Iran. J. Ichthyol. (2026) 13(1): 13-22
P-ISSN: 2383-1561; E-ISSN: 2383-0964

ORIGINAL ARTICLE

Application of geometric morphometrics to characterize morphological variation in *Schizocypris altidorsalis* (Actinopterygii: Cyprinidae) from the Hamun–Hirmand aquatic system, Southeastern Iran

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Article history:
Accepted 25 December 2025

Abstract
The present study employed geometric morphometric analysis to investigate morphological variation of a cyprinid fish *Schizocypris altidorsalis* from the Hamun–Hirmand aquatic system in the Sistan Basin, southeastern Iran. A total of 55 specimens (26 from the Chahnimeh reservoirs and 29 from the Hamun wetland) were collected using hand and cast nets. Sixteen homologous landmarks were digitized from two-dimensional images of each specimen using TPSDig2 software. Shape variation was analyzed using Generalized Procrustes Analysis (GPA), followed by Principal Component Analysis (PCA), Discriminant Function Analysis (DFA), and Hotelling's T^2 test. The DFA revealed significant morphological differentiation between the two populations. Wireframe deformation analysis based on the consensus configuration indicated that the primary differences were associated with body depth and caudal peduncle length. These findings suggest that *S. altidorsalis* exhibits habitat-associated morphological plasticity, likely reflecting phenotypic responses to contrasting environmental conditions within the Hamun–Hirmand aquatic system.

Keywords: Cypriniformes, Phenotypic plasticity, Freshwater Fishes, Discriminant Function Analysis

INTRODUCTION

Iran is situated within the southern Palearctic biogeographic region and serves as an important transitional zone for freshwater fish fauna between the western and eastern Palearctic. To date, approximately 300 freshwater fish species belonging to 110 genera and 38 families have been recorded from the inland waters of Iran (Sayyadzadeh & Esmaeili 2024). The Sistan Basin, located in southeastern Iran, is geographically isolated from other inland drainage systems of the country and forms part of the transboundary Helmand (Hirmand) River basin shared between Iran and Afghanistan. The Hamun wetland complex and the Chahnimeh reservoirs (Chahnimeh 1–4), covering approximately 15,000 ha and storing nearly 1.5 billion m³ of freshwater, constitute one of the principal habitats of the endemic Anjak fish. However, prolonged droughts and hydrological alterations have resulted in a substantial decline in the abundance of this species (Rahdari, 2019).

Schizocypris altidorsalis Bianco & Bănărescu, 1982 (Cyprinidae: Schizothoracinae), commonly known as the Anjak fish, is a native benthopelagic and commercially valuable freshwater species inhabiting the Hamun Lake–Helmand River system (Ghanbari et al. 2019). The species is endemic to the Sistan Basin and is restricted to the Hamun wetlands, the Helmand River and its tributaries, and possibly adjacent waters in Afghanistan (Coad 2013). Compared with other cyprinid species occurring in the basin, such as *Schizothorax zarudnyi*, *S. altidorsalis* occupies a narrower ecological niche and is considered both ecologically and culturally important in the Sistan region (Shamsi et al. 2024). It is distinguished by a moderately elongated body, a bluish dorsum with silvery flanks and ventral surface, a long dorsal fin bearing a robust serrated spine, a transverse subterminal mouth with a protruding snout, and characteristic scale patterns, including a naked strip anterior to the dorsal fin and enlarged scales around the pectoral fin base, anus, and anterior lateral line

Journal homepage: ijichthyol.org/ DOI: https://doi.org/10.22034/iji.v13i1.1145

(Keivany et al. 2016).

Body shape analysis is widely used in ichthyology to investigate taxonomy, population structure, ecology, evolution, behavior, and fisheries management, and to improve our understanding of species diversity (Slice 2005; Mouludi-Saleh et al. 2022b). Morphological variation among fish populations often reflects the combined effects of environmental conditions, phenotypic plasticity, and natural selection (Gammanpila et al. 2017). Numerous studies have demonstrated that environmental factors, including habitat characteristics, hydrological conditions, and resource availability, can strongly influence body morphology, whereas genetic differentiation may contribute to a lesser extent in some populations (Acar & Kaymak 2023).

Geometric morphometrics (GM) has become one of the most powerful quantitative approaches for analyzing biological shape variation. Unlike traditional morphometric methods, which rely primarily on linear measurements, GM uses homologous anatomical landmarks to capture and visualize shape differences while preserving the geometric relationships among landmarks (Geiger et al. 2016; Martin et al. 2023; Luo 2024). This approach enables more accurate detection, visualization, and statistical analysis of subtle morphological differences among populations.

Geometric morphometric techniques have been widely applied to Iranian freshwater fishes (Eagderi et al. 2013; Nasri et al. 2013, 2018; Zamani Faradonbeh et al. 2014; Razavipour et al. 2015; Mouludi-Saleh & Keivany 2018a, 2018b, 2022 a,b; Mouludi-Saleh et al. 2019; Ganjali et al. 2021). Previous studies have demonstrated that GM generally provides greater discriminatory power than traditional morphometric approaches for detecting morphological divergence (Loy et al. 1996; Radkhah et al. 2016; Ganjali et al. 2021; Mouludi-Saleh et al. 2021), although both methods may produce either similar or contrasting results depending on the species and study design (Mouludi-Saleh & Keivan, 2018a; Salehinia et al., 2016; Ganjali et al. 2021; Ganjali 2023).

Despite the ecological and conservation importance of *Schizocypris altidorsalis*, information on morphological variation among its populations remains limited. Therefore, the present study aimed to evaluate body shape variation between two populations inhabiting the Hamun–Hirmand aquatic system using landmark-based geometric morphometric analysis. The findings provide insights into habitat-associated morphological differentiation and contribute to the conservation and management of this endemic freshwater species.

MATERIALS AND METHODS

A total of 55 specimens of *Schizocypris altidorsalis* were collected from two localities in the Sistan Basin, southeastern Iran: 26 specimens from the Chahnimeh reservoirs (30°50'21.7500"N, 61°41'39.8004"E) and 29 specimens from the Hamun Wetland flood embankment (61°23'57.0"E, 31°09'20.1"N in March 2025 (Figs. 1 and 2). Fish were captured using hand nets and cast nets. Following capture, specimens were anesthetized in a 1% clove oil solution, fixed in 4% buffered formaldehyde, and transported to the laboratory for subsequent analyses. The Mean standard length (SL) range of specimens were recorded as 125.53mm for Chahnimeh reservoirs and 106.34mm for Hamun.

The left lateral side of each specimen was photographed using a standardized copy stand equipped with a Canon G7 digital camera. Sixteen homologous anatomical landmarks were selected and digitized on two-dimensional images using TPSDig2 software (version 2.31) (Fig. 2).

To eliminate non-shape variation associated with position, orientation, and scale, landmark configurations were superimposed using Generalized Procrustes Analysis (GPA) (Rohlf & Bookstein 1990). The resulting Procrustes coordinates were subjected to multivariate statistical analyses, including Principal Component Analysis (PCA), Discriminant Function Analysis (DFA), and Hotelling's T^2 test, using PAST software v. 2.17 (Hammer et al. 2001). Cross-validation (leave-one-out classification) for DFA results was performed and studied populations were divided to groups. Morphological differences between

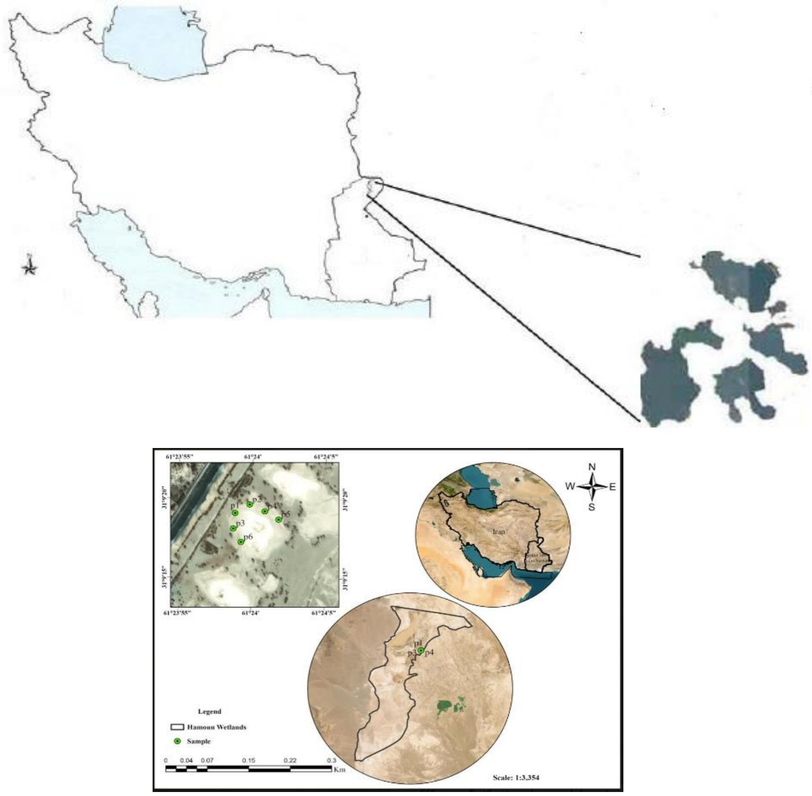

Fig.1. Map of the study area showing the sampling locations in the Chahnimeh reservoirs (upper panel) and the Hamun Wetland (lower panel, Ganjali & Ghorbani 2025), Sistan Basin, southeastern Iran.

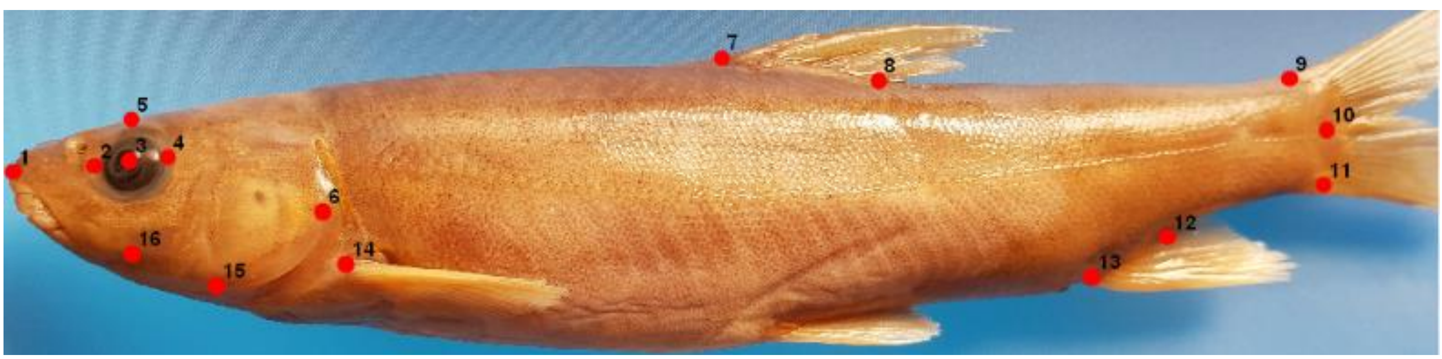

Fig.2. Defined landmark-points to extract the body shape data of *Schizocypris altidorsalis*: (1) anterior-most point of the snout tip on the upper jaw, (2) the beginning of the eye socket, (3) center of the eye, (4) the end of the eye socket, (5) the dorsal surface of the head is perpendicular to the center of the eye, (6) the end point of the gill operculum, (7) the origin point of the dorsal- fin base, (8) the insertion point of the dorsal- fin base, (9) the end of the caudal peduncle - the beginning of the procrand radius, (10) the middle part of the most end of the caudal peduncle, (11) the lower part of the most recessed of the caudal peduncle, (12) the origin point of the anal- fin base, (13) the insertion point of the anal- fin base, (14) most anterior point of the pectoral fin, (15) the most ventral point of the gill slit and (16) ventral surface of the head perpendicular to the center of the eye.

populations were visualized using wireframe deformation grids generated in MorphoJ v. 1.02j (Klingenberg 1998). All geometric morphometric and statistical analyses were performed using PAST and MorphoJ software.

RESULTS

Principal Component Analysis (PCA) indicated that the first four principal components exceeded the Jolliffe cut-off criterion and were therefore considered informative for describing shape variation among the studied populations. These components explained 49.92% (PC1), 18.93% (PC2), 7.86% (PC3), and 5.84% (PC4) of the total variation, accounting for a cumulative variance of 82.55%. The first two principal components together explained 68.85% of

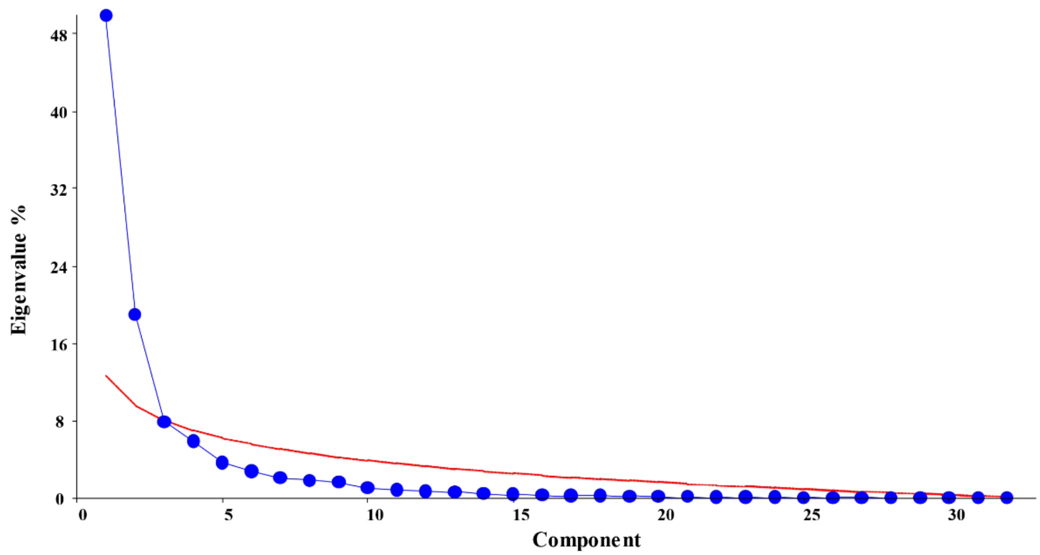

Fig.3. The screen plot diagram of PCA and the Jollief cutoff point (red line), showing the main 2 significant components Jolliffe line.

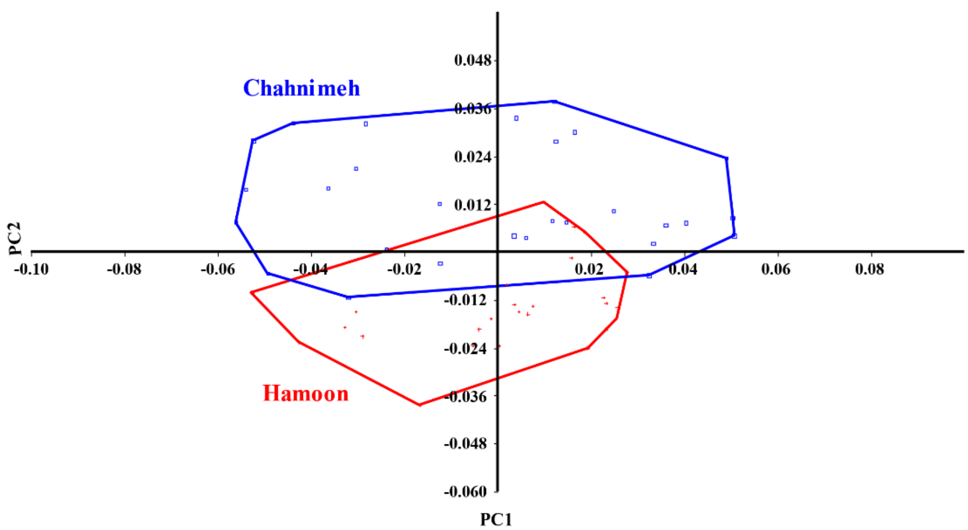

Fig.4. Principal Component Analysis diagram of Anjak, *Schizocypris altidorsalis* in the Sistan Basin.

the total shape variation (Fig. 3). Although the PCA scatter plot revealed some grouping of specimens according to sampling locality, considerable overlap was observed between the two populations, indicating limited separation based solely on the first two principal components (Fig. 4).

In contrast, Discriminant Function Analysis (DFA) demonstrated a clear morphological separation between the Chahnimeh and Hamun populations. This differentiation was statistically supported by Hotelling's T^2 test (T^2= 710.66, P<0.001) (Fig. 5). Furthermore, the Mahalanobis distance (6.723) and Procrustes distance (0.0282) between the two populations were both statistically significant, confirming the presence of distinct body shape differences. Wireframe deformation analysis illustrated the patterns of morphological variation between the populations (Fig. 6). The Hamun population was characterized by a relatively shallower body and a shorter caudal peduncle compared with the Chahnimeh population, indicating habitat-associated differences in body shape.

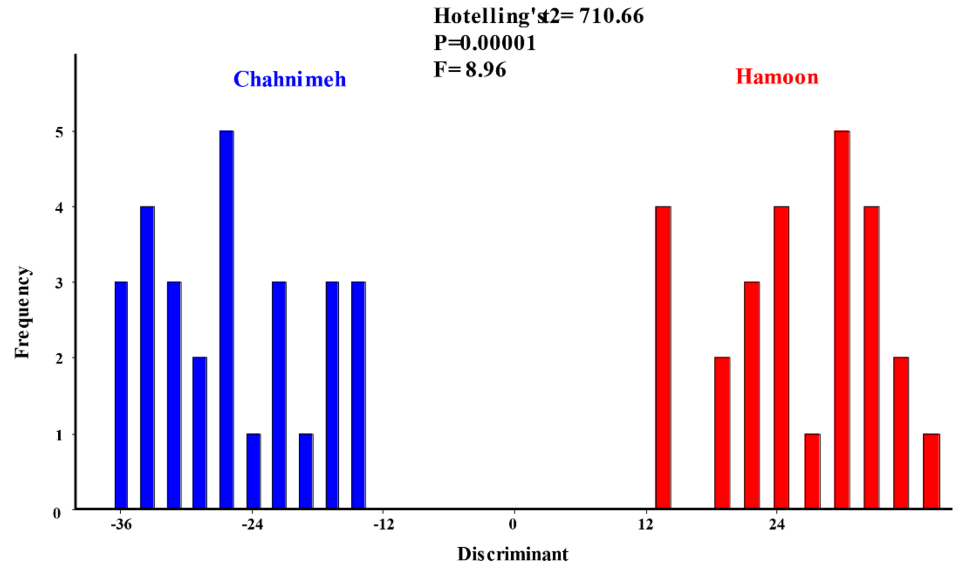

Fig.5. Analysis Chart - DFA Body Shape Populations of Anjak, *Schizocypris altidorsalis* in the Sistan Basin.

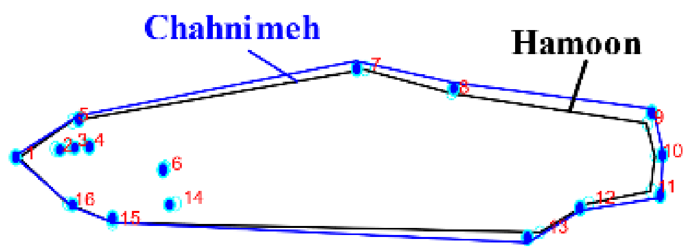

Fig.6. Comparison of the average body shape of Anjak, *Schizocypris altidorsalis* populations in the Sistan Basin using the deformation Wireframe network.

DISCUSSION

Freshwater ecosystems are among the most valuable and vulnerable environments, supporting high levels of biodiversity while being increasingly threatened by climate change and human activities. Environmental variation among aquatic habitats can strongly influence water quality and ecological conditions, ultimately affecting the morphology and population structure of freshwater fishes (Tadesse & Lakew 2025).

Fish are among the most morphologically diverse groups of vertebrates and often exhibit considerable phenotypic plasticity in response to environmental conditions (Shuai et al., 2018; Mouludi-Saleh & Keivany 2019). Although morphological variation has traditionally been attributed primarily to genetic differences, numerous studies have demonstrated that environmental factors, including habitat characteristics, water flow, temperature, food availability, and salinity, can induce substantial phenotypic variation through developmental plasticity (Smith & Skúlason 1996; Turan et al. 2004; Acar & Kaymak 2023). Consequently, body shape variation among fish populations often reflects the combined effects of genetic differentiation and environmental influences.

The present study revealed significant morphological differentiation between the Chahnimeh and Hamun populations of *Schizocypris altidorsalis* based on geometric morphometric analysis. Although the PCA showed partial overlap between populations, the DFA clearly discriminated the two groups, and the significant Hotelling's T^2 test, together with the Mahalanobis and Procrustes distances, confirmed that the observed body shape differences were statistically significant. This pattern suggests that subtle morphological differences, which are not fully captured by the major principal components, can be effectively detected using discriminant analyses.

Wireframe analysis indicated that the principal morphological differences involved body depth and caudal peduncle length. Individuals from the Hamun population exhibited a shallower body and a shorter caudal peduncle than those from the Chahnimeh reservoirs. Similar habitat-associated variation in body shape has been reported in numerous freshwater fishes, where differences in hydrological conditions, habitat complexity, food resources, and swimming performance contribute to morphological divergence (Smith & Skúlason 1996; Turan et al. 2004).

The present study did not directly measure environmental variables; therefore, the mechanisms underlying the observed morphological differences cannot be determined conclusively. Nevertheless, several ecological factors may have contributed to the detected variation. The Chahnimeh reservoirs provide relatively stable aquatic habitats, whereas the Hamun wetlands experience pronounced seasonal fluctuations in water level owing to prolonged droughts and variable inflow from the Helmand River. Such contrasting environmental conditions may influence growth patterns and developmental plasticity, ultimately resulting in differences in body shape. Future studies integrating morphometric, environmental, and molecular data will be necessary to distinguish phenotypic plasticity from genetically based differentiation.

Our findings are generally consistent with previous morphometric studies conducted on fishes of the Sistan Basin. Ganjali (2023) reported morphological variation between male and female populations of *S. altidorsalis*, although considerable overlap among individuals was observed. Likewise, Gholami et al. (2025) documented significant body shape differentiation among populations of *Alburnus hohenackeri* using geometric morphometrics, despite partial overlap in PCA space. These studies, together with the present results, demonstrate the effectiveness of geometric morphometric techniques for detecting subtle morphological variation in freshwater fishes.

Geometric morphometrics offers several advantages over traditional morphometric approaches because it preserves the geometric relationships among anatomical landmarks and allows detailed visualization of shape variation. In the present study, this approach successfully identified differences in body depth and caudal peduncle morphology that may have been difficult to detect using conventional linear measurements alone. Therefore, geometric morphometrics represents a valuable tool for investigating population differentiation, phenotypic plasticity, and conservation units in endemic freshwater fishes.

Because *S. altidorsalis* is an endemic species with a restricted distribution in the Sistan Basin, its conservation deserves particular attention. Prolonged droughts, alterations in river flow, habitat degradation, and fishing pressure have substantially reduced suitable habitats within the Hamun–Helmand system. Continued monitoring of morphological and genetic diversity will be important for assessing population status and developing effective conservation and management strategies for this ecologically and economically important species.

CONCLUSION

This study demonstrated the usefulness of landmark-based geometric morphometric analysis for detecting body shape variation in *Schizocypris altidorsalis* from two habitats within the Hamun–Hirmand aquatic system. Although Principal Component Analysis revealed partial overlap between the two populations, Discriminant Function Analysis and Hotelling's T^2 test identified significant morphological differentiation. The primary differences were associated with body depth and caudal peduncle length, with individuals from the Hamun population exhibiting a shallower body and a shorter caudal peduncle than those from the Chahnimeh reservoirs.

These findings suggest that populations of *S. altidorsalis* exhibit habitat-associated morphological variation, which may reflect phenotypic plasticity in response to contrasting environmental conditions. However, because environmental variables and genetic data were not examined in the present study, the mechanisms underlying the observed differences remain uncertain. Future research integrating geometric morphometrics with molecular analyses and environmental assessments is recommended to distinguish phenotypic plasticity from genetic differentiation.

Given the restricted distribution of *S. altidorsalis* and the increasing threats posed by prolonged drought, habitat degradation, hydrological alterations, and fishing pressure in the Sistan Basin, continued monitoring of its populations is essential. The present study provides a valuable baseline for future ecological, evolutionary, and conservation studies and supports the application of geometric morphometric methods as an effective tool for assessing population differentiation in endemic freshwater fishes.

ACKNOWLEDGMENTS

I would like to thank Mr. Shahroudi for helping with fish collection.

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Iran. J. Ichthyol. (2026) 13(1): 13-22
P-ISSN: 2383-1561; E-ISSN: 2383-0964
http://www.ijichthyol.org

doi: 10.22034/iji.v13i1.1145

مقاله کامل

کاربرد ریخت‌سنجی هندسی برای توصیف تنوع ریختی *Schizocypris altidorsalis* (Actinopterygii: Cyprinidae) از اکوسیستم‌های آبی هامون-هیرمند، جنوب شرقی ایران

زهره گنجعلی*

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چکیده: مطالعه حاضر با استفاده از آنالیز ریخت‌سنجی هندسی، تنوع ریخت‌شناسی ماهی انجک، *Schizocypris altidorsalis* را از اکوسیستم آبی هامون-هیرمند در حوضه سیستان، جنوب شرقی ایران، بررسی کرد. در مجموع ۵۵ نمونه (۲۶ نمونه از مخازن چاه نیمه و ۲۹ نمونه از تالاب هامون) با استفاده از تورهای دستی و پرتابی جمع‌آوری شدند. شانزده لندمارک همولوگ از تصاویر دوبعدی هر نمونه با استفاده از نرم‌افزار TPSDig2 رقومی‌سازی شدند. تنوع شکل با استفاده از آنالیز پروکراست (GPA) و به‌دنبال آن آنالیز مؤلفه‌های اصلی (PCA)، آنالیز تابع تشخیص (DFA) و آزمون T^2 هتلینگ تجزیه‌وتحلیل شد. تحلیل DFA تمایز ریخت‌شناسی معنی‌داری را بین دو جمعیت نشان داد. آنالیز تغییر شکل نمودار قاب سیمی براساس میانگین شکل کل نشان داد که تفاوت‌های اولیه با عمق بدن و طول ساقه دمی مرتبط هستند. این یافته‌ها نشان می‌دهد که *S. altidorsalis* انعطاف‌پذیری ریختی مرتبط با زیستگاه را نشان می‌دهد که احتمالاً منعکس‌کننده پاسخ‌های فنوتیپی به شرایط محیطی متفاوت در اکوسیستم آبی هامون-هیرمند است.

کلمات‌کلیدی: کپورماهیان، انعطاف‌پذیری فنوتیپی، ماهیان آب شیرین، تحلیل تابع تشخیصی