Iran. J. Ichthyol. (2025) 12(3): 266-276
P-ISSN: 2383-1561; E-ISSN: 2383-0964

ORIGINAL ARTICLE

Geometric-morphometric evidence of environmentally driven shape divergence and adaptive morphometric variation in *Glossogobius giuris* from the Vembanad Kol wetlands and associated wetland areas of Kerala

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Article history:
Accepted 23 December 2025

Abstract

In the current study Landmark-based geometric morphometrics (GM), ecomorphological metrics and statistical analyses were used to explore divergence associated with gradients in physicochemical parameters among *Glossogobius giuris*, sampled from four ecologically significant zones of Vembanad-Kol Wetlands and associated wetland systems of Kerala. Procrustes ANOVA, discriminant analysis, regression, and Kendall's tau consistently supported strong associations between environmental variables and body shape variables. Correlations for traits such as body depth, standard length, head and fin measurements with parameters like salinity, pH, and hardness reflect a pattern of adaptive phenotypic plasticity. Kendall's tau revealed negative relationships between salinity/hardness and major metrics such as total and head length ($\tau \approx -0.55$, $P<0.01$), while regression analysis confirmed shape allometry ($P<0.001$). Discriminant function analysis distinguished freshwater (Thannermukkom, Kumarakom) and brackish (Kumbalangi, Thekkumkara) populations, with shape partitioning evident from Mahalanobis distances (up to 32.7) and Procrustes values (0.022–0.050; all $P<0.001$). Thin-plate spline wireframe analysis revealed distinct variations in jaw orientation, eye position, and fin morphology corresponding to environmental gradients which clarifies both the magnitude and anatomical integration of shape change among populations, providing direct evidence for adaptive phenotypic plasticity and spatial structuring in *G. giuris* in response to environmental heterogeneity. These findings highlight the integrative power of geometric morphometrics for ecological and evolutionary inference in wetland fishes.

Keywords: Eco-morphology, Phenotypic plasticity, Environmental gradient, Gobiids

INTRODUCTION

Glossogobius giuris (Hamilton 1822) a member of the Gobiidae (gobiiformes) is the principal and most widely distributed species of the genus *Glossogobius* in India, where over 220 gobiid species have been documented in recent taxonomic checklists (Sreeraj & Sen 2024). It is an amphidromous and benthopelagic species, broadly distributed from East Africa to Southeast Asia and is ecologically prominent in Indian inland and estuarine ecosystems (Hossain et al. 2009; Dinh et al. 2017; Ghosh et al. 2021). It is distinguished by its elongated, cylindrical body with a flattened head, large projecting lower jaw, separated dorsal fins, and united pelvic fins forming a sucking disc, with coloration ranging from olive-green to brown and dark spotting on the sides and fins and also exhibits a wide range of body sizes, with total lengths reported from as small as 4.3cm up to 30cm TL in South Asian river populations and a maximum observed standard length of 50 cm in broader surveys (Talwar & Jhingran 1991; Hossain et al. 2009; Azad et al. 2018).

Intraspecific morphological and morphometric variation among fish populations reflects a complex interplay of genetic and environmental factors, with early attention to phenotypic diversity recognized as foundational for evolutionary and ecological studies

(Bookstein 1991; Cadrin & Friedland 1999). Gobiids, one of the largest vertebrate families, display extraordinary adaptability across marine, brackish, and freshwater systems due to their ecological plasticity and habitat fidelity (Gill & Mooi 2012; Hoese et al. 2015).

In Kerala, the Vembanad-Kol Wetlands constitute a major Ramsar site, supporting rich fish diversity and facing pronounced temporal and spatial environmental variation due to salinity intrusion, changing hydrology, and anthropogenic inputs (Mogalekar et al. 2015; Shibu et al. 2021). Such gradients offer a unique context for investigating how physicochemical variables drive adaptive phenotypic plasticity in fish populations (Mollah et al. 2012; Kudsiah et al. 2022).

The use of traditional morphometrics and landmark-based geometric morphometric techniques is now standard for resolving population boundaries in gobioid fishes, allowing precise quantification of shape differences while retaining the spatial configuration of morphological features (Bookstein 1991; Rohlf 1998; Adams et al. 2013). In *G. giuris*, these methods have clarified population structure and adaptation to environmental gradients across river basins and estuaries (Viswambharan et al. 2015; Azad et al. 2018). This approach has proven particularly valuable in studies of fish morphology, where subtle shape variations can reflect adaptive responses to environmental pressures, feeding strategies, or hydrodynamic constraints (Andres et al. 2019). Correlating morphometric and geometric morphometric data with physicochemical parameters using multivariate statistics provides insight into how environmental gradients drive fish morphological adaptation (Klingenberg 2011; Zelditch et al. 2012; Andres et al. 2019). This approach strengthens the validity and ecological interpretation of observed shape variation by directly linking it to key habitat variables such as salinity, water hardness, electrical conductivity (EC), Total Dissolved Solids (TDS),

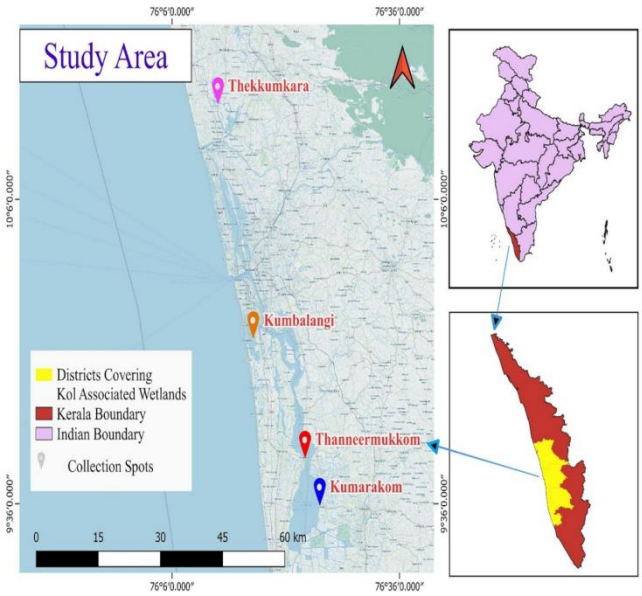


Fig.1. Map showing the collection sites of *G. giuris* from Vembanad Kol Wetlands.

dissolved oxygen (DO), and pH.

Despite previous studies elsewhere, integrative analyses of *G. giuris* in the Vembanad-Kol Wetlands remain limited. This study employs geometric morphometrics alongside fine scale ecological and environmental data to clarify how local habitat variation shapes body form in this species (Mogalekar et al. 2015; Hoese et al. 2015).

MATERIALS AND METHODS

Sampling was conducted between January and December, 2024 in the Vembanad-Kol Wetland system, Kerala, covering approximately 151,250 hectares and spanning 9°16′–10°36′N and 76°01′–76°35′E. Four ecologically significant locations were selected: Thanneermukkom Bund (9.40319°N, 76.23341°E), Kumarakom (9.597703°N, 76.425064°E), Kumbalangi (9.87113°N, 76.28864°E), and Thekkumkara (10.256219°N, 76.201299°E) (Fig. 1). A total of 100 specimens of *G. giuris*, comprising 25 individuals from each study site, were captured using fishing gears like gill nets (mesh size: 1.5-2.0cm), cast net (mesh size: 1.5-2.5cm) and square lift net (mesh size ~ 2.0cm). Freshly collected fish samples were transported in a plastic insulated box after being preserved in ice and then brought to the laboratory. Each specimen was photographed

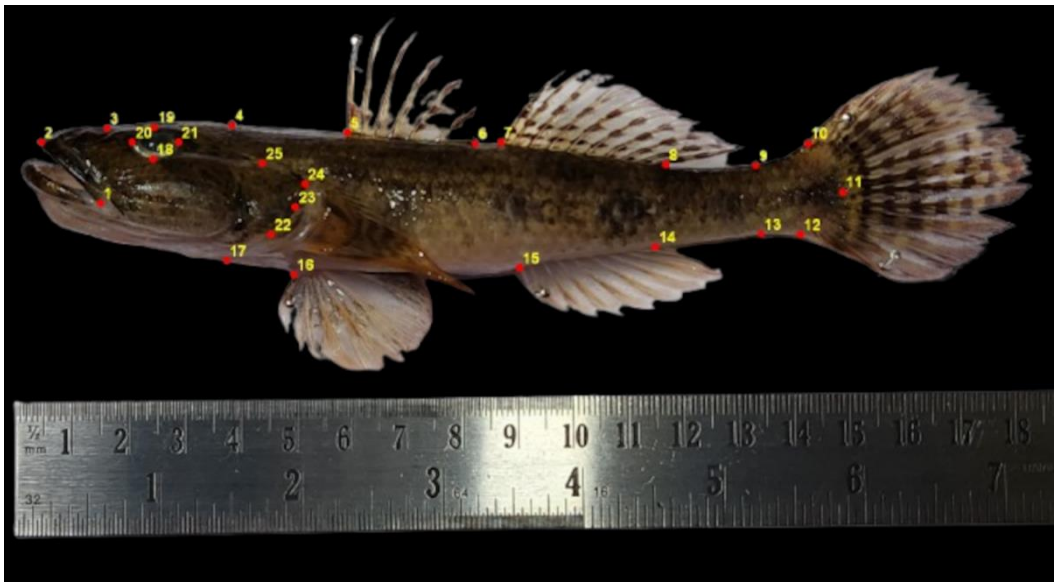


Fig.2. *G. giuris* image showing twenty-five landmarks used for GM analysis.

laterally and 25 morphometric traits were measured to the nearest 0.01mm using digital calliper, Total Length (TH), Standard Length (SL), Body Depth (BD), Head Length (HL), Head Depth (HD), Head Width (HW), Eye Diameter (ED), Snout Length (SNL), Pre Dorsal Length (PDL1), Post Dorsal Length (PDL2), Pre Pelvic Length (PPL), Pre Anal Length (PAL), Snout Anus (SA), Ventral Fin Anus (VFA), Caudal Peduncle Length (CPL), Caudal Peduncle Depth (CPD), First Dorsal Fin Base (DFB1), Second Dorsal Fin Base (DFB2), Anal Fin Base (AFB), Caudal Fin Length (CFL), Pectoral Fin Length (PFL), Ventral Fin Length (VFL), Anal Fin Length (AFL), Body Width (BW), Distance between Eyes (DE) along with 6 meristic characters was also included: First dorsal fin (D1), Second dorsal fin (D2), Pectoral fin rays (P1), Pelvic fin rays (P2), Anal fin rays (A), Caudal fin rays (C) as described in Azad et al. (2018). Physicochemical parameters including salinity, water hardness, EC, TDS, DO and pH were measured on site following APHA (2017) protocols. Depth, substrate type, and habitat structure were also noted. *G. giuris* specimen was photographed in strict left lateral view to analyse the biological shape of the specimens. Images will be converted into TPS files in tpsUtl v.1.68 and 25 homologous anatomical landmarks were digitized using TPS Dig2 v.2.26 software (Rohlf 2015). Coordinates were aligned through Generalized Procrustes Analysis to produce shape variables independent of size, position, and orientation, thus capturing only true morphological differences among individuals (Klingenberg 2011; Zelditch et al. 2012).

Left flank of the sample (Fig. 2) showing the locations of 25 landmarks that were used for body shape analysis. These landmarks corresponds to: (1) the axis of the jaws; (2) the tip of the snout; (3-4) dorsal portion of the head; (5-6) anterior-and-posterior-most edges of the first dorsal fin; (7-8) anterior and posterior most edges of the second dorsal fin; (9-13) caudal; (14-15) the posterior and anterior most edges of the anal fin at the points where it emerges from the ventral surface; (16) the pelvic fin; (17) ventral portion of the head; (18-21) orbital and (22-25) edges of the gill feature.

Multivariate statistics included Principal Component Analysis (PCA) for shape variance, Canonical Variate Analysis (CVA) was employed to maximize shape differentiation among sampling sites and, Discriminant Function Analysis (DFA) to identify variables most responsible for group separation, Mahalanobis and Procrustes distances for quantifying inter-location differences, as well as Procrustes ANOVA, regression and Kendall's tau for

exploring associations between morphometrics and environment. Wireframe diagrams and grid transformation plots were used to visually summarize shape variation among populations. Wireframes connected landmark configurations, illustrating differences between consensus shapes, while deformation grids highlighted patterns of localized shape change across ecological gradients using thin-plate spline interpolation (Rohlf 2015; Cabuga 2016). All data processing and plotting were carried out using the Paleontological Statistics software package for education and data analysis (PAST version 4.17) (Hammer et al. 2001) and MorphoJ version 1.08.02 (Klingenberg 2011) software with results validated by permutation testing.

RESULTS

Physicochemical data: Salinity ranged from 0ppt (Thanneermukkom; Kumarakom) to 20ppt (Thekkumkara), with intermediate values at Kumbalangi (5ppt). Water hardness and conductivity showed low values in freshwater (25–35mg/L, 72–110µS/cm), rising to 900–3250mg/L and >2000 µS/cm in brackish sites. TDS (36–1682ppm), DO (3.2–9.1mg/L) and pH ranged from 7.1–7.7 followed a similar gradient. Depth varied 0.5–2m, Substrate texture varied along the freshwater–brackish continuum.

Correlation with morphometric traits: Kendall's tau analysis revealed negative correlations between salinity and total length ($\tau \approx -0.55$, $P<0.01$), body depth ($\tau \approx -0.40$, $P<0.05$), head length ($\tau \approx -0.42$, $P<0.05$), and various morphometric measures across all sites. Hardness also correlated negatively with standard length ($\tau \approx -0.53$, $P<0.05$) (Fig. 3).

Geometric morphometrics: PCA of Procrustes coordinates produced 46 components (100% variance). The first six PCs explained 76.7% of total variance: PC1 (22.8%), PC2 (21.6%), PC3 (12.1%), PC4 (10.2%), PC5 (6.1%), PC6 (3.9%) (Fig. 4). PC1 and PC2 reflected population-level divergence in trunk depth, jaw projection, and caudal area e.g., PC1 (x1=0.1178, y1=-0.1519), PC2 (x1=-0.1075, y1=0.0967).

The scatter plot of principal component 1 (PC1) against principal component 2 (PC2) visualizes the shape variation among *G. giuris* populations from different sampling locations. Each point represents an individual specimen, and the coloured ellipses indicate 95% confidence intervals for each locality group. The clustering and overlap of data points display the degree of morphological differentiation between populations, with distinct groupings suggesting shape divergence and overlapping regions indicating shared morphometric characteristics among sites. This plot effectively summarizes the main axes of shape variation and facilitates the comparison of morphometric patterns across groups (Fig. 5).

Regression and Matrix Correlation: Shape regression on salinity, TDS, and hardness gave $R^2=0.52–0.66$, $P<0.01$. Matrix correlation between Procrustes distances and environmental dissimilarity was 0.519 (10,000 permutations, $P=0.0001$). CVA revealed three significant axes with eigenvalues of 6.13, 4.70, and 2.86, accounting for 44.8%, 34.3%, and 20.9% of total variance, respectively. Procrustes ANOVA for shape: Site effect SS=0.047, df=138, MS=0.00034, F=6.35, Pillai's trace=2.42, $P<0.0001$. Centroid size ANOVA: F=6.37, P=0.0006. Residual variance was 0.237 (4416 df). Matrix permutation test: $P=0.0001$.

Wireframe and Thin-Plate Spline Visualization (deformation grids) graphically illustrated anatomical changes across the ecological spectrum: fishes from brackish/saline sites showed anterior jaw elongation, deeper heads, and modified pectoral and caudal fin placement relative to those from freshwater areas. Greatest shape variation is observed around the head region (landmarks 1–6, 17–25) and the caudal peduncle/tail area (landmarks 10–15). Comparisons involving Kumarakom (Fig. 6a–6c , 7a–7c) frequently show pronounced differences at the snout and operculum (landmarks 1, 4, 17, 18, 23, 24), reflecting

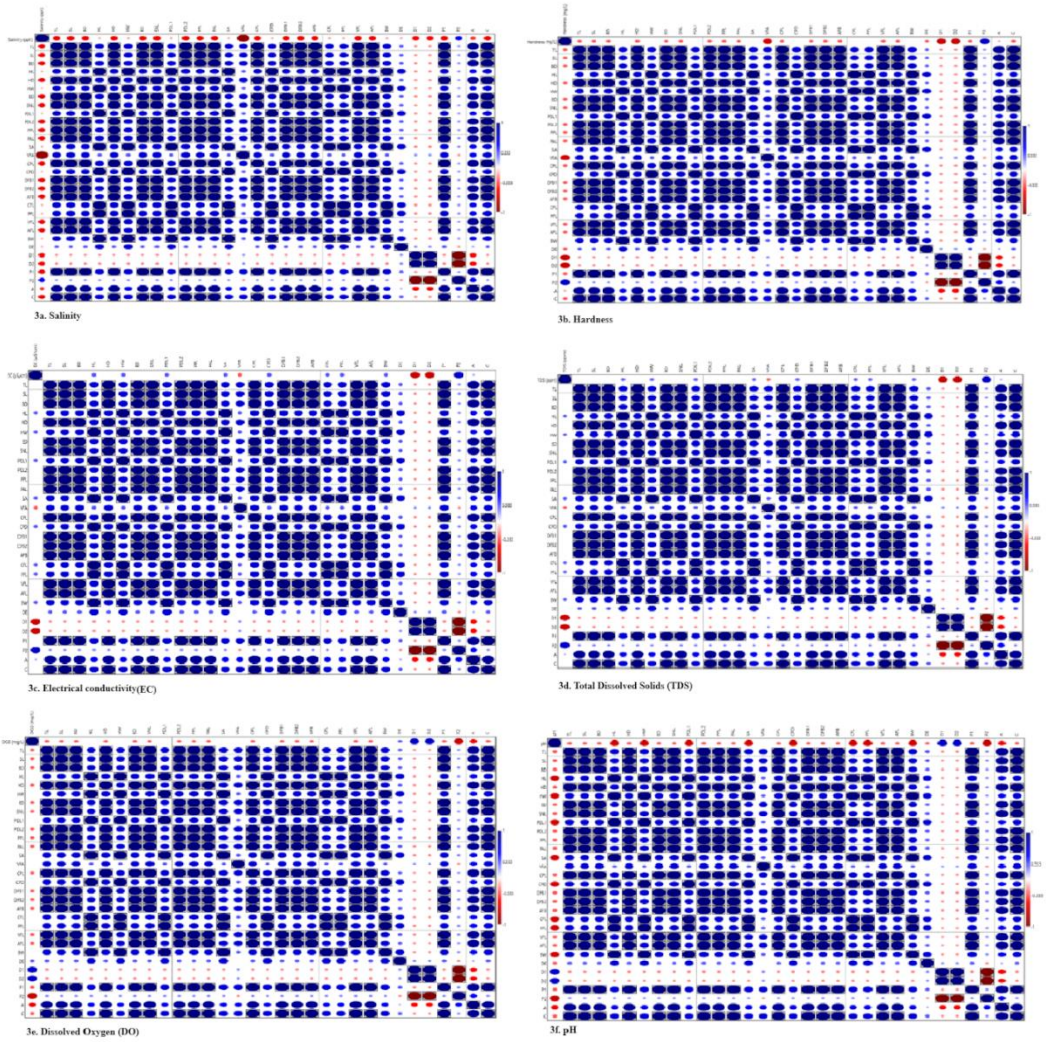


Fig.3. Correlation matrix plot representing correlation between morphometric parameters and physicochemical parameters (3a – 3f). Blue ellipse indicates positive correlation; red ellipse indicates negative correlation and ellipse width corresponding to strength of correlation.

shifts in head width and mouth position. In contrast, differences involving Thanneermukkom Bund and Thekkumkara (Fig. 6f, 7f) display deformation at the dorsal and ventral margins of the caudal region (landmarks 10–15). Kumbalangi-related comparisons (Fig. 6b, 6d, 6e; 7b, 7d, 7e) reveal intermediate patterns, with notable differences at landmarks adjacent to the fin bases and lateral line.

DFA shows pairwise population comparisons which revealed distinct and statistically significant differentiation among all sites with largest Procrustes distance of 0.0495 (Kumarakom vs Thekkumkara) and Mahalanobis distance >32.69 indicated the greatest population divergence, while the smallest distances (Procrustes: 0.0221, Mahalanobis >31.37) were observed between Kumarakom and Thanneermukkom Bund; all group pairs were statistically significant (permutation P<0.001–0.035), confirming substantial shape differentiation. The discriminant function histograms (Fig. 8) reveal distinct, non-overlapping distributions for each of the six site pairs. The absence of overlap between most site-specific histograms confirms strong discriminatory power of shape variables, underscoring significant morphological divergence among all population pairs.

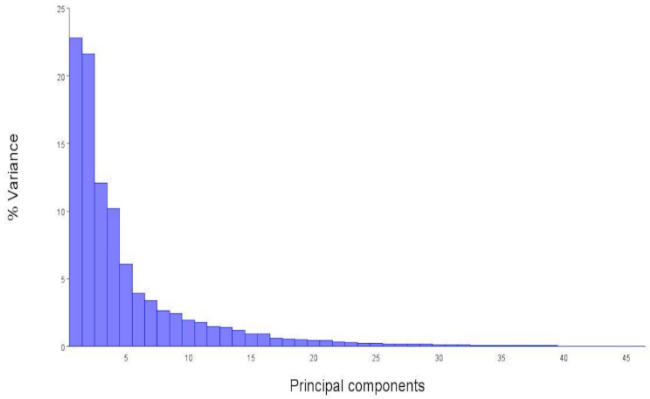


Fig.4. Scree plot showing the percentage variance explained by each principal component in the GM analysis, as computed by MorphoJ.

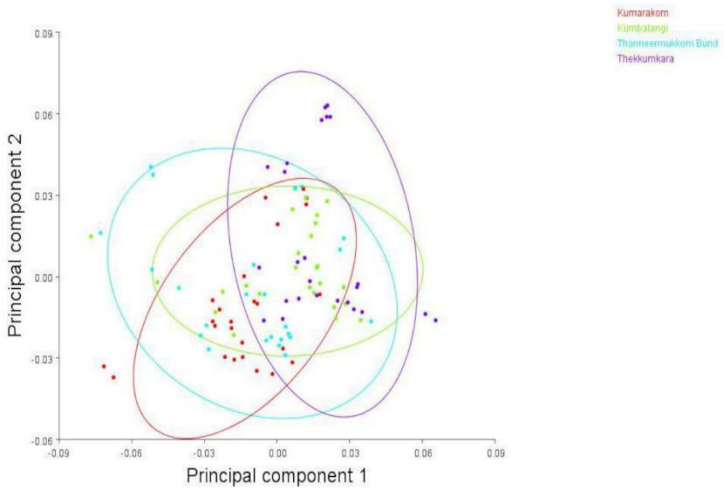
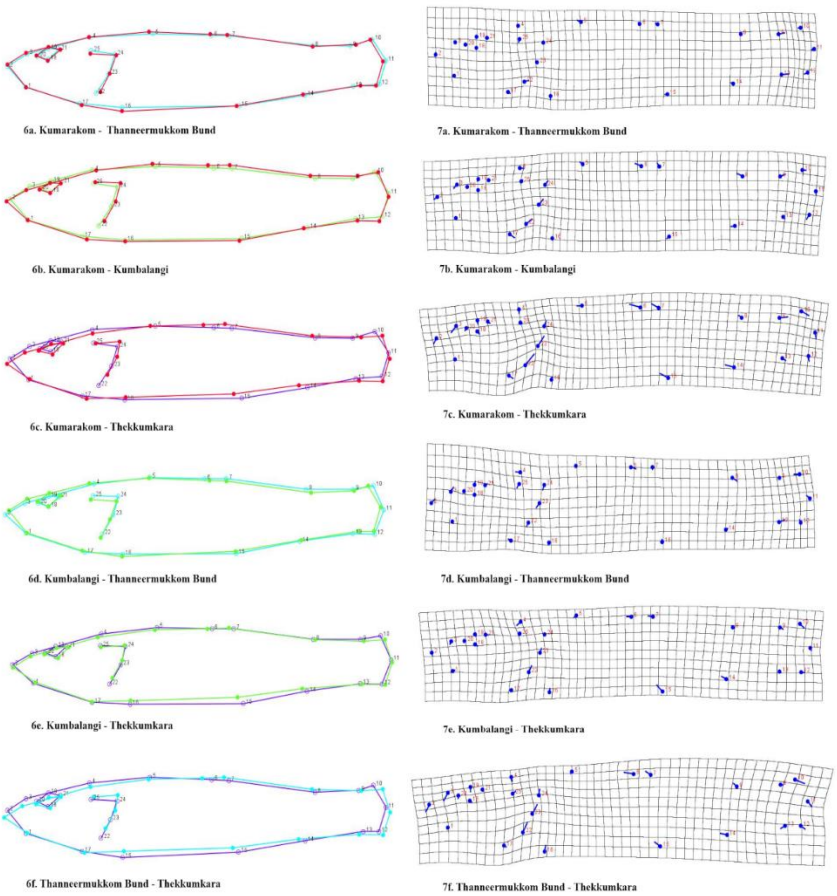


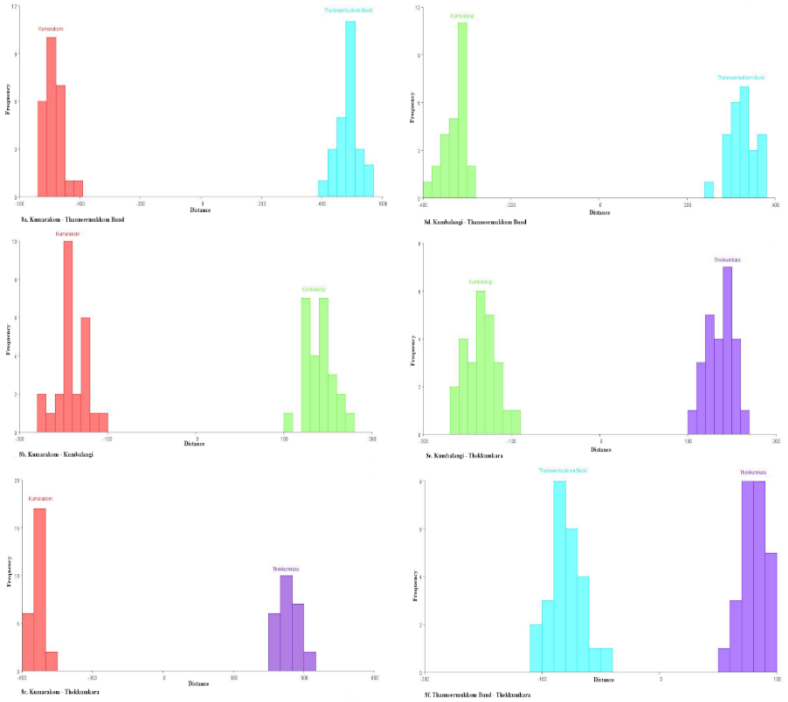
Fig.5. Scatter plot of the first two principal components (PC1 vs. PC2).

DISCUSSION

The present study establishes clear and statistically significant shape differentiation among *G. giuris* populations inhabiting different ecological zones of the Vembanad-Kol Wetlands and associated wetland systems. Marked variation in salinity (0–20ppt) and water hardness (25–3250mg/L) shaped distinct differences in body proportions of *G. giuris* across the Kol wetlands. In our study, significant negative Kendall's tau associations between salinity and morphometric traits such as: standard length, total length, and body depth underline the influence of physicochemical gradients in structuring population variability. This pattern is strongly reflected in Azad et al. (2018), who found that body elongation, jaw prominence, and overall shape in *G. giuris* from Bangladesh varied systematically with habitat and water properties, demonstrating the sensitivity of this species' morphology to local environmental conditions. Our geometric morphometric analysis identified clear shape divergence among sites, where the first two axes of PCA separated populations according to differences in salinity and substrate, and Procrustes ANOVA revealed a strong effect of location ($F = 6.35$, Pillai's trace = 2.42, $P<0.0001$). Klingenberg (2011) demonstrated that PCA and Procrustes based analyses are effective in uncovering nuanced, biologically meaningful population structure in fishes, even across continuous gradients. Recent work from Hoang et al. (2024) on Vietnamese *G. giuris* showed that geometric morphometric methods successfully revealed population expansions, habitat



Figs.6 &7. The wireframe diagrams and grid transformation illustrate shape differences among *G. giuris* populations from six pairwise site comparisons: Kumarakom, Thanneermukkom Bund, Kumbalangi, and Thekkumkara. Wireframes (6a–6f) highlight landmark displacement while the thin plate spline grids (7a–7f) show localized deformation patterns.



Figs.8. Histograms of discriminant function scores showing distinct morphological separation between each site pair (8a -8f).

linked divergence, and eco-phenotypic clusters paralleling environmental transitions, a pattern in line with our observations.

Wireframe models and thin-plate spline grids from the present study reveal pronounced anterior jaw elongation, reduced head depth, and posterior repositioning of the dorsal and pectoral fin bases in brackish, high salinity populations relative to freshwater sites. Azad et al. (2018) found similar landmark shifts in gobies along salinity gradients, while Brodnicke et al. (2022) recently demonstrated that increased jaw allometry and extension is typical for gobioid taxa adapting to challenging or variable habitats as it is a pattern associated with enhanced feeding efficiency and ecological specialization.

Adaptations in fin positioning and body shape, in general, are common among fishes inhabiting variable environments, supporting greater stabilization and manoeuvrability. In gobies, the fusion of pelvic fins into an adhesive disc represents a key evolutionary innovation that facilitates substrate attachment and stability in dynamic habitats (Thacker & Roje 2011). The observed reduction in caudal peduncle thickness and the subtle decrease in overall body length among fish from saline sites match patterns reported by Styga et al. (2019), who identified streamlined body shapes linked to higher flow rates and greater salinity in *Fundulus* and other euryhaline taxa.

CVA and DFA showed clear separation among *G. giuris* populations. The first three axes of the CVA together explained 100% of the shape variance. Site wise Mahalanobis distances were highest between Kumarakom and Thekkumkara (>32.69), followed by Kumarakom–Thanneermukkom Bund (>31.37) and Kumarakom–Kumbalangi (>16.79), indicating maximal population differentiation along the salinity and habitat gradient. Procrustes distances mirrored this trend, peaking at 0.0495 between Kumarakom and Thekkumkara, with lower values (0.0221) between Kumarakom and Thanneermukkom Bund. All pairwise permutations confirmed significant divergence ($p < 0.05$ for every comparison). These results validate the high discriminatory power of Mahalanobis and Procrustes metrics for ecological partitioning. Freudiger *et al.* (2021) applied Procrustes ANOVA to reveal significant morphological differentiation among wild-caught fish populations in response to ecological variation, directly linking morphometric divergence to environment. Similarly, Bishop et al. (2022) used Procrustes ANOVA to partition shape variation among populations of fishes as a function of dissolved organic carbon and basin structure, offering fine scale diagnosis of environmentally driven divergence. Morphometric disparity estimates and regression approaches further support the power of Procrustes metrics to diagnose ecological axes of divergence in fish populations.

In landmark-based geometric morphometric analysis, earlier foundational guidance by Zelditch et al. (2012) explained how careful placement of anatomical landmarks and the use of principal component analyses allow researchers to capture both subtle and dramatic shape variation in fishes, including differences in caudal peduncle thickness and head shape related to ecological function. Subsequent studies, such as Hoang et al. (2024), used these methods to show that *G. giuris* populations from estuarine and riverine environments display significant divergence in head, jaw, and fin positions, with habitat driving adaptive modifications across populations. Building on these advances, Vukić et al. (2025) demonstrated that convergent evolution in European gobies results in recurring patterns of jaw, trunk, and fin structure aligned with ecological niche, documenting both elongated nektonic forms and deep bodied cryptobenthic shapes as direct outcomes of environmental adaptation. Together, these findings highlight that combining geometric morphometrics with fine-scale environmental profiling is a powerful approach for interpreting adaptive morphological change in fishes.

The present study demonstrates that *Glossogobius giuris* in the Vembanad-Kol Wetlands displays clear, statistically validated morphometric and shape variation in response to local environmental differences, mainly with change in salinity, pH, hardness. By coupling conventional and geometric morphometric analyses, the study not only

distinguishes population structuring at fine ecological scales but also visualizes specific anatomical adaptations such as jaw elongation and fin repositioning across different habitats. Findings confirm that ecological context, captured through precise physicochemical profiling, leaves a distinct signature on fish body form. These insights advance our understanding of adaptive morphological plasticity in tropical wetland ecosystems and underscore the importance of integrated quantitative approaches for fisheries management, conservation, and future evolutionary research.

ACKNOWLEDGEMENT

The authors are grateful to the University of Kerala for the award of University Junior Research Fellowship and Research Centre, Department of Zoology, University College for providing facility and essential resources and to the fishermen for their assistance in the sampling.

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Iran. J. Ichthyol. (2025) 12(3): 266-276
P-ISSN: 2383-1561; E-ISSN: 2383-0964
http://www.ijichthyol.org

doi: 10.22034/iji.v12i3.1103

مقاله کامل

شواهد هندسی-ریختی از واگرایی شکل ناشی از محیط و تنوع ریخت‌سنجی تطبیقی در *Glossogobius giuris* از تالاب‌های Vembanad-Kol و مناطق تالابی مرتبط با آن در کرالا

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چکیده: در مطالعه حاضر، از ریخت‌سنجی هندسی مبتنی بر لندمارک (GM)، معیارهای اکومورفولوژیکی و تحلیل‌های آماری برای بررسی واگرایی مرتبط با گرادیان در پارامترهای فیزیکوشیمیایی درون گونه‌ای *Glossogobius giuris* که از چهار منطقه ب مهم تالاب‌های Vembanad-Kol و سیستم‌های تالابی مرتبط با آن در کرالا نمونه‌برداری شده بودند، استفاده شد. آنالیز واریانس پروکراست، تحلیل تشخیصی، رگرسیون و تائو کندال از ارتباط قوی بین متغیرهای محیطی و شکل بدن پشتیبانی کردند. همبستگی صفاتی مانند عمق بدن، طول استاندارد، اندازه سر و باله با پارامترهایی مانند شوری، pH و سختی، الگویی از انعطاف‌پذیری فنوتیپی تطبیقی را منعکس می‌کند. تائو کندال روابط منفی بین شوری/سختی و معیارهای اصلی مانند طول کل و سر را نشان داد (τ=-۰/۵۵، P<۰/۰۱)، در حالی‌که تجزیه و تحلیل رگرسیون، آلومتری شکل را تأیید کرد (P<۰/۰۰۱). تجزیه و تحلیل تابع تشخیص، جمعیت‌های آب شیرین (تانرموکوم، کوماراکوم) و لب‌شور (کومبالانگی، تکومکارا) را از هم متمایز کرد، به‌طوری که تفکیک شکل از فواصل ماهالانوبیس (تا ۳۲/۷) و مقادیر پروکرراست (۰/۰۵-۰/۰۲۲؛ P<۰۰۱) مشهود بود. تجزیه و تحلیل نمودار قاب سیمی، تغییرات متمایزی را در جهت فک، موقعیت چشم و ریخت باله مربوط به گرادیان‌های محیطی نشان داد که هم بزرگی و هم ادغام آناتومیکی تغییر شکل در بین جمعیت‌ها را آشکار می‌کند و شواهد مستقیمی برای انعطاف‌پذیری ریختی تطبیقی و ساختار فضایی در *G. giuris* در پاسخ به ناهمگونی محیطی ارائه می‌دهد. این یافته‌ها قدرت یکپارچه ریخت‌سنجی هندسی را برای استنتاج اکولوژیک و تکاملی در ماهیان تالابی برجسته می‌کند.

کلمات‌کلیدی: ریخت‌شناسی زیستی، انعطاف‌پذیری ریختی، گرادیان محیطی، گاوماهیان