



How the morphology of two closely related riverine sympatric species are reflected in ecological niche overlapping? A case study of two *Capoeta* species

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Abstract

This study investigated morphological differences, habitat preference, and ecological niche overlap in two sympatric *Capoeta* species i.e., *Capoeta damascina* and *Capoeta umbla* collected from the Sirvan river drainage. Ten environmental factors, including pH, temperature, electrical conductivity (EC), total dissolved solids (TDS), river width, river depth, flow velocity, altitude, slope, and dissolved oxygen (DO) were measured during sampling time. A total of 17 morphometric characteristics were measured using digital calipers for traditional morphometrics (TM). For the geometric morphometric method (GM), 2D pictures were taken from the left side of the fresh samples, by tpsDig2 software, and 16 landmark points were defined and digitalized to extract body shape data. The data were analyzed using *t*-test, Mann–Whitney, principal component analysis (PCA), and discriminant function analysis based on the *P*-value of Hotelling's T-squared. The ratio of the common area under the graph to the total area of habitat suitability indices was defined as the ecological niche overlap. The results showed significant differences in eye diameter, predorsal, caudal peduncle length, preanal, preventral, ventral-pectoral, body depth, and caudal peduncle depth traits ($P < 0.05$) in TM, and those differences in the GM were related to the position of the snout, head and body depth and caudal peduncle length i.e., *C. damascina* had the deeper body shape and head, and anterior the snout and caudal peduncle length. Based on the results, *C. damascina* prefers areas with higher pH and temperature and by increasing other studied factors, its habitat suitability decreased. The preference for *C. umbla* with increasing river depth and DO was increased. These two species showed low niche overlap i.e., they avoid competition in their habitat by opting for different areas in terms of river width, flow velocity, and temperature that have more depth with higher slope microhabitats.

Keywords Sirvan river · Morphological traits · Habitat preference · Discriminant function analysis

Introduction

Sympatric speciation occurs when two species evolved from an ancestral species in the same geographical area. Some models have been proposed for evolving sympatric speciation (Smith 1966), however, there is no consensus to put all sympatric speciation in defined models. Two closely related species of *Capoeta damascina* and *Capoeta umbla* inhabit the Iranian part of the Sirvan River drainage as sympatric (Alwan 2011; Esmaeili et al. 2016; Eagderi and

Mousavi-Sabet 2021; Mouludi-Saleh et al. 2022a). These sympatric species could be proper candidates to examine how they have differentiated in terms of morphology while living in the same habitat with probably overlapped niche preferences.

Levin et al. (2012) reported that the genus *Capoeta*, includes Mesopotamian, Anatolian–Iranian, and Aralo-Caspian groups. Alwan (2011) reported western and eastern lineages within the Mesopotamian group or *C. damascina* species complex, and those of the western group comprise *C. damascina*, *Capoeta kosswigi*, *Capoeta caelestis*, and *C. umbla*. Some works suggest the conspicuousness of this lineage (Turan 2008; Alwan et al. 2016a, b; Ghanavi et al. 2016; Zareian and Esmaeili 2017; Zareian et al. 2018; Bektaş et al. 2019). *Capoeta caelestis* and *C. umbla* are valid species because of their morphological differences from *C. damascina* despite their molecular similarity (Çiçek

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et al. 2021a). However, *C. kosswigi* was considered a junior synonym of *C. damascina* (Çiçek et al. 2021a). *Capoeta damascina* is a widespread species in the Persian Gulf basin, Jordan River drainage, and Orontes basin (Alwan 2011; Alwan et al. 2016a; Esmaeili et al. 2016; Eagderi et al. 2022).

Fish morphology is a reflection of its adaptation to its habitat (Eklöv and Svanbäck 2006; Costa and Cataudella 2007). Morphological study of coexisting fishes may lead to understanding their resource use (Helland et al. 2009). Morphological differences can be a strategy to decrease competition, directly related to fitness. In a given species, its preference for environmental parameters can be found using the habitat suitability index (HSI) i.e., a similar HSI of sympatric species may be an indication of their ecological niche overlap (McNyset 2005).

Based on the above-mentioned background, this study evaluates morphological differentiation patterns, habitat preferences, and ecological niche overlapping and their relationships based on some large-scale parameters in two closely related sympatric *Capoeta* species i.e., *C. damascina* and *C. umbla* inhabiting the Sirvan River drainage. The results will help to understand how morphological differences may be a mechanism allowing congeneric species to coexist, which has led to evolving distinct species despite their molecular similarity (Jawad and Alwan 2020).

Materials and methods

Sampling

During the summer of 2021, 104 specimens (62 *C. damascina* and 42 *C. umbla*) were collected from six stations (ST1: 35°32'08.87"N; 46°18'25.22"E, 8 *C. damascina* and 5 *C. umbla*; ST2: 35°33'05.87"N; 46°18'38.19"E, 9 *C. damascina* and 7 *C. umbla*; ST3: 35°24'13.48"N; 46°17'15.01"E, 13 *C. damascina* and 11 *C. umbla*; ST4: 35°21'13.03"N; 46°16'52.55"E, 15 *C. damascina* and 6 *C. umbla*; ST5: 35°20'40.02"N; 46°17'34.23"E, 8 *C. damascina* and 7 *C. umbla*; ST6: 35°15'56.77"N; 46°24'45.88"E, 9 *C. damascina* and 9 *C. umbla*) (three times for each station) in the upper part of the Sirvan River drainages using an electrofishing device (SAMUS 750, Poland) (Fig. 1). The specimens were anesthetized and the left side of the fresh specimens were photographed, and then they were fixed into 10% buffered formalin and transferred to the laboratory.

Morphology

Following Armbruster (2012), and for the traditional morphometric method (TM), 18 morphometric traits were measured using digital calipers to the nearest 0.05 mm



Fig. 1 *Capoeta damascina* (upper) and *C. umbla* (below) collected from the Sirvan River drainage

(Table 1). The data were transformed to remove the effects of size using PAST version 2.17b software based on the allometric growth method (Elliott et al. 1995). Then, the results derived from the allometric method were confirmed by the testing significance of the correlation between transformed variables and standard length (Çiçek et al. 2021b). The t-test and Mann–Whitney tests were used to analyze the extracted traditional morphometric data. The studied species were compared using multivariate analysis of discriminant function analysis (DFA) with T-squared.

For the geometric morphometric method (GM), the left side of the fresh samples was photographed using a digital camera (Canon, 18MP, Thailand). Sixteen landmark points were defined and digitalized using tpsDig2 software (Rohlf 2001; <http://www.sbmorphometrics.org/soft-dataa cq.html>) on 2D pictures (Fig. 2). For data analysis, multivariate analysis of DFA with T-squared was performed after superimposition of data by Generalized Procrustes Analysis. All analysis was performed in SPSS 26 (IBM Corp 2019), PAST v 2.17b (Hammer et al. 2001), and MorphoJ (Klingenberg 2011, https://morphometrics.uk/MorphoJ_page.html).

Table 1 The results of the Mann–Whitney and *t* test for difference in the morphometric traits (mean \pm SD) between *C. damascina* and *C. umbla* in the Sirvan River

Traits	Abbreviations	<i>C. damascina</i>	<i>C. umbla</i>	<i>t</i>	<i>P</i>
Standard length	SL	118.68 \pm 00	118.68 \pm 00	–	–
Head length	HL	27.03 \pm 1.73	26.51 \pm 1.22	1.409	0.161
Snout length	SnL	7.37 \pm 0.99	7.34 \pm 1.05	0.139	0.889
Post orbital length	PoO	12.95 \pm 1.00	13.13 \pm 1.08	0.847	0.398
Eye diameter	ED	6.58 \pm 0.87	6.21 \pm 0.76	0.421	0.022
Predorsal	PrD	57.98 \pm 2.29	59.55 \pm 1.93	3.23	0.002
Post dorsal	PoD	38.42 \pm 2.58	37.36 \pm 1.9	1.91	0.058
Pre anal	PrA	90.78 \pm 2.33	92.15 \pm 2.16	2.67	0.008
Caudal peduncle length	CPL	14.89 \pm 2.51	15.9 \pm 2.85	2.82	0.005
Pre ventral	PrV	64.47 \pm 2.32	66.13 \pm 2.69	3.2	0.002
Pre pectoral	PrP	25.56 \pm 1.99	25.95 \pm 2.43	0.805	0.422
Pectoral-anal	P-A	64.88 \pm 2.41	65.77 \pm 2.2	1.63	0.444
Pectoral-ventral	P-V	37.54 \pm 2.15	39.10 \pm 1.5	3.42	0.000
Ventral-anal	V-A	26.34 \pm 1.97	26.53 \pm 2.07	0.399	0.691
Body depth	BD	29.43 \pm 1.64	30.46 \pm 1.17	3.01	0.001
Caudal peduncle depth	CPD	13.55 \pm 0.78	14.08 \pm 0.68	3.1	0.004

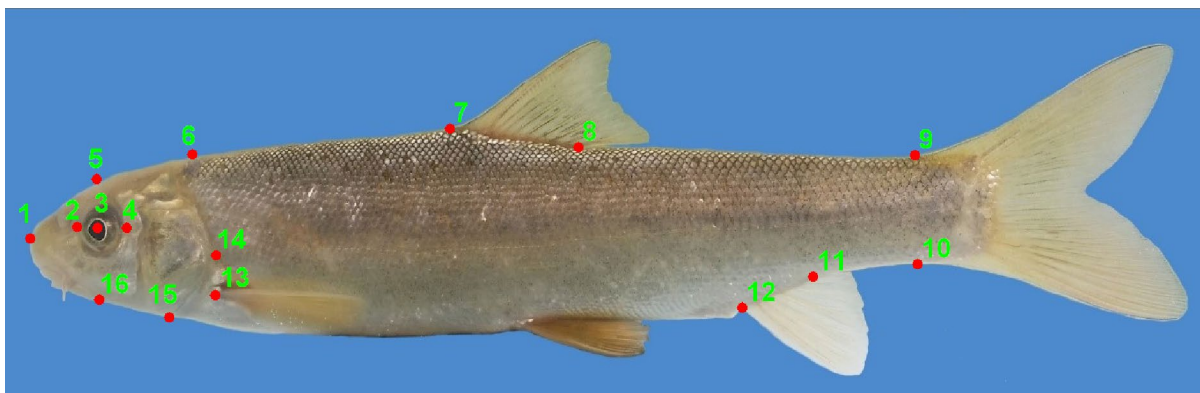


Fig. 2 Sixteen defined landmark points for extracting the body shape data of *Capoeta* species in the Sirvan River. (1) anterior-most point of the snout tip on the upper jaw, (2) anterior point perpendicular to the center of the eye, (3) center of the eye, (4) posterior point dorsal perpendicular to the center of the eye (5) edge of the head perpendicular to the center of the eye, (6) boundary between smooth and scaly skin, (7) origin and (8) insertion point of the dorsal-fin base, (9) postero-

dorsal end of the caudal peduncle at its connection to caudal fin, (10) postero-ventral end of the caudal peduncle at its connection to caudal fin, (11) insertion and (12) origin point of the anal-fin base, (13) most anterior point of the pectoral fin, (14) posterior edge of the opercle, (15) ventral end of the gill slit and (16) ventral edge of the head perpendicular to the center of eye

Habitat parameters

Ten parameters were measured in three replicates for each location: pH, Temperature (°C), Electrical conductivity ($\mu\text{S}/\text{cm}$), Total dissolved solids (mg/L) (using a portable device for measuring environmental factors), altitude (m), river depth (m) and width (m) using a tape measure, flow velocity (m/s) using the floating object method (Hasanli 1999), river bed slope (%) using google earth software, and DO ($\text{mg}-\text{O}_2/\text{L}$) VAHEB Oxygen measuring kit (Shimi sanat, Iran) were recorded in each station with three replicates.

Suitability index calculation

Kernel smoothing was used to find the suitability index. To find the bandwidth of the kernel smoothing, a polynomial regression was calculated to model the predicted values. The predicted values were standardized to find the SI graphs using the following equation: $\{x_i - \min(x)\} / (\max(x) - \min(x))$, where, x_i = the environment variable, $\min(x)$ = the minimum value of each variable, and $\max(x)$ = the maximum value of each variable. Then, the graphs of these values were standardized and plotted for each environmental variable, including pH, temperature, EC, TDS, altitude, river depth and width, flow velocity, slope, and DO (Pourmoghadam et al. 2019).

Niche overlap

The overlap of ecological niches was investigated using suitability indices curves of every habitat parameter drawn by kernel smoothing. The proportion of area overlapping between two species drawn by SI curves for the two species was defined as the ecological niche overlap according to the

following equation, where A and B are the fitted sub-smooth areas for both species. This part was done in the R (version 4.2.2) packages (“caret” version 6.0–94 (Kuhn et al. 2020) and “sfsmisc” (Maechler et al. 2023) version 1.1–16).

$$\text{Niche overlap} = \frac{A \cap B}{A \cup B - (A \cap B)}$$

Results

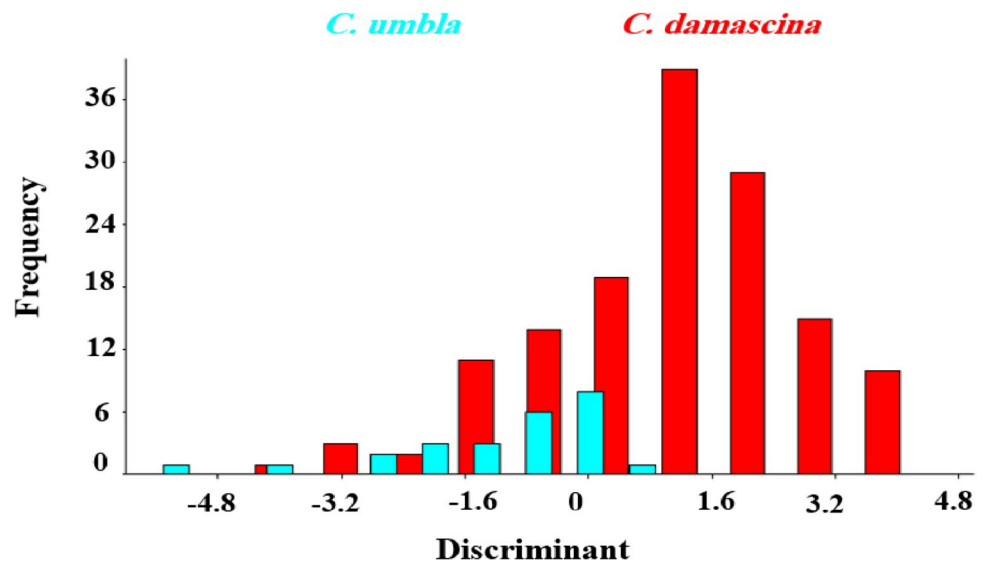
Traditional morphometry method

Normality test showed all studied traits were normal except eye diameter, predorsal, preventral, ventral-pectoral, body depth, and caudal peduncle depth ($P > 0.05$). Normal and non-normal data were compared between two species using the *T*-test and Mann–Whitney test, respectively. The results showed a significant interspecific difference in eye diameter, predorsal, caudal peduncle length, preanal, pre-ventral, ventral-pectoral, body depth, and caudal peduncle depth ($P < 0.05$, Table 1). The DFA with *T*-squared analysis showed separations of *C. damascina* and *C. umbla* (*T*-squared = 45.67, $F = 5.47$, $P < 0.001$; (Fig. 3). The pre-pectoral (0.523) and caudal peduncle (0.779) lengths had high discriminatory roles.

Geometric morphometry method

Principal component analysis of the body shape showed that the first three principal components accounted for 69.85% of the variance. The DFA with *T*-squared showed that *C. damascina* and *C. umbla* are different in body shape

Fig. 3 DFA for traditional morphometric traits of *C. damascina* and *C. umbla* collected from the Sirvan River



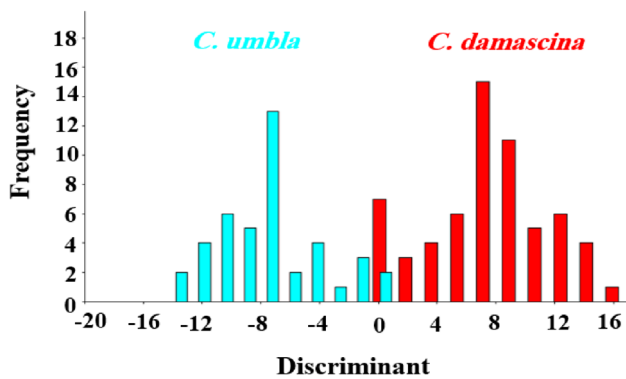


Fig. 4 DFA for geometric morphometric traits of *C. damascina* and *C. umbla* collected from the Sirvan River

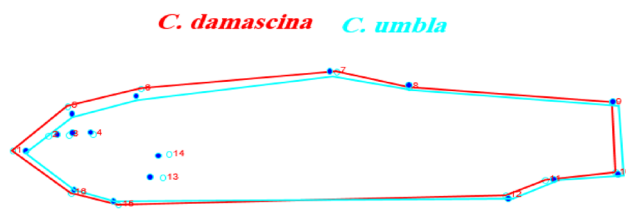


Fig. 5 Wireframe diagram consensus body shape graph of *Capoeta damascina* and *C. umbla* in the geometric morphometric method

(T -squared = 384.77, $F = 8.36$, $P < 0.001$; Fig. 4). Based on the wireframe diagram, *C. damascina* had a deeper body and head, and its snout and caudal peduncle were longer (Fig. 5). The Mahalanobis distance was 3.91 between the two species.

Habitat preference

The highest SI values for *C. damascina* were calculated as pH \approx 9.6, temperature = 22 °C, TDS \approx 230 mg/L, EC \approx 450 mS/cm, altitude = 1150 m, river depth \approx 34 cm, river width = 3 m, flow velocity \approx 0.2 m/s, river bed slope = 6% and DO = 6 mg-O₂/L. The highest SI values of *C. umbla* were recorded as pH \approx 8, temperature = 19 °C, TDS = 200 mg/L, EC = 350 μ S/cm, altitude = 1250 m, river depth \approx 23 cm, river width \approx 2.5 m, flow velocity = 0.2 m/s, river bed slope = 1% and DO = 9 mg-O₂/L (Figs. 6 and 7).

Niche overlap

The average ecological overlap for the two studied species was approximately 0.32% (Table 2). In Fig. 8, the overlapping area under the diagram is shown as the ecological niche overlap. Based on the results, the overlap curves of the ecological niche show the highest overlap for the river bed slope (0.69) and river depth (0.502), and the lowest values for EC

(0.0136) and temperature (0.11). The SI curves of pH were not overlapped between the two species.

Discussion

In the current work, two closely related and sympatric species of *C. damascina* and *C. umbla* were studied to examine how morphological differences may be a mechanism allowing congeneric species to inhabit the same habitat. Based on previous studies (Jawad and Alwan 2020; Çiçek et al. 2021a), these two species are close to each other based on molecular data, but they have morphological differences (Berg 1949; Saadati 1977; Esmaeili et al. 2016; Jawad and Alwan 2020). Berg (1949) and Saadati (1977) distinguished *C. damascina* and *C. umbla* by their morphological traits, the larger number of lateral line scales (87–99), higher dorsal fin branched rays (9–10), longer dorsal fin, longer caudal, a markedly transverse mouth, and a weaker dorsal fin spine in *C. umbla*. Similar results were reported by Esmaeili et al. (2016), in which these species are differentiated by their body traits, including the number of scales between dorsal-fin origin and lateral line, the number of scales between lateral line and anal-fin origin, the number of scales encircling the least circumference of caudal peduncle, and by the number of scales in the lateral-line series. Such morphological differences may have led to the evolution of these two sympatric species with probably overlapped niche preferences.

The Mahalanobis value indicates a high degree of morphological differentiation between the two sympatric species. The two studied sympatric *Capoeta* species have significant differences in their morphological traits, including diameter, predorsal, caudal peduncle length, preanal, preventral, ventral-pectoral, body depth, and caudal peduncle depth in TM, and the position of the snout, head, and body depth, and caudal peduncle length in GM. Based on the results, *C. damascina* can be distinguished from *C. umbla* by having a longer snout and caudal peduncle and a deeper trunk and caudal peduncle. Phenotypic plasticity is a common phenomenon in fish species (Eagderi et al. 2019; Ghafouri et al. 2021; Seçer et al. 2022), as expected in widespread species such as *C. damascina* in different habitats (Çiçek et al. 2021a). Closely related species sharing the same habitat will lead to differences in their morphology to reveal ecological partitions, as seen in these two *Capoeta* species in the Sirvan River. According to the results, the two species showed a low niche overlap (0.3149) based on some large-scale habitat parameters. This indicates that they avoid competition in their habitat by choosing different areas in terms of river width, flow velocity, and temperature. However, the adult specimens of both species prefer deeper areas with a higher slope that have higher DO content.

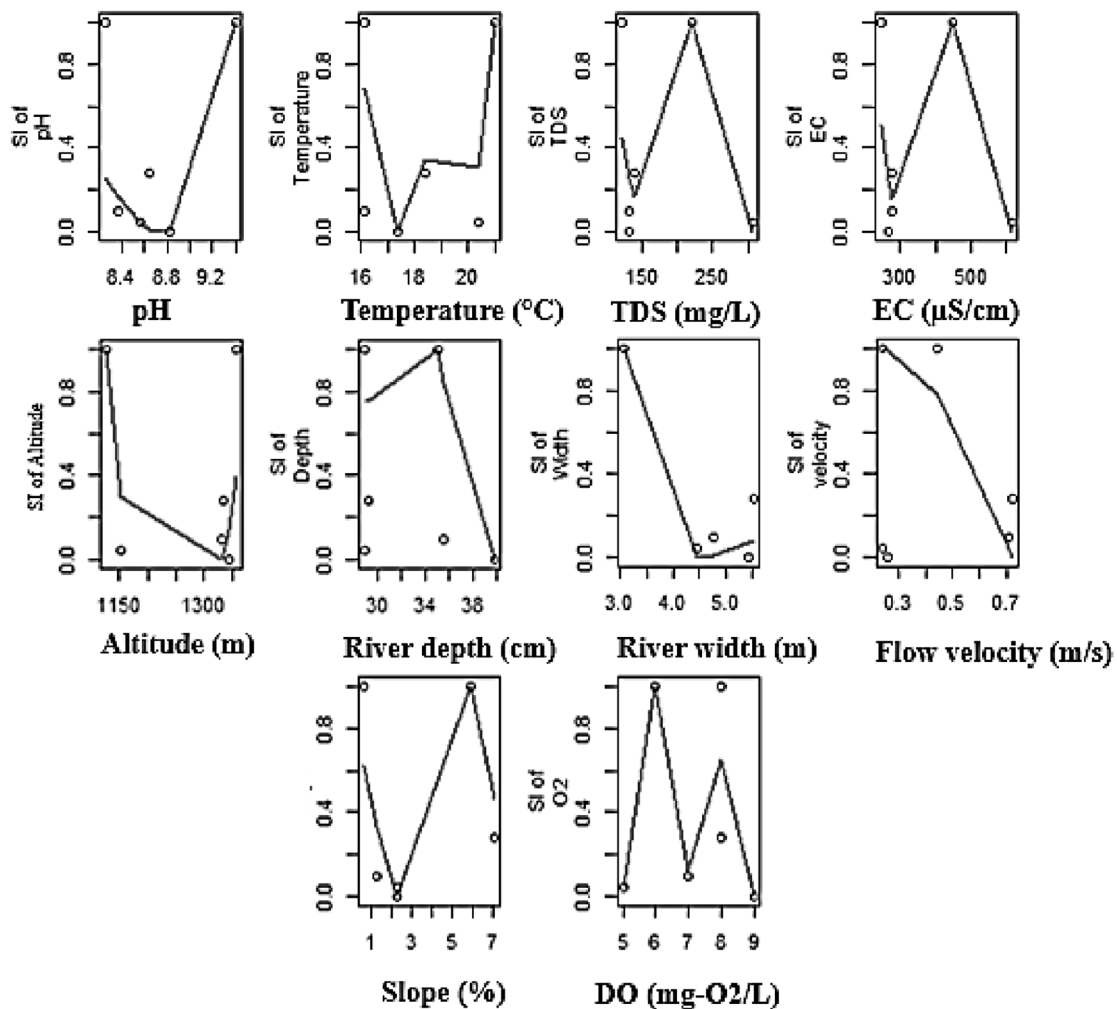


Fig. 6 SI charts of environmental variables for *C. damascina* in the Sirvan River

Both *Capoeta* species in this river drainage migrate upstream for spawning but they use their reproductive grounds separated by breeding in different places to avoid interbreeding. However, our sampling was done outside of the spawning season to avoid any effect of sexual dimorphism. Our examination showed no morphological differences between the two sexes of both *C. damascina* and *C. umbla* (Samaee and Patzner 2011; Esmaili et al. 2016). Small specimens of these fish that have the same size and food are very sensitive due to intraspecific and interspecific competition (Wootton 1990). Hence, they avoid competition due to reproduction in different grounds of upstreams. However, the presence of fish in the upper part of the river is due to the repeated migration from downstream to those areas.

HSI results showed the two studied species prefer different ranges of environmental factors i.e., *C. umbla* prefers low pH, temperature, TDS, EC, altitude, river width, and river bed slope of the habitats, whereas in *C. damascina*,

preference decreased by increasing TDS, EC, river depth and width, flow velocity and DO. The preferred habitats of *C. damascina* during autumn in the Sirvan River are areas with a pH of approximately 6, temperature of 9 °C, TDS of 200 mg/L, EC of 300 µS/cm, altitude of 1130 m, depth of 50 cm, river width of 9 m, flow velocity of 0.8 m/s, river bed slope of 2% and DO of 9 mg-O₂/L (Mouludi-Saleh et al. 2022b). Different range preferences in the physico-chemical environmental parameters may be because of their habitat selection.

Capoeta damascina has a deeper body that is suitable for occurring in deeper parts of the river with low velocity but *C. umbla* has a long head and caudal peduncle and a shallow body depth, or in other words, it has a more streamlined body shape that is suitable for inhabiting parts of the river with higher flow, so this morphological difference can be explained by the micro-habitat selection within the same habitats of the main river channel. River width and water velocity have a reverse relationship i.e., by increasing river

Fig. 7 SI charts of environmental variables for *C. umbla* in the Sirvan River

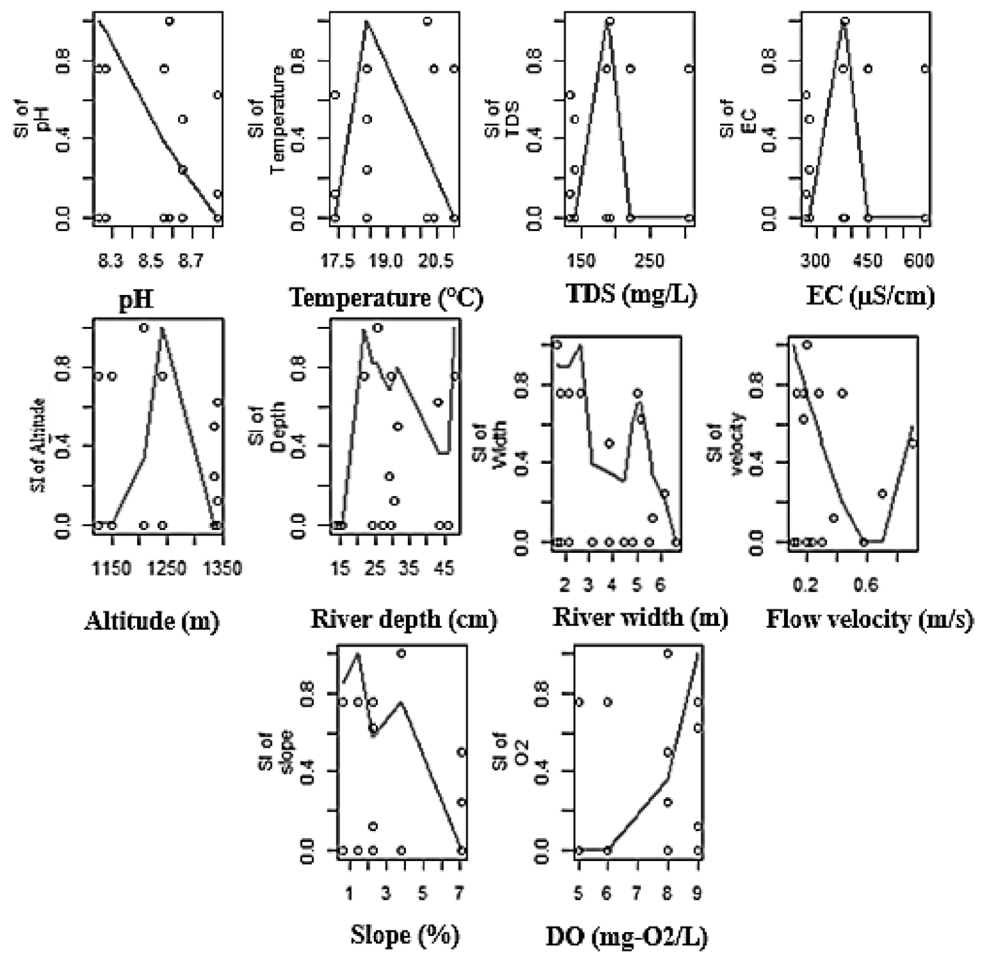


Table 2 Values of ecological niche overlap between *C. damascina* and *C. umbla* related to different environmental parameters in the Sirvan River

Parameters	Niche overlap value
pH	–
Temperature	0.11
TDS	0.211
EC	0.013
Altitude	0.372
Depth	0.502
Width	0.273
Velocity	0.186
Slope	0.69
DO	0.46
Average	0.314

width, flow velocity decreases (Zamani Faradonbe et al. 2015). Therefore, the selection of a deep region of the river with low flow velocity by *C. damascina*, alongside the presence of *C. umbla* in deeper areas of the river with higher flow velocity, can justify the niche overlapping between

these two species in terms of depth (0.502) and slope (0.69) factors.

The separation of the habitat between the two studied sympatric *Capoeta* species will be a mechanism to reduce their competition. The selection of different habitats by different species is a well-known strategy for coexistence in river systems, even in species such as *Capoeta* species that feed on the same food (Keivany et al. 2016) because their habitat appears to be a resource-rich environment. There should be no problem with being constrained to compete between the two omnivorous species in terms of nutrition, which is known as voluntary segregation, by selecting the habitat location instead of using food resource partitioning.

In conclusion, the evolution of two sympatric *Capoeta* species, which are generalists to adapt to different habitats, with morphological differentiation, has made it possible for them to coexist by utilization of different microhabitats. As shown in the current study based on their habitat preferences and niche overlap. This pattern of sympatric evolution in genetically close species with high morphological differences in riverine systems can be considered an evolutionary model for stream congeneric fish species.

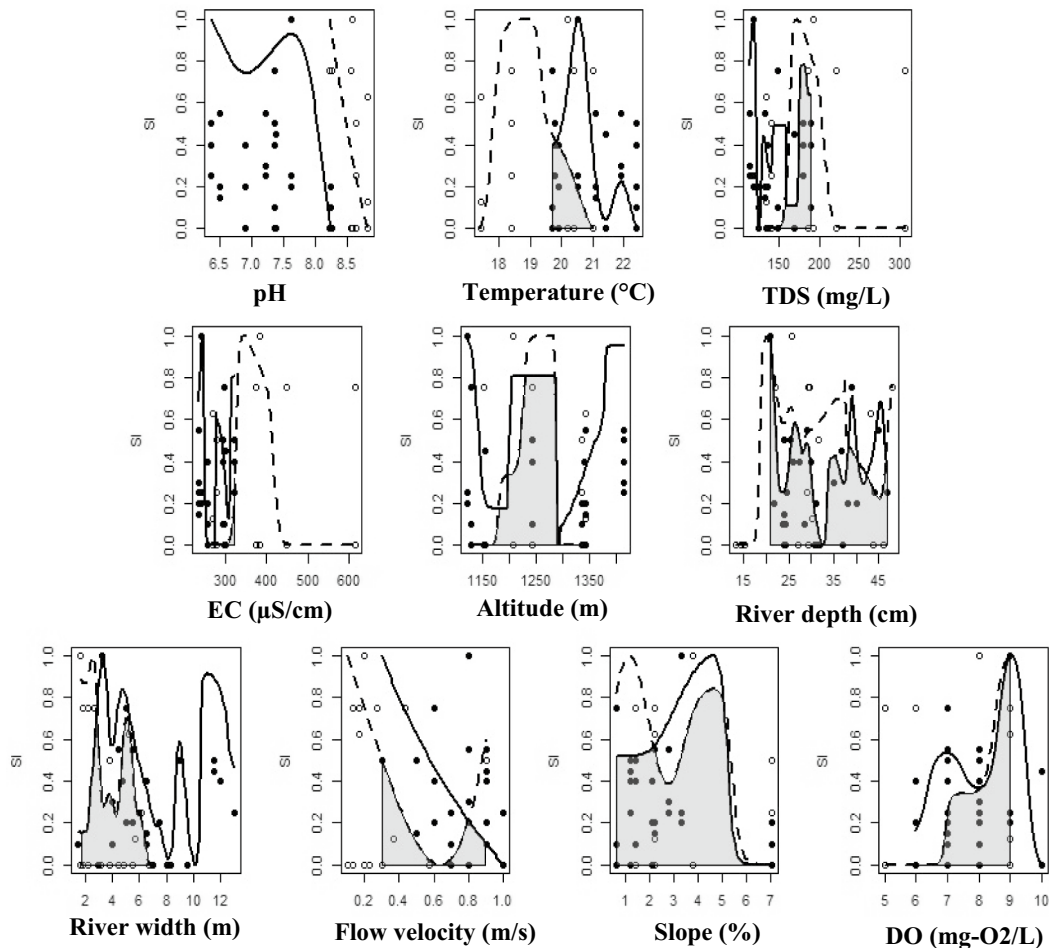


Fig. 8 Values of ecological niche overlap between *C. damascina* (●, —) and *C. umbla* (○, --) based on the studied environmental parameters in the Sirvan River

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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 there are no competing interests.

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