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**Demographic history, genetic connectivity, and conservation
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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.

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). Exposé synoptique des données biologiques sur *Heterotis niloticus* (Cuvier, 1829). Food and Agriculture Organization Synopsis de Pêches 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 or 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.