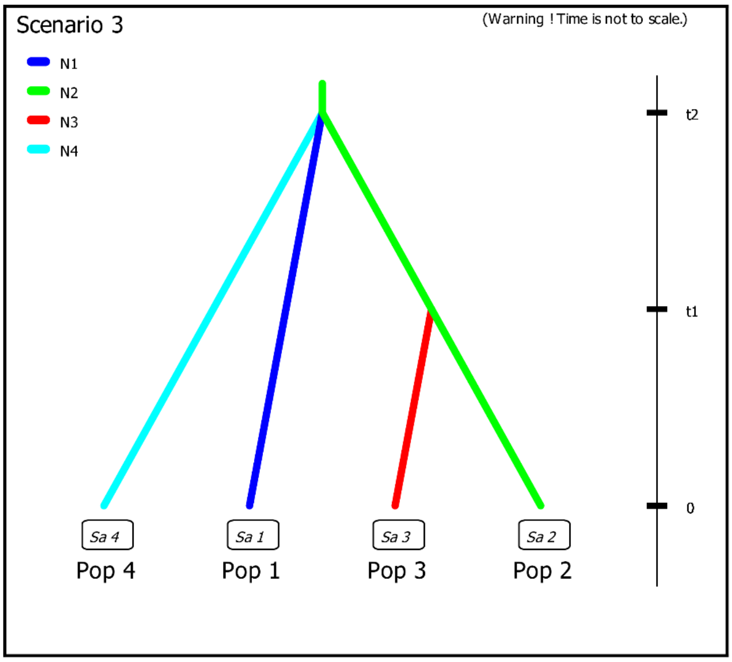


Fig. 5. Schematic Representation of the Best Demographic Scenario (Scenario 3) obtained from DIYABC simulations of the *H. niloticus* populations

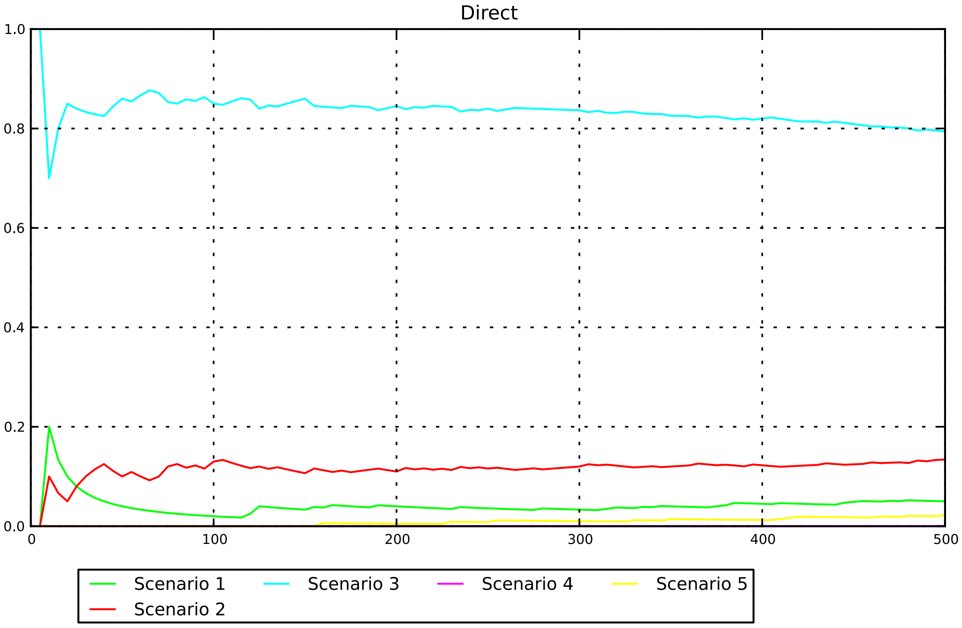


Fig. 6. Direct regression across all tested scenarios, showing that Scenario 3 has the highest posterior probability.”

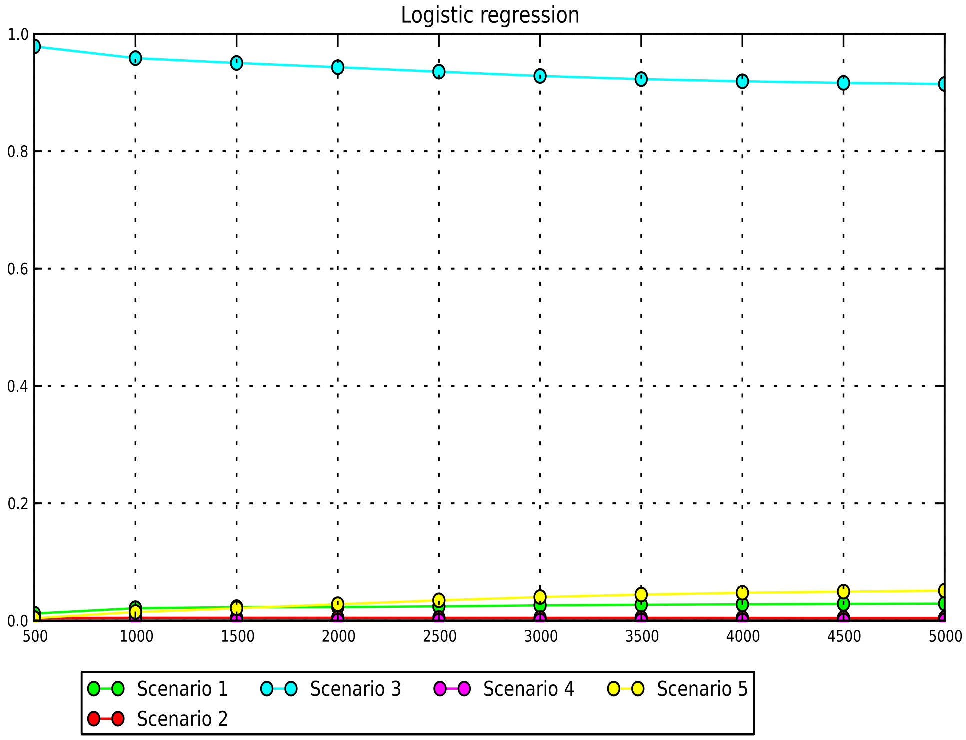


Fig. 7. Logistic regression across all tested scenarios, showing that Scenario 3 has the highest posterior probability.

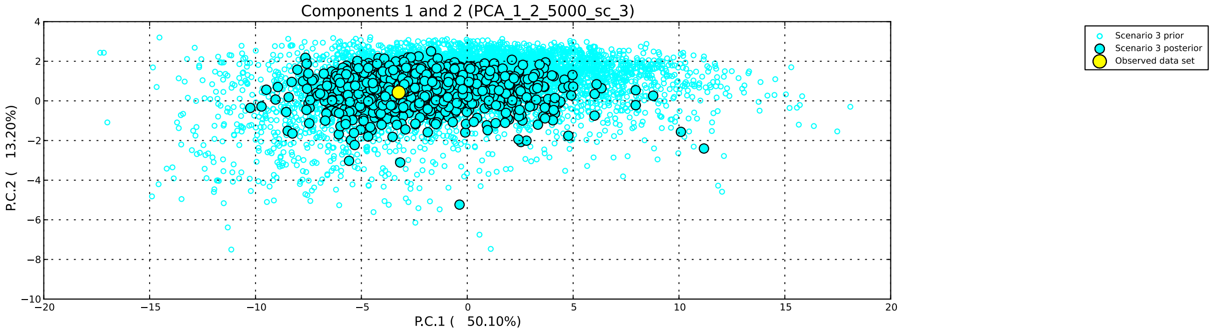


Fig. 8. PCA model check of scenario 3, showing the observed data set within the simulated data set.

Table 4. Estimate of Demographic Parameters for the best Demographic Scenario (Scenario 3) as indicated by DIYABC

Parameter	Median	Q5%	Q95%
N1	5.53E+03	1.89E+03	9.67E+03
N2	2.43E+03	9.00E+02	6.82E+03
N3	3.17E+03	7.96E+02	8.82E+03
N4	7.03E+02	2.61E+02	1.80E+03
T1	7.75E+02	2.81E+02	9.85E+02

T2	2.19E+03	8.36E+02	4.60E+03
µmic_1	5.70E-04	2.04E-04	9.47E-04
pmic_1	2.28E-01	1.17E-01	3.00E-01
snimic_1	2.86E-07	1.16E-08	5.45E-06

Key: N1 effective population size of population 1 (Kainji Lake); N2, effective population size of population 2 (Southern Nigeria); N3, effective population size of population 3 (Southern Benin); N4, effective population size of population 4 (Southern Nigeria); T1 divergence time at the second split event; T2, divergence time at the first split event

Discussion

Although the genetic structure of *H. niloticus* populations has previously been examined separately in Nigeria (Oladimeji *et al*., 2021) and Benin (Hurtado *et al*., 2013), the present study provides new insights into the demographic history and genetic connectivity of populations from both countries, representing a significant portion of its distribution in West Africa. This focus is justified, as the largest wild capture of this species in Africa is reported for these countries, with 409,784 metric tons (representing 85.3% of total catch in Africa) in Nigeria, between 1990 and 2021, and 21,640 metric tons in Benin, between 1987 and 2021 (FAO, 2021; Hurtado *et al*., 2023).

The population differentiation findings reported here, including STRUCTURE and DAPC, allowed us to group the 15 sampling localities of *H. niloticus* from Nigeria and Benin into four major populations. Two of these groups are geographically close. Kainji Lake and Malanville were identified as separate populations with very restricted connectivity with the others, despite their physical proximity. Kainji Lake is the impoundment of the Niger River and is situated far north of Nigeria, while Malanville is also a city on the Niger River in Northern Benin. Malanville and Kainji are both connected through the Niger River system. The Niger River flows southward from Malanville, forming part of the natural border between Benin and Nigeria before entering Nigeria fully. Though Kainji and Mallanville are naturally connected, the Kainji dam, which was constructed in 1968, has obstructed fish dispersal, constituting a strong barrier to gene flow between the two populations. This barrier is evident in the pattern of genetic differentiation as revealed by both STRUCTURE and DAPC. The separation of the Kainji Lake and Malanville from the other Southern populations in Nigeria and Benin, respectively, could partly be attributed to the considerable geographic distance between the Lake and other populations down south.

The geographic distance between Kainji Lake in the far north and the southern populations (Epe Lagoon, Ethiope River, and Igbokoda River) approximately ranges from 550 to 700 km, while the geographic distance between Malanville and the southern populations (Oueme-So River flood plains, Mono River) in Benin approximately ranges from 670 to 735km. The impoundment is also another significant factor that could have restricted gene flow between *H. niloticus* from Kainji Lake and the other populations, as noted by Oladimeji *et al* (2022). This genetic divergence at the local scale could therefore be a consequence of man-made structures such as dams and other barriers that could modify the natural course of rivers and disrupt functional connectivity (Davis *et al*., 2019). The Epe Lagoon, Ethiope River, and Igbokoda River were collectively identified as a single population, while the nine localities in the Oueme´-So River floodplain system and the Mono River were also grouped as a single population.

The strong gene flow and genetic connectivity between the southern localities in both Nigeria and Benin could be attributed to the hydrological connectivity of the rivers and the absence of physical barriers to fish dispersal among these water bodies. In Nigeria, the Igbokoda River and Epe Lagoon are connected through a water channel that joins the Lekki Lagoon, which is connected to the eastern portion of Epe Lagoon, while the Ethiope River and Igbokoda River are connected indirectly through the creeks, swamps, and distributaries of the Niger Delta. In Benin, the genetic connectivity observed among the nine localities sampled in the Oueme´-So River floodplain system alongside the Mono River is expected due to seasonal flooding, which enhances fish dispersal within this region (Adite *et al.*, 2006). This is consistent with the report of Hurtado *et al.* (2013), who reported low levels of population genetic differentiation within the Oueme-So River floodplain system. Marandel *et al.* (2017) similarly identified four large metapopulations of rays and skates from 11 putative populations in the Mediterranean and on the Northeast Atlantic shelf using genetic simulations. Their result indicated that the level of genetic differentiation among the populations reflected the interplay between gene flow and genetic drift (Palumbi, 2003; Waples and Gaggiotti, 2006).

The demographic history of *H. niloticus* from study sites across Nigeria and Benin, as revealed by the DIYABC analysis, suggests a north-to-south divergence pattern of the four identified populations. The northern populations (Kainji and Malanville) are genetically older, ~ 4380 years old, representing an ancestral lineage, while the southern populations (Nigeria and Benin) have recently diverged ~ 1,550 years ago. Kainji Lake has the largest effective population size (*Ne*) of 5530, indicating an ancestral population. This is reasonable, as *H. niloticus* was first reported in the Kainji Lake according to Moreau (1982) in a FAO synopsis/report. Also, Kainji Lake has the highest genetic diversity estimate of all four genetic groups with a negative inbreeding coefficient value (H_E = 0.704; F_{IS} = -0.012; Table 3), supporting the hypothesis of a large population size. The Southern Nigeria and Southern Benin populations have moderately large *Ne,* 2430 and 3170, respectively, likely attributed to recent expansion. Malanville has the smallest *Ne* (703), which suggests past demographic contraction (bottleneck), genetic isolation, and restricted gene flow. Hurtado *et al*. (2024) similarly reported the lowest value of *Ne* in Malanville compared to other localities in Nigeria and Benin. They attributed this to the genetic isolation of Malanville relative to the other populations sampled down south of Benin. The estimate for effective population size reported in this study varies from those reported by Hurtado *et al.* (2023). This is expected because different methods were used in the estimation. In the study by Hurtado *et al.* 2024, each sampling site was analysed separately using Linkage Disequilibrium methods, while in this study, the Ne estimates were derived from Approximate Bayesian Computation (ABC) simulations in DIYABC based on the four genetic groups identified by STRUCTURE and DAPC.

Conclusion

The *H. niloticus* populations from Southern Nigeria and Southern Benin represent a metapopulation sharing a common origin, while the northern populations are genetically distinct. The Kainji Lake population is more viable relative to the other populations, while Malanville is threatened, as evidenced by the genetic contraction observed in this population. The southern populations in both Nigeria and Benin are relatively stable. Improved conservation efforts are therefore recommended to ensure the sustainability of this economically important species.

References

Adite, A., Winemiller, K.O. & Fiogbé, E.D. (2005). Ontogenetic, seasonal, and spatial variation in the diet of *Heterotis niloticus* (Osteoglossiformes: Osteoglossidae) in the Sô River and Lake Hlan, Benin, West Africa. *Environmental Biology of Fishes*. 73, 367–378.

Agostinho, A. A. (2003). Migratory fishes of the upper Parana River basin, Brazil. In: Gomes LC, Fernandes DR, Suzuki HI, Ju´lio HF Jr, Carolsfeld J, Harvey B, Ross C, Baer A (eds) Migratory fishes of South America: biology, fisheries and conservation status. IDRC-World Bank-World Fisheries Trust, Victoria, pp 19–98

Balogun J. K. & Ibeun, M. O. (1995). Additional Information on Fish Stocks and Fisheries of Lake Kainji (Nigeria). In: Current Status of Fisheries and Fish Stocks of the Four Largest African Reservoirs: Kainji, Kariba, Nasser/Nubia and Volta (eds R. C. M. Cul and Roest. F. C.) CIFA Technical Paper No. 3. Food and Agriculture Organization. Rome. Pp 1-18.

Chen, Q., Li, Q., Lin, Y., Zhang, J., Xia, J., Ni, J., et al. (2023). River damming impacts on fish habitat and associated conservation measures. *Reviews of Geophysics*, 61, e2023RG000819. https:// doi.org/10.1029/2023RG000819

Cornuet, J.M., Pudlo, P., Veyssier, J., Loire, E., Santos, F., Dehne-Garcia, A. & Estoup, A. (2014) DIYABC v2.0: A software to make approximate Bayesian computation inferences about population history using single-nucleotide polymorphism, DNA sequence, and microsatellite data. *Bioinformatics* **30**, 1187‑1189.

Criscuolo, N.G. & Angelini, C. (2020). StructuRly: A novel shiny app to produce comprehensive, detailed, and interactive plots for population genetic analysis. *PLoS ONE* 15(2): e0229330. https://doi.org/10.1371/journal.pone.0229330.

Darwall, W. R. T., Smith, K. G., Allen, D. J., Holland, R. A., Harrison, I. J. & Brooks, E. G. E. (2011). *The diversity of life in African freshwaters: Underwater, under threat*. IUCN

Davis, C. D., Epps, C. W., Flitcroft, R. L., & Banks, M. A. (2019). Beyond Isolation by Distance: Riverscape Effects on Genetic Structure of Fall-Run Chinook Salmon. American Fisheries Society Symposium 90:35-56.

Evanno, G., Regnaut, S. & Goudet, J. (2005). Detecting the number of clusters of individuals using the software structure: a simulation study. 14 (8): 2611-2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Falush D., Stephens M. & Pritchard J. (2003). Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, 164:1567-1587.

FAO (2020). Fishery Statistical Collections: Global Capture Production 1950‑2018. http:// www. fao. org/ fishery/ statistics/ global- capture- production/ query/en

FAO (2021). Global Capture Production Quantity (1950‑2021). Available online: https://www.fao.org/fishery/statistics-query/en/capture/capture_quantity (accessed on 5 November 2023).

Ferraris Jr., C.J. (2003). Arapaimatidae (Bonytongues). In: Reis, R.E., Kullander, S.O., Ferraris Jr., C.J. (Eds.), Checklist of the Freshwater Fishes of South and Central America. Porto Alegre: Edipucrs, Brasil. 31 pp.

Hoeinghaus, D. J., Agostinho, A. A., Gomes, L. C., Pelicice, F. M., Okada, E. K., Latini, J. D., Kashiwaqui, E.A.L. & Winemiller, K. O. (2009) Effects of river impoundment on ecosystem services of large tropical rivers: embodied energy and market value of artisanal fisheries. *Conservation Biology* 23:1222–1231

Hurtado, L. A., Carrera, E., Adite, A. & Winemiller, K. O. (2013). Genetic differentiation of a primitive teleost, the African bony tongue *Heterotis niloticus*, among river basins and within a floodplain river system in Benin, West Africa. *Journal of Fish Biology*. **83**, 682‑690.

Hurtado, L.A., Mateos, M., Caballero, I.C., Oladimeji, T.E., Adite, A., Awodiran, M.O., Winemiller, K.O. & Hamilton, M.B. (2024). Critically Small Contemporaneous Effective Population Sizes Estimated for Stocks of the African Bonytongue in Western Africa. *Fishes*, 9, 196. https://doi.org/10.3390/fishes9060196.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers.” *Bioinformatics* 24(11): 1403-1405. doi:10.1093/bioinformatics/btn129

Jombart, T. & Ahmed, I. (2011). adegenet 1.3‑1: New tools for the analysis of genome-wide SNP data. *Bioinformatics* **27(21)**, 3070‑3071. doi:10.1093/bioinformatics/btr521

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A. & Mayrose, I. (2015). Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. *Molecular Ecology Resources 15(5)*

Levêque, C., Paugy, D. & Teugels, G.G. (1990). Faunes des Poissons d'Eaux Douces et Saumâtres de l'Afrique de l'Ouest, éd. Orstom/Mrac, Paris. 384 pp.

Li, G.Q. & Wilson, M.V.H., (1996). In: Stiassny, M.L.J., Parenti, L.R., Johnson, G.D. (Eds.), Phylogeny of Osteoglossomorpha. Interrelationships of Fishes-Academic Press, New York, pp. 163–174

Li, Y. & Liu, J. (2017). StructureSelector: A web-based software to select and visualize the optimal number of clusters using multiple methods. *Molecular Ecology Resources* 18(1) DOI: 10.1111/1755-0998.12719

Lischer, H. E. L. & Excoffier, L. (2012). PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics* 28, 298–299.

Marandel, F., Lorance, P., Andrello, M., Charrier, G., Le Cam, S., Sigrid Lehuta, S., &Trenkel, V. M. (2017). Insights from genetic and demographic connectivity for the management of rays and skates. *Canadian Journal of Fisheries and Aquatic Sciences.* **75**: 1291‑1302 (2018) dx.doi.org/10.1139/cjfas-2017-0291

Mbega, J. D. (2004). Biodiversité des poissons du bassin inférieur de l'Ogooué (Gabon). Thèse de Docteur en Sciences, Facultés Universitaires Notre-Dame de la Paix, Namur, 607 pp.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA pp 1 - 8. DOI: 10.1109/GCE.2010.5676129

Moreau, J. (1982). Expose´ synoptique des donne´es biologiques sur *Heterotis niloticus* (Cuvier, 1829). Food and Agriculture Organization Synopsis de Peˆches 131: 1–45.

Morin, P. A., Manaster, C., Mesnick, S. L., & Holland, R. (2009). Normalization and binning of historical and multi-source microsatellite data: Overcoming the problems of allele size shift with allelogram. *Molecular Ecology Resources* 9, 1451–1455. doi:10.1111/j.1755-0998.2009.02672.x

Ofori-Darkwah, P., Adjei-Boateng, D., Edziyie, R.E., Agbo, N.W. & Lund, I. (2024). Early ontogeny of the African Bony-tongue (Heterotis niloticus) and the effect of Artemia and rotifer live feeds on larval digestive enzyme activity and performance. *Frontiers in Aquaculture* 3, 1310429

Oladimeji, T. E., Caballero, I. C., Mateos, M., Awodiran, M. O., Winemiller, K. O., Adite, A. & Hurtado, L. A. (2022). Genetic identification and diversity of stocks of the African bonytongue, *Heterotis niloticus* (Osteoglossiformes: Arapaiminae), in Nigeria, West Africa. *Scientific Report.* 19;12(1):8417. doi: 10.1038/s41598-022-12428-6.

Palumbi, S.R. (2003). Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13(sp1): 146‐158. doi:10.1890/1051-0761(2003)013[0146:PGDCAT]2.0.CO;2.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155:945-959.

Waples, R.S., Punt, A.E. & Cope, J.M. 2008. Integrating genetic data into management of marine resources: how can we do it better? *Fish.* **9**(4): 423‐449. doi:10.1111/j.1467-2979.2008.00303.x.

Wikondi, J., Meutchieye, F., Adenyo, C., Osei-Amponsah, R., Kayang, B. B. & Tomedi, M. E. T. (2023). Genetic diversity of bonytongue fish *Heterotis niloticus* (Cuvier, 1829) in Cameroon, Central Africa. *Scientific African*, 22. https://doi.org/10.1016/j.sciaf.2023.e01975

Mentoring and supervision

No mentoring of supervision activity was carried out. However, it is noteworthy that Dr. Tofunmi’s contribution to the Molecular Ecology laboratory was academic, scientific, and cultural. Through group-level biweekly discussion, it became evident to the lab members composed of undergraduate and graduate students the differences between academic setting in Nigeria and Brazil, also how scientists may approach research from different perspectives depending, at least partially, on their geographic origins. It was a positive, expected outcome of a visiting researcher from a country like Nigeria.

Courses and outreach activities

No teaching or outreach activity was carried out as it was part of the requirements of the funding agency, TETfund. Thus, research activity was the focus of Dr. Tofunmi period as a postdoctoral researcher at UNESP, Institute of Biosciences, São Vicente.