



Original article

Inter - and intraspecific phenotypic variation in co-occurring invasive and introduced cyprinid fish species

Can Mert Gören, Nehir Kaymak*

Akdeniz University, Faculty of Science, Department of Bioogy, Antalya, Turkey



ARTICLE INFO

Keywords:

*Carassius gibelio**Cyprinus carpio*

Inter and intraspecific variation

Phenotypic differences

Geometric morphometrics

Cyprinidae

ABSTRACT

A species introduced outside of its native range will likely encounter unusual abiotic and biotic conditions, and may exhibit phenotypic traits that may facilitate survival and persistence. Phenotypic plasticity drives non-native species' development of adaptive traits in the new environment, increases their fitness, and as a result, contributes to invasion success. In this study, we examined inter and intraspecific phenotypic variation (body size and shape) for an invasive (*Carassius gibelio*) and introduced (*Cyprinus carpio*) cyprinid fish species (Teleostei: Cyprinidae) in the Düden Stream, Turkey, which is a small-scale river system. We hypothesized that interspecific phenotypic variation correlates with fish-specific variables and river site. We further hypothesized that these two species may exhibit similar phenotypic variation patterns between populations. The MANCOVA revealed that species-specific traits, river site, had significant effects on body shape variation and size along the stream. The differences in the shape of the head, the central portion of the body, and fins in both species most probably reflected differences in the swimming and feeding of the fish, possibly to avoid interspecies competition. The intraspecific phenotypic variation observed in both species may indicate rapid local adaptation, triggered by multiple founding event, or/and phenotypic plasticity.

1. Introduction

The growth, development, and maturation of individuals within a species may be directly or indirectly affected by abiotic and biotic factors, and may result in the emergence of diverse morphologies (Novomeská et al., 2013). This may be due to the interactive effects of natural selection, genetics, and as well as the environmental influences on individual ontogenies (Cadrin, 2000). Intraspecific variation can affect community structure and ecosystem functioning through the differential contributions of individuals to trophic interactions, ecosystem productivity, nutrient cycling, and/or ecosystem engineering (Lang et al., 2021). This kind of morphological variations can occur in a continental area, regional scale, or local scale such as a single river system, or even within a single lake (Park and Bell, 2010; Webster et al., 2011; Radojković et al., 2018; Scott et al., 2022).

The ability of species introduced outside of their natural range to survive in the new environment and successful in establishing sustainable populations is the result of their ability to use new resources (phenotypic plasticity) and/or to adapt (Sakai et al., 2001). Morphology and reproductive traits that reflect the ability of a species to adapt to

new conditions, expand its range and survive, and mitigate the effects of environmental variation during invasion are linked to phenotypic plasticity (Záhorská et al., 2017), founder effects and genetic drift (Cerwenka et al., 2023). In fact, when introduced or invasive species enter a different region not within their natural range, they may be exposed to different environmental conditions than they have experienced throughout their evolutionary history. In such a situation, sufficient numbers of individuals may not survive until they acquire the necessary genetic traits to exhibit phenotypic adaptations. At this stage, adaptive plasticity (phenotypic plasticity) can increase invasion success by producing favorable traits acquired through directional selection by each subsequent generation (Yavno and Fox, 2013). Phenotypic plasticity based on morphology is quite common in invasive species (Záhorská et al., 2009; Cerwenka et al., 2014; Mangit et al., 2018). Thus, external morphometry is one of the most accessible ways to assess how species cope with environmental plasticity. (Novomeská et al., 2013).

In this study, we investigated the patterns of phenotypic variability of an invasive and introduced cyprinid fish species: a gibel carp *Carassius gibelio* (Bloch, 1782), and the common carp *Cyprinus carpio* (Linnaeus, 1758), respectively. Gibel carp was first introduced to Türkiye in the

* Corresponding author.

E-mail addresses: 20193401030@ogr.akdeniz.edu.tr (C. Mert Gören), nehirkaymak@akdeniz.edu.tr (N. Kaymak).

1980s (Baran and Ongan, 1988). Rapid increases in abundance and distribution, reproductive strategy, resistance to unfavorable conditions, and phenotypic plasticity of the gibel carp increase its invasion success (Tarkan et al., 2012). Although the common carp, *C. carpio* is a native species for some regions of Turkey (Atalay et al., 2017), it has been transported to almost all parts of Turkey due to aquaculture production and stocking programs and has subsequently been reported as an introduced fish. The gibel carp was also unintentionally and/or accidentally introduced as contaminant in common carp stocking (Tarkan et al., 2015). Since there is no previous study on the fish biodiversity of the Düden Stream, it is not known when this species was introduced. The only data we have is the study of Küçük and İkiz (2004) in the Kirkgöz Spring-Düden Stream between 1994 and 1996 and 2002–2003, these two carp species were not reported. The system offers the possibility to examine phenotypic variation and assess the invasive potential of non-native species in such a small-scales and in less than 20 years after the introduction. In this context, this study aimed to reveal the interspecific and intraspecific phenotypic variation (body size and shape) patterns of sympatric the gibel and the common carps by using geometric morphometric analyses. We hypothesized that interspecific phenotypic variation to increase in relation to fish-specific adaptive traits and/or river site. Because the adaptive responses of species expanding in new environments to changing selection regimes may be species-specific, and sympatric species that share the same habitat and compete for resources may tend to develop different

phenotypes to reduce competition (Cerwenka et al., 2014). river site Since both cyprinids species exhibit similarities in habitat use (both fishes inhabit still, slow-flowing, and well-vegetated water bodies) and feeding habits (both fishes feed on a variety of benthic organisms and plant material) (Froese and Pauly, 2023), we hypothesized that these two sympatric species, due to their similar ecological preferences, may demonstrate comparable phenotypic variation patterns among populations depending on the river site.

2. Material and method

2.1. Study area

The Düden Stream, is 14 km long, originates from the karst Kirkgöz Springs and drains into the Mediterranean Sea (Fig. 1). The stream mostly flows through Antalya city center. In the upper basin of the river, the natural flow of water was disrupted a long time ago (~1967) and confined within a channel. A large part of the water coming out of the spring is taken into the canal for Kepez Hydroelectric Power Plant (HPPs), and some of it goes underground through the karst waterways in the sinkhole and permeable travertine (Environmental Research Turkey, 2020). The sinkhole emerging at the Kirkgöz spring forms a lake, and many times the water disappears at the mouth of a cave, passing a few kilometers underground and coming out again through the rocks. It passes over a waterfall (the upper Düden waterfall) where it emerges



Fig. 1. Satellite image of the Düden Stream and the position of the three study sites (O), two HPPs (Kepez 1 and 2 Hydroelectric Power Plants), and waterfall (the upper Düden waterfall).

for the last time, flows to the shore as a stream without sinking again, and pours into the Mediterranean Sea (the lower the Düden waterfall) over a 40 m high cliff. Annual precipitation is 856 mm, and the mean annual flow of the stream is 23.8 m³/s (Ayaz et al., 2013).

Both fish species were sampled from three different sites along the Düden Stream. Site 1 was located above the HPPs (about 2 km) and in the water retention pond of HPPs. Site 2 was in the main channel of the stream and Antalya city center which was under the influence of urbanization, agriculture, and industrial activities (pollution from manure, industrial and domestic sewage and wastewater) below the HPPs and waterfall. Site 3 which is close to the area where the river falls into the sea from the waterfall was approximately 4.5 km below site 2. In addition, the water current of this site was partially blocked by a small barrier, thus reducing the flow velocity.

2.2. Fish sampling

Fishes were captured from these three sites between May to September 2022 using fyke-nets with a 12 – 35 mm mesh size, and trawl nets with different mesh sizes (8–55 mm). Collected fish were anesthetized with MS-222, and then fixed in 10 % formalin and transferred to 70 % ethanol for storage. The standard lengths of the fish individuals were measured in the laboratory. To further reduce the effects of size, only individuals with SL range from 6.6 cm to 18.1 (mean = 11.54, SD = 2.98) in gibel carp and from 3.4 to 20.4 cm (mean = 11.36, SD = 6.10) in common carp were included in the analysis.

2.3. Geometric morphometric analysis

Photographs of the lateral left side of each individual were taken at a constant distance of ca. 50 cm using a digital camera (Nikon® D90) attached to a tripod at approximately 50 cm above the sample. Photographs were converted into.tps files, using tpsUtil software (Rohlf, 2015). Both geometric and linear morphometric measurements were recorded for each sample by the same person using the tpsDIG2 software (Rohlf, 2015). Twenty-two landmarks (Fig. 2) digitized x and y coordinates were generated. Raw landmark coordinates were subject to a Procrustes superimposition to remove size, position, and orientation

effects and standardize each specimen (Zelditch et al., 2012). The only variation after this process is particularly shaped variation, and this also allows shape comparisons free from allometric growth associated with early ontogeny between populations (Hooker et al., 2022). The centroid size is used as a measure body size (Zelditch et al., 2012). All these processes were performed using MorphoJ version 1.05f (Klingenberg, 2011).

2.4. Statistical analysis

Interspecies variation: Normality and homogeneity of variances of centroid size values assumptions were evaluated with Shapiro-Wilk ($p < 0.05$) and Levene tests ($p > 0.05$), respectively. Centroid sizes were compared using the Kruskal-Wallis followed by pairwise Dunn's post-hoc tests. Principal Component Analysis (PCA) was used to analyze the interspecific shape variation of both species. PCA reveals both the amount of variation and the shape variation associated with each component using Procrustes coordinates (Bravi et al., 2013). Following these analyses, Multivariate analysis of covariance (MANCOVA) was performed to determine whether body shape varied among the species and river site using IBM SPSS Statistics 23 (IBM Corporation). In the MANCOVA, PC scores (explaining at least 1 % of shape change) served as dependent variables describing body shape, species (the gibel and the common carps), river site (three sites), and the interaction between species and river site while centroid size was a covariate (to test for allometry). MANCOVA was followed by Wilks' λ test to determine the degree of shape difference explained.

Intraspecific variations: Spatial differences in centroid sizes of populations were tested using Kruskal-Wallis followed by pairwise Dunn's post-hoc tests. Because PCA represents the overall variation in all samples, Discriminant analysis (DFA) was used to further quantify and visualize inter-population differences (intraspecific variation) (Zelditch et al., 2012). The "Jackknife Groupings" test was used for group assignments. Whether the group differences based on the shape revealed by the DFA score were statistically significant was tested with ANOVA. All these analyses were performed using PAST 4.0.4 exe.

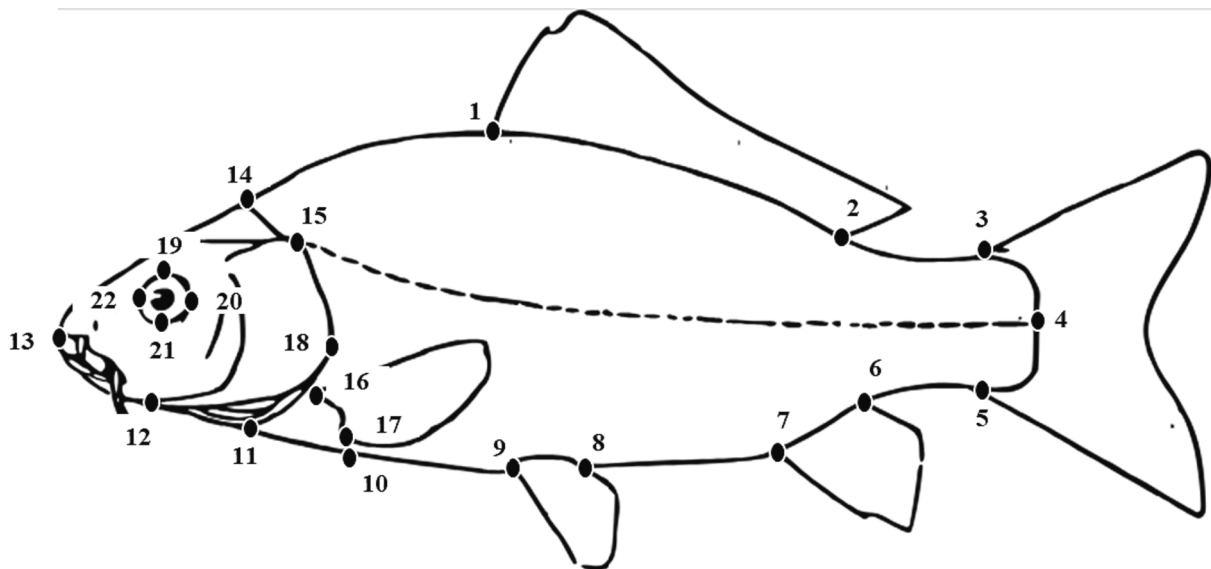


Fig. 2. Location of the 22 landmarks used for geometric morphometric analysis (fish illustration is taken from Matschie et al., 2023): 1: anterior point of dorsal fin base, 2: posterior point of dorsal fin base, 3: dorsal point of peduncle-caudal fin junction, 4: the middle point of caudal peduncle, 5: ventral point of peduncle-caudal fin junction, 6: posterior point of anal fin base, 7: anterior point of anal fin base, 8: anterior point of pelvic fin base, 9: posterior point of pectoral fin base, 10: ventral projection of the operculum, 11: ventral end of the gill slit, 12: injection point of operculum and preoperculum, 13: mouth tip, 14: dorsal head-body junction, 15: upper portion of the operculum, 16: anterior point of pelvic fin base, 17: posterior point of pelvic fin base, 18: posterior portion of the operculum, 19: the upper margin of the orbital socket, 20: posterior medial edge of orbital socket 21: the lower margin of the orbital socket, 22: anterior medial edge of orbital socket.

3. Results

3.1. Interspecific variations in morphology of invasive and introduced fishes

A total of 65 common carp and 26 gibel carp were analyzed for shape and size variation. There was no statistically significant difference between the two species in centroid size ($\chi^2 = 2.34$, $p = 0.126$). MANCOVA revealed that the covariate and all factors had significant effects on body shape variation (Table 1). Species and species-river site interaction had the strongest effect on body shape ($\eta_p^2 = 0.37$, $\eta_p^2 = 0.42$, respectively), whereas river site was significant, but its effects were relatively weak in explaining body shape variation ($\eta_p^2 = 0.07$).

Although the PCA biplot showed a range of overlap in body shape between gibel and common carps, the plot that best visualizes the shape distinction was between PC 1 and PC 3. The PCA's PC 1, 2, and 3 explained 29.60, 17.98, and 14.30 % of the total variation in the two fish species. PC1 compared head length, eye sizes, and body depth, while PC 3 compared dorsal fin position and length, anal and pelvic fin positions (Fig. 3). The relative total amount of variation explained by the regression between centroid size and shape variables was 24.95 % for common carp and 19.97 % for the gibel carp.

3.2. Intraspecific variations in morphology of invasive and introduced fishes

The populations of both species differ in body size (centroid size). Populations from site 1 had the smallest, and populations from sites 2 and 3 had the largest size for the gibel and common carp ($\chi^2 = 16.43$, $p < 0.001$, $\chi^2 = 21.16$, $p < 0.001$, respectively). Discriminant function analyses (DFA) indicated that there was a significant shape difference among river sites in both species (Wilk's $\lambda = 0.009$, $\chi^2 = 204.99$, $p < 0.0001$, Wilk's $\lambda = 0.000$, $\chi^2 = 92.33$, $p < 0.0001$). DFA correctly classified 75.4 % of common carp and 51.6 % of gibel carp into the correct habitat. The highest classification rate was recorded for site 1, while the lowest classification rates were recorded from sites 2 and 3 for common and the gibel carp (Table 2).

In the common carp, the first DF accounted for 89.30 %, and the second accounted for 10.70 % of the between-group variability, explaining 100 % of the total between groups variability (Fig. 4a). DF 1 reflected variation associated with landmarks 1, 2, 9 (central body depth), 5 (the caudal peduncle length), 11, 12, 13, 14, 15 (head length), and 16, 17 (position of pectoral fin), and 19, 21, 22 (eyes position). DF 2 was associated with variation in landmarks 1 (dorsal fin length), 3 (mouth position), 5 (ventral point of caudal peduncle), 8—9 (the positions of the pelvic fin), and 15—18 (operculum position) (Fig. 4a). In the gibel carp, the first two DFA axis contributed 96.6 % (DF 1) and 3.4 % (DF 2) of the total variation (Fig. 4b). Wireframe deformation plot explained the variation associated with the position of the caudal peduncle (landmarks 3, 4, 5), and both the position of the anal and pelvic fin and depth of the central body (7, 8, 9, 10), and position of the head and operculum (12, 13, 14, 15, 18) for DF 1. DF 2 reflected the shape variation associated with the body depth (7, 8, 9) and the position of the dorsal fin (1, 14), and the pectoral fin (Fig. 4b).

DFA analysis, revealing the effect of river site on body morphology,

Table 1

MANCOVA tests result for the effects of species, river site, and their interaction on body shape for *C. carpio* and *C. gibelio*.

Effect	Partial variance (%)	F	df	p
species (S)	0.368	12.88	10.75	< 0.001
river site (RS)	0.074	20.13	20.150	< 0.001
S x RS	0.424	4.02	20.150	< 0.001
Centroid size	0.230	25.06	10.75	< 0.001

grouped the three populations significantly apart from each other for both fish species (Fig. 5a–b). The DF1 clearly differentiated populations from sites 2–3 to site 1. In the common carp, some individuals from the site 1 population with positive DF1 and negative DF2 values were characterized by larger eyes, and enlarged operculum in contrast to individuals from the site 3 population. Individuals of site 2 populations with negative DF1 and DF2 values had smaller eyes, and deeper central body part relative to some individuals from site 1 with positive DF1 and DF2 (Fig. 5a). The gibel carp population from site 1 which was associated with the positive extreme along DF1 had a deeper central body part and head region. The population from site 2 with negative DF1 and positive DF2 was characterized by an elongated body, narrower operculum, and slightly longer dorsal fin than the population from site 3 (associated with the negative DF1 and DF2) which had a narrower central body region, larger head region and operculum, larger eyes, and extended caudal peduncle (Fig. 5b). The DF1 axis which explained the highest proportion of total shape variation between groups revealed that river site was responsible for shape variation among populations for the common carp (ANOVA, $F = 851.4$, $P < 0.0001$) and gibel carp (ANOVA, $F = 222.1$, $P < 0.0001$). The shape of the site 1 population of the common carp is clearly different from the other two populations (from sites 2 and 3), this was well illustrated by the box plot for DF1 scores. A similar situation was valid for the gibel carp, but there was a significant shape difference among all three populations.

4. Discussion

The common carp (*Cyprinus carpio*) has been introduced to almost all parts of Turkey through stocking programs to enhance fisheries (Vilizzi et al., 2015). The gibel carp also emerged accidentally through batches of *C. carpio* and has become the most abundant species in Turkey today by establishing populations in reservoirs, lakes, ponds, and river channels (Tarkan et al., 2012). In this study of sites along the Düden River, both fish species were found to coexist. However, in general, common carp was more abundant than the gibel carp in fishing gear (personal observation of N. Kaymak). Although it was known that these two species experience trophic niche overlap especially in the summer season (but not in the winter season) when sympatric (Kaymak et al., 2023), their competitive interactions with each other are not yet fully understood. However, in the study conducted by Dominguez Almela et al. (2021) on the competitive interactions of the common carp with the crussian carp (*Carassius carassius*), it was reported that the common carp have the ability to consume more resources in a shorter period of time and, therefore, were much stronger competitors. In many cases, if two closely related species with similar life histories and behaviors live on a single resource, the one with a slight advantage will out-compete the other: Complete competitors cannot coexist. This is known as the competitive exclusion principle (Capitan et al., 2015). However, character displacement may facilitate species coexistence through niche partitioning and/or interspecific niche differences (Stroud et al., 2019). The differences in body shapes of the two species in this study may be a result of ecological character displacement. For example, differences in functional trait related to feeding (head and eye size), habitat use (body depth), and swimming (fin length) may reflect ecological characters displacement and niche differences. This process may facilitate the coexistence of sympatric non-native species in a new environment. More detailed studies are needed to better explain coexistence patterns and interspecific phenotypic variation.

Sympatric species that share the same habitat and compete for resources tend to develop different phenotypes, thereby increasing interspecific morphologic variability (Luiz et al., 2022). As a result of both morphological and behavioral adaptations, interspecific competition can be reduced (Platell et al., 2006). PCA biplot graphs showed that body shapes partially overlapped between the two species. However, the results of multivariate covariance analysis revealed that the impact of species-specific traits on phenotypic variation was greater compared to

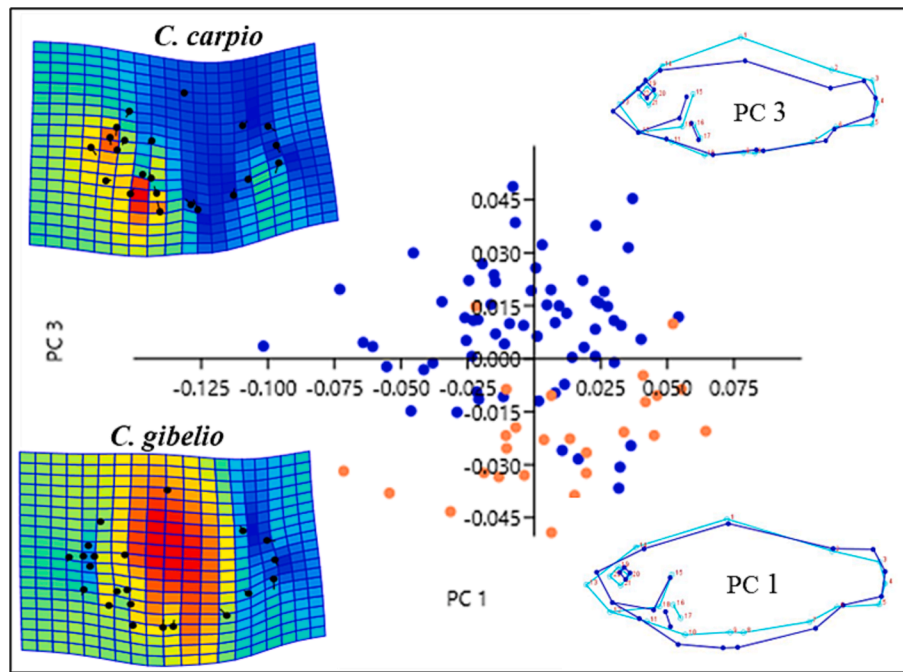


Fig. 3. PCA ordination of body shape between *C. carpio* (blue dots) and *C. gibelio* (red dots) from the Düden Steam. PC 1 explained 29.60% and PC 3 explained 14.30% of the total variation. Shape variation of fishes depicted by thin-plate spline using a deformation heat map (dark red spots represent the fish's body shape expanding beyond its mean shape, blue spots represent the fish's body shape shrinking relative to the average shape).

Table 2

Jackknife grouping test results show the number and percentage of individuals assigned to a river site for both fish species.

<i>C. carpio</i>	N	site 1	site 2	site 3
site 1	30	27 (90 %)	1	2
site 2	19	0	12 (63.2 %)	7
site 3	16	1	5	10 (62.5 %)
<i>C. gibelio</i>				
site 1	8	5 (62.5 %)	0	3
site 2	13	4	6 (46.15 %)	3
site 3	5	2	1	2 (40 %)

the effect of river site alone. Additionally, the interactive effect of river site and species-specific traits was also quite significant. These results are found to be consistent with our first hypothesis. Because an organism's phenotype (body shape and size) could exhibit different patterns not only based on species-specific traits but also in response to abiotic factors such as resource availability (Raffard et al., 2020), habitat suitability (Thuiller et al., 2010), and disturbance (Mouillot et al., 2013). Many studies have investigated the relationship between interspecific variation in morphology such as body shape and size, and environmental conditions (Langerhans and Reznick, 2009; Leavy and Bonner, 2009; Wellenreuther et al., 2010).

We hypothesized that these two sympatric species, due to their similar ecological preferences, could exhibit similar patterns of phenotypic variation among populations based on river site. Overall, our results have partially supported this hypothesis. In both species, they showed a partially similar trend in morphological variation at lentic-characterized site 1 and lotic-characterized site 2. However, their shapes were completely different at lotic-characterized site 3. Both species have larger head widths, larger eyes, and wider operculum at site 1 compared to site 2. Differences observed in head shape among habitats may reflect variations in feeding, such as foraging mode or dietary composition (Langerhans et al., 2003; O'Reilly and Horn, 2004). The similar variation in head shape observed in both species may indicate their specialization on habitat-specific similar food sources. Both the

gibel carp and common carp are generalist omnivores, and they particularly consume larger zooplankton and benthic invertebrates (such as Cladocerans, Copepods, Ostracods, Dipterans, etc.) in lakes and reservoirs (Balık et al., 2003; Gül et al., 2010), and algae, detritus, and small invertebrates in rivers (Partal and Özdilek, 2019; Imran et al., 2021). Habitat-dependent differences in food preferences can influence operculum and eye size, consequently affecting head width. For instance, Wilson et al. (2015) reported that cichlids feeding on small benthic invertebrates have a narrower operculum, while those feeding on larger zooplankton have a broader operculum.

In both species, the shape differences were primarily observed in the head region as well as the width of the central portion of the body, the position of dorsal, anal, and pelvic fins, and the width of the caudal peduncle. However, this time, these characters exhibited different variation trends in both species: at site 1, the body of the common carp was narrower and longer, while the gibel carp's body was deeper. On the other hand, the situation was reversed at site 2. When considering this character, our results were not consistent with our second hypothesis. The central body width and fin shape differences that arise particularly due to variations in water velocity between lentic and lotic habitats are often associated with swimming and maneuvering capabilities in fish. Specifically, selection in lotic habitats can result in fusiform (narrow and elongated) body shapes that reduce friction and allow for prolonged swimming, thus reducing energy expenditure. On the other hand, in lentic systems, increased body depth enhances swimming speed and maneuverability (Franssen, 2011). Indeed, many species can exhibit different responses to environmental changes. For instance, Atlantic salmon (*Salmo salar*) had a deeper body in lotic systems, whereas brown trout (*Salmo trutta*) had a more fusiform body (Pakkasmaa and Piironen, 2001). In this study, the two fish species have developed different solutions to cope with water velocity challenges. In a lotic system, various microhabitats such as pools, riffles, and runs provide shelter from the constant water flow, reducing the need for well-defined traits (Brinsmead and Fox, 2002). Both species could enhance invasion success through adaptive phenotypic plasticity by utilizing different microhabitats within the same river site (Caño et al., 2008), thus avoiding interspecific competition for habitat.

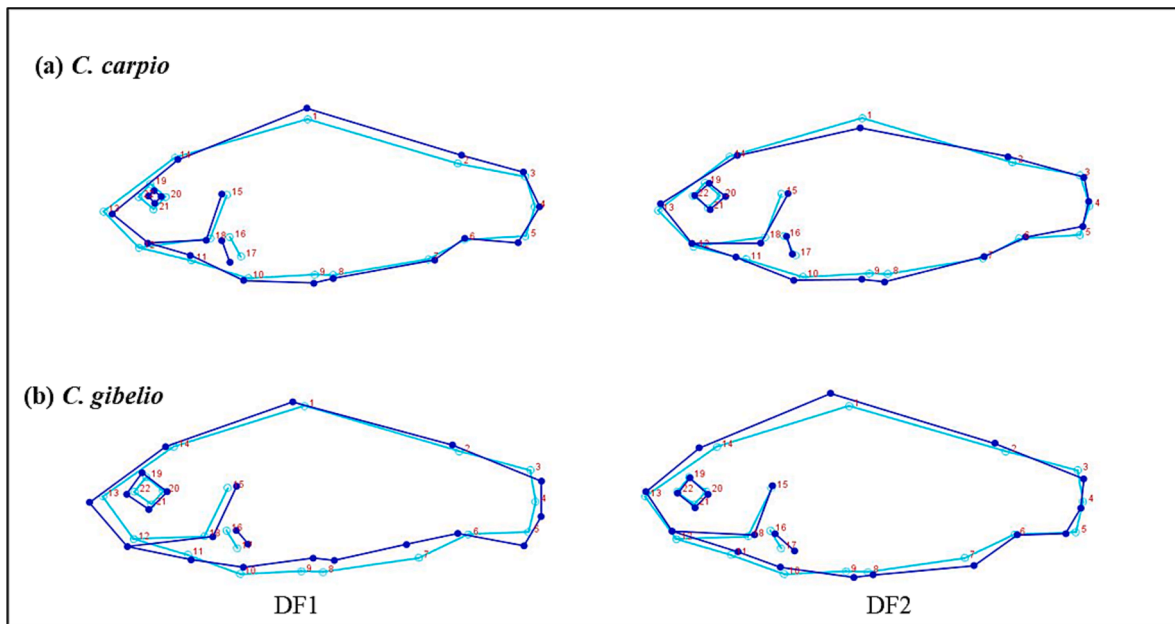


Fig. 4. Wireframe obtained from Discriminant analysis (DFA) for both fish species (the light blue lines are the average shape, and dark blue lines show the shape variation). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

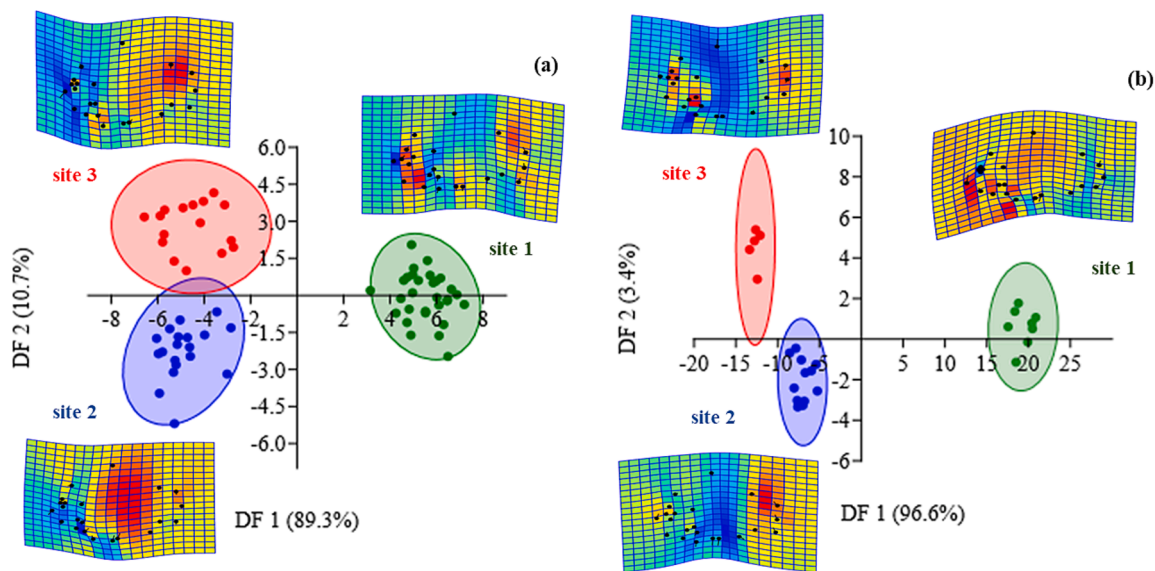


Fig. 5. Discriminant analysis and thin-plate spline showing the shape variation of *C. carpio* (a) and *C. gibelio* (b) among sites along the Düden Stream.

The invasive gibel carp have shown higher phenotypic variation compared to introduced common carp. While common carp exhibited two different phenotypes (or shapes) along the Düden River (one phenotype from site 1 and another from sites 2 and 3) (Fig. 5a), the gibel carp displayed three different phenotypes (one for each population) (Fig. 5b). The common carp had a deeper body at sites 2 and 3, and a narrower body with large eyes and a broader operculum at site 1. The body shape differences in common carp may also be related to allometry, where shape variation is associated with size variation (Klingenberg and Marugán-Lobón, 2013). Because the populations from sites 2 and 3 had a larger body size (centroid size) compared to the population from site 1. Additionally, another reason for this variation could be that these fish might have been introduced by a single founder population, but populations in the upper and lower reaches could have become isolated from each other due to natural and artificial barriers

(hydroelectric power plants and waterfall) below site 1. This isolation can lead to reduced gene flow between populations from site 1 and populations from sites 2 and 3, hence genetically distinct populations due to the resulting population bottlenecks and inbreeding (Willis et al., 2012; Garner et al., 2013). The population of gibel carp from site 3 was characterized by a broader head, caudal peduncle, and a narrower body compared to the other two populations. Since we don't have genetic data for both species in the Düden Stream, it is challenging to precisely explain the reasons behind this variation. However, possible reasons could include habitat use and feeding-related phenotypic plasticity, rapid local genetic adaptation, multiple founder populations, the effect of sexual dimorphism (Cerwenka et al., 2014), and barrier effects.

5. Conclusion

In this study, it has been found that sympatric invasive (the gibel carp) and introduced (the common carp) fish species exhibit strong inter- and intraspecific morphological variations. Especially, river site-dependent ecological factors and species-specific traits have been found to play a crucial role in promoting phenotypic divergence. We have observed that even in small-scale river systems, these species can have different functional and trophic characteristics. Although this may vary depending on the geographic scale and the invasive species, this situation can have diverse effects on ecosystem functioning and food web structure. Determining the ecological and evolutionary processes that cause phenotypic variations of invasive species populations is of great importance for invasive species management. Therefore, we suggest that future studies focus primarily on the population genetics of invasive fish, and then test the phenotypic plasticity of these two species with sex, environmental (abiotic and biotic), and ecological factors (food preferences, foraging tactics) to further increase our understanding of what triggers the invasive success of invasive species.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to thank Mustafa Gürdal and Elif Acar for their help during the laboratory and field studies.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Authors' contributions

Can Met Gören: collected samples, analyzed them in the laboratory, and wrote the draft manuscript. Nehir Kaymak: designed and supervised the study, performed data analysis, and reviewed the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.sjbs.2024.103943>.

References

- Atalay, M.A., Kirankaya, Ş.G., Ekmekçi, F.G., 2017. The current status of gibel carp and sand smelt in Turkey's inland fisheries. *Aquacult. Stud.* 17, 41–57. <https://doi.org/10.17693/yunusae.v17i26557.281581>.
- Ayaz, S., Erdoğan, N., Beşiktaş, M., Ayıtç, E. A., Dereli, E. M., Aynur, S., et al. 2013. Havza koruma eylem planlarının hazırlanması projesi batı akdeniz havzası nihai raporu. Tübitak MAM Project Report no 5118601, 593 p. 2013.
- Balık, I., Kardeşin, B., Özkök, R., Çubuk, H., Uysal, R. 2003. Diet of silver crucian carp *Carassius gibelio* in Lake Eğirdir. *Turkish J. Fish. Aquat. Sci.*, 3.
- Baran, I. and Ongan, T. 1988. Gala Gölü'nün limnolojik özellikleri Balıkçılık Sorunları ve Öneriler [Limnological features of Lake Gala, Fisheries Problems and Suggestions]. İstanbul: Gala Gölü ve Sorunları Sempozyumu, Doğal Hayatı Koruma Derneği Bilimsel Yayınlar Serisi, pp. 46–54.
- Bravi, R., Ruffini, M., Scalici, M., 2013. Morphological variation in riverine cyprinids: a geometric morphometric contribution. *Ital. J. Zool.* 80, 536–546. <https://doi.org/10.1080/11250003.2013.829129>.
- Brinsmead, J., Fox, M.G., 2002. Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. *J. Fish Biol.* 61, 1619–1638. <https://doi.org/10.1111/j.1095-8649.2002.tb02502.x>.
- Cadrin, S.X., 2000. Advances in morphometric identification of fishery stocks. *Rev. Fish Biol. Fish.* 10, 91–112. <https://doi.org/10.1023/A:1008939104413>.
- Caño, L., Escarré, J., Fleck, I., Blanco-Moreno, J.M., Sans, F.X., 2008. Increased fitness and plasticity of an invasive species in its introduced range: a study using *Senecio*

- pterophorus*. *J. Ecol.* 96, 468–476. <https://doi.org/10.1111/j.1365-2745.2008.01363.x>.
- Capitan, J.A., Cuenda, S., Alonso, D., 2015. How similar can co-occurring species be in the presence of competition and ecological drift? *J. R. Soc. Interface* 12, 20150604. <https://doi.org/10.1098/rsif.2015.0604>.
- Cerwenka, A.F., Alibert, P., Brandner, J., Geist, J., Schliwien, U.K., 2014. Phenotypic differentiation of Ponto-Caspian gobies during a contemporary invasion of the upper Danube River. *Hydrobiologia* 721, 269–284. <https://doi.org/10.1007/s10750-013-1668-5>.
- Cerwenka, A.F., Brandner, J., Dashinov, D., Geist, J., 2023. Small but Mighty: The Round Goby (*Neogobius melanostomus*) as a Model Species of Biological Invasions. *Diversity* 15 (4), 528. <https://doi.org/10.3390/d15040528>.
- Dominguez Almela, V., South, J., Britton, J.R., 2021. Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species. *J. Anim. Ecol.* 90, 2651–2662. <https://doi.org/10.1111/1365-2656.13571>.
- Environmental Research Turkey, 2020. Antalya İli 2020 Yılı Çevre Durum Raporu (Türkiye). accessed 01 June 2023. https://webdosya.csb.gov.tr/db/ced/icerikler/antalya_2020_cdr-20210812095503.pdf.
- Franssen, N.R., 2011. Anthropogenic habitat alteration induces rapid morphological divergence in a native stream fish. *Evol. Appl.* 4, 791–804. <https://doi.org/10.1111/j.1752-4571.2011.00200.x>.
- Froese, R. and Pauly, D. 2023. FishBase. World Wide Web electronic publication. www.fishbase.org, (9.01.2023).
- Garner, S.R., Bobrowicz, S.M., Wilson, C.C. 2013. Genetic and ecological assessment of population rehabilitation: Walleye in Lake Superior. *Ecol Appl.* 23, 594–605. <https://doi.org/10.1890/12-1099.1>. PMID: 23734488.
- Gül, A.L., Yılmaz, M., Kuşçu, A., Benzer, S., 2010. Feeding properties of common carp (*Cyprinus carpio* L, 1758) living in Hirfanlı dam lake. *Kastamonu Educ. J.* 18, 545–556.
- Hooker, O.E., Adams, C.E., Chavarie, L., 2022. Arctic charr phenotypic responses to abrupt generational scale temperature change: an insight into how cold-water fish could respond to extreme climatic events. *Environ. Biol. Fishes* 104, 458–472. <https://doi.org/10.1111/azo.12431>.
- Imran, M., Khan, A.M., Waseem, M.T., 2021. Dietary Overlap between Native and Exotic Fishes revealed through Gut Content Analysis at Head Baloki, Punjab, Pakistan. *JBM* 8, 10. <https://doi.org/10.35691/JBM.1202.0169>.
- Kaymak, N., Emre, N., Yalim, F.B., Toslak, C., Emre, Y., Akin, Ş., 2023. Seasonal variation in trophic niches and niche overlap between native and introduced cyprinid fishes. *Spectrosc. Lett.* 56, 227–237. <https://doi.org/10.1080/00387010.2023.2202229>.
- Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. *Mol. Ecol. Resour.* 11, 353–357.
- Klingenberg, C.P., Marugán-Lobón, J., 2013. Evolutionary covariation in geometric morphometric data: analyzing integration, modularity, and allometry in a phylogenetic context. *Syst. Biol.* 62, 591–610. <https://doi.org/10.1093/sysbio/syt025>.
- Küçük, F., İkiz, R., 2004. Antalya Körfezi'ne Dökülen Akarsuların Balık Faunası. *Su Ürünleri Dergisi* 21.
- Lang, I., Paz-Vinas, I., Cucherousset, J., Loot, G., 2021. Patterns and determinants of phenotypic variability within two invasive crayfish species. *Freshw. Biol.* 66, 1782–1798. <https://doi.org/10.1111/fwb.13792>.
- Langerhans, R.B., Reznick, D.N., 2009. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. In: Domenici, P., Kapoor, B.G. (Eds.), *Fish Locomotion: an Etho-Ecological Perspective*. Science Publishers, Enfield, pp. 200–248.
- Langerhans, R.B., Layman, C.A., Langerhans, A.K., Dewitt, T.J., 2003. Habitat-associated morphological divergence in two Neotropical fish species. *Biol. J. Linn. Soc.* 80, 689–698. <https://doi.org/10.1111/j.1095-8312.2003.00266.x>.
- Leavy, T.R., Bonner, T.H., 2009. Relationships among swimming ability, current velocity association, and morphology for freshwater lotic fishes. *N. Am. J. Fish Manag.* 29, 72–83. <https://doi.org/10.1577/M07-040.1>.
- Luiz, O.J., Olden, J.D., Kennard, M.J., Crook, D.A., Douglas, M.M., Saunders, T.M., Wedd, D., Adair, B., King, A.J., 2022. Substantial Intraspecific Trait Variation across a Hydrological Gradient in Northern Australian Fishes. *Ecosphere* 13, e4169.
- Mangit, F., Korkmaz, M., Yerli, S.V., 2018. Morphological variation of pumpkinseed (*Lepomis gibbosus*) with emphasis on allometry. *Turk. J. Zool.* 42, 53–61. <https://doi.org/10.3906/zoo-1703-45>.
- Matschie, P., Reichenow, A., Tornier, G., Pappenheim, P. 1909: *Mammalia, Aves, Reptilia, Amphibia, Pisces*. In: Brauer, A. (Hrsg.): *Die Süßwasserfauna Deutschlands. Eine Exkursionsfauna*. Heft 1, Gustav Fischer Verlag, Jena, S. 206. ([https://commons.wikimedia.org/wiki/File:Cyprinus_carpio.Linnaeus_1758_Fig_126_\(Matschie_et_al.,1909\).svg](https://commons.wikimedia.org/wiki/File:Cyprinus_carpio.Linnaeus_1758_Fig_126_(Matschie_et_al.,1909).svg)) (accessed 05. July 2023).
- Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W., Bellwood, D.R., 2013. A Functional Approach Reveals Community Responses to Disturbances. *Trends Ecol. Evol.* 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>.
- Novomeská, A., Katina, S., Copp, G.H., Pedicillo, G., Lorenzoni, M., Pompei, L., Cucherousset, J., Kováč, V., 2013. Morphological variability of black bullhead *Ameiurus melas* in four non-native European populations. *J. Fish Biol.* 82, 1103–1118. <https://doi.org/10.1111/jfb.12035>.
- O'Reilly, K.M., Horn, M.H., 2004. Phenotypic variation among populations of *Atherinops* affinis (*Atherinopsidae*) with insights from a geometric morphometric analysis. *J. Fish Biol.* 64, 1117–1135. <https://doi.org/10.1111/j.1095-8649.2004.00379.x>.
- Pakkasmaa, S., Piironen, J., 2001. Water velocity shapes juvenile salmonids. *Evol. Ecol.* 14, 721–730.

- Park, P.J., Bell, M.A., 2010. Variation of telencephalon morphology of the threespine stickleback (*Gasterosteus aculeatus*) in relation to inferred ecology. *J. Evol. Biol.* 23, 1261–1277. <https://doi.org/10.1111/j.1420-9101.2010.01987.x>.
- Partal, N., Özdilek, Ş.Y., 2019. Ontogenetic Diet Shift of Invasive Gibel Carp (*Carassius gibelio*, Bloch 1782) in Karamenderes River (Turkey). *J. Limnol. Freshw. Fisheries Res.* 5, 6–16. <https://doi.org/10.17216/limnofish.461758>.
- Platell, M.E., Orr, P.A., Potter, I.C., 2006. Inter- and intraspecific partitioning of food resources by six large and abundant fish species in a seasonally open estuary. *J. Fish Biol.* 69, 243–262. <https://doi.org/10.1111/j.1095-8649.2006.01098.x>.
- Radojković, N., Marinović, Z., Milošković, A., Radenković, M., Đuretanović, S., Lujčić, J., Simić, V., 2018. Effects of stream damming on morphological variability of fish: Case study on large spot barbell *Barbus balcanicus*. *Turkish J. Fish. Aquat. Sci.* 19, 231–239. <https://doi.org/10.4194/1303-2712-v19.03.06>.
- Raffard, A., Santoul, F., Blanchet, S., Cucherousset, J., 2020. Linking Intraspecific Variability in Trophic and Functional Niches along an Environmental Gradient. *Freshw. Biol.* 65, 1401–1411. <https://doi.org/10.1111/fwb.13508>.
- Rohlf, F.J., 2015. *TpsDig, Version 2.22*. Department of Ecology and Evolution. State University of New York, Stony Brook, New York.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The Population Biology of Invasive Species. *Annu. Rev. Ecol. Evol. Syst.* 32, 305–332. <http://www.jstor.org/stable/2678643>.
- Scott, R.J., Haines, G.E., Biedak, N.R., Baker, J.A., 2022. Variation in morphology among populations of threespine stickleback (*Gasterosteus aculeatus*) from western Newfoundland, Canada. *Biorxiv* 2022–09. <https://doi.org/10.1101/2022.09.08.507156>.
- Stroud, J.T., Giery, S.T., Outerbridge, M., Feeley, K.J., 2019. Ecological character displacement alters the outcome of priority effects during community assembly. *Ecology* 100 (8), e02727.
- Tarkan, A.S., Copp, G.H., Top, N., Özdemir, N., Önsoy, B., Bilge, G., Filiz, H., Yapıcı, S., Ekmekçi, F.G., Kirankaya, Ş., Emiroğlu, Ö., Gaygusuz, Ö., Gürsoy Gaygusuz, Ç., Oymak, A., Özcan, G., Saç, G., 2012. Are introduced gibel carp *Carassius gibelio* in Turkey more invasive in artificial than in natural waters? *Fish. Manag. Ecol.* 19, 178–187. <https://doi.org/10.1111/j.1365-2400.2011.00841.x>.
- Tarkan, A.S., Marr, S.M., Ekmekçi, F.G., 2015. Non-native and translocated freshwater fish species in Turkey. *FISHMED* 003.
- Thuiller, W., Albert, C.H., Dubuis, A., Randin, C., Guisan, A., 2010. Variation in habitat suitability does not always relate to variation in species' plant functional traits. *Biol. Lett.* 6, 120–123. <https://doi.org/10.1098/rsbl.2009.0669>.
- Vilizzi, L., Ekmekçi, F.G., Tarkan, A.S., Jackson, Z., 2015. Growth of common carp *Cyprinus carpio* in Anatolia (Turkey), with a comparison to native and invasive areas worldwide. *Ecol. Freshw. Fish* 24, 165–180. <https://doi.org/10.1111/eff.12141>.
- Webster, M.M., Atton, N., Hart, P.J., Ward, A.J., 2011. Habitat-specific morphological variation among threespine sticklebacks (*Gasterosteus aculeatus*) within a drainage basin. *PLoS One* 6, e21060.
- Wellenreuther, M., Brock, M., Montgomery, J., Clements, K.D., 2010. Comparative morphology of the mechanosensory lateral line system in a clade of New Zealand triplefin fishes. *Brain Behav. Evol.* 75, 292–308. <https://doi.org/10.1159/000317061>.
- Willis, S.C., López-Fernández, H., Montaña, C.G., Farias, I.P., Ortu, G., 2012. Species-level phylogeny of 'Satan's perches' based on discordant gene trees (Teleostei: Cichlidae: *Satanoperca* Günther 1862). *Mol. Phylogenet. Evol.* 63, 798–808. <https://doi.org/10.1016/j.ympev.2012.02.018>.
- Wilson, L.A., Colombo, M., Sánchez-Villagra, M.R., Salzburger, W., 2015. Evolution of opercle shape in cichlid fishes from Lake Tanganyika-adaptive trait interactions in extant and extinct species flocks. *Sci. Rep.* 5, 16909. <https://doi.org/10.1038/srep16909>.
- Yavno, S., Fox, M.G., 2013. Morphological change and phenotypic plasticity in native and non-native pumpkinseed sunfish in response to sustained water velocities. *J. Evol. Biol.* 26, 2383–2395. <https://doi.org/10.1111/jeb.12230>.
- Záhorská, E., Kováč, V., Falka, I., Beyer, K., Katina, S., Copp, G.H., Gozlan, R.E., 2009. Morphological variability of the Asiatic cyprinid, topmouth gudgeon *Pseudorasbora parva*, in its introduced European range. *J. Fish Biol.* 74, 167–185. <https://doi.org/10.1111/j.1095-8649.2008.02121.x>.
- Záhorská, E., Balázová, M., Bhagat, Y., Copp, G.H., 2017. Does latitude drive the phenotypic plasticity of morphological traits in non-native pumpkinseed populations from Europe? *Knowledge & Management of Aquatic Ecosystems* 418, 219. <https://doi.org/10.1051/kmae/2017021>.
- Zelditch, M.L., Swiderski, D.L., Sheets, H.D., 2012. Geometric morphometrics for biologists: a primer. Academic Press. <https://doi.org/10.1016/C2010-0-66209-2>.