Phenotypic responses to piscivory in invasive gibel carp populations

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Abstract

The establishment of introduced fishes can be inhibited by biotic resistance from species in the receiving environment, including strong consumptive resistance from specific piscivorous fishes. In response to predation pressure, prey fish population responses include predator-induced morphological changes, where an extreme example is seen in crucian carp *Carassius carassius*, which form deep-bodied morphs in predator presence that reduces individual predation risk. As its congener gibel carp *Carassius gibelio* is a highly invasive fish across in its non-native range in Eurasia, here we test whether their introduced populations also respond to the presence of piscivorous fishes by altering their body shape and trophic ecology by testing differences across 16 non-native lentic populations in Turkey that provided groups of piscivorous fish presence versus absence. In piscivore presence, gibel carp had a higher ratio of body length-to-depth than in piscivore absence, but with their body condition factor being higher in absence. Stable isotope mixing models predicted that gibel carp had diets that were more animal-based (gastropods and zooplankton) in piscivore absence, but plant-based in piscivore presence. Moreover, diet predictions of piscivore diet suggested gibel carp were consistently consumed less than other prey fishes. These results suggest that these alien gibel carp were responding to piscivory as per crucian carp, reducing their predation risk at the individual level by forming deep-bodied morphs. We suggest these morphological responses then decrease the strength of the biotic resistance against their invasion at the population level.

Keywords: *Carassius gibelio*; fish shape; induced morphology; predator–prey interactions; inducible defence

Introduction

The establishment of sustainable populations of introduced species can be inhibited by biotic resistance in the receiving environment (Alofs and Jackson 2014; Britton, 2023). While commonly associated with native species richness, the strength of biotic resistance has also been associated with niche availability and the presence of a few species that make key contributions to the resistance (Henriksson et al. 2015). In freshwater habitats, empirical evidence suggests that the strongest resistor against the establishment of introduced fishes can be piscivory. For example, the presence of one piscivorous species in Swedish lakes, Northern pike *Esox lucius*, was a stronger explanatory variable on the outcome of multiple introductions of an alien salmonid fish than species richness (Henriksson et al. 2015). Indeed, when compared to competitive resistance of the establishment of freshwater alien species, consumptive resistance tends to be relatively strong (Alofs and Jackson 2014).

An immediate response of prey fishes to elevated predation risk is behavioral changes, such as forming schools, increasing vigilance, seeking refuge and/or reducing their activity (Walls 1990; Ioannou et al. 2017). Longer term responses in the population include altered life history traits and predator induced chemical defences (Walls et al. 1990). A further long-term response in predated fish populations is in morphology, where predation acts as a strong selection pressure that shifts body shapes. For example, the roach *Rutilus rutilus* in predator presence becomes more streamlined and with caudally inserted dorsal fins, features that facilitate escape from predators (Schanweber et al. 2013).

An extreme example of strong anti-predator morphological responses is in populations of the crucian carp *Carassius carassius* (Andersson et al. 2006). In the presence of Northern pike, individuals within crucian populations develop deeper body shapes, reducing their predation risk due to pike gape limitation, but with deep-bodied individuals also being able to attain higher speed, acceleration and turning rate during their behavioural anti-predator responses than shallow-bodied individuals (Domenici et al. 2008). Pike handling times are also higher for deep-bodied than shallow-bodied individuals and experiments indicate pike prefers to predate on shallow bodied crucians (Nilsson et al. 1995; Holopainen et al. 1997). This phenotype shift to deep bodied morphs is driven by a chemical signal released from epidermal club cells in the skin of crucian carp on injury (Stabell and San Lwin 1997) or by a diet based on chironomid larvae instead of zooplankton (Andersson et al. 2006). As shallow-bodied morphs also have higher zooplankton foraging success than deep-bodied morphs, these body shape changes might also impact foraging success and diet composition (Andersson et al. 2006). The ecosystem type, however, can also be an important variable for defining the body shape and condition factor of fish, because different types of ecosystems provide different levels of resources and environmental conditions that can influence the growth and development of fish (Záhorská et al. 2009).

This phenotypic morphological shift in crucian carp in predator presence is then potentially important in a biological invasion context. This is because if a similar process is also apparent in its congener gibel carp *Carassius gibelio*, then its ability to establish sustainable populations following introductions could be facilitated through shifts to deep-bodied morphs reducing the strength of their consumptive biotic resistance (Alofs and Jackson 2014). Gibel carp is recognised as a highly invasive freshwater fish in many areas of Eurasia (Lusková et al. 2010; Perdikaris et al. 2012). In Turkey, gibel carp has been accidentally introduced around the country through batches of common carp *Cyprinus carpio* that were stocked for enhancing reservoir fisheries (Vilizzi et al. 2015) in response to local demand (Gaygusuz et al. 2015). Gibel carp has since expanded its invasive distribution range (Gaygusuz et al. 2015) and is now the most abundant introduced species in Turkey, having established populations in stagnant water bodies such as reservoirs, lakes, and ponds (Tarkan et al. 2012a). It is widely reported to have ecological impacts in its invasive range, including the significant decline of native cyprinid populations through reproductive interference and competition (e.g., Emiroğlu et al. 2012; Tarkan et al. 2012b). Some of these invaded reservoirs have also received introductions of piscivorous fishes, including pike, perch *Perca fluviatilis*, pikeperch *Sander lucioperca* and European catfish *Silurus glanis*. While it has not yet been quantified as to the extent of predation pressure exerted on the fish community (including gibel carp) by these piscivores (Saç and Okgerman 2015), they provide the opportunity to test whether their presence has affected the invasive populations of gibel carp in relation to their body shape.

Correspondingly, the aim here was to test phenotypic differences in lentic populations of invasive gibel carp in the presence and absence of piscivorous fishes, with assessment of the phenotypic morphological response of populations to the presence/absence of predation pressure from piscivorous fishes while also considering their trophic information (from a bulk stable isotope approach; $\delta^{13}C$, $\delta^{15}N$). We posit that gibel carp express a different morphological phenotype response (as the body length/depth ratio) and diet consumption in the presence of piscivorous fishes that minimises their contribution to the diets of those fishes compared with other prey fishes and, in doing so, reduces the strength of consumptive biotic resistance.

Materials and methods

Study area

Gibel carp were collected from 16 water bodies in Turkey (Fig. 1), seven of which were reservoirs established for irrigation purposes, with areas ranging from 0.05 to 9.60 km^2 and average maximum depths of approximately 35 m, while the other nine study sites are natural lakes of various sizes ranging from 0.1 to 300 km^2 and mostly shallow ranging between 1-3 m (Table 1). Except two water bodies located in Thrace, all waters are located in western Anatolia (Fig. 1). All of these water bodies have gibel carp present in either the presence or absence of piscivorous fishes (piscivores hereafter). Among the sampled sites, perch was the dominant piscivore, being present in Bayat, Gala, and Seyitler, followed by European catfish, which was present in Gala and İznik, and pikeperch was present in Gala and Sığırcı (Table 1).

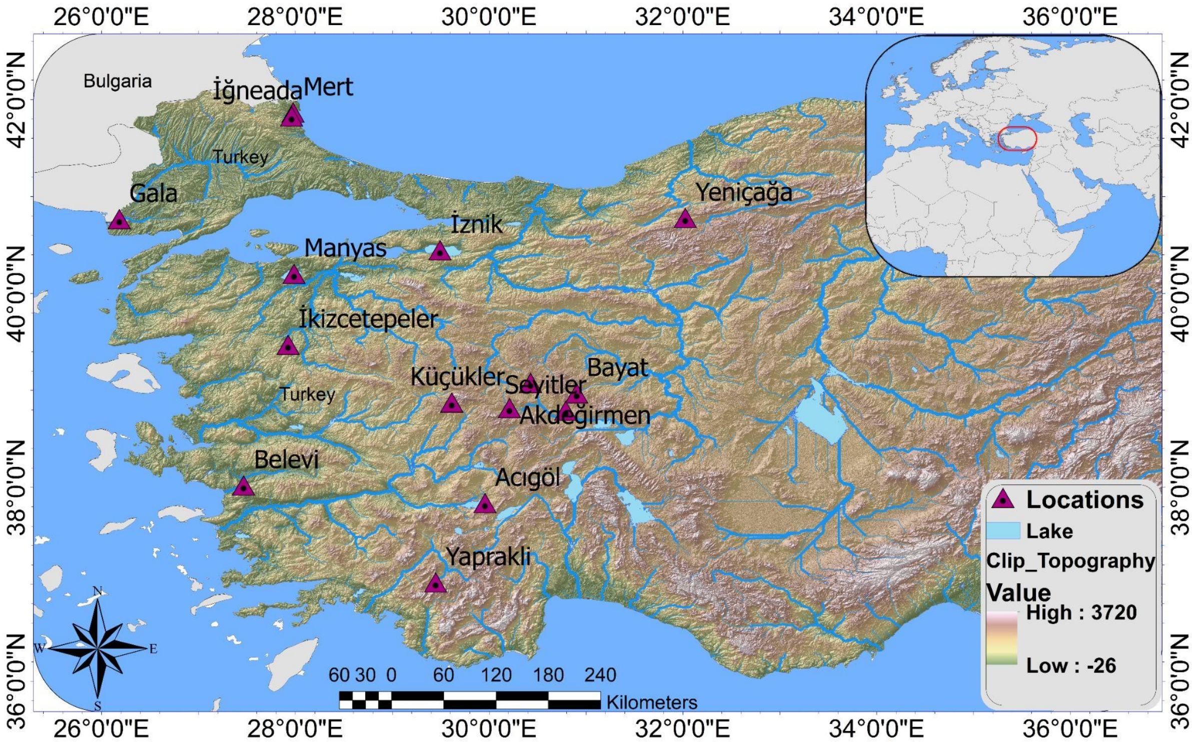

Fig. 1. The sampling sites in western Anatolia, Turkey.

Table 1. Coordinates, cover area and depth of the sampling sites as well as the respective predator species present, including the sample number of the respective species.

Lake	Ecosystem type	Latitude	Longitude	Area (km^2)	Depth (m)	Predator (sample number)
Acıgöl	Natural lake	38.56	34.48	69.5	2.1	Not applicable
Akdeğirmen	Reservoir	38.82	30.21	6	34.5	Not applicable
Bayat	Reservoir	38.97	30.9	0.05	28	*Perca fluviatilis* (15)
Belevi	Natural lake	38.02	27.47	2.5	2	
Gala	Natural lake	40.77	26.19	5.6	2	*Sander lucioperca* (10)*, Perca fluviatilis* (9)*, Silurus glanis* (7)
İğneada	Natural lake	41.83	27.93	0.1	2.1	Not applicable
İkizcetepeler	Reservoir	39.48	27.93	9.6	17	Not applicable
İznik	Natural lake	40.45	29.53	300	70	*Silurus glanis* (10)
Küçükler	Reservoir	38.88	29.61	1.2	9.5	Not applicable
Manyas	Natural lake	40.2	27.95	169	3	Not applicable
Mert	Natural lake	41.87	27.97	2.2	1.5	Not applicable
Seyitler (north)	Reservoir	38.8	30.79	4.5	25.5	*Perca fluviatilis* (10)
Seyitler (south)	Reservoir	38.8	30.79	4.5	25.5	*Perca fluviatilis* (10)

Sığırcı	Natural lake	40.83	26.32	6.5	6	*Sander lucioperca* (11), *Perca fluviatilis* (10)
Üçlerkayası	Reservoir	39.08	30.43	0.04	19.5	Not applicable
Yapraklı	Reservoir	37.02	29.44	6.5	22.6	Not applicable
Yeniçağa	Natural lake	40.78	32.02	2.78	12	Not applicable

Sampling and sample processing

Sampling was conducted in autumn (October-November) of 2021, with fish captured using multi-mesh gillnets (12 panels varying from 5 to 55 mm mesh sizes). Following capture, representative samples of all captured fish were transported to the laboratory on an ice water slurry. Also, samples of other co-occurring fish species and fish putative prey resources (algae, submerged macrophytes, detritus, bivalves, gastropods, phytoplankton, and zooplankton) were collected from each sampling site, where available.

In the laboratory, the collected fishes were measured (total length, body depth, i.e. distance from insertion of dorsal fin to insertion of pelvic fin, and weight to the nearest mm and g). The weight-length (WL) relationships of gibel carp were determined using the slopes (b) of the linear regression models between log-transformed length and weight measures. If $b > 3$, fish growth was defined as hyperallometric (growth in weight is faster than in length) and where $b < 3$ then growth in length was faster than in weight (Karachle and Stergiou 2012). Fitting of WL relationships was performed in R (ver. 4.2.1, R Core Team) using the libraries 'FSA' (ver. 0.9.3) and 'nlstools' (ver. 1.0–2; Ogle et al. 2000). Gibel carp body condition was evaluated by Fulton's condition coefficient (Le Cren 1951) calculated as Fulton's condition (KF) = $100{,}000 \times W / TL^3$, where: W = total body weight [g], TL = total length [cm].

Stable isotope analysis

For the analysis of bulk carbon and nitrogen stable isotopes ($\delta^{13}C$, $\delta^{15}N$), a sample of dorsal muscle tissue was taken from the area between lateral line and dorsal fin of each individual fish sampled (Table S1). All samples were dried at a constant temperature (60 °C) for 24 h and ground to fine powder using an agate pestle and mortar. Because lipids can be depleted in $\delta^{13}C$ compared with the whole organism (Post et al. 2007), lipids were extracted from all animal tissues using a 2:1 chloroform: methanol solution. The plant and invertebrate samples were processed as a whole, without any chemical treatment. The analyses of the samples were then performed with a continuous flow interface (ConFlo IV, Thermo Fisher Scientific, Germany) and an isotopic ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Germany). All stable isotope values are reported in the δ notation: $\delta^{13}C$ or $\delta^{15}N = [((R_{sample} / R_{standard}) - 1) \times 1000]$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios, and the standards are atmospheric nitrogen and Pee Dee Belemnite. The standard errors of the replicates of all the analyses were 0.03 ‰ for $\delta^{13}C$ and 0.11 ‰ for $\delta^{15}N$.

Statistical analyses

The slope (*b*) of the gibel carp weight-length relationships was tested against the effect of the ecosystem type and piscivore presence using ANOVA. Moreover, we inspected the body length to depth ratio (L:D; reflecting the fish's phenotypic adaptation; Domenici et al. 2008) and Fulton's condition factor (as a proxy of the fish's health; Le Cren 1951) across all sites as a response to the presence of piscivores using a t-test, where the test compares the means of two groups and determines if a factor (i.e., piscivore presence) has an effect on the dependent variable (i.e., the L:BD and Fulton factor). We further used the *cor* function of the `corplot` R-package and Spearman's rank correlation coefficient to identify correlations between various variables of gibel carp (W, TL, body depth, $\delta^{13}C$, $\delta^{15}N$, type of water body, Fulton factor and predator presence). We then used a series of linear mixed models (with the *lmer* function implemented in the `lme4` package; Bates 2010) and analysed whether: (*i*) system type (two levels: reservoirs; natural lakes), Fulton factor (continuous variable), and the presence of piscivores (two levels: present; absent) significantly predicted gibel carp L:BD ratios, and (ii) if the presence of piscivores and ecosystem significantly predicted gibel carp condition (as Fulton's condition factor), in either case including 'site' as a random effect.

Stable isotope mixing models were run to predict (1) gibel carp dietary differences in piscivore presence/absence, and (2) contributions of gibel carp to piscivore diets and in relation to other prey fishes in the sites. For (1), the included sites were Acıgöl, Akdeğirmen and Üçlerkayası in piscivore absence, and Bayat, Gala, İznik, Seyitler and Sığırcı in piscivore presence. Putative prey resources included in models were animal (gastropods, bivalves and zooplankton), plant resources (algae, phytoplankton) and detritus. For (2), all the sites with piscivores were included and prey sources were mainly cyprinid species including gibel carp and some non-native fish species, e.g. *Atherina boyeri*, *Lepomis gibbosus*, *Gambusia holbrooki* (Fig. 2). To predict the diet composition of the piscivorous fishes and thus to identify the relative importance of gibel carp, as well as to identify potential differences in the diet of gibel carp in sites with and without piscivorous fishes, stable isotopes mixing models were run using the R package `simmr` (Parnell and Parnell 2016). For this, we considered no priors and used the trophic discrimination factors (TDFs) proposed by Post (2002), namely 1 for $\delta^{13}C$ and 3.4 for $\delta^{15}N$.

Results

Relative contributions of gibel carp to piscivores' diet

For the piscivorous fishes present in each lake (perch, pikeperch, European catfish), the stable isotope mixing models predicted that gibel carp were consistently consumed in lower dietary proportions than other putative prey fishes (Fig. 2). This was the case whether there were multiple prey species present (i.e., in İznik and Gala) or only one other prey species present (i.e., Seyitler; Fig. 2). For gibel carp diet, predictions were that dietary contributions of gastropods and zooplankton were higher in sites of piscivore absence, whereas in piscivore presence, their diets were based more on plants and detritus (Fig. 3).

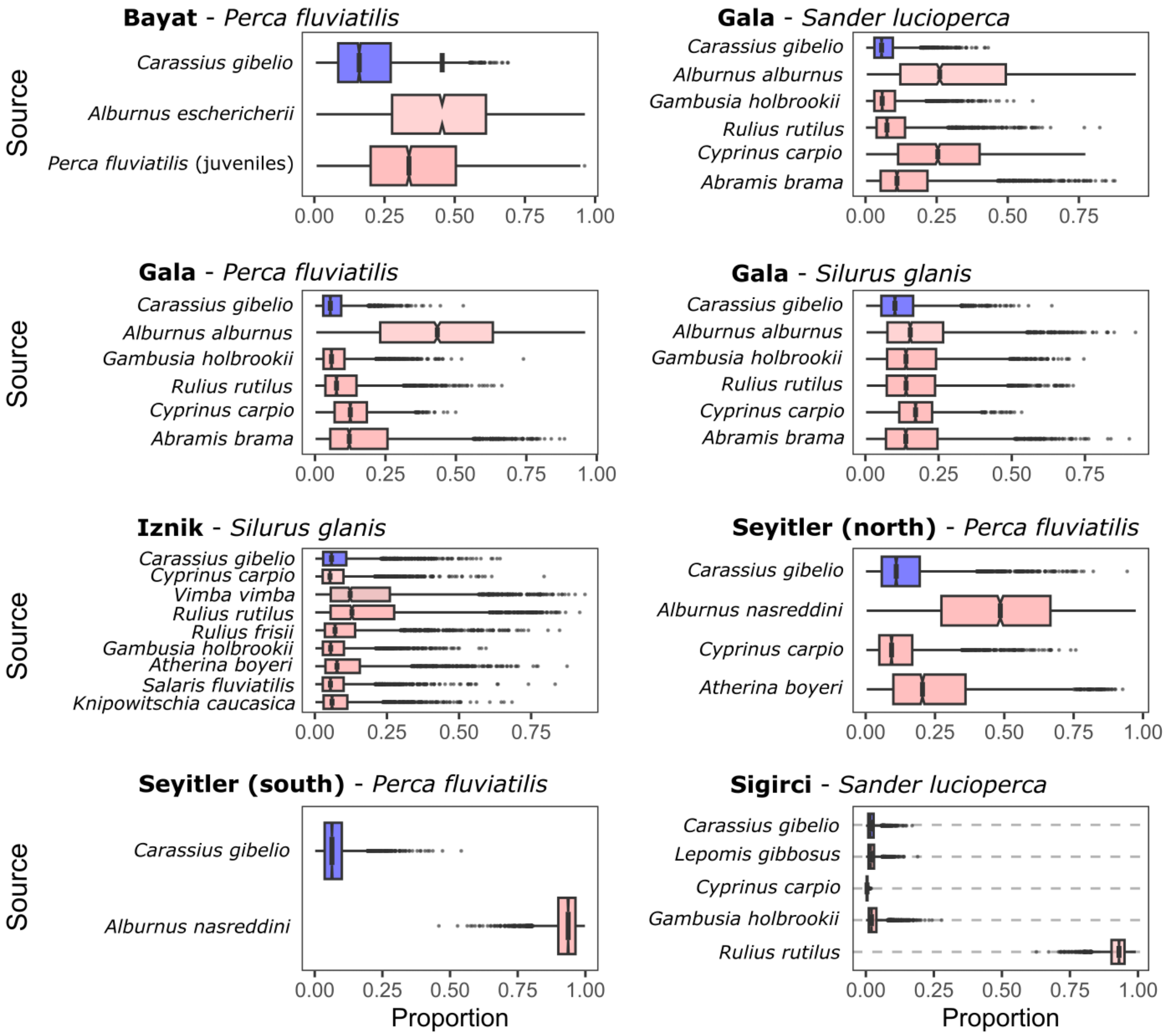

Fig. 2. Mixing models results without priors indicating the probabilistic distribution of prey for the respective predator(s) at each site, highlighting *Carassius gibelio* (blue) vs. other consumed prey (red).

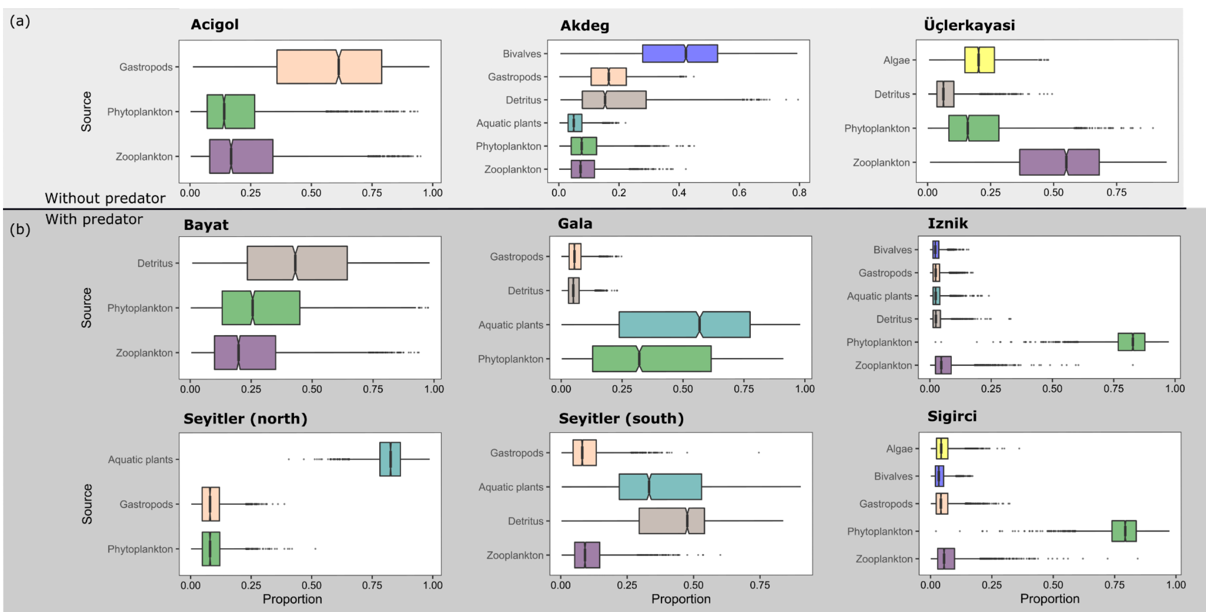

Fig. 3. Mixing models results indicating the probabilistic distribution of prey in the diet of gibel carp (*Carassius gibelio*) at each site separated into sites without and with piscivores.

Gibel carp morphological and condition differences

Across all 15 sites, the mean of the L:BD ratio between sites with and without piscivores differed significantly (t = -7.5031; df = 93.11; $P < 0.05$), indicating a higher ratio in sites with piscivores (Fig. 4a). The estimated values of b in the LW relationship (as 95% CI) were mostly above 3 except for the Seyitler and Akdeğirmen reservoirs, which was below 3, and ranged from 3.0 (İğneada and Üçlerkayası reservoirs, and İznik and Sığırci lakes) to 3.5 in Gala (Table S1). However, differences in b between waters with and without piscivores were not significant ($F_{2, 14} = 0.74$, $P > 0.05$), with this also the case between natural lakes and reservoirs ($F_{2,14} = 0.32$, $P > 0.05$). However, the mean of the Fulton condition factor of gibel carp across sites did differ significantly between the sites with and without piscivores (t = 5.6036; df = 176.14; $P < 0.05$; Fig. 4b).

Significant correlations were found between Fulton condition, L:BD ratio, and the presence of piscivores, where Spearman correlations were $r_{sp} > 0.5$ (Fig. S1). There was a negative correlation between presence of piscivores and condition, with the latter being positively correlated with the body depth of gibel carp and its presence in reservoirs. Body length and depth were further significantly negatively correlated with $\delta^{13}C$ (Fig. S1). Linear mixed models identified the presence of piscivores as significantly positive and Fulton conditioning factor as significantly negative predictors of the L:BD ratio ($P < 0.05$; Fig. 5a, b), whereas ecosystem type was not a significant predictor ($P > 0.05$). Neither presence of piscivores nor ecosystem type significantly predicted Fulton condition factor ($P > 0.05$; Fig. 5c).

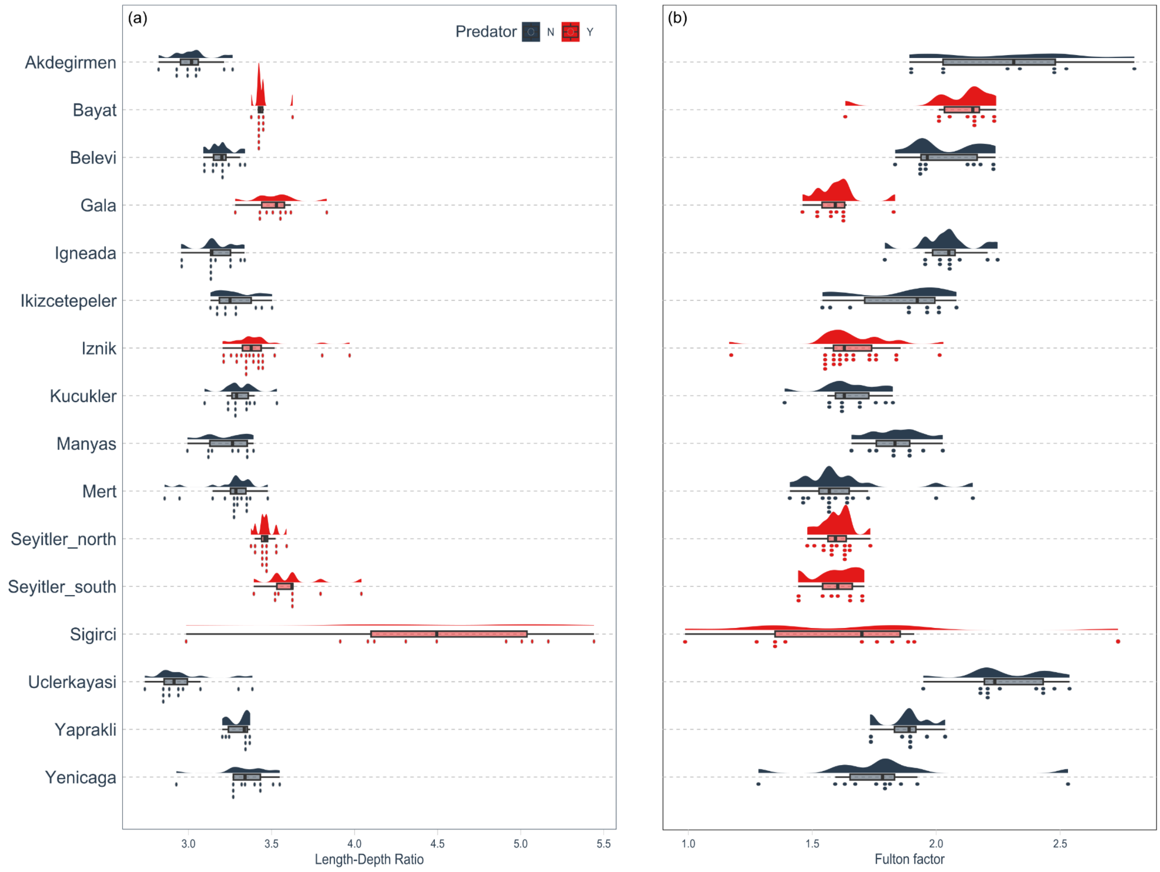

Fig. 4. Body length-depth ratio (left) and Fulton condition factor (right) by water bodies.

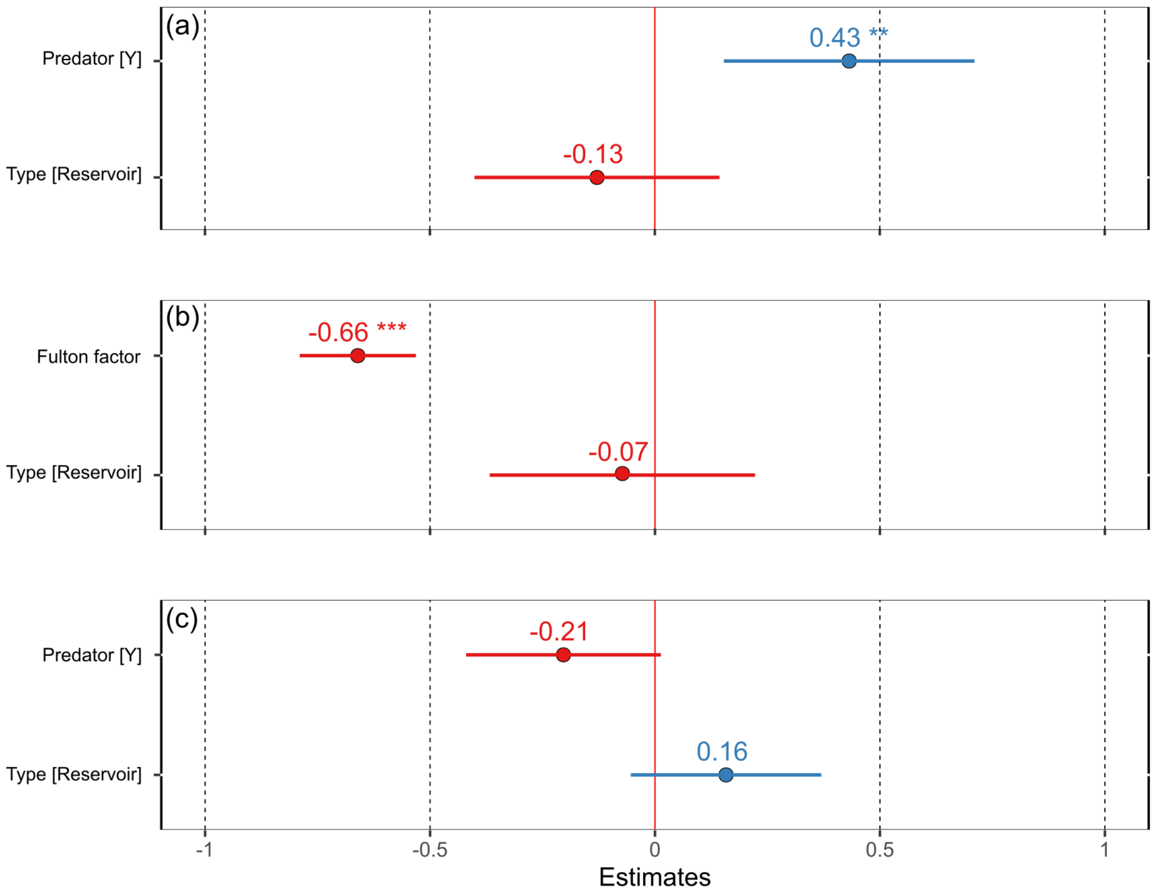

Fig. 5. (a) Linear mixed effect model average of the L:D ratio as (a) function of predator presence and ecosystem type, (b) Fulton factor and ecosystem type, (c) and Fulton factor as function of predator presence and ecosystem type. Each model considered the site as a random factor.

Discussion

The wide environmental tolerance and the ability of alien species to adapt to and thrive under a broad variety of environmental conditions is a prerequisite for their invasion success. While there have been reports highlighting the behavioural and phenotypic plasticity of alien species from their invasive range (Rolla et al. 2020; Haubrock et al. 2021), information is often scant and anecdotal. Here, we identified a significant change in the ratio between body length to body depth in gibel carp in the presence of piscivores. While we cannot account for additional or alternative drivers that may have led to the observed morphological changes in gibel carp, our results can be seen as the first indications of a morphological adaptation of an invasive fish species to the presence of predatory pressure.

In accordance with our predictions, we detected significant morphological changes (as body length to depth ratio) in gibel carp under piscivory, a phenotypic response that is regularly observed in the congener crucian carp (Brönmark and Miner 1992). While mixing models suggested that gibel carp were not subject to strong predation pressure, this is possibly due to these morphological adaptations, given pike prey choice experiments suggest preference for shallow-bodied over deep-bodied crucians (Nilsson et al. 1995). Our models identified that the presence of piscivores led to shorter and slimmer individuals. This might relate to their direct response to piscivore presence or direct predatory stress (Nilsson et al. 1995), and/or relate to induced behavioural changes, such as in their foraging (e.g., their diets being more plant-based in piscivore presence) (Domenici 2002). Indeed, the ability of crucian carp to recognize the presence of predators through chemical cues from predators might be the mechanism driving this phenotypic adaptation in gibel carp (Brönmark and Pettersson 1994).

The increased length to depth ratio in crucian carp as a response to predation is an adaptation that decreases the risk of predation by gape-limited piscivorous fish like pike (Stabell and San Lwin 1997) and could have resulted individuals also increasing their ability to evade capture through increased burst swimming capabilities and an ability to turn more quickly (Domecini et al. 2008). We also detected differences in both $\delta^{13}C$ and overall diet between the gibel carp groups, with deeper-bodied fish consuming more plant-based materials. Such predator avoidance mechanisms or behavioural adaptations have - at least to our knowledge - not yet been reported for the gibel carp, making our results the first of its kind for this widely distributed and impactful invader. While it is difficult to identify if the observed adaptation was the result of direct predation pressure or occurred as the response of e.g. chemical cues (i.e., from predators or injured congeners), nonetheless, the altered body morphology in piscivore pressure was likely to decrease gibel carp predation risk, thus reducing the extent of consumptive biotic resistance to their populations in the invaded reservoirs.

The Fulton condition factor may not necessarily reflect a fish's health or fitness, indicated by a negative relationship between the factor and the body length to depth ratio, but rather indicating a change in condition rather than a decrease in fitness. While this relationship likely originated from the length of individuals used to estimate both Fulton factor and body length to depth ratio, it cannot be ignored that a lower fish depth can be indicative of a change in condition. Commonly, a value of ~1 is considered as ideal. Here, values decreased from on average >2 , indicating that fish display an increase in condition by being less ‘plump’. The lower Fulton factor in sites with predators may therefore not necessarily reflect a worse condition, which would be in line with our third hypothesis, but rather the decreased body depth (Emiroğlu et al. 2012). This is further underlined by neither predator presence nor habitat having a significant effect on the Fulton factor while being lower at sites with predators. The phenotypic response in the gibel carp to predator presence could also be mediated by the co-occurrence of congeners. This could provoke a maximisation of somatic growth potential and growth rates, which was already observed in the crucian carp (i.e., adversely affected by intra-specific competition when the food shortage increases; Holopainen et al. 1997).

Conclusion

Our results suggest that gibel carp shift their body shape in piscivore presence, with deeper bodied morphs being present compared with populations in piscivore absence, although the exact mechanism by which the deep bodied morphs formed could not be tested directly here. These results suggest that the invasions of gibel carp could be facilitated by this phenotypic response to piscivore presence, which we suggest reduces the biotic resistance on their establishing populations, elevating their probability of becoming highly invasive.

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Author contributions

Ali Serhan Tarkan: Conceptualization, Methodology, Writing – original draft, review & editing. **Sadi Aksu & Özgür Emiroğlu**: Conceptualization, Methodology, Visualization. **Oğuzcan Mol, Esengül Köse, Irmak Kurtul, Sercan Başkurt, Emre Çınar, Pınar Öztopçu-Vatan:** Investigation & Data curation. **Phillip Haubrock & Paride Balzani:** Methodology, Visualization, Writing – original draft, review & editing. **Robert Britton**: Conceptualization, Writing – review & editing, Supervision.

Data availability

All data generated or analyzed during this study are included in this published article and are available from the corresponding author.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Consent to publication All authors have consented to publish this version of the manuscript.

References

Alofs KM, Jackson DA (2014) Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. Ecology 95:3259–3270.

Andersson J, Johansson F, Söderlund T (2006) Interactions between predator-and diet-induced phenotypic changes in body shape of crucian carp. P Roy Soc B-Biol Sci 273:431–437.

Bates DM (2010) lme4: Mixed-effects modeling with R.

Britton JR (2023) Contemporary perspectives on the ecological impacts of invasive freshwater fishes. J Fish Biol https://doi.org/10.1111/jfb.15240

Brown GE (2003) Learning about danger: chemical alarm and local risk assessment in prey fishes. Fish Fish 4:227–234.

Brönmark C, Miner JG (1992) Predator-induced phenotypical change in body morphology in crucian carp. Science 258:1348–1350.

Brönmark C, Pettersson LB (1994) Chemical cues from piscivores induce a change in morphology in crucian carp. Oikos 70:396–402.

Domenici P (2002) The visually-mediated escape response in fish: predicting prey responsiveness and the locomotor behaviour of predators and prey. Mar Freshw Behav Phy 35:87–110.

Domenici P, Turesson H, Brodersen J, Brönmark C (2008) Predator-induced morphology enhances escape locomotion in crucian carp. P Roy Soc B-Biol Sci 275:195–201.

Emiroğlu Ö, Tarkan AS, Top N, Başkurt S, Sülün Ş (2012) Growth and life history traits of a highly exploited population of non-native gibel carp, *Carassius gibelio* from a large eutrophic lake (Lake Uluabat, NW Turkey): is reproduction the key factor for establishment success? Turk J Fish Aquat Sci 12:925–936.

Gaygusuz Ö, Tarkan AS, Aydın H, Dorak Z, Top N, Karakuş U, Vilizzi L (2015) Stocking of Common Carp (*Cyprinus carpio*) into Some newly-established reservoirs of north-west Anatolia may enhance the spread of non-native Fish. Turk J Fish Aquat Sci 15:833–840.

Haubrock PJ, Balzani P, Matsuzaki SS, Tarkan AS, Kourantidou M, Haase P (2021) Spatio-temporal niche plasticity of a freshwater invader as a harbinger of impact variability. Sci Total Environ 777:145947.

Henriksson A, Yu J, Wardle DA, Englund G (2015) Biotic resistance in freshwater fish communities: species richness, saturation or species identity? Oikos 124:1058–1064.

Holopainen IJ, Tonn WM, Paszkowski CA (1997) Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L.)) in northern Europe. Ann Zool Fenn 34:1–22.

Ioannou CC, Ramnarine IW, Torney CJ (2017) High-predation habitats affect the social dynamics of collective exploration in a shoaling fish. Sci Adv 3:p.e1602682.

Karachle PK, Stergiou KI (2012) Morphometrics and allometry in fishes. Morphometrics, (c), 65–86. Retrieved from. http://www.intechopen.com/books/morphometrics.

Le Cren ED (1951) The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J Anim Ecol 20:201–219.

Lusková V, Lusk S, Halačka K, Vetešník L (2010) *Carassius auratus gibelio* —The most successful invasive fish in waters of the Czech Republic. Russ J Biol Invasions 1:176–180.

Nilsson PA, Brönmark C, Pettersson LB (1995) Benefits of a predator-induced morphology in crucian carp. Oecologia 104:291–296.

Parnell A, Parnell MA (2019) Package ‘simmr’. In (2016) Aquaculture big numbers. Food and Agriculture Organization of The United Nations Rome, Italy.

Perdikaris C, Ergolavou A, Gouva E, Nathanailides C, Chantzaropoulos A, Paschos I (2012) *Carassius gibelio* in Greece: the dominant naturalised invader of freshwaters. Rev Fish Biol Fisher 22:17–27.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189.

Ogle DH, Wheeler P, Dinno A (2000) FSA: fisheries stock analysis. R package Retrieved from. https://github.com/droglenc/FSA.

Rolla M, Consuegra S, Garcia de Leaniz C (2020) Trophic plasticity of the highly invasive topmouth gudgeon (*Pseudorasbora parva*) inferred from stable isotope analysis. Front Ecol Evol 8:212.

Saç G, Okgerman H (2015) Growth and reproduction of a non-native fish species *Carassius gibelio* (Bloch, 1782) from Büyükçekmece Lake (İstanbul, Turkey). IUFS J Biol 74:1–12.

Scharnweber K, Watanabe K, Syväranta J, Wanke T, Monaghan MT, Mehner T (2013) Effects of predation pressure and resource use on morphological divergence in omnivorous prey fish. BMC Evol Biol 13:132.

Stabell OB, San Lwin M (1997) Predator-induced phenotypic changes in crucian carp are caused by chemical signals from conspecifics. Environ Biol Fish 49:145–149.

Tarkan AS, Copp GH, Top N, Özdemir N, Önsoy B, Bilge G, Filiz H, Yapıcı S, Ekmekçi FG, Kırankaya Ş, Emiroğlu Ö, Gaygusuz Ö, Gürsoy Gaygusuz Ç, Oymak A, Özcan G, Saç G (2012a) Are introduced gibel carp *Carassius gibelio* in Turkey more invasive in artificial than in natural waters? Fisheries Manag Ecol 19:178–187.

Tarkan AS, Gaygusuz Ö, Gürsoy Gaygusuz Ç, Saç G, Copp GH (2012b) Circumstantial evidence for gibel carp *Carassius gibelio* reproductive competition exerted on native fish species in a mesotrophic reservoir. Fisheries Manag Ecol 19:167–177.

Vilizzi L, Ekmekçi FG, Tarkan AS, 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.

Walls M, Kortelainen I, Sarvala J (1990) January. Prey responses to fish predation in freshwater communities. In Annales Zoologici Fennici (pp. 183-199). Finnish Zoological Publishing Board, formed by the Finnish Academy of Sciences, Societas Scientiarum Fennica, Societas Biologica Fennica Vanamo and Societas pro Fauna et Flora Fennica.

Záhorská E, Kováč V, Falka I, Beyer K, Katina S, Copp GH, Gozlan RE (2009) Morphological variability of the Asiatic cyprinid, topmouth gudgeon *Pseudorasbora parva*, in its introduced European range. J Fish Biol 74: 167–185.