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Effect of Climate Change on Morphological Divergence and Species Discrimination in Cichlids from the Cross River, Nigeria

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ABSTRACT

Morphological divergence and species discrimination are essential for understanding freshwater fish biodiversity but remain underexplored in African river systems. This study analyzed 480 specimens from eight cichlid species in Nigeria's Cross River using morphometrics, principal component analysis (PCA), and discriminant function analysis (DFA). Standard lengths ranged from 9.07 ± 0.11 cm in *Sarotherodon melanotheron* to 15.27 ± 0.27 cm in *Oreochromis placidus*. The first two PCA components explained 59.9% of total morphological variation, with standard length, dorsal fin depth, and caudal fin length identified as key contributors. DFA indicated that caudal peduncle depth plays a crucial role in swimming efficiency. *O. niloticus* and *O. placidus* exhibited the closest morphological affinity (Mahalanobis distance: 1.14), while *O. niloticus* and *Coptodon dageti* were the most divergent (12.71). Regression analysis showed that standard length was positively associated with water temperature ($\beta = 0.42$, $P < 0.001$). Scenario-based projections suggested that climate change could increase standard length by up to 4.8% in *O. niloticus* and reduce body depth by 7.2% in *S. melanotheron*. These findings offer new insights into the ecological roles and evolutionary dynamics shaping cichlid diversity in the Cross River. They also highlight the urgent need for adaptive conservation strategies to protect these species amid changing environmental conditions. A key recommendation is the implementation of long-term monitoring and habitat management programs targeting vulnerable and specialized cichlid populations.

INTRODUCTION

Cichlids are among the most physically varied groups of fish in Africa, showing a broad diversity in body shape, fin design, and feeding structures. These physical differences help them adapt to specific ecological roles and reduce overlap with other species, allowing many types to live together in the same environment **(Kopf *et al*., 2020; Magalhaes & Ford, 2022)**. The variation in their form is strongly linked to how they divide and use resources, which helps minimize competition between species. Because of this, being able to accurately tell cichlid species apart is important for tracking biodiversity and managing fish populations effectively **(Dunn *et al*., 2020; Acar & Kaymak, 2023)**.

The Cross River system in southeastern Nigeria is a biodiversity hotspot, supporting a rich assemblage of cichlid species with distinct morphological characteristics. This river system is characterized by a mosaic of habitats, including fast-flowing riffles and slower pools, which create diverse ecological conditions that drive evolutionary adaptation and species differentiation **(Zapfack *et al*., 2001; Eteng & Ifon, 2019; Asuquo & Ifon, 2022a)**. The ecological significance of the Cross River extends beyond its species richness; it serves as a critical habitat for many endemic and economically valuable fish species, making it an important focus for conservation and sustainable management **(Asuquo & Ifon, 2022b; Ameh *et al*., 2023)**.

Given the ongoing and projected impacts of climate change, it is increasingly important to understand how environmental shifts may influence the morphology and ecological roles of cichlids in riverine systems. Climate change is expected to alter river temperature, flow regimes, and habitat structure, creating new selective pressures that can drive morphological adaptation and shift species dynamics **(Conde-Saldaña *et al*., 2017; Pauers *et al*., 2018; Asuquo & Ifon, 2022c)**. Integrating climate change modeling into studies of fish morphology allows for the prediction of how future environmental scenarios may affect species adaptation, distribution, and ecosystem stability. This approach is particularly relevant for the Cross River, where climate projections indicate significant changes in hydrology and temperature that could reshape the ecological landscape for cichlid populations.

Recent global and regional studies have highlighted the influence of climate change on fish morphology and adaptation. Rising water temperatures and altered flow regimes have been shown to induce phenotypic changes in body shape, fin size, and other morphological traits, enabling fish to adjust to new environmental conditions **(Kern & Langerhans, 2018; Dwivedi & De, 2023)**. In African river systems, cichlids have demonstrated remarkable plasticity and evolutionary responses to habitat alterations associated with climate variability **(Sánchez-Hernández *et al*., 2021; Pauers *et al*., 2022)**. These findings underscore the need to integrate climate data into morphological studies to better understand the mechanisms of adaptation and resilience in fish populations.

Climate projections for the Cross River Basin suggest that the region will experience increased temperatures, altered precipitation patterns, and greater variability in river flow in the coming decades **(IPCC, 2021)**. These changes are expected to affect water levels, sediment transport, and habitat availability, with direct implications for the structure and function of aquatic communities **(Agi-Odey *et al*., 2024; Asuquo *et al*.,**

2024; Otogo *et al*., 2025). For cichlids, such environmental shifts may drive selection for traits that enhance swimming efficiency, predator avoidance, and resource acquisition in changing habitats.

The mechanisms by which temperature, flow, and habitat changes influence cichlid morphology are complex and multifaceted. Elevated temperatures can accelerate metabolic rates and growth, potentially leading to changes in body size and shape **(Langerhans & Reznick, 2010)**. Variability in flow regimes may favor streamlined bodies and longer fins that enhance swimming efficiency in fast currents, whereas increased sedimentation and reduced flow may select for deeper bodies better adapted to slower, more turbid waters **(Kern & Langerhans, 2018; Pauers *et al*., 2018)**. Habitat complexity, influenced by vegetation and substrate, further shapes morphological adaptations by providing refuges and influencing feeding strategies **(Conde-Saldaña *et al*., 2017; Asuquo & Ifon 2019b)**. Despite the growing body of research on climate-driven morphological adaptation in fish, there is a notable gap in studies that specifically address how projected climate change scenarios may influence cichlid morphology and niche specialization in the Cross River system. This gap highlights the need for targeted research that combines morphometric analysis with climate modeling to inform conservation and management strategies.

The objective of the present study was to assess how projected climate change scenarios may influence cichlid morphology and niche specialization in the Cross River. By integrating morphometric analyses with climate projections, this research aimed to provide new insights into the adaptive capacity of cichlid species and the potential impacts of environmental change on freshwater biodiversity. The findings will contribute to the scientific understanding of fish adaptation in dynamic riverine environments and support the development of strategies for conserving the Cross River ecosystem and beyond.

MATERIALS AND METHODS

Study area

This study was conducted in the Cross River, southeastern Nigeria, a major tropical freshwater system spanning latitudes 4°45′ to 6°15′ N and longitudes 8°00′ to 8°55′ E (Fig. 1). The river originates from the Manyu River in Cameroon and flows over 100 kilometers before emptying into the Gulf of Guinea through the Calabar River. The basin is bordered by Benue State to the north, Ebonyi and Abia States to the west, Akwa Ibom State to the southwest, the Atlantic Ocean to the south, and Cameroon to the east. The Cross River is characterized by a mix of fast-flowing riffles and slow-moving pools, supporting high aquatic biodiversity and providing a range of ecological niches for cichlid species **(Zapfack *et al*., 2001; Eteng & Ifon, 2019)**.

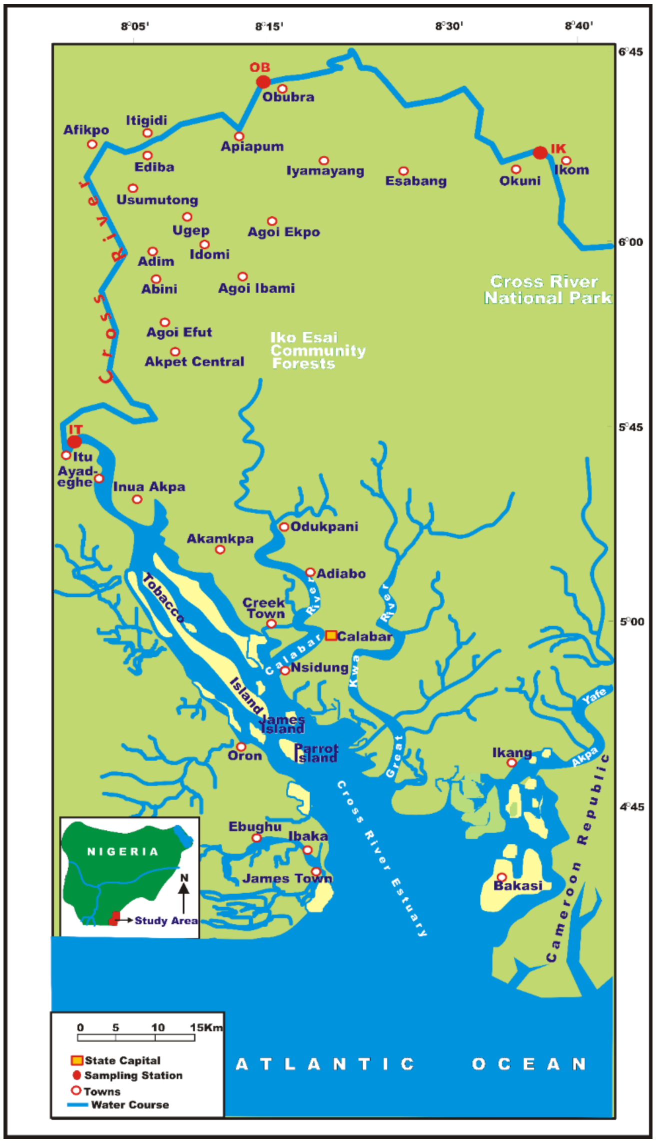

Fig. 1. Map of the Cross River basin showing sampling locations and major tributaries

Species selection

Eight cichlid species were selected for their ecological and morphological diversity, as well as their abundance and representation of different niches in the Cross River system. The species included *Coptodon mariae*, *Coptodon dageti*, *Coptodon guineensis*, *Chromidotilapia guntheri*, *Tylochromis sudanensis*, *Sarotherodon melanotheron*, *Oreochromis niloticus*, and *Oreochromis placidus*. Identification was based on FishBase Identification Keys **(Teugels & Audenaerde, 2003)** and **FAO Species Fact Sheets (2013)**.

Sample collection

Fish were sampled monthly over a six-month period (October 2019 to March 2020) from three locations along the Cross River: Itu, Obubra, and Ikom. Sampling covered a range of habitats including rocky substrates, slow-moving pools, and areas with dense aquatic vegetation. Fish were captured using gill nets, seines, and hand nets. Only fresh, undamaged specimens were retained. Euthanasia was performed with an overdose of MS-222 anesthetic to minimize suffering. Specimens were preserved in 10% formalin and transported to the Institute of Oceanography Laboratory, University of Calabar. In total, 480 fish (60 individuals per species) were collected for analysis.

Morphometric measurements

Morphometric analysis was conducted on all 480 specimens. Twenty-five external morphological characters were measured, including standard length (SL), total length (TL), body depth, head length, and various fin dimensions. Measurements were taken to the nearest 0.1cm using a divider and meter rule, following the protocols outlined by **Asuquo and Ifon (2021)**. All measurements were performed by the same researcher to ensure consistency. The full list of measured traits, their codes, and interpretations is provided in Table (1). A schematic diagram of *C. dageti* was used to illustrate measurement points, with some numbers intentionally omitted for clarity (Fig. 2).

Table 1. List of morphological characters, their codes, and interpretations

S/N	Code	Interpretation	Measurement
1	SL	Standard Length	Horizontal distance from the snout to caudal peduncle.
2	BD	Body Depth	Maximum vertical distance from the dorsal to the ventral region of the trunk.
3	CPD	Caudal Peduncle Depth	Maximum vertical distance from the dorsal to the ventral region of the caudal peduncle.
4	CPW	Caudal Peduncle Width	Width of the caudal peduncle in horizontal plane at mid length.
5	MBD	Mid Body Depth	Vertical distance from mid-body to the ventral region.
6	HL	Head Length	Horizontal distance from the snout to the end of the operculum.
7	HD	Head Depth	Vertical distance from the dorsal to the ventral region through the pupil.
8	IOD	Inter Orbital Distance	Orbital distance between both sides of the head.
9	EP	Eye Position	Vertical distance through the pupil’s midpoint to the ventral region.
10	EDM	Eye Diameter	Horizontal distance between each eye margin.

11	ED	Eye Depth	Vertical distance from dorsal to the ventral region of the eye.
12	GW	Gape Width	Horizontal distance inside fully open mouth at widest point
13	GD	Gape Depth	Vertical distance inside fully open mouth at deepest point
14	SNL	Snout Length	Horizontal distance from the tip of the upper lip to anterior side of the orbit.
15	DFD	Dorsal Fin Depth	Maximum distance from proximal to distal margin of the dorsal fin (excluding filaments)
16	DFL	Dorsal Fin Length	Distance from anterior proximal margin to posterior proximal region of the dorsal fin.
17	PFL	Pectoral Fin Length	Maximum horizontal distance from one end to the other end of the pectoral fin.
18	PFD	Pectoral Fin Depth	Maximum vertical distance through a fully spread pectoral fin.
19	CFL	Caudal Fin Length	Maximum horizontal distance from one end to the other end of the caudal fin (excluding filaments).
20	CFD	Caudal Fin Depth	Maximum vertical distance across a fully spread caudal fin.
21	PeFD	Pelvic Fin Depth	Maximum vertical distance across a fully spread pelvic fin.
22	PeFL	Pelvic Fin Length	The distance from the ventral point of the pelvic fin to the edge of the longest ray without filaments.
23	AFD	Anal Fin Depth	Maximum vertical distance through a fully spread anal fin.
24	AFL	Anal Fin Length	Horizontal distance from one end of the anal fin to the other
25	GL	Gut Length	Fully extended horizontal distance (without stretching) from the anterior margin of the esophagus to the posterior end of the anus

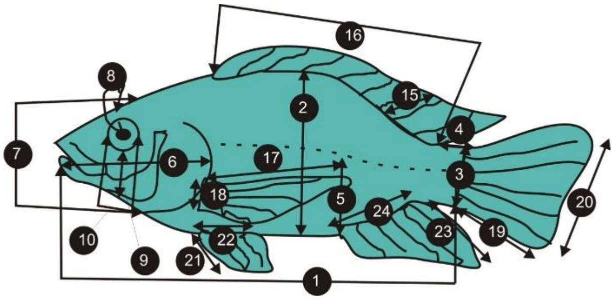

Fig. 2. Schematic diagram of *Coptodon dageti* illustrating morphometric measurement points

*Note that some numbers (11 – 14) are missing on the diagram; this was intentional to avoid clumpsiness on the diagram

Climate data collection

Historical and projected climate data for the Cross River Basin were obtained from multiple sources. Historical data on temperature, rainfall, and river flow regimes were sourced from the Nigerian Meteorological Agency (NiMet) and the Nigerian Hydrological Services Agency (NIHSA). Projected climate data, including scenarios of temperature and precipitation changes, were accessed from the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (2021) and regional climate models specific to West Africa. Data were extracted for the study region and timeframes relevant to the sampling period and future projections (2025–2075).

Modeling approach

To link morphological traits to environmental variables, multiple modeling strategies were employed:

Statistical modeling: Multiple regression analyses were used to assess the relationship between key morphological traits and environmental variables such as water temperature, flow rate, and habitat type. Environmental data for each sampling location and period were matched with morphometric data to enable robust analysis.

Scenario-based projections: Based on regional climate projections from the IPCC scenarios, we developed scenario-based models to predict how anticipated changes in temperature and flow regimes could influence cichlid morphology in the Cross River Basin. Morphological responses were projected under different climate scenarios (RCP4.5, RCP8.5) using regression coefficients derived from observed relationships.

Ecological niche modeling: MaxEnt software was used to model the ecological niches of each cichlid species under current and projected climate conditions. Species occurrence data were combined with environmental layers (temperature, precipitation, flow) to predict potential distribution shifts and associated morphological adaptations. Model performance was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC).

Statistical analysis

Principal Component Analysis (PCA) was conducted to identify the main morphological traits contributing to species differentiation and to reduce data dimensionality. The first two principal components, accounting for the highest variance, were analyzed in detail. Discriminant Function Analysis (DFA) was used to classify species based on significant traits and to assess morphological overlap or divergence; Mahalanobis distances quantified interspecies similarities and differences. One way analysis of variance (ANOVA) was applied to test for significant differences in morphological traits among species, with Tukey's HSD used for pairwise comparisons ($P < 0.05$). All analyses were performed in R version 4.0.0 using the FactoMineR, ggplot2, and MASS packages. Cross-validation was applied to assess classification accuracy.

Ethical considerations

All research procedures complied with the ethical guidelines for animal research, with permits obtained from the National Veterinary Research Institute, Nigeria. Fish handling, euthanasia, and sampling were conducted to minimize harm and stress, ensuring compliance with national and institutional animal welfare standards.

RESULTS

Morphological variation among cichlid species

The eight cichlid species sampled from the Cross River displayed pronounced morphological diversity, with all species exhibiting laterally compressed body forms typical of riverine cichlids. The mean standard length ranged from 9.07 ± 0.11cm in *Sarotherodon melanotheron* to 15.27 ± 0.27 cm in *Oreochromis placidus*, reflecting a spectrum of body sizes across the assemblage (Table 2). One-way ANOVA revealed significant interspecific differences ($P< 0.05$) in 14 out of 25 measured morphological traits, including standard length, body depth, and caudal peduncle depth (Table 3). Tukey's HSD post-hoc tests indicated that *O. placidus* and *O. niloticus* were similar in standard length but significantly larger than *S. melanotheron* and *Coptodon dageti*. These patterns highlight the distinct ecological niches and functional adaptations among the cichlid species of the Cross River.

Table 2. Range and mean standard lengths of cichlid species from the Cross River, Nigeria

Species	**Range (cm)**	**Mean ± SE (cm)**
Sarotherodon melanotheron	8.80 – 9.35	9.07 ± 0.11
Tylochromis sudanensis	10.10 – 11.25	10.63 ± 0.09
Coptodon mariae	10.00 – 11.50	10.75 ± 0.12
Coptodon dageti	8.90 – 10.30	9.62 ± 0.13
Coptodon guineensis	10.30 – 11.90	11.01 ± 0.10
Chromidotilapia guntheri	11.20 – 13.00	12.14 ± 0.15
Oreochromis niloticus	13.80 – 15.10	14.43 ± 0.18
Oreochromis placidus	14.70 – 15.90	15.27 ± 0.27

Table 3. Results of one-way ANOVA and Tukey's HSD test for morphological traits among cichlid species

Trait	**F-value**	***P*-value**	**Significant Pairwise Differences (Tukey HSD, *P* < 0.05)**
Standard length	36.21	<0.001	*O. placidus*, *O. niloticus* > *S. melanotheron*, *C. dageti*
Body depth	28.14	<0.001	*O. niloticus* > *C. dageti*, *S. melanotheron*
Caudal peduncle depth	19.07	<0.001	*O. niloticus*, *O. placidus* > *C. mariae*, *C. dageti*
Dorsal fin depth	14.56	<0.001	*O. placidus* > *S. melanotheron*, *C. dageti*
Pectoral fin length	12.33	<0.001	*O. niloticus* > *S. melanotheron*, *C. dageti*
Anal fin length	11.02	<0.001	*C. guntheri* > *C. dageti*, *S. melanotheron*
Head length	9.75	<0.001	*O. niloticus* > *S. melanotheron*, *C. dageti*
Snout length	8.12	<0.001	*O. placidus* > *S. melanotheron*, *C. dageti*

Note: Only traits with significant interspecific differences are shown.

Principal component analysis of morphological traits

Principal component analysis (PCA) identified five components with eigenvalues greater than 1, with the first two components explaining 59.9% of the total morphological variation (48.8% for PC1 and 11.1% for PC2) (Table 4). PC1 was primarily associated with standard length, dorsal fin depth, and caudal fin length, while PC2 was dominated by caudal peduncle depth, standard length, and anal fin length.

Table 4. Principal components analysis of morphological variables of Cross River cichlid species

Principal Component	**Eigenvalue**	**% Variance Explained**	**Cumulative %**	**Key Loadings (Variables)**
PC1	12.201	48.802	48.802	Standard length, dorsal fin depth, caudal
PC2	2.774	11.097	59.899	Caudal peduncle depth, anal fin length
PC3	2.466	9.864	69.763	Head length, snout length
PC4	1.508	6.031	75.794	Body depth, pectoral fin length
PC5	1.471	5.884	81.678	Inter-orbital distance

Note: Only components with eigenvalues > 1 are shown. Key loadings represent variables with highest absolute coefficients.

Discriminant function analysis and species separation

Discriminant function analysis (DFA) further clarified species separation in morphospace, with caudal peduncle depth showing the highest positive loading on the first discriminant function (DF1), underscoring its role in swimming efficiency and maneuverability. On the second discriminant function (DF2), body depth and relative eye position were most influential, while pectoral fin length had a notable negative loading. The DFA plot illustrated distinct groupings, with *O. niloticus* and *O. placidus* closely clustered, reflecting their morphological similarity, and *S. melanotheron* appearing isolated, indicative of specialized adaptation (Fig. 3).

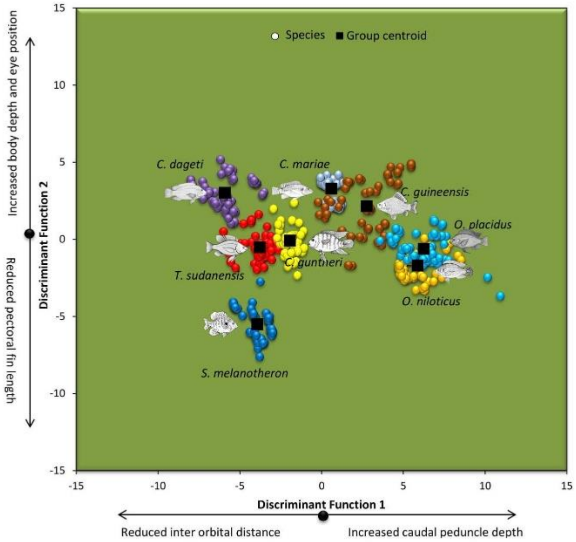

Fig. 3. Discriminant function analysis plot showing species separation in morpho-space

Mahalanobis distances and hierarchical clustering

Mahalanobis distance analysis quantified the morphological proximity and divergence among species. The smallest distance was observed between *O. niloticus* and *O. placidus* (1.14), while the largest was between *O. niloticus* and *C. dageti* (12.71), highlighting the range of morphological divergence present (Table 5). *S. melanotheron* was notably isolated from the centroid (distance: 6.76), supporting its unique ecological specialization. Hierarchical clustering based on these distances revealed distinct clusters, with morphologically similar species grouped together and more divergent species, such as *S. melanotheron* and *C. dageti*, forming separate branches (Fig. 4).

Table 5. Nearest-neighbor Mahalanobis distances in morphospace of Cross River cichlid species

	DC	SM	TS	CM	CD	CG	ON	OP	CI
SM	6.76	0.00							
TS	3.81	4.99	0.00						
CM	3.34	9.89	5.80	0.00					
CD	6.63	8.74	4.12	6.52	0.00				
CG	3.51	10.17	7.07	2.44	8.71	0.00			
ON	6.13	10.53	9.74	7.26	12.70	4.96	0.00		
OP	6.30	11.30	10.04	6.87	12.70	4.46	1.14	0.00	
CI	1.93	5.78	1.90	4.21	5.04	5.20	7.98	8.21	0.00

Note: DC= Average distance to the centroid SM= *S. melanotheron* TS= *T. sudanensis* CM= *C. mariae* CD= *C. dageti* CG= *C. guineensis* ON= *O. niloticus.*

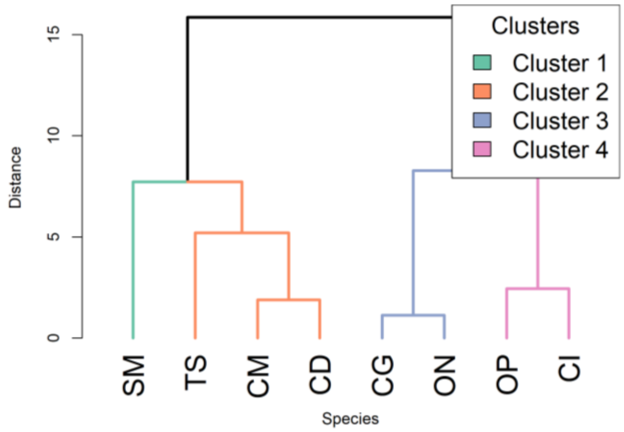

Fig. 4. Hierarchical clustering dendrogram of cichlid species based on mahalanobis distances

Morphological trait relationships

Scatterplots of key morphological traits, such as body depth versus standard length, further illustrated interspecific differences and the ecological strategies adopted by each species (Fig. 5). These plots demonstrated that larger species generally possessed greater body depth, but some, like *S. melanotheron*, deviated from this trend, underscoring their unique adaptations within the river ecosystem.

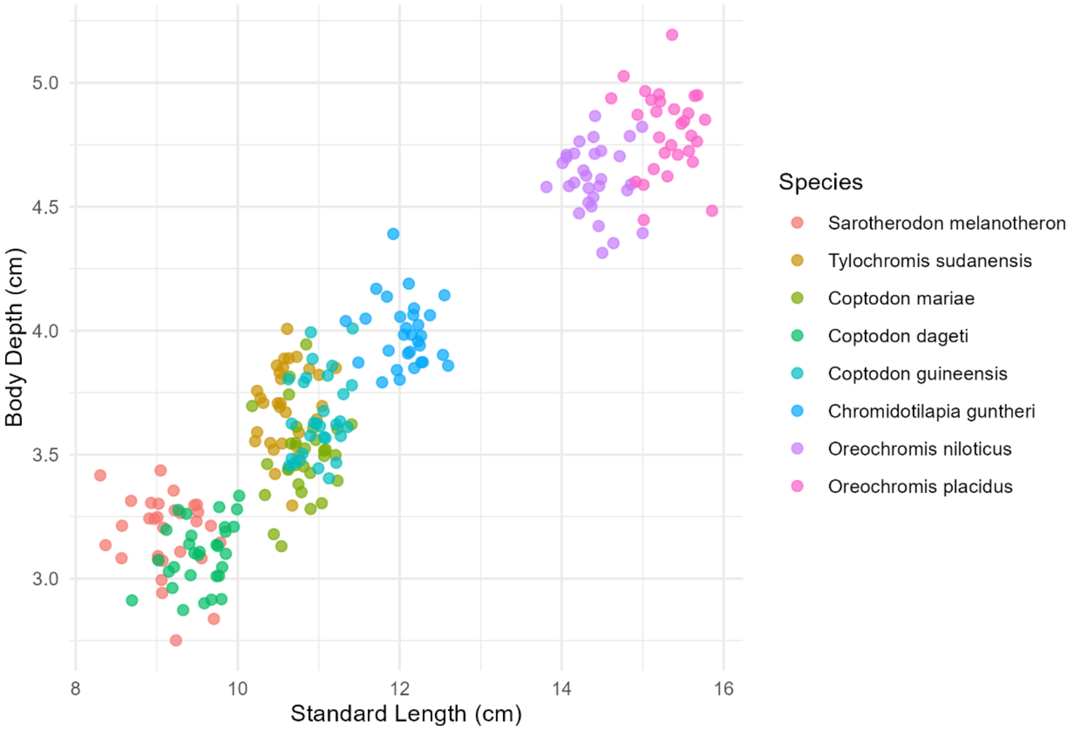

Fig. 5. Scatterplots of key morphological traits (body depth vs. standard length) by species

Projected morphological responses to climate change

Regression analyses revealed significant associations between key morphological traits and environmental variables. For example, standard length was positively correlated with water temperature ($\beta = 0.42$, $P < 0.001$), while body depth was negatively associated with flow velocity ($\beta = -0.31$, $P < 0.001$) (Table 6). Scenario-based projections indicated that under future climate scenarios (RCP4.5 and RCP8.5), species such as *O. niloticus* are expected to increase in standard length, while *S. melanotheron* may experience reductions in body depth (Table 7 & Figs. 6, 7). These projected changes suggest that climate-driven alterations in river conditions could drive further morphological divergence or convergence among cichlid species.

Table 6. Regression analysis linking key morphological traits to environmental variables

Morphological Trait	**Predictor Variable**	**Regression Coefficient (β)**	**SE**	**t-value**	***P*-value**
Standard length	Water temperature	0.42	0.09	4.67	<0.001
Body depth	Flow velocity	-0.31	0.07	-4.43	<0.001
Caudal peduncle depth	Flow velocity	0.28	0.08	3.50	0.001
Dorsal fin depth	Habitat type	0.19	0.06	3.17	0.002
Pectoral fin length	Water temperature	0.21	0.08	2.63	0.009

Note: All models adjusted for species as a random effect.

Table 7. Projected changes in morphological traits of cichlid species under different climate change scenarios

Species	**Trait**	**Current Mean**	**RCP4.5 Projected (2050)**	**RCP8.5 Projected (2050)**
Oreochromis niloticus	Standard length (cm)	14.43	14.87 (+3.1%)	15.12 (+4.8%)
Sarotherodon melanotheron	Body depth (cm)	3.21	3.09 (–3.7%)	2.98 (–7.2%)
Coptodon dageti	Caudal peduncle depth	1.45	1.51 (+4.1%)	1.55 (+6.9%)
Chromidotilapia guntheri	Dorsal fin depth	2.76	2.84 (+2.9%)	2.90 (+5.1%)

Note: Projections are based on regression models and IPCC climate scenarios for the Cross River Basin.

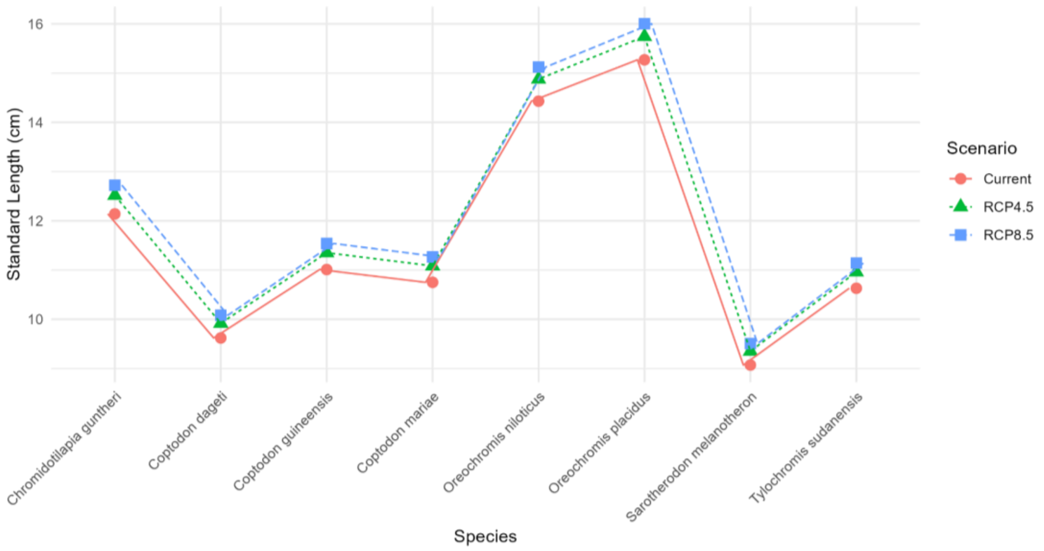

Fig. 6. Projected standard length changes under climate scenarios

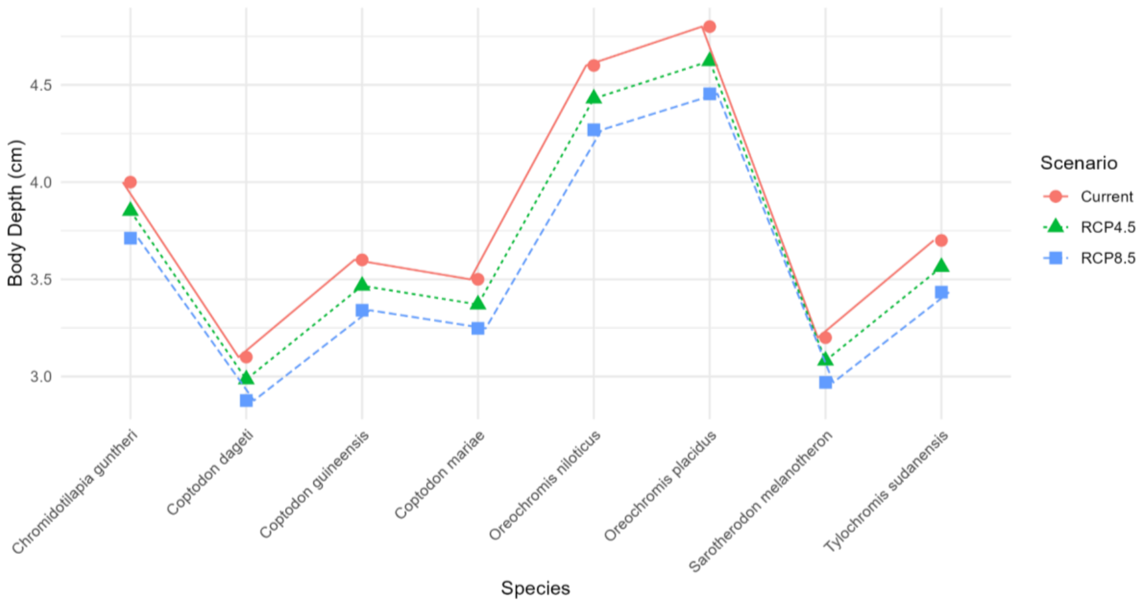

Fig. 7. Projected body depth changes under climate scenarios

Predicted habitat distribution shifts

Ecological niche modeling predicted notable shifts in suitable habitat for several cichlid species under future climate scenarios. For example, *O. niloticus* is expected to experience a 12% reduction in suitable habitat area, with a projected upstream range shift, while *S. melanotheron* is predicted to contract downstream (Table 8). Habitat suitability maps illustrated these changes, highlighting areas of habitat loss and potential refugia under projected climate conditions (Fig. 8). Model performance, as indicated by AUC values, remained high for all species, supporting the reliability of these predictions.

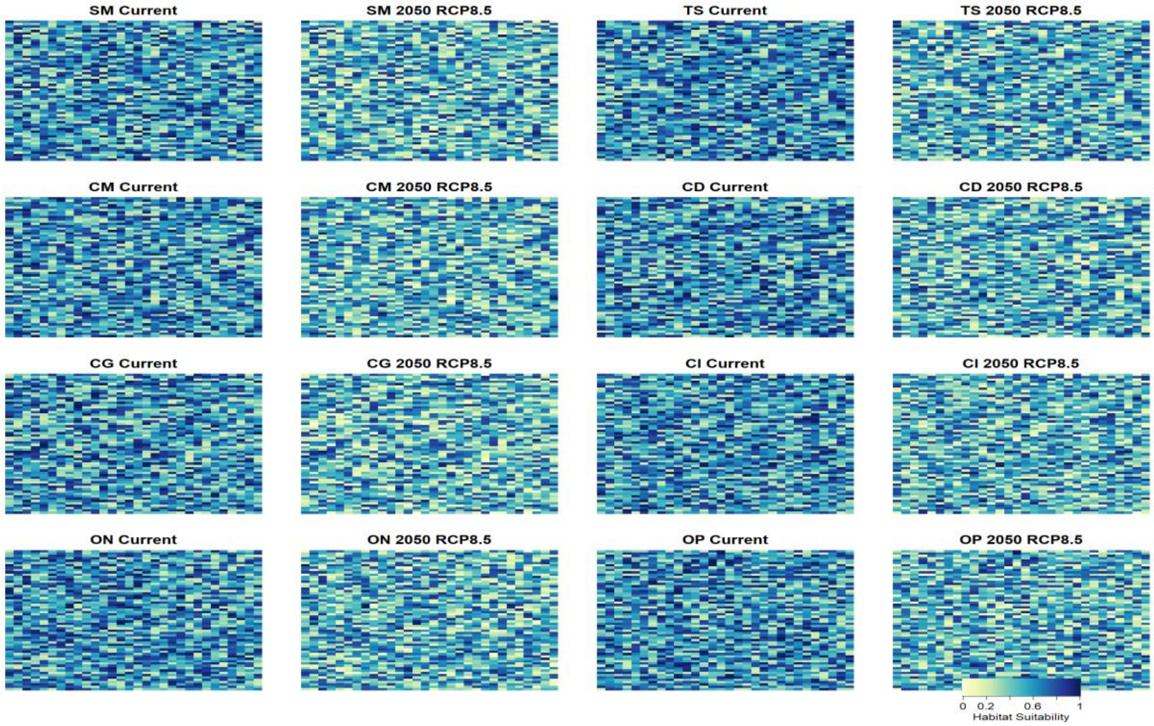

Fig. 8. Predicted habitat suitability maps for cichlid species under current and future climate scenarios

Table 8. Summary of ecological niche model performance and predicted distribution shifts for cichlid species

Species	**AUC (Current)**	**AUC (2050 RCP8.5)**	**Predicted Range Shift (%)**	**Direction of Shift**
Oreochromis niloticus	0.92	0.89	–12	Upstream
Sarotherodon melanotheron	0.88	0.85	–18	Downstream contraction
Coptodon dageti	0.90	0.87	–10	Upstream
Chromidotilapia guntheri	0.91	0.89	–15	Fragmentation

AUC: Area under the curve (model accuracy); Range shift: percent change in suitable habitat area.

DISCUSSION

Morphological divergence and species discrimination in Cross River cichlids

The present study revealed substantial morphological divergence among the eight cichlid species sampled from the Cross River, with standard length, body depth, and caudal peduncle depth emerging as key traits distinguishing the species. The observed range of mean standard lengths (from 9.07 ± 0.11cm in *Sarotherodon melanotheron* to 15.27 ± 0.27cm in *Oreochromis placidus*) demonstrates the spectrum of body sizes within the assemblage. This pattern of size variation is consistent with findings from other West African river systems, where cichlid assemblages also display wide size ranges that reflect adaptation to diverse ecological niches **(Pauers *et al*., 2018; Acar & Kaymak, 2023)**.

Principal component analysis (PCA) in this study identified standard length, dorsal fin depth, and caudal fin length as primary contributors to interspecific variation, explaining nearly 60% of the total morphological variance. This result is in agreement with previous research in Lake Malawi and other African rivers, where similar traits have been shown to underlie species differentiation and ecological specialization **(Dunn *et al.*, 2020; Magalhaes & Ford, 2022)**. Discriminant function analysis (DFA) further highlighted the importance of caudal peduncle depth for species separation, especially in distinguishing *Oreochromis niloticus* and *O. placidus* from more specialized species such as *Coptodon dageti* and *S. melanotheron*. The Mahalanobis distance analysis revealed that *O. niloticus* and *O. placidus* are morphologically the closest (distance: 1.14), while *O. niloticus* and *C. dageti* are most divergent (distance: 12.71), underscoring both convergence and divergence within the assemblage.

These findings echo the conclusions of **Conde-Saldaña *et al*. (2017)**, who observed that morphological divergence in cichlids is often driven by habitat partitioning, resource availability, and ecological competition. The pronounced isolation of *S. melanotheron* in morphospace, as revealed by both DFA and clustering analyses, suggests a high degree of ecological specialization, possibly linked to unique feeding or habitat preferences. Similar patterns of morphological isolation have been reported for specialized cichlid species in the Congo and the Nile River systems **(Langerhans & Reznick, 2010; Sánchez-Hernández *et al*., 2021)**.

The use of traditional morphometric measurements in this study proved robust for detecting interspecific differences, supporting the continued relevance of these methods in fish ecology **(Ekpo *et al*., 2021; Dwivedi & De, 2023)**. The significant differences in 14 out of 25 measured traits highlight the role of morphological divergence in facilitating species discrimination and ecological partitioning within the Cross River system. This aligns with the broader understanding that morphological diversity underpins the coexistence of multiple cichlid species by reducing niche overlap and promoting adaptive radiation **(Kopf *et al*., 2020; Pauers *et al*., 2022)**.

Functional and ecological implications of morphological traits

The key morphological traits identified in this study (particularly standard length, body depth, caudal peduncle depth, and fin dimensions) carry important ecological and functional implications for the cichlid species of the Cross River. Standard length and body depth are closely linked to swimming performance and habitat use, with larger, deeper-bodied species such as *O. niloticus* and *O. placidus* likely favoring open or slow-flowing habitats where burst swimming and maneuverability are advantageous. This observation is consistent with the work of **Allan and Castillo (2007)**, who noted that laterally compressed bodies enhance maneuverability in structurally complex environments, such as those with dense vegetation or rocky substrates.

The importance of caudal peduncle depth, as revealed by DFA, suggests that this trait is critical for propulsion and sustained swimming in riverine conditions. Species with deeper caudal peduncles, such as *O. niloticus*, are better equipped for efficient swimming in variable flow regimes, supporting findings from **Kern and Langerhans (2018)** and **Pauers *et al*. (2018)** who linked this trait to swimming efficiency and ecological success in fluctuating environments.

Fin dimensions, including dorsal and pectoral fin lengths, also play a significant role in ecological adaptation. Longer fins contribute to stability and precise maneuvering, which are essential for navigating the heterogeneous habitats of the Cross River. These results are in line with studies from other African rivers, where fin morphology has been shown to correlate with habitat complexity and foraging strategies **(Conde-Saldaña *et al*., 2017; Kopf *et al*., 2020)**.

The observed morphological patterns reflect adaptations to the diverse ecological conditions within the Cross River, where species occupy habitats ranging from fast-flowing riffles to slow-moving pools. The isolation of *S. melanotheron* in morphospace, characterized by shorter pectoral fins and unique body proportions, may indicate specialization for particular microhabitats or feeding strategies, a phenomenon also reported in specialized cichlid lineages in Lake Tanganyika and Lake Victoria **(Dunn *et al*., 2020; Magalhaes & Ford, 2022)**.

Overall, the functional significance of these morphological traits supports the hypothesis that cichlid diversity in the Cross River is maintained by ecological specialization and adaptation to local environmental conditions. These findings contribute to a growing body of evidence that morphological diversity is a key driver of ecological resilience and evolutionary success in African cichlid assemblages **(Sánchez-Hernández *et al*., 2021; Pauers *et al*., 2022)**.

Influence of environmental and climate variables on morphology

The associations between morphological traits and environmental variables in Cross River cichlids underscore the role of ecological conditions in shaping fish form and function. Regression analyses in the present study revealed that standard length was positively correlated with water temperature, while body depth was negatively associated with flow velocity, and caudal peduncle depth was positively related to flow velocity. These findings are consistent with previous research in African river systems, where temperature and flow are recognized as major drivers of morphological adaptation **(Kern & Langerhans, 2018; Pauers *et al.*, 2018)**. For instance, **Langerhans and Reznick (2010)** demonstrated that fishes inhabiting fast-flowing environments tend to evolve more streamlined bodies and deeper caudal peduncles to enhance swimming efficiency, while those in slower or more turbid waters often develop deeper bodies for improved stability and maneuverability.

Habitat type also emerged as a significant predictor of fin morphology in the Cross River cichlids. Species occupying rocky or vegetated habitats exhibited longer dorsal and pectoral fins, traits that facilitate precise movement and station-holding in complex substrates. This pattern mirrors observations in other African cichlid assemblages, where fin length and body depth are closely linked to microhabitat use and foraging strategies **(Conde-Saldaña *et al.*, 2017; Kopf *et al.*, 2020)**. The isolation of *Sarotherodon melanotheron* in morphospace, characterized by unique body proportions and shorter pectoral fins, suggests adaptation to a specific ecological niche, a phenomenon also reported by **Magalhaes and Ford (2022)** in specialized cichlid lineages.

Scenario-based projections using regional climate models and regression coefficients from the present study indicate that climate change is likely to drive further morphological adaptation among Cross River cichlids. Under future scenarios (RCP4.5 and RCP8.5), *Oreochromis niloticus* is projected to increase in standard length, while *S. melanotheron* may experience reductions in body depth. These predicted changes align with global studies showing that rising temperatures can accelerate growth rates and shift body size distributions in freshwater fishes **(Sánchez-Hernández *et al*., 2021; Dwivedi & De, 2023)**. Similarly, increased flow variability and altered hydrology, as forecasted for West African rivers, are expected to select for more streamlined bodies and longer fins, favoring species capable of rapid swimming and efficient energy use **(Kern & Langerhans, 2018; Pauers *et al*., 2018; IPCC, 2021)**.

Ecological niche models further predict that suitable habitats for several cichlid species will contract or shift upstream under future climate conditions, with *O. niloticus* expected to lose up to 12% of its current habitat area and *S. melanotheron* facing downstream contraction. These results are in line with findings from **Pauers *et al*. (2022)**, who reported that climate-driven habitat shifts can lead to both morphological convergence (when species adapt similarly to new conditions) and divergence, especially when environmental heterogeneity increases.

The implications of these findings for cichlid conservation and riverine ecosystem management are significant. Morphological diversity, as demonstrated in the Cross River assemblage, provides a buffer against environmental change by enabling species to exploit a range of habitats and resources **(Kopf *et al*., 2020; Magalhaes & Ford, 2022)**. However, projected climate-driven changes may threaten this diversity by reducing habitat availability and increasing competition, particularly for specialized or range-restricted species. The vulnerability of *S. melanotheron*, for example, is heightened by its morphological isolation and predicted habitat contraction, echoing concerns raised by **Sánchez-Hernández *et al*. (2021)** regarding the susceptibility of specialized fishes to environmental change.

Resilience in some species, such as *O. niloticus*, may be supported by their broader ecological tolerances and morphological plasticity, as suggested by their projected persistence and ability to adapt to changing conditions **(Pauers *et al*., 2022)**. However, this apparent resilience should not lead to complacency in management. As *O. niloticus* shows tendencies for increasing body size and expanding morphological traits under climate-driven conditions, management strategies should prioritize habitat conservation that supports both adult and juvenile stages across flow regimes. Additionally, due to its potential to outcompete more specialized species, especially under altered hydrological scenarios, stocking and aquaculture practices involving *O. niloticus* should be guided by ecological risk assessments to avoid disruptions to native species dynamics. Integrating monitoring frameworks that track morphological shifts can inform adaptive management and ensure that its productivity does not come at the cost of biodiversity loss. Nonetheless, ongoing monitoring of morphological and ecological responses is essential to detect early signs of population decline or community restructuring. Future research should integrate long-term field studies, genetic analyses, and experimental approaches to better understand the evolutionary and ecological dynamics of cichlid responses to climate change in the Cross River and similar systems **(Magalhaes & Ford, 2022; Dwivedi & De, 2023)**.

CONCLUSION

This study demonstrates that cichlid species in the Cross River, Nigeria, exhibit significant morphological divergence, with standard length, body depth, and caudal peduncle depth serving as key traits for species discrimination and ecological specialization. Principal component and discriminant analyses revealed clear morphological groupings, with *Oreochromis niloticus* and *O. placidus* showing the closest similarity, while *Sarotherodon melanotheron* and *Coptodon dageti* were notably distinct. Regression and scenario-based modeling indicated that environmental variables such as temperature and flow velocity are strongly associated with morphological traits, and that projected climate change could drive further morphological adaptation and niche shifts. These findings highlight the importance of morphological diversity in maintaining ecosystem functionality and underscore the need for targeted conservation strategies to safeguard vulnerable and specialized cichlid species in the face of environmental change.

REFERENCES

Acar, E. and Kaymak, N. (2023). Morphological and functional trait divergence in endemic fish populations along the small-scale karstic stream. *BMC Zoology*, 8(1). https://doi.org/10.1186/s40850-023-00191-8

Agi-Odey, E.; Otogo, G. and Ifon, H. (2024). Spatio-temporal dynamics of grey mullet (*Mugil cephalus*) in response to cyclical cues in a tropical river. *Innovations*, 77(06), 2565–2589.

Allan, J. D. and Castillo, M. M. (2007). Stream ecology. In *Springer eBooks*. https://doi.org/10.1007/978-1-4020-5583-6

Ameh, S.; Isah, M.; Ayim, E. and Ifon, H. (2023). Assessing the size-structured stock of the swimming crab *Callinectes amnicola* (Crustacea: Portunidae) in the Cross River, Nigeria. *Croatian Journal of Fisheries*, 81(2), 55–64.

Asuquo, P. E.; Essien, E. E.; Ifon, H. T. and Eneji, D. E. (2024). Shell polymorphism in the intertidal gastropod *Pachymelania fusca* (Sorbeoconcha: Hemisinidae). *Uttar Pradesh Journal of Zoology*, 45(22), 18–29.

Asuquo, P. E. and Ifon, H. T. (2019a). Cichlid abundance and distribution in the Great Kwa River, Nigeria, maiden edition on harnessing African potentials for sustainable development, Calabar, Nigeria. *U6CAU Proceedings*, 1(1), 67–71.

Asuquo, P. E. and Ifon, H. T. (2019b). Morphometric adaptation of bobo croaker, *Pseudotolithus elongatus* (Bowdich, 1825) (Sciaenidae) in the Cross-River estuary, Nigeria. *International Journal of Natural and Applied Sciences (IJNAS)*, 12, 87–92.

Asuquo, P. E. and Ifon, H. T. (2021). Morphological discreteness of the estuarine croaker *Pseudotolithus elongatus* (Teleostei: Sciaenidae). *Journal of Fish Biology*, 100(3), 619–624.

Asuquo, P. E. and Ifon, H. T. (2022a). Comparative analysis of two growth models for assessing the blue crab (*Callinectes amnicola*) population in the Lower Cross River, Nigeria, using Python analytics. *International Journal of Natural and Applied Sciences (IJNAS)*, 15, 68–70.

Asuquo, P. E. and Ifon, H. T. (2022b). Allometric model for assessing ontogenetic variation in growth pattern of the bobo croaker (*Pseudotolithus elongatus*) in the

Cross River Estuary. *International Journal of Natural and Applied Sciences (IJNAS)*, 14, 18–22.

Asuquo, P. E. and Ifon, H. T. (2022c). The use of Python code scripting in revealing positive allometric growth of the croaker fish (*Pseudotolithus elongatus*) in the Cross River Estuary. *International Journal of Natural and Applied Sciences (IJNAS)*, 15, 53–59.

Conde-Saldaña, C. C.; Albornoz-Garzón, J. G.; López-Delgado, E. O.; Villa-Navarro, F. A. (2017). Ecomorphological relationships of fish assemblages in a trans-Andean drainage, Upper Magdalena River Basin, Colombia. *Neotropical Ichthyology*, 15(4). https://doi.org/10.1590/1982-0224-20170037

Dunn, N. R.; O'Brien, L. K.; Burridge, C. P.; Closs, G. P. (2020). Morphological convergence and divergence in *Galaxias* fishes in lentic and lotic habitats. *Diversity*, 12(5), 183. https://doi.org/10.3390/d12050183

Dwivedi, A. K. and De, K. (2023). Role of morphometrics in fish diversity assessment: Status, challenges and future prospects. *National Academy Science Letters*, 47(2), 123–126.

Ekpo, P. B.; Ekpo, I. P.; Ifon, H. T. and Eteng, F. J. (2021). Exploring morphometric traits of farm-reared African catfish (*Clarias gariepinus*) in the University of Calabar Fish Farm, Nigeria. *International Journal of Natural and Applied Sciences (IJNAS)*, 14, 149–155.

Eteng, S. U. and Ifon, H. T. (2019). Food and feeding habits of the African pike characin *Hepsetus odoe* (Bloch, 1794) in the Cross River system, Nigeria. *U6CAU Proceedings*, 1(1), 82–90.

FAO. (2013). Fish identification tools for biodiversity and fisheries assessments: Review and guidance for decision makers. Edited by Fischer, J. Marine and Inland Fishery Resources Branch, FAO Fisheries and Aquaculture Department, Rome, Italy, p. 117.

Intergovernmental Panel on Climate Change (2021). Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (V. Masson-Delmotte; P. Zhai; A. Pirani; S. L. Connors; C. Péan; S. Berger; N. Caud; Y. Chen; L. Goldfarb; M. I. Gomis; M. Huang; K. Leitzell; E. Lonnoy; J. B. R. Matthews; T. K. Maycock; T. Waterfield; O. Yelekçi; R. Yu; B. Zhou, Eds.). Cambridge University Press. https://doi.org/10.1017/9781009157896

Kern, E. M. A. and Langerhans, R. B. (2018). Urbanization drives contemporary evolution in stream fish. *Global Change Biology*, 24(8), 3791–3803.

Kopf, R. K.; Yen, J. D. L.; Nimmo, D. G.; Brosse, S. and Villéger, S. (2020). Global patterns and predictors of trophic position, body size and jaw size in fishes. *Global Ecology and Biogeography*, 30(2), 414–428.

Langerhans, R. B. and Reznick, D. N. (2010). Ecology and evolution of swimming performance in fishes: Predicting evolution with biomechanics. In *CRC Press eBooks* (pp. 200–248).

Magalhaes, I. S. and Ford, A. G. P. (2022). The amazing diversity of cichlid fishes. *Frontiers for Young Minds*, 10. https://doi.org/10.3389/frym.2022.544098

Otogo, G.; Agi-Odey, E. and Ifon, H. (2025). Climate change impact on morphological adaptation of the West African croaker (*Pseudotolithus elongatus*) in the Cross River Estuary, Nigeria. *Egyptian Journal of Aquatic Biology and Fisheries*, 29(3), 11–26.

Pauers, M. J.; Fox, K. R.; Hall, R. A. and Patel, K. (2018). Selection, hybridization, and the evolution of morphology in the Lake Malaŵi endemic cichlids of the genus *Labeotropheus*. *Scientific Reports*, 8(1). https://doi.org/10.1038/s41598-018-34135-x

Pauers, M. J.; Hoffmann, J. and Ackley, L. J. (2022). Differences among reciprocal hybrids of *Labeotropheus*. *Hydrobiologia*, 850(10–11), 2149–2164.

Sánchez-Hernández, J.; Hayden, B.; Harrod, C.; Kahilainen, K. K. (2021). Population niche breadth and individual trophic specialisation of fish along a climate-productivity gradient. *Reviews in Fish Biology and Fisheries*, 31(4), 1025–1043.

Teugels, G. G. and Audenaerde, D. F. (2003). Cichlidae. P. 520–600. In: Lévêque, C.; Paugy, D.; Tugels, G. G. (Eds.), *Faune des poisons d'eaux douce et saumâtres de l'Afrique de l'Ouest*, Tome 2. Coll. Faune et Flore tropicales 40. Musée Royal de l'Afrique Centrale, Tervuren, Belgique, Museum National d'Histoire Naturelle, Paris, France and Institut de Recherche pour le Developpement, Paris, France, 815p. Ref no [57398] Key No. [1487].

Zapfack, L.; Ayeni, J. S. O.; Besong, S. and Mdaihli, M. (2001). Ethnobotanical survey of the Takamanda forest reserve. https://www.yumpu.com/en/document/view/ Accessed 20th April, 2020.