



Exploring shape and size variation in *Schizodon fasciatus* (Characiformes: Anostomidae) across the Catatumbo river basin, Colombia

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Abstract

Colombia is home to a rich diversity of freshwater species, including *Schizodon fasciatus*, an important fish in the Catatumbo sub-basin that serves as a critical resource for local food security. However, agricultural activities and ecosystem alterations threaten its populations. This study examines the morphological variability of *S. fasciatus* from two tributaries of the Catatumbo sub-basin, the Grita and El Zulia rivers, using geometric morphometrics to assess how habitat conditions influence body shape. The results showed significant shape variation between populations. Specimens from Puerto Santander (Grita River) revealed longer pectoral fins, while those from El Zulia showed more compact bodies. These differences were influenced by environmental parameters such as conductivity, pH, salinity, temperature, and dissolved oxygen. The Grita River, with better-conserved riparian zones, provided conditions supporting more hydrodynamically adapted shapes, whereas the El Zulia River, heavily impacted by deforestation and agricultural runoff, was associated with compact body shapes and higher phenotypic variability. This research highlights the importance of habitat quality in shaping the morphology of *S. fasciatus*. By linking environmental stressors to morphological adaptations, the findings contribute to understanding the ecomorphological behavior of *S. fasciatus*, providing a foundation for its conservation and sustainable management in the Catatumbo sub-basin.

Keywords Morphological variation · Geometric morphometrics · Shape · Fishes · Catatumbo

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Introduction

Colombia is home to 1610 freshwater fish species, making it the second most biodiverse country in this category after Brazil (DoNascimento et al. 2017; Maldonado-Ocampo et al. 2019). The Catatumbo River sub-basin, a region with exceptionally high ichthyological diversity per unit area, hosts 127 recorded freshwater fish species, 61 of which have restricted distributions (Lasso-Alcalá et al. 2012; Ortega-Lara et al. 2012). The Catatumbo River spans an area of 25,600 km², flowing from Colombia into Venezuela. The upper and part of the middle basin are located within Colombian territory, encompassing 16,565 km² (76.5% of the sub-basin), including the department of Norte de Santander (IGAC 2003; Ortega-Lara et al. 2012). The lower basin lies in Venezuela, covering 9035 km² (23.5% of the sub-basin), traversing a protected area—the Juan Manuel Wildlife Refuge, Aguas Blancas, and Aguas Negras—before draining into Lake and Bay El Tablazo, an estuarine zone within the Maracaibo Lake system in Zulia State (Yépez et al. 2009; Ortega-Lara et al. 2012).

The sub-basin features a heterogeneous landscape and complex topography, supporting a variety of ecosystems such as páramos and piedmonts (Galvis et al. 1997). However, it faces significant environmental challenges, including frequent oil spills, water extraction for irrigation, deforestation of riparian forests, and pesticide contamination. These factors contribute to the degradation of aquatic ecosystem health (Colonnello and Lasso-Alcalá 2011). Such disturbances reduce biodiversity by decreasing population sizes, restricting gene flow, and promoting contaminant bioaccumulation. As a result, ecosystem equilibrium is disrupted, fishery resources are diminished, and the food security of communities relying on these ecological systems is jeopardized (Dias et al. 2017; Mohanty et al. 2019). Most people living in the Catatumbo region rely on subsistence fishing as their main source of food. This practice, which is carried out in an artisanal way, uses nets and hooks and aims to satisfy local food needs. Among the fish species in Catatumbo used for subsistence fishing, *Schizodon fasciatus* (Spix and Agassiz 1829), locally known as “Piro,” stands out. This fish belongs to the family Anostomidae, characterized by its elongated, cylindrical body, small head. It can grow up to 23 cm, is territorial, and forms schools (Atencio 2001). Given the anthropogenic pressures affecting the Catatumbo region, understanding the relationship between fish morphological variations and their environment is essential, particularly within the field of ecomorphology. This discipline seeks to explain morphological adaptations in response to ecological conditions, examining how environmental interactions drive or influence observed structural variations (Betz 2006).

One widely used tool for examining variations in organism shapes is geometric morphometrics (GM), a technique integrating geometry, multivariate statistics, and biology to investigate shape and morphological variability in organisms, providing more precise biological interpretations. Unlike traditional morphometry, GM directly analyzes shape using anatomical landmarks as its foundation (Rohlf and Slice 1990; Zelditch et al. 2004; Slice 2007). Geometric morphometrics has been effectively used to explore ecomorphological patterns in fish assemblages. For example, Bower and Piller (2015) demonstrated how body shape can predict niche relationships among fish in the Tickfaw River, revealing significant correlations between shape and ecological roles, such as trophic guilds and flow regimes or Páez-Collao et al. (2024) which analyzed the ontogenetic shape changes in cryptobenthic fishes during their shift from pelagic larvae to benthic juveniles, revealing that head and fin structures adapted significantly to new ecological roles during settlement. Applying this tool allows the identification of morphological variation patterns indicative of underlying evolutionary and ecological processes. Furthermore, this methodology enables more effective population comparisons, identifying differences that may result from phenotypic plasticity or evolutionary divergence (Hernández et al. 2022, 2023).

Therefore, this article uses geometric morphometrics (GM) to analyze the morphological variation of *Schizodon fasciatus* within the Catatumbo sub-basin by examining body shape differences in populations from two of its Colombian tributaries: The El Zulia and Grita rivers. These rivers exhibit distinct socio-environmental dynamics and varying levels of ecosystem conservation. This study hypothesizes that differences in environmental conditions, such as water quality and riparian vegetation, between these rivers will be reflected in the body morphology of *S. fasciatus*, with individuals from more conserved habitats (e.g., Grita River) expected to display more streamlined and hydrodynamically adapted shapes, while those from disturbed environments (e.g., El Zulia River) will show more compact or variable body shape. Studying such morphological variation is critical for understanding ecological adaptations in freshwater fishes, assessing environmental health, and providing baseline data for the conservation and sustainable management of *S. fasciatus*, a species important to subsistence fisheries in the region.

Materials and methods

Geographic location

The study area is located in the municipalities of Puerto Santander and El Zulia, in the department of Norte de Santander (Fig. 1), specifically in the Grita and Zulia rivers, tributaries of the Catatumbo River.

The Grita River is a natural drainage system that originates in the highlands of the municipality of La Grita, Táchira State (Venezuela). Most of its course runs through Venezuelan territory, with its final five kilometers forming a border between Venezuela and Colombia, before flowing into the Zulia River in the municipality of Puerto Santander. The Zulia River covers a total area of 348,540.99 hectares and is part of the Caribbean hydrographic zone. Altitudinally, the basin is located on the eastern slope of the Eastern Cordillera of Colombia, between 50 and 4200 m above sea level, which provides a wide diversity of ecosystems and environmental gradients (CORPONOR 2010). Additionally,

the Catatumbo River basin is globally recognized for the Catatumbo lightning phenomenon, an atmospheric event that produces frequent electrical discharges over Lake Maracaibo, highlighting the climatic uniqueness of this region (Valjarević 2025).

Despite this natural and climatic richness, the region faces high anthropogenic pressure. Agricultural and live-stock expansion, along with the consolidation of monocultures such as African oil palm and illicit crops, have been identified as the main drivers of deforestation and land cover change (Portillo-Quintero et al. 2012; Negret et al. 2019). Furthermore, the construction of roads and oil pipelines associated with the oil boom has promoted ecosystem fragmentation and facilitated access to previously conserved areas (Barrera et al. 2022). These dynamics are reinforced by the persistence of armed conflict, which intensifies pressure on natural resources and has caused forced displacement of civilians (Barrera et al. 2022; Negret et al. 2019). Likewise, water systems show signs of declining quality

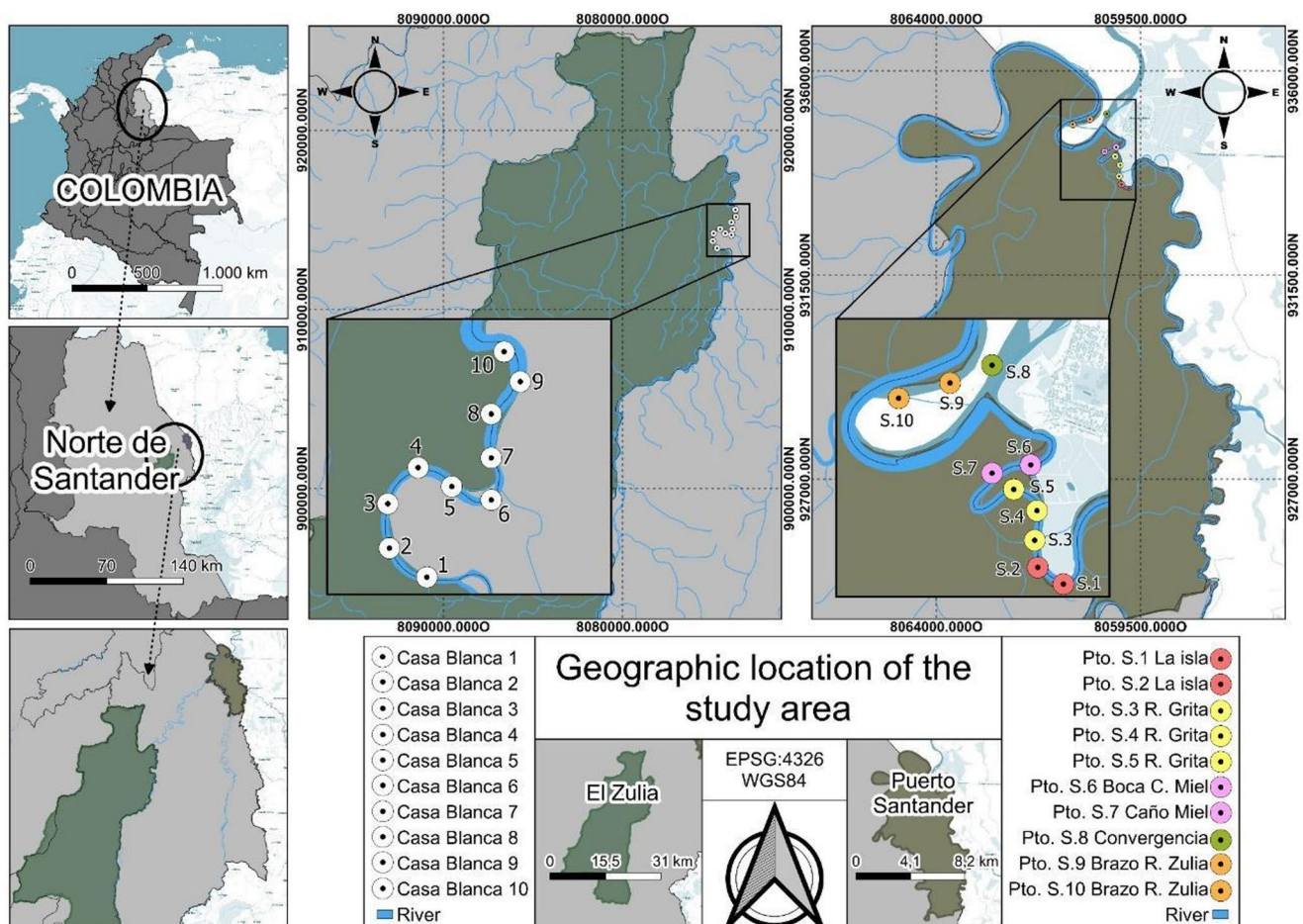


Fig. 1 Geographic location of the sampling area in the Catatumbo River Basin, Norte de Santander Department, Colombia. The map shows the general location of the study area within Colombia and the department of Norte de Santander. The enlarged insets detail the sampling sites:

Casas Blancas (1–10) and the river sites (S.1–S.10). White numbered circles correspond to sampling sites in the Casas Blancas sector, while colored circles indicate the sampling sites in the Zulia, Grita, and Catatumbo rivers. Blue lines represent the main hydrographic system

Table 1 Means and standard deviations of the water parameters measured at each study location between April 2023 and May 2024

Water parameters	Localities			
	El Zulia		Puerto Santander	
	Mean±SD	Min–Max	Mean±SD	Min–Max
Temperature (°C)	27.7±1.7	25.5–30.3	30.6±0.8	29.4–31.1
pH	7.7±0.1	7.5–7.8	8±0.1	7.8–8.1
Conductivity (µS/cm)	162.9±3.4	154.9–166.6	293±14.3	255.8–301.4
Salinity (PSU)	0.1±0.0	0.1–0.1	0.1±0.0	0.1–0.1
Dissolved oxygen (ppm)	3.7±1.9	2.1–8.0	4.8±3.5	2.8–11

Table 2 Mean and standard deviation of the total length and standard length at the study localities

Measurements	Localities			
	El Zulia		Puerto Santander	
	Mean±SD	Min–Max	Mean±SD	Min–Max
Total length (cm)	28.1±1.8	24.8–33.0	28.0±2.0	22.8–33.0
Standard length (cm)	24.3±1.7	20.6–28.8	24.4±1.6	21.8–29.0

due to untreated domestic discharges, intensive use of agrochemicals, and extractive activities.

In each municipality, 10 sampling stations were selected, taking into account accessibility, conservation status, and water flow. Finally, each station was georeferenced using GPS.

Data acquisition

Sampling activities were conducted between April 2023 and May 2024 at ten stations located in El Zulia and Puerto Santander, respectively. Four cast net throws were performed per station for fish collection, collecting 80 specimens of *S. fasciatus* (25 from El Zulia and 55 from Puerto Santander). Simultaneously, water parameters such as temperature (°C), pH, conductivity (µS/cm), salinity (PSU), and dissolved oxygen (ppm) were measured in situ at each station using a Hanna Instruments HI 94,194 multiparameter probe (Table 1). Subsequently, the specimens were stored under refrigerated conditions and then transported to the laboratory of the Universidad Francisco de Paula Santander, Ocaña, where they were photographed and biometric measurements were recorded, including total length (TL) and standard length (SL) (Table 2).

The identification of the organisms was carried out in the laboratories of Universidad Francisco de Paula Santander, Ocaña campus, using the identification guides by Cabrera et al. (2006) and Angulo et al. (2013, 2021).

Table 3 Anatomical description of landmarks in *Schizodon fasciatus*

Landmark	Anatomical position
1	Tip of the Mouth
2	Upper base of the head
3	Anterior insertion of the first dorsal fin
4	Posterior insertion of the first dorsal fin
5	Anterior insertion of the second dorsal fin
6	Upper base of the caudal fin
7	Caudal peduncle
8	Lower base of the caudal fin
9	Posterior insertion of the anal fin
10	Anterior insertion of the anal fin
11	Anterior insertion of the ventral fin
12	Lower base of the head
13	Upper base of the pectoral fin
14	Lower base of the pectoral fin
15	Pupil

Morphometrics analysis

To capture the images, the individuals were pinned and placed on a surface in an anteroposterior position, with the fins extended, using a ruler to establish the scale. The photographs were taken with a Canon EOS RP camera with a 24–105 mm f/4–7.1 IS STM lens at a resolution of 27.1 megapixels. Fifteen landmarks were defined following the protocol of Hernández et al. (2022), with some modifications detailed in Table 3. These landmarks were digitized and converted into coordinates in a two-dimensional plane using the software TpsDig2 (Rohlf 2013).

Data analysis

A Generalized Procrustes Analysis (GPA) was used to process the Cartesian coordinates derived from the landmark positions (Rohlf 1990). Measurement error for the landmarks was calculated by digitizing landmarks twice in a sample of individuals, followed by a Procrustes ANOVA, where the mean squares of individuals were compared to the mean squares of the error (Arnqvist and Martensson 1998; Fruciano 2016). A principal component analysis (PCA) was conducted using the individual covariance matrix, generating a scatter plot that graphically displayed the first two shape dimensions (PC1 vs PC2). Subsequently, the average shapes of the samples by locality were obtained to observe shape changes. For this, a new PCA was performed using the mean shape covariance matrix. A partial least squares (PLS) analysis was carried out to determine the influence of environmental parameters on shape. To understand how the environmental variables measured in the field (temperature, pH, conductivity, salinity, and dissolved oxygen) influence the body shape of *S. fasciatus* individuals, a PCA was performed on the scaled covariates to determine their influence

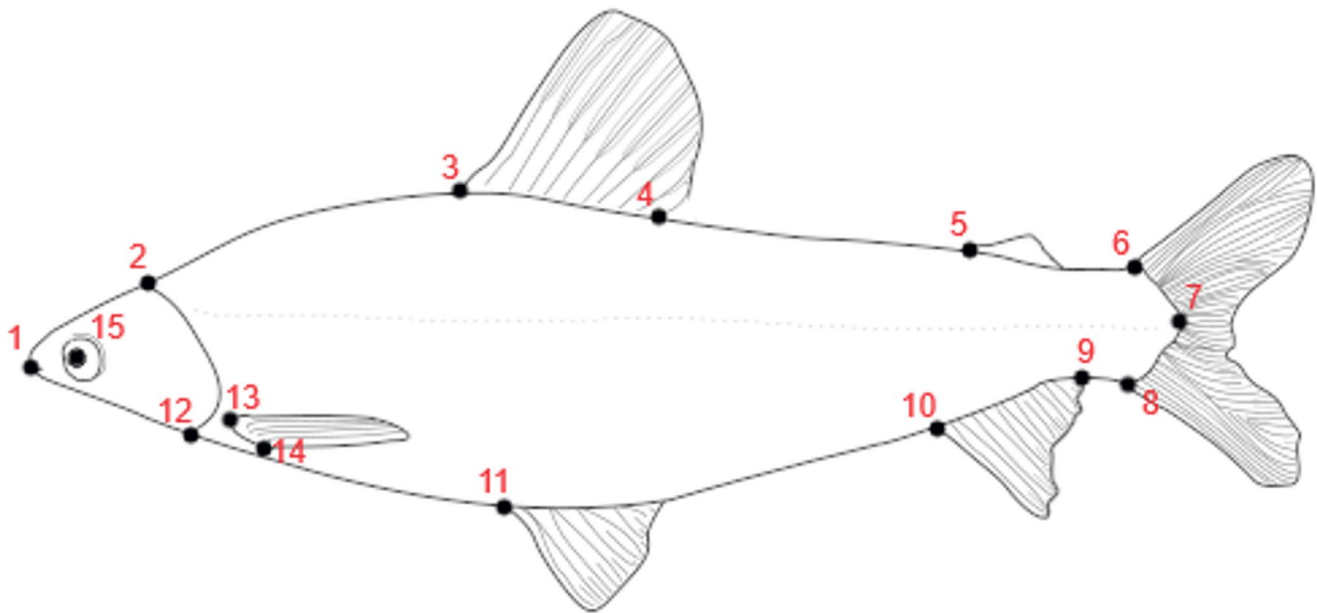


Fig. 2 Schematic reference of *Schizodon fasciatus* body shape with 14 landmarks

Table 4 Procrustes ANOVA for the analysis of measurement error of *Schizodon fasciatus*

Effect	SS	MS	df	F	P (param.)		
Centroid size							
Individual	1494829.448	18921.89	79	0.44	0.9988		
Error 1	1253555.746	13154.32	36				
Effect	SS	MS	df	F	P (param.)	Pillai tr.	P (param.)
Shape, procrustes ANOVA							
Individual	0.091	0.000044	2054	11.44	<0.0001	23.47	<0.0001
Error 1	0.0036	0.0000039	936				

on shape. An ANOVA was conducted under a linear model using the first three components containing the relevant ecological information for morphological shape. All analyses were performed using the MorphoJ 2.0 software and the Geomorph package in R (Klingenberg 2016; Adams et al. 2013) (Fig. 2).

Results

The measurement error calculation through Procrustes ANOVA indicated that the mean squares of the individuals were greater than that of the error (MS Error 0.0000039136 < MS Individuals 0.0000447749), indicating no digitization error in the landmarks. This means that the variance found is due to biological variation in the shape of the samples (Table 4). On the other hand, the PCA (Fig. 3) showed shape disparities between the localities. The first three axes of the PCA explained 55.65% of the shape variation (PC1: 30.53%; PC2: 13.85%; PC3: 11.26%) (Fig. 3). The individuals from Puerto Santander had a longer pectoral

fin base than those from El Zulia. Meanwhile, the individuals from El Zulia had slightly more compact bodies than those from Puerto Santander (Fig. 4).

The violin diagram of the centroids of the populations from Puerto Santander appears to have a more centered distribution around the values of 35–40, with a higher concentration of data in this range. Zulia has a more dispersed distribution, with data extended from values around 20 to more than 40, indicating greater variability in the size of the centroid (Fig. 5). On the other hand, the violin diagram (Fig. 5) showed that individuals from Puerto Santander and El Zulia tend to have little variable sizes between them.

The PLS graph associated with ecological variables and body shape (Fig. 6) shows a positive correlation between the variables and shape in both populations. The analysis of variance (ANOVA) and principal component analysis (PCA) highlight the significant influence of several environmental covariates on fish shape variation. The significant principal components (PC1, PC2, and PC3) explain 5.43%, 3.70%, and 3.15% of shape variance, respectively (Fig. 7). PC1, with high loadings for Conductivity (0.4947),

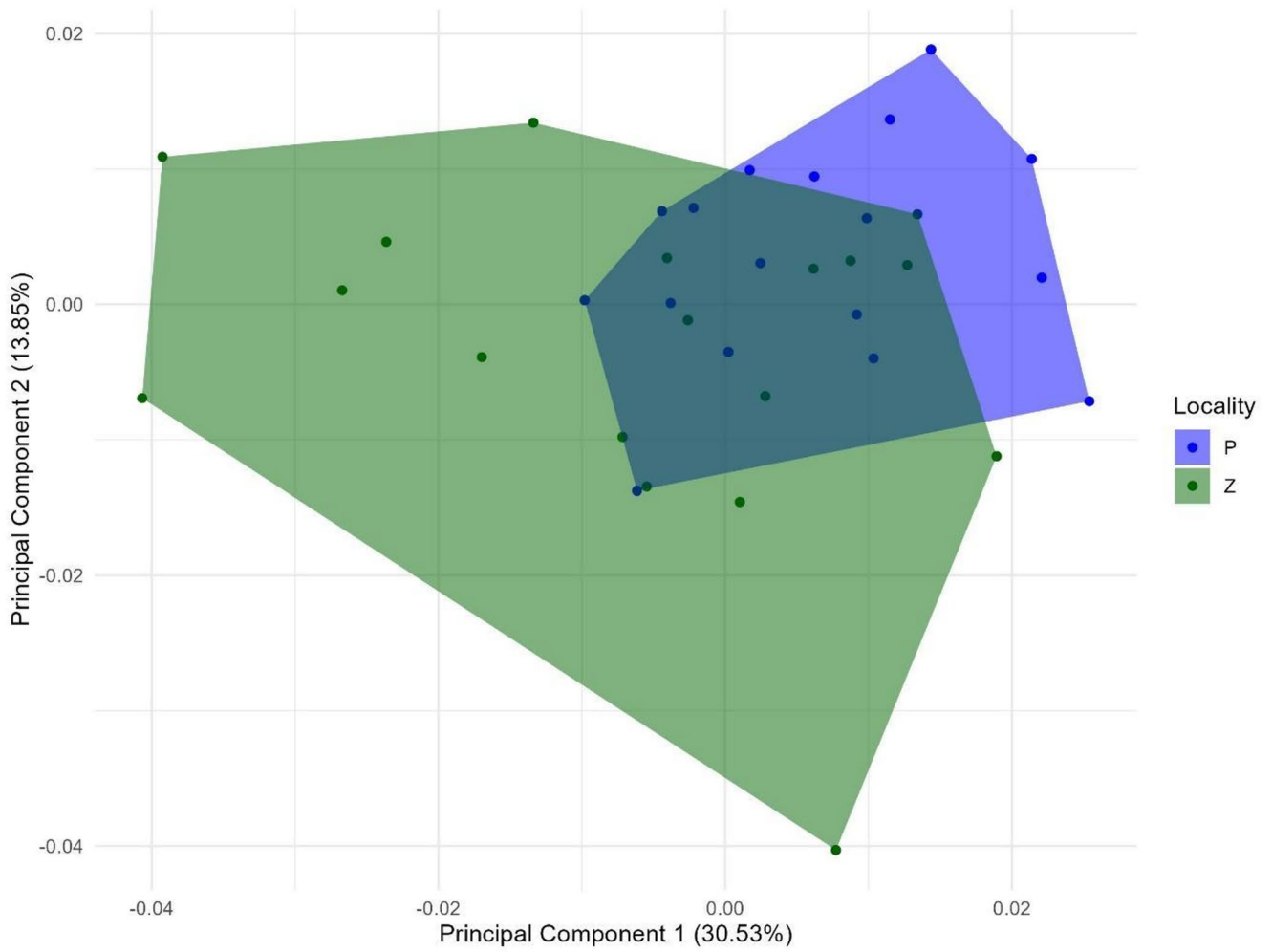


Fig. 3 Principal component analysis of the body shape in *Schizodon fasciatus*. Colors represent the localities El Zulia (Z) (green) and Puerto Santander (P) (blue)

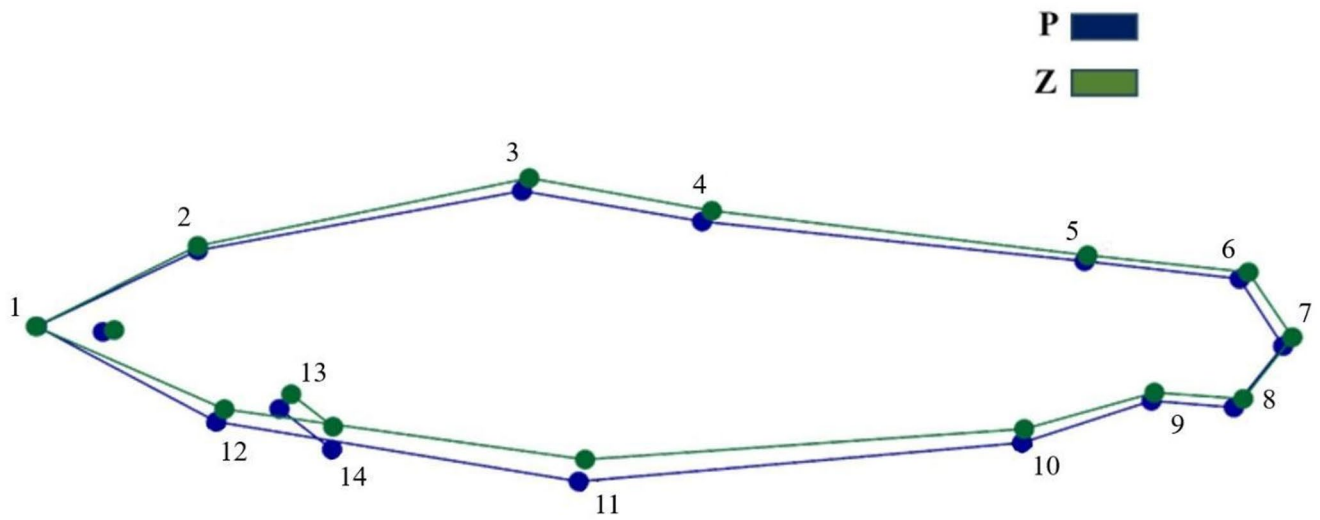


Fig. 4 Average shape superposition of *Schizodon fasciatus* of Puerto Santander (P) (Blue) and El Zulia (Z) (Green)

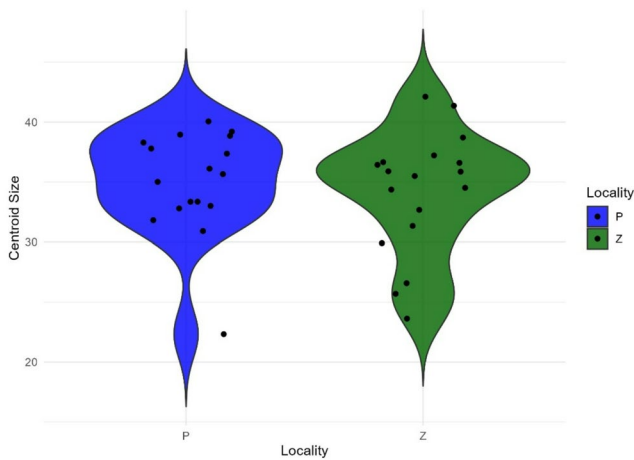


Fig. 5 Violin diagram of the centroids of the *Schizodon fasciatus* populations of Puerto Santander (P) (Blue) and El Zulia (Z) (Green)

pH (0.4898), Salinity (0.4888), and Temperature (0.4839), indicates that these covariates collectively contribute to shape variation, with Conductivity having a slightly greater influence. PC2 is dominated by Dissolved Oxygen (DO) (-0.8739), suggesting that variations in oxygen levels significantly affect fish shape. PC3 is primarily influenced by Temperature (-0.8171) and Salinity (0.4253), indicating strong but opposing effects of these covariates on shape variation.

The proportion of variance shows that PC1 accounts for 72.77% of the variance, PC2 21.65%, and PC3 4.11%, cumulatively explaining 98.52% of the total variance. These PCs' large effect sizes (Z) and low p -values further confirmed their significant role in explaining shape differences. The graphical representation of loadings visually confirms these influences, reinforcing the critical impact of environmental factors such as conductivity, pH, salinity, temperature, and DO on the morphological characteristics of the fish.

Discussion

The use of geometric morphometrics as a tool revealed morphological variations among *S. fasciatus* individuals from El Zulia and Puerto Santander. The results suggest that environmental pressures shape population morphology. GM analysis identified notable differences in the body shape of *S. fasciatus* between the study locations. Specifically, individuals from El Zulia exhibited a narrower pectoral fin insertion (landmarks 13 and 14) and a slightly more compact dorsoventral body shape compared to individuals from Puerto Santander, who displayed a broader pectoral fin insertion and a less compact body shape.

Field observations revealed that *S. fasciatus* populations inhabit rivers with distinct and variable ecological

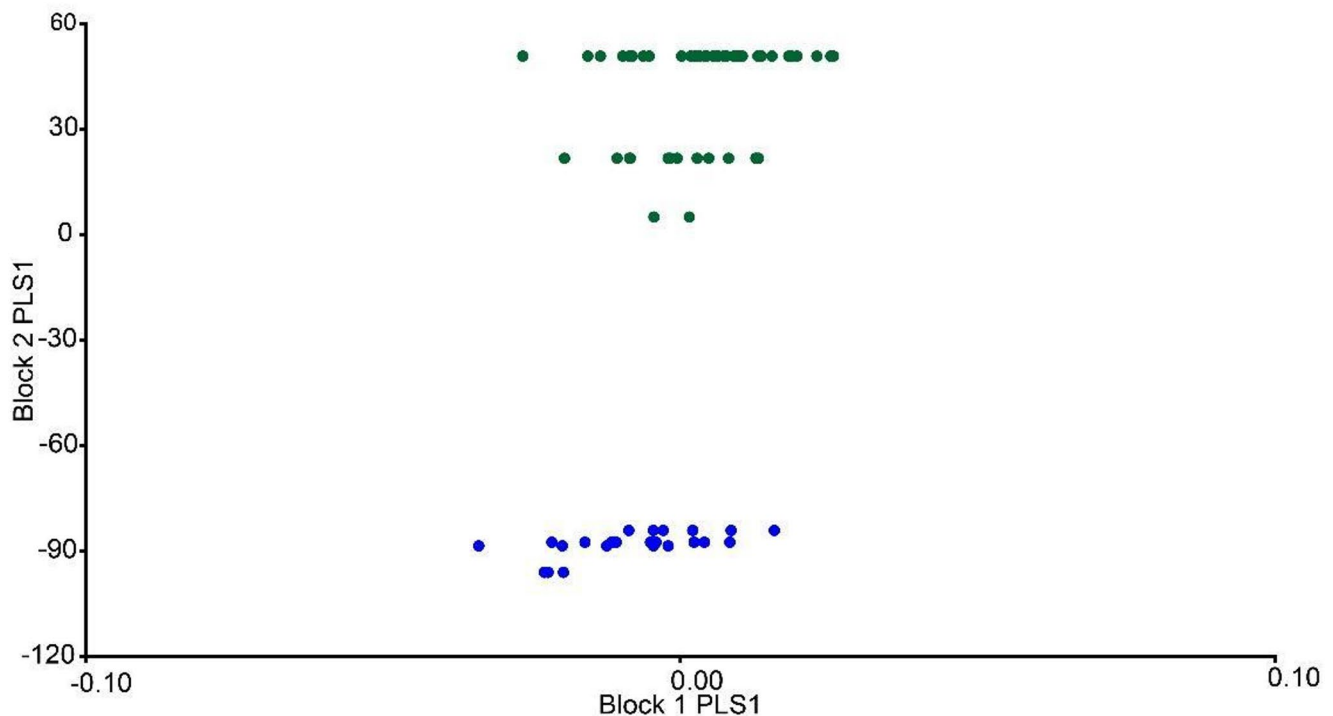


Fig. 6 Partial least squares (PLS) analysis of *Schizodon fasciatus* body shape in relation to environmental parameters (temperature, pH, dissolved oxygen, salinity, and conductivity). The plot displays the distribution of individuals along the first two PLS axes (PLS1 and PLS2).

Green dots correspond to the El Zulia locality, while blue dots represent the Puerto Santander locality, showing differences in morphological variation associated with the environmental conditions of each site

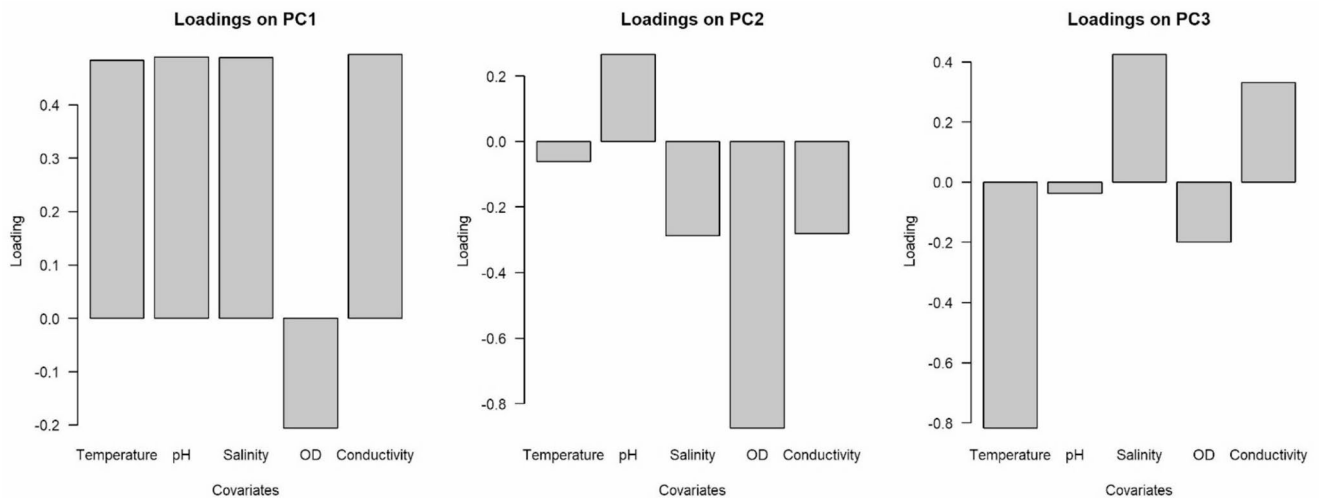


Fig. 7 Principal component loadings (PCA) of environmental variables recorded in habitats of *Schizodon fasciatus*. The plots show the loadings of each environmental variable on the first three principal components (PC1, PC2, and PC3). Temperature, pH, salinity, dissolved

oxygen (DO), and conductivity display different levels of contribution to each component, reflecting their relative importance in explaining the observed environmental variation

conditions. The El Zulia River, located in El Zulia, represents a highly transformed ecosystem, where the riparian zone has been almost entirely deforested to establish rice monocultures. This has increased sedimentation in the water body, altering the structure of aquatic habitats. Additionally, agricultural chemicals used in these crops are carried into the river through runoff, deteriorating water quality. In contrast, the Grita River, located in Puerto Santander, features a riparian zone with a landscape matrix composed of subsistence crops and abundant shrub and forest vegetation, resulting in less direct agrochemical contamination.

Deforestation in watersheds has been documented to increase nutrient and dissolved solid input into aquatic systems through runoff and deposition (de Mello et al. 2018). Moreover, the establishment of monocultures and the use of fertilizers and pesticides near water bodies can cause ecosystem imbalances, directly impacting aquatic fauna (de Jong et al. 2015). Therefore, we consider that differences in the physicochemical variables between the study locations were mediated by these anthropogenic pressures. The PLS results indicated that water quality conditions in the Grita and El Zulia rivers differ and may explain the morphological differences observed in *S. fasciatus* individuals across study locations. Martínez-Leiva et al. (2023) noted that organisms exposed to varying environmental pressures might exhibit body modifications mediated by phenotypic plasticity or rapid adaptive changes (Páez-Collao et al. 2024).

Several authors agree that the physical and chemical conditions of water bodies can drive evolutionary and ecological processes that promote changes in fish morphology (Drake et al. 2008; Haas et al. 2010; Ahnich et al. 2024). In particular, we hypothesize that hydrological changes associated

with natural physical processes in the study areas may have contributed to the morphological variation observed in *S. fasciatus*. By applying Geometric Morphometrics (GM), we were able to objectively quantify subtle shape differences that might not be detectable through traditional morphological approaches, thus reinforcing the robustness of our inference regarding environmentally driven shape variation. The differences observed in the pectoral fin may be linked to hydrodynamic disturbances caused by wind-driven currents and gravity, generating turbulence that affects the swimming capacity of fish, including their direction and swimming speed in the water column. This, in turn, has direct implications for their behavior and anatomy (Lauder and Drucker 2004; Belarmino et al. 2024). We hypothesize that these wind currents have a greater impact on individuals from El Zulia due to the area's severe deforestation and the presence of low-height, low-foliage crops (rice), which lack the ability to act as windbreaks to mitigate this factor's impact on the river.

Furthermore, the differences observed in body shape are likely related to dissolved oxygen availability in the water. Fish inhabiting low-oxygen zones (conditions in El Zulia) tend to have more compact bodies compared to those in high-oxygen zones (Schofield et al. 2009; Hernández et al. 2022). A more compact body facilitates gill ventilation and water pumping over the gill lamellae, and also reduces the energy demand per unit length in environments prone to hypoxia (Nilsson 2007; Crispo and Chapman 2010).

Our findings align with the study by Crispo and Chapman (2010), who analyzed body shape variation in *Pseudocrenilabrus multicolor* (Schöller 1903) and found that oxygen concentrations in water were critical to species variation.

Similar findings have been reported in Neotropical studies linking fish body shape variation to habitat-selective pressures. For example, Hernández et al. (2022) examined the relationship between physicochemical water parameters and the body shape of *Caquetaia kraussi* (Steindachner, 1878), discovering that natural physical conditions (e.g., currents) along with pH, temperature, and dissolved oxygen caused environmental stress linked to sexual dimorphism. Similarly, Asaduzzaman et al. (2024) found differences in mouth position and caudal fin shape in *Polynemus paradiseus* Linnaeus, 1758 individuals, potentially influenced by salinity concentrations and water flow interactions.

Additionally, *S. fasciatus* individuals from El Zulia exhibited greater variation in body size compared to those from Puerto Santander, which had more conserved sizes. Environmental pressures also have implications for reproductive patterns and individual growth (Asaduzzaman et al. 2024). The observed size variations may also be habitat-related. For example, Dubuc et al. (2024) evaluated environmental conditions and their effects on the physiology and phenotype of *Siganus lineatus*, demonstrating the species' adaptive morphological and physiological capacities to habitat variations. Likewise, Martin and Leberg (2011) assessed the influence of environmental stress on the age and size at maturity of *Gambusia affinis* (Baird and Girard, 1853) and *Heterandria formosa* Agassiz, 1853 along a water salinity gradient. They determined that fish exhibited physiological compensations in response to elevated salinity levels and morphological changes associated with size during sexual maturity, with *G. affinis* males and *H. formosa* females maturing at smaller sizes and older ages.

It is important to note that the study locations are slightly over 50 km apart within the same hydrographic sub-basin, where the Grita and El Zulia rivers, tributaries of the Cataumbo River, have fluvial connectivity. Despite this connectivity, the territorial nature of *S. fasciatus* (Atencio 2001) suggests that this distance may act as a geographic barrier. Therefore, conducting molecular studies to gain a better understanding of population status is an interesting and necessary topic to explore.

Conclusions

The *S. fasciatus* individuals exhibit morphological differences across locations. Furthermore, variations in body shape were associated with physicochemical water variables (conductivity, salinity, pH, temperature, and dissolved oxygen), indicating that habitat conditions influence the morphology of individuals. In this context, it is necessary to continue developing studies that integrate morphometric, physiological, and genetic approaches in order to identify

the mechanisms responsible for the observed variations and to gain a more precise understanding of the species' environmental requirements. This knowledge is essential not only to advance our understanding of its biology and ecology but also to guide conservation and management strategies in fluvial systems subjected to increasing anthropogenic pressures.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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