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RESEARCH PAPER

Phenotypic Plasticity of Angora Loach, *Oxynoemacheilus angorae* (Steindachner, 1897) in Inland Waters of Turkey

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Abstract

In the present study, we studied the morphological variations in four populations of *Oxynoemacheilus angorae* distributed in three basins of Turkish inland waters using a geometric morphometric technique. For this purpose, a total of 55 specimens were collected from the Kızılırmak, Sakarya and Marmara basins. To extract body shape data, the left side of the specimens was photographed, and 15 landmark points on the 2D pictures were defined and digitized. After generalized procrustes analysis, the body shape data were analyzed using multivariate analyses, such as principal component analysis, canonical variation analysis and cluster analysis. The deformation grids were used to show how the body shape changed. Based on the results, two groups, namely Nevşehir and Ankara, by having a deeper body and head and a somewhat longer caudal peduncle, and Yalova and Eskişehir due to lower body and shorter caudal peduncle were clustered. Based on the results, *O. angorae* adapts itself to different habitats by adjusting head and body depth and caudal peduncle length based on habitat parameters.

Keywords Phenotype plasticity · Turkish inland waters · Landmarks · Cluster analysis

1 Introduction

The morphological features in fishes are used for identifying population units and morphological variations (Zelditch et al. 2004; Mouludi-Saleh and Eagderi 2021a; Yedier and Bostanci 2021; Rodrigues-Oliveira et al. 2022). Traditional morphometric is a set of distance measurements of the biological structures, whereas, in the geometric morphometric technique, the landmark points or outlines are used to extract shape data (Mouludi-Saleh et al. 2020a). The geometric method has been described as an effective method in morphological studies compared to the traditional one (Loy et al. 1996; Radkhah et al. 2016) due to its higher efficiency in extracting shape data (Mouludi-Saleh et al. 2019; Nasri et al. 2019).

In Turkey, the nemacheilid fishes possess 59 species belonging to five genera, including *Oxynoemacheilus*, *Paracobitis*, *Schistura*, *Seminemacheilus,* and *Turcinoemacheilus* of which the genus *Oxynoemacheilus* is the most diverse one, with 48 species (Çiçek et al. 2015, 2018, 2019, 2020, 2021; Yedier et al. 2021a, b; Freyhof et al. 2021; Yoğurtçuoğlu et al. 2021). Among the members of the *Oxynoemacheilus*, Angora loach, *O. angorae* (Steindachner, 1897), described from the Çubuk Stream (Sakarya Basin), has a wide distribution covering other inland waters of Turkey, including the Marmara, Susurluk, Sakarya and Kızılırmak basins (Çiçek et al. 2019). This species has been reported from Iranian inland waters; however, Freyhof et al. (2011) rejected its occurrence in the Caspian Sea Basin of Iran and considered it as an endemic species of the western and Central Anatolian and Black Sea basins. Nemacheilid species particularly some member of the genus *Oxynoemacheilus* show high morphological variations as reported in *O. seyhanensis* (Seçer et al. 2020), and *O. bergianus* (Mohammadi et al.

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2020; Mouludi-Saleh and Eagderi 2021b), revealing their high phenotypic plasticity in their different populations.

Given the wide distribution range of this species, the aim of our study was to assess whether *O. angorae* populations display morphological variations in different river basins and these probable morphological variations are habitat-dependent. Therefore, we specifically compared the morphological characteristics in four populations of *O. angorae* from three Turkish inland basins, and explored whether some habitat characteristics such as river width or altitude could potentially explain inter-population morphological differences.

2 Martial and Methods

During the spring of 2019, a total of 55 specimens of *O. angorae* were collected from three basin of Turkish inland waters, including 14 from output of the Doyduk Dam Lake in Nevşehir (Kızılırmak Basin), 15 from Çubuk Stream (Ankara), 11 from Düden Stream (Eskişehir) (Sakarya Basin) and 15 from Altınova Stream (Yalova) (Marmara Basin) using an electrofishing device (Figs. 1, 2 and Table 1). After anesthesia, the specimens were fixed in 4% buffered formalin and transferred to the Hydrobiology Laboratory at Nevsehir Haci Bektas Veli University.

During sampling, some environmental characteristics of the habitats, including altitude, river depth, width, the average size of the substrate stones, slope, and water velocity, were measured. The coordinates and altitude of the sampling point were recorded using a hand-held GPS (Garmin eTrex 30x). The river widths were measured using a tape measure at the anterior, middle, and posterior points of the sampling station, and their average was considered the river width of the station. The river depth was measured across the river at twenty points with about 1 m distance using a graduated wooden pole that was averaged and considered as the depth of a given sampling point. The slope of the river bed was measured using a Suunto device (PM-PC Clinometer). The water velocity was measured three times and averaged at each sampling point using the floating object method (Hasanli 1999).

For extracting shape data in geometric morphometric, the left sides of the fresh specimens were photographed using a copy-stand equipped with a digital camera (Canon EOS 700D with 18 MP resolution). Then, 15 homologous landmark-points were digitized using tpsDig2 software (Rohlf 2004 version 1.04) on 2D images (Fig. 3). The extracted data were analyzed using Generalized Procrustes Analysis (GPA) to remove non-shape data, including size, position and direction (Zeldtich et al. 2004). Then, data were analyzed using Principal Components Analysis (PCA), Canonical Variate Analysis (CVA) and Cluster Analysis (CA) as a complement to CVA by adopting the Euclidean square distance as a measure of dissimilarity. Permutation test was used to prepare a pairwise distance of

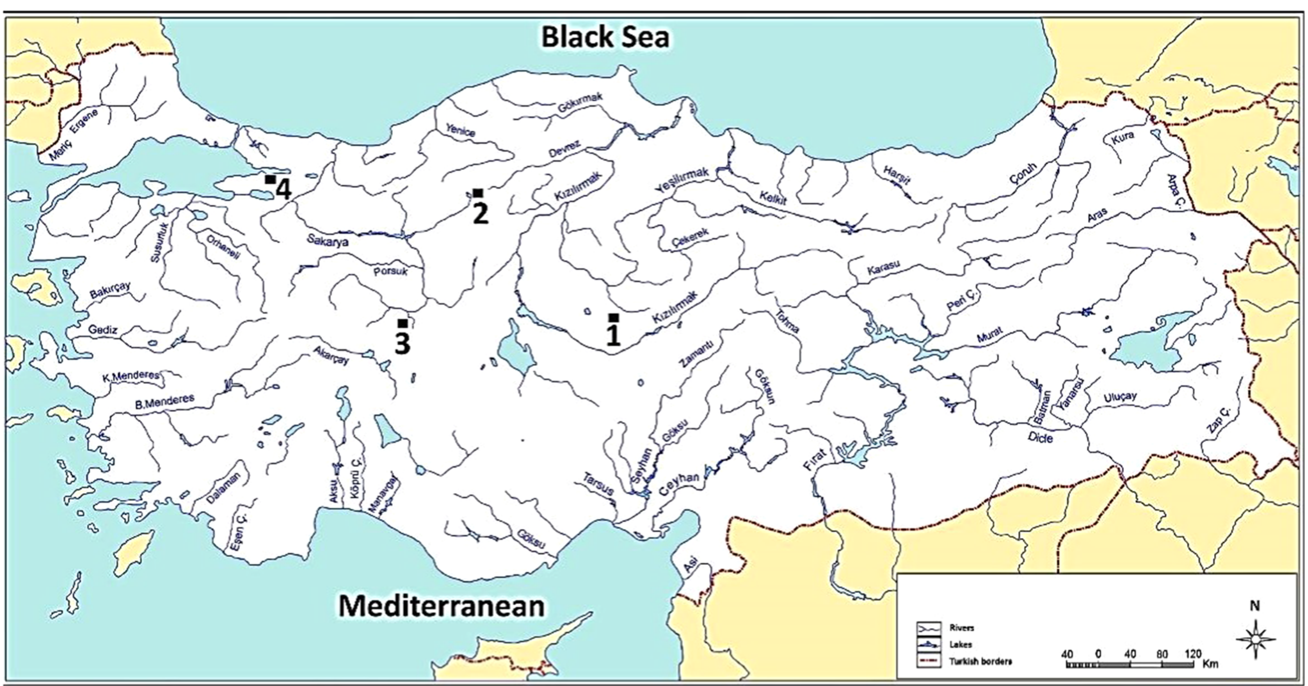

Fig. 1 Sampling sites of *Oxynoemacheilus angorae* from Turkish inland waters. (1: Nevşehir; 2: Ankara; 3: Eskişehir; 4: Yalova)

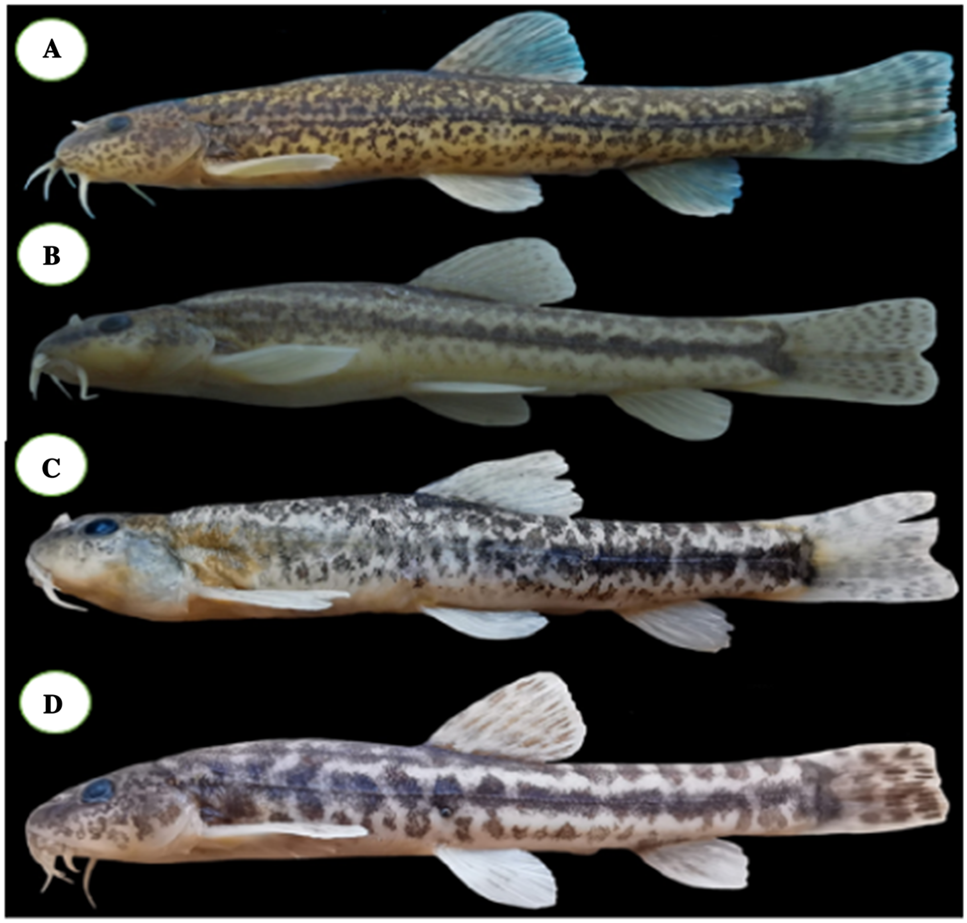

Fig. 2 *Oxynoemacheilus angorae*; A = Ankara, 64.7 mm SL; B = Nevşehir, 57.5 mm SL; C = Yalova, 56.4 mm; D = Eskişehir, 66.2 mm SL

Table 1 Ecological parameters of the study areas, Turkish inland water

Populations	Geographical coordinate	Habitat	Bed type	Velocity	Slope	Width (m)	Deep (m)	Height above sea level (m)
Nevşehir	39°12′22“N 34°44′19”E	Output of Doyduk Dam Lake	Mud	Moderate	0.5	4	0.50	1062
Ankara	40°20′38“N 33°02′19”E	Çubuk Stream	Mud + Gravel	Moderate	1	6	0.70	1161
Eskişehir	39°09′04“N 31°36′55”E	Düden Stream	Mud	Fast	0.5	7	0.90	884
Yalova	40°40′38“N 29°31′54”E	Altınova Stream	Sand + Gravel	Moderate to fast	1.5	2	0.35	43

the studied populations based on MANOVA/CVA analysis with 10,000 repetitions in MorphoJ software version 1.02j.

The Mahalanobis and Procrustes distances (as the degree of differentiation of the body shape in canonical variate analysis) were calculated to explore the degree of the morphological distance between the studied populations. For shape differences, each population was compared with the consensus configuration visualized as deformation grids presented with CA. All analyses were performed in PAST V2.17b (Hammer et al. 2001) and MorphoJ (version 1.02j) (Klingenberg 2011) software. A procrustes regression was used to find the environmental variables that significantly influenced the morphology of the populations (Sherratt 2014). For morphological data, we used procrustes distance as a descriptor for the variation in shape (Bookstein 1991). The regression was performed in R 3.6.1 using the package geomorph (Adams et al. 2021).

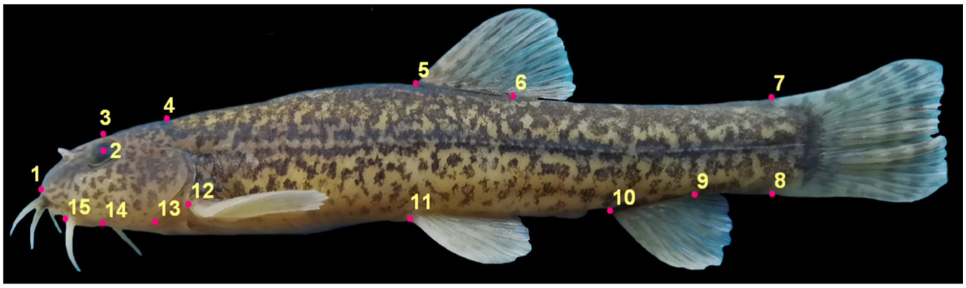

Fig. 3 The **15** defined landmark-points to extract the body shape data of *Oxynoemacheilus angorae*. **1.** Anterior-most point of the snout tip on the upper jaw. **2.** Center of eye. **3.** Dorsal edge of the head perpendicular to the center of eye. **4.** The line extends perpendicularly to the ventral edge of the opercle above the head. **5.** Origin and **6.** Insertion point of the dorsal-fin base. **7.** Postero-dorsal end of the caudal peduncle at its connection to caudal fin. **8.** Postero-ventral end of the caudal peduncle at its connection to caudal fin. **9.** insertion and **10.** Origin point of the anal-fin base. **11.** Most anterior point of the ventral fin. **12.** Most anterior point of the pectoral fin. **13.** Ventral end of the gill slit and **14.** Ventral edge of the head perpendicular to the center of eye. **15.** Mandibular barbel

3 Results

In PCA, the first three principal components accounted for a total of 66.54% (PC1 + PC2 + PC3) of the variance (PC1 = 42.59, PC2 = 14.66 and PC3 = 9.28; Fig. 4). The distribution of the studied populations is presented in Fig. 5, and the body shape changes along the PC1 and PC2 axes in Fig. 6. By moving along the PC1 axis, the position of the nape (landmark-points: LM 4), the position of the dorsal (LM 5 and 6) and anal (LM 9 and 10) fins' bases are altered, and in the PC2 axis, the position of the pectoral (LM 12), dorsal (LM and 6) and ventral fins' bases were altered.

Canonical Variate Analysis (CVA) based on the *P*-value obtained from a permutation test with 10,000 replications showed a significant difference (Wilks-lambda = 0.001, F = 8.878, $P < 0.01$) in the body shape of the four studied populations (Fig. 7). The results of the through permutation test showed that the studied populations have significant differences in their morphological patterns ($P < 0.001$, Table 2).

The Mahalanobis and Procrustes distances as the degree of body shape differentiation between the studied populations are given in Tables 3 and 4. According to the results, the greatest Mahalanobis and Procrastes were found between the Yalova and Ankara populations. The cluster

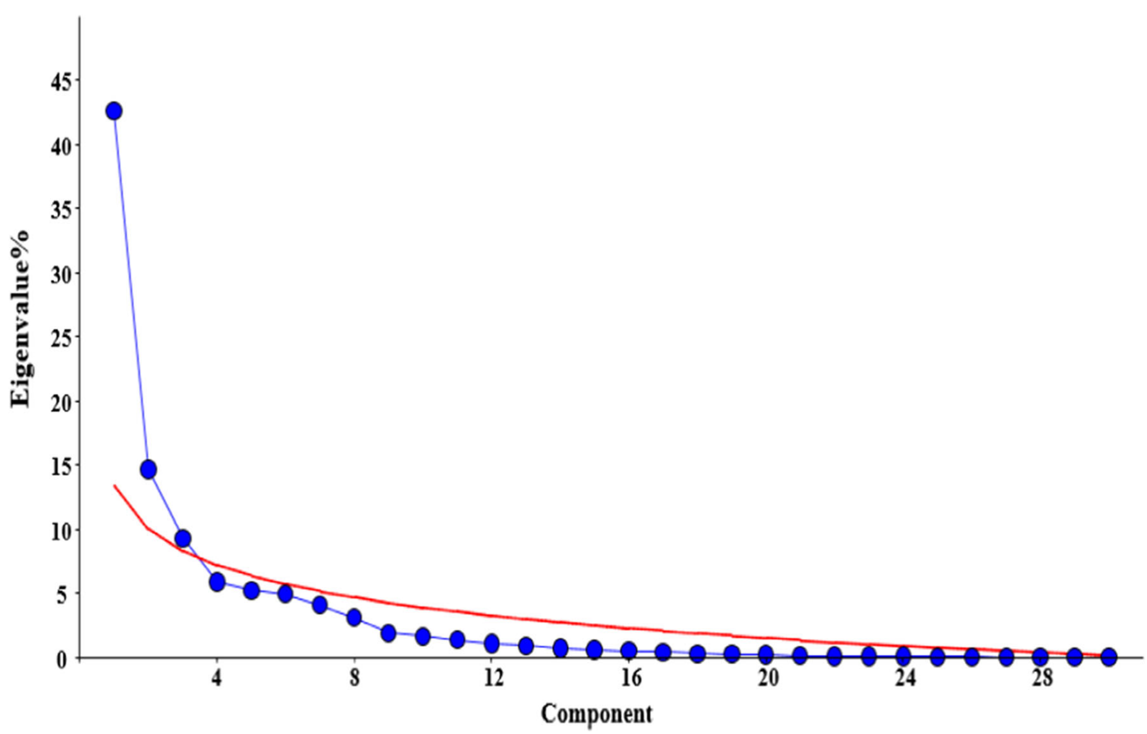

Fig. 4 The scree plot diagram of PCA and the Jolliffe cutoff point (red line), showing the main significant components

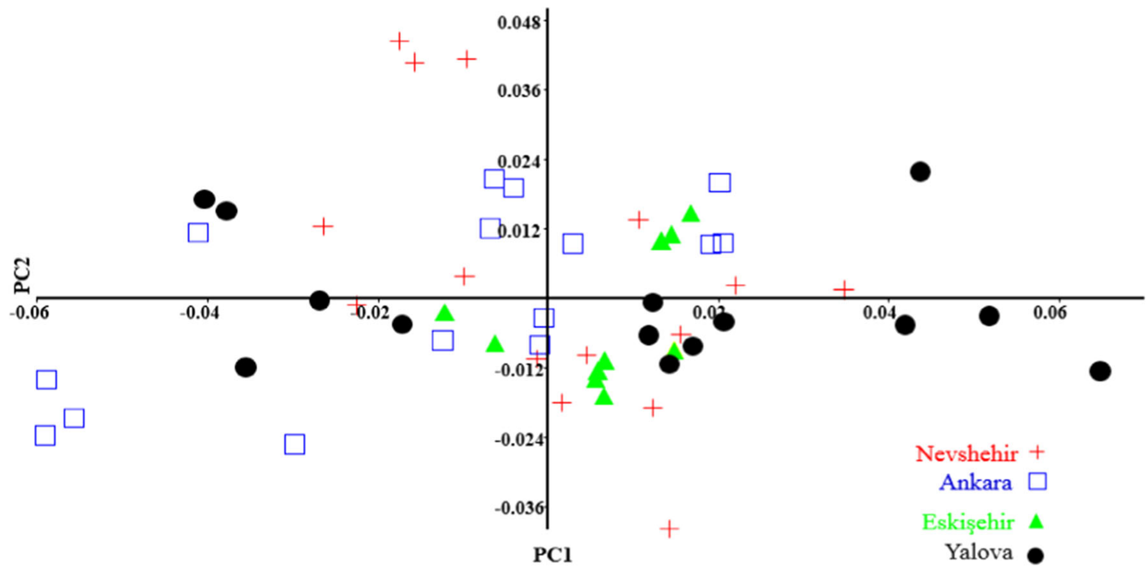

Fig. 5 Principal components analysis (PCA) graph of *Oxynoemacheilus angorae* populations

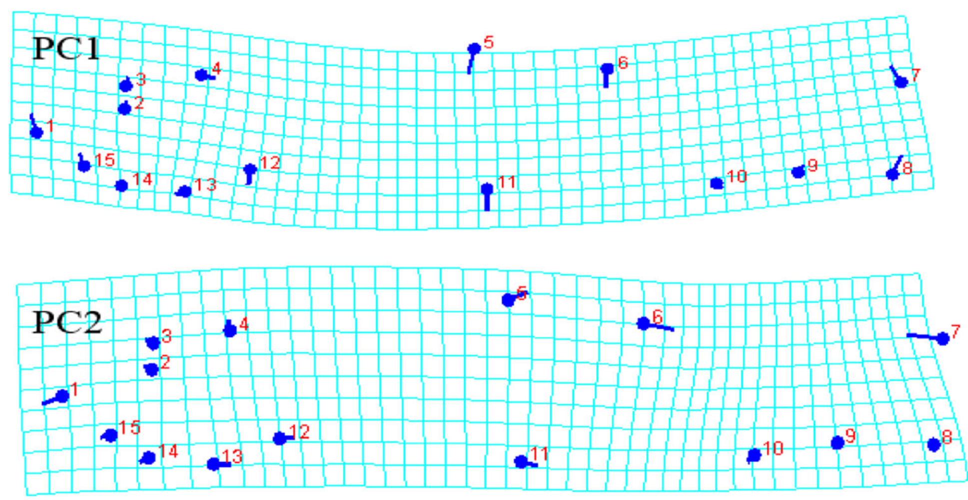

Fig. 6 Positive extreme body shape changes along the PC1 and PC2 axes

analysis of the studied populations based on the body shape pattern showed two main branches, including the Nevşehir + Ankara due to having a higher body and head depth and a longer caudal peduncle, and Yalova + Eskişehir by having lower body and a shorter caudal peduncle (Fig. 8).

The procrustes regression indicated that the width and depth of the rivers had a significant effect on the morphology of the specimens (Table 5). The rest of the environmental variables were redundant and therefore eliminated from the analysis.

4 Discussion

Morphological variations between different populations of a single species can be due to environmental characteristics, i.e., water flow, substrate and vegetation types and genetic differences (Nicieza 1995; Guill et al. 2003; Nasri et al. 2015), leading to morphological flexibility (Cadrin and Silva 2005; Mouludi-Saleh et al. 2020b). In the present study, four populations of *O. angorae* were studied to investigate the body shape variations for understanding the pattern of their morphological adaptations in different

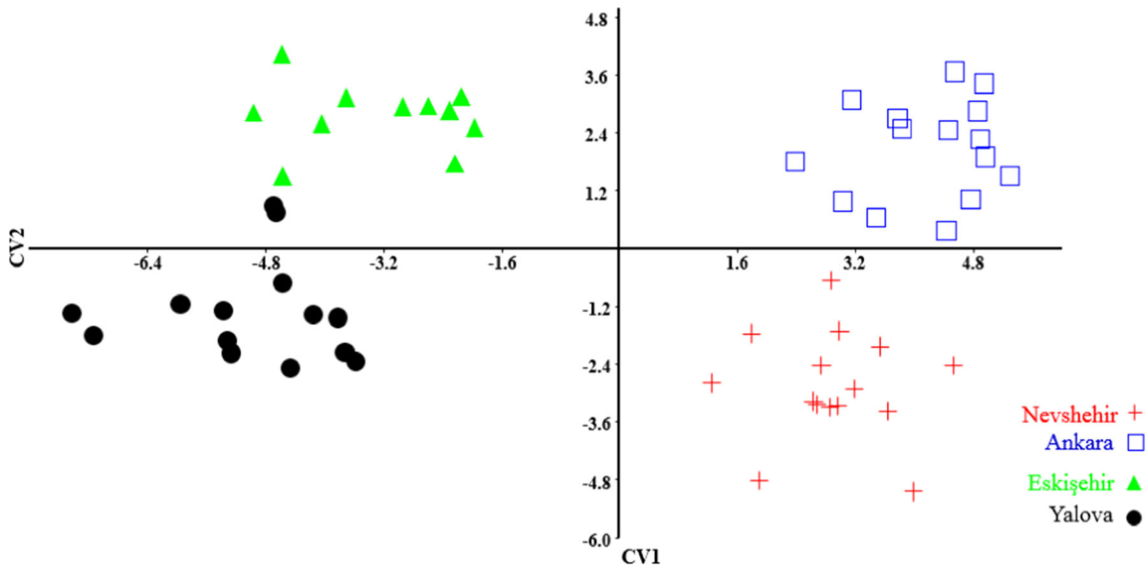

Fig. 7 Canonical variate analysis (CVA) graph of *Oxynoemacheilus angorae* populations

Table 2 The results of permutation test based on MANOVA/CVA

	Ankara	Nevşehir	Eskişehir
Nevşehir	< 0.0001		
Eskişehir	< 0.0001	< 0.0001	
Yalova	< 0.0001	< 0.0001	< 0.0001

Table 3 Mahalanobis distances of the body shape of the studied populations of *Oxynoemacheilus angorae*

	Ankara	Nevşehir	Eskişehir
Nevşehir	5.13		
Eskişehir	7.75	7.65	
Yalova	9.65	8.7	5.67

Table 4 Procrustes distances of the body shape of the studied populations of *Oxynoemacheilus angorae*

	Ankara	Nevşehir	Eskişehir
Nevşehir	0.024		
Eskişehir	0.029	0.031	
Yalova	0.036	0.03	0.021

habitats. Based on the results, the differences between the body shapes of the studied populations were those of the body and head depth and caudal peduncle length. The higher body depth is more efficient in low flow areas and marginal vegetation to increase rapid maneuverability (Blake 1983) as seen in the Nevşehir and Ankara populations, whereas the lower body depth is reported to be proper in water bodies with high flow to reduce friction (Barlow 1961) as seen in the Yalova and Eskişehir populations.

As seen in Fig. 7, Angora loach has an eel-like body shape and, based on the results, this species is adapted to different habitats by adjusting its caudal peduncle length and body depth, i.e., as its morphological adaptation pattern. The tail is a serious locomotive organ in fish species, and its size and shape effect its swimming performance (Plaut 2000; Yang et al. 2013). A longer caudal area is an adaptation to have higher swimming performance but higher drag, whereas in a shorter one, both swimming performance and drag force are decreased (Fu et al. 2013). In Yalova and Eskişehir populations, the shorter tail is accompanied by deeper body, i.e., having a fusiform body shape that is proper for the swift current of Yalova and Eskişehir water bodies (Donley and Dikson 2000). In Nevşehir and Ankara samples, longer caudal peduncles can provide powerful swimming performance in the slower currents of their habitats (Watson and Balon 1984). In addition, a longer caudal peduncle enhances fast-start swimming performance (Langerhans 2009), and this is elicited by increasing prediction and prey capture (Langerhans 2009; Langerhans and Reznick 2010). As seen in the Eskişehir and Yalova populations, the smaller head, longer caudal peduncle and relatively lower body are suitable for living in fast-flowing water at a lower depth (Darcy 1985; Zamani-Faradonbe et al. 2015). The results revealed that two environmental factors, i.e., depth and width of rivers, have an effect on the morphology of the

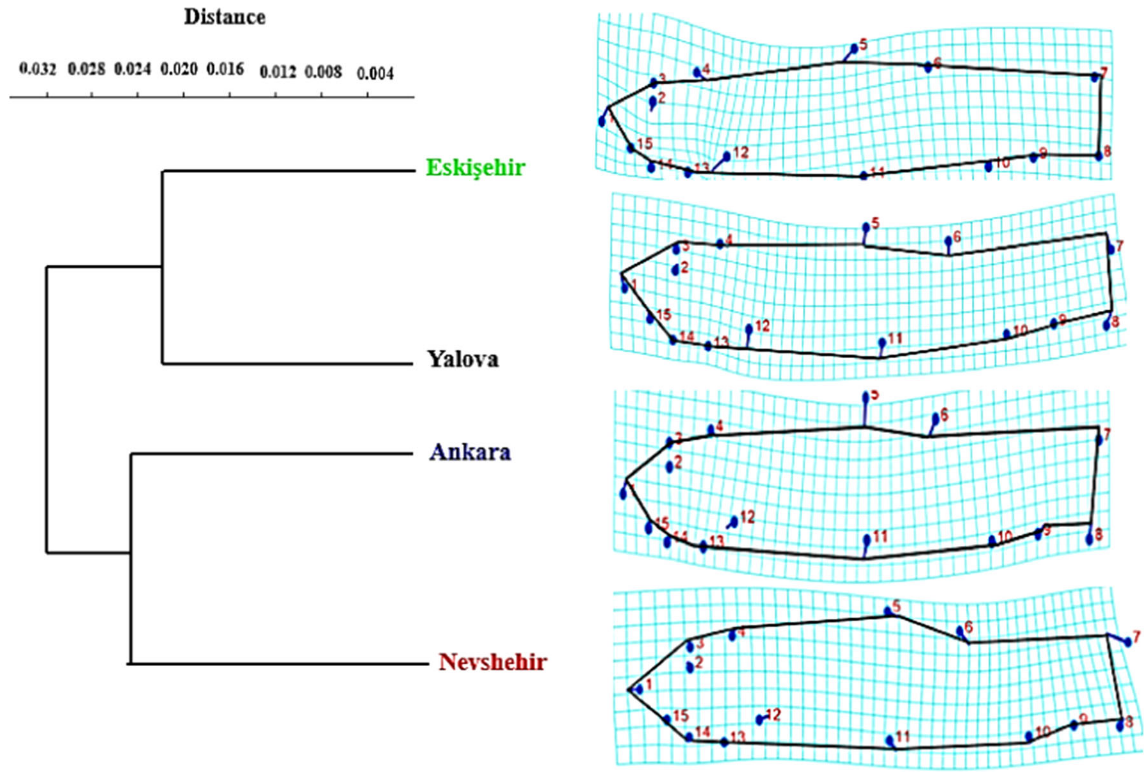

Fig. 8 Cluster analysis (CA) graph of *Oxynoemacheilus angorae* populations

Table 5 The results of the procrustes regression performed to find the environmental variables having significant effects on morphology of the specimens

Variables	df	SS	MS	Rsq	F	Z	Pr(> F)
River width	1	0.005585	0.0055855	0.05368	3.3904	2.0655	0.03
River depth	1	0.009484	0.0094839	0.09114	5.7566	2.8422	0.01
Altitude	1	0.003319	0.0033192	0.03190	2.0147	1.3800	0.09
Residuals	52	0.085668	0.0016475	0.82328			
Total	55	0.104057					

studied populations of *O. angorae*. These results of environmental parameters are in agreement with morphological changes in the Yalova and Eskişehir populations. However, in the Eskişehir, having deeper habitat with a wider river and increasing the river width can lead to decreasing its depth or providing some microhabitat with lower depths, especially in the littoral area, as was the case with this habitat (Fig. 9). In previous studies on the member of *Oxynoemacheilus* species, important morphological traits in separating their populations were those of inter orbital and maxillary barbell lengths (Seçer et al. 2020), pectoral fin height, distance between pelvic and anal fins (Mohammadi et al. 2020) and caudal peduncle length and depth, body depth, head length and position of the dorsal, anterior and pectoral fins (Mouludi-Saleh and Eagderi 2021b). These variations in the morphological variation of other members of this genus show different strategies to adapt their morphology to various habitats.

Various environmental parameters (temperature, turbidity, salinity, depth, and velocity of water bodies) can cause a change in the morphological traits, resulting in the morphological separation of populations (Eagderi et al. 2013, 2020). Based on the results, habitat-dependent morphological patterns in the studied species were head and body depth and caudal peduncle length, i.e., this species adapts itself to different habitats by adjusting these mor-

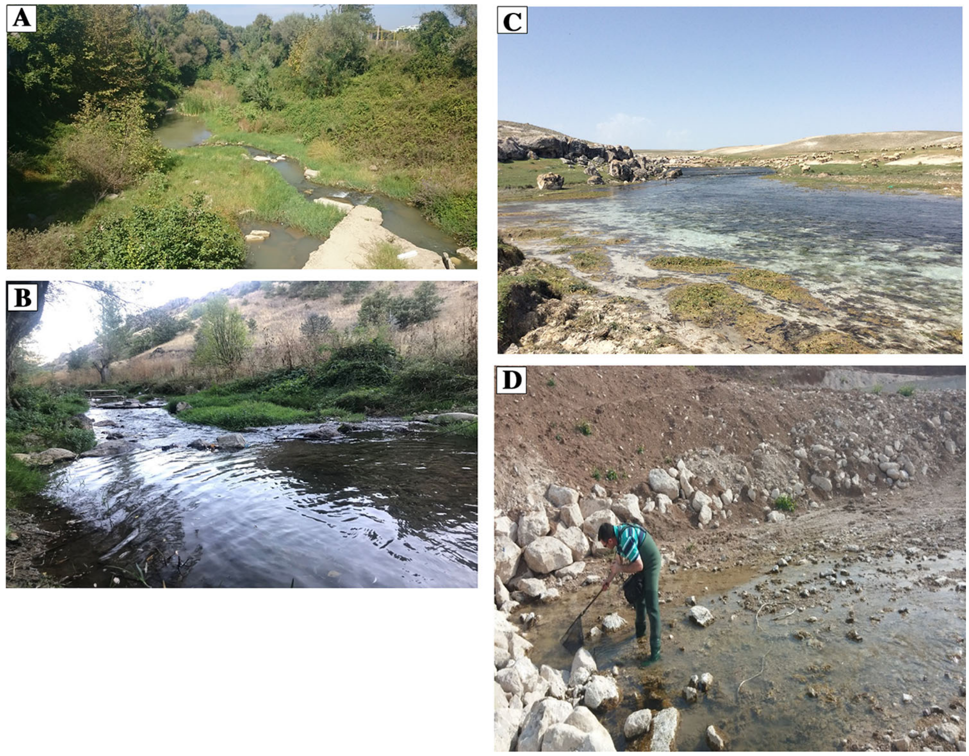

Fig. 9 Natural habitat of the studied rivers **A** Yalova; **B** Ankara; **C** Eskişehir; **D** Nevşehir

phological features based on habitat parameters. However, the morphological change patterns indicate the high plasticity ability of this species to develop its distribution area in different inland waters of Turkey.

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Data Availability The data that support the findings of this study are available on request from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical Approval We confirm that all procedures performed in this study involving animals were in accordance with the ethical standards.

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