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Niche segregation of a newly introduced invasive and co-occurring native fish species in a productive shallow lake (Manyas, NW Anatolia)

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Abstract. The impacts of aquatic invasive species vary from the population to ecosystem level most strikingly through modifications to native communities, often leading to a decline in native species. A primary impact mechanism is competitive displacement of native by invasive species through resource partitioning. However, the trophic interactions between native and invasive species occupying the same habitat remain poorly understood, particularly at the early stages of invasion. This study used stable isotope analysis of two co-occurring populations of invasive topmouth gudgeon, *Pseudorasbora parva* and native Caucasian dwarf goby, *Knipowitschia caucasica* in a highly productive shallow lake to characterize overlap of potential trophic niches. The trophic niches of both species were divergent, with no overlap. Mixing models suggest some inter-specific dietary differences. The trophic niche of the Caucasian dwarf goby was slightly and non-significantly larger than that of topmouth gudgeon. These results suggest that when introduced outside of their natural range, topmouth gudgeon might integrate into new fish communities via the exploitation of resources that are underexploited by native fishes, which could also explain the high invasion success of the species.

Key words: Caucasian dwarf goby, fish diet, isotopic niche, resource partitioning, topmouth gudgeon, trophic level

Introduction

Introduction of non-native fish species is an important threat to native and particularly to endemic species (Gozlan et al. 2010) and is capable of affecting ecosystems directly or indirectly (Gaygusuz et al. 2013, Copp et al. 2017). One of the main ways for understanding the impact of non-native fishes is from their trophic interactions with extant native species, such as through convergence or divergence in resource use (Copp et al. 2017). These impacts have been reported across a range of families covering different feeding guilds (Crowl et al. 1992, Martin et al. 2010, Weber & Brown 2011). Niche partitioning has been observed in invasive species which enables their stable coexistence with other community members (Chesson 2000, Kylafis & Loreau 2011). This partitioning could be realized by becoming less generalized in their diet (Van Valen 1965), and thus, declining in niche width (Olsson et al. 2009). Conversely, when competition for resources is increased, expansion of trophic niches by invasive species can be observed (Svanbäck & Bolnick 2007).

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Topmouth gudgeon *Pseudorasbora parva* Temminck & Schlegel, 1846 is native to East Asia and one of the most successful invasive freshwater fishes in the world (Gozlan et al. 2010). Severe ecological effects were reported after their introduction to novel ecosystems (Bianco 1988, Wildekamp et al. 1997, Pollux & Korosi 2006). They compete with native species for prey and habitat (Britton et al. 2007, Carpentier et al. 2008) and have invaded numerous countries from Central Asia to North Africa (Gozlan et al. 2010). There are contrasting reports on its competitive impact on native fishes in many invaded fish communities, i.e. adverse ecological impacts (Britton et al. 2010) *vs.* minimal sharing of food resources (e.g. Jackson & Britton 2013, 2014).

Concern with the dispersal and impact of non-native fishes in freshwater ecosystems has been increasing in Turkey (Yoğurtçuoğlu & Ekmekçi 2018, Ozulug et al. 2019, Emiroğlu et al. 2020, Saç et al. 2020). The first record of topmouth gudgeon in Turkish freshwaters was in the 1980s (Erk'akan 1984) and it has subsequently spread across Anatolia, mainly through human-mediated accidental introductions (Ekmekçi & Kırankaya 2006). The species has now been reported from ~70 water bodies in Turkey (Özcan & Tarkan 2019) and has continued to spread (Bostancı et al. 2020, Saç et al. 2020). Topmouth gudgeon has been recently reported from Lake Manyas (Saç et al. 2020), which has been designated as a Ramsar Site since 1994 (Yeniyurt & Hemmami 2011). In addition to habitat degradation and environmental pressures, non-native fish introductions have become one of the main threats to the conservation of biodiversity at this site. The Caucasian dwarf goby *Knipowitschia caucasica* Berg, 1916 is a small Ponto-Caspian gobiid that is capable of surviving in a range of ecosystems, from fresh to hypersaline. It is mostly endemic with limited distribution in waters along coasts of the Black, Azov, Caspian and Aegean Seas (Kottelat & Freyhof 2007). The current study reports that the Caucasian dwarf goby and topmouth gudgeon broadly share the same macrohabitat (turbid, shallow, muddy and rocky sediment) in Lake Manyas, and therefore they are potential competitors for resources. Despite the fact that Gobiids and gudgeons can often co-exist, especially in the littoral zones of stagnant water bodies (e.g. Tarkan et al. 2018), no studies have uncovered niche interactions of topmouth gudgeon and members of the Gobiidae family. The same is also true for the competitive interactions of these species, which have rarely been the subject of studies at an early stage of invasion.

Here we identify the possible interaction of these species using stable isotope analyses. This method allows an estimation of the overlap of the isotopic niches of competing species to infer potential food competition (Balzani et al. 2016, 2020) or niche partitioning (Polačik et al. 2014) and the method has been demonstrated to be useful in revealing the ecological impacts of introduced fishes (Cucherousset et al. 2012). Our specific objectives were to understand the trophic ecology and niche breadth of a topmouth gudgeon invasion, particularly in its early stages, which could give further insights of the likely establishment success of the species. In addition, knowledge of the feeding ecology of the Caucasian dwarf goby and its interactions with a non-native species is likely to be important for assessing its ecological flexibility in an invaded ecosystem, as it has been reported to be introduced and to have successfully established in freshwater bodies around the Black Sea and Mediterranean region (e.g. Didenko et al. 2020).

Material and Methods

Study area

Lake Manyas, also called Lake Bird, is an important hosting area for migrant birds. It is located in north-west Anatolia (40.2000, 27.9333) and is a shallow eutrophic lake (mean depth ca. 4 m) at a height of 15 m above sea level and a surface area of 150 km^2 (Balik 1989). This natural lake has several streams that debouch into it (Kocaçay, Akıntı, Dutlu and Sığırcı streams) and the lake water flows into the Sea of Marmara through the River Kara, connecting to the River Susurluk. Topmouth gudgeon were first reported from Lake Manyas in 2020 (Saç et al. 2020) though the species was observed in the lake earlier (present study in 2016). Apart from the two species under current study, several fish species belonging to Cyprinidae family have been reported from the lake, including white bream *Blicca bjoerkna* Linnaeus, 1758; Danube bleak *Alburnus chalcoides* Güldenstädt, 1772; common carp *Cyprinus carpio* Linnaeus, 1758; roach *Rutilus rutilus* Linnaeus, 1758; rudd *Scardinius erythropthalmus* Linnaeus, 1758; vimba bream *Vimba vimba* Linnaeus, 1758 (Öztürk 2011), Manyas spirlin *Alburnoides manyasensis* Turan et al., 2013 (Turan et al. 2013) and gibel carp *Carassius gibelio* Bloch, 1782 (Çiçek et al. 2009), as well as species from Gobiidae family; western

tubenose goby *Proterorhinus semilunaris* Heckel, 1837; monkey goby *Neogobius fluviatilis* Pallas, 1814 (Tarkan et al. 2018).

Sampling and stable isotope analysis (SIA)

Sampling was carried out in January 2016 by backpack electrofishing (SAMUS-725G) in littoral areas of the lake. In the field, all captured fishes were euthanized, total length (TL, cm, accuracy nearest mm) and weight (W, g, nearest 0.1 g) were measured. All specimens were stored at –20 °C until a sample of dorsal muscle tissue was taken from each individual for SIA. Environmental samples of putative food resources of the fishes, including submerged macrophytes, zooplankton, macrobenthos (i.e. only Insecta and Oligochaeta), which were previously identified in the diet by gut content analysis of the fishes (e.g. Güçlü & Erdoğan 2017, Didenko et al. 2020), were also collected from the lake. Macrobenthos and macrophytes were collected with a grab and a scoop from the lake bottom and surface, while zooplankton was collected with a zooplankton net. Macrophyte samples were washed in tap water and, after removing insects/other organic materials, stored separately for SIA.

Samples were dried in an oven for 24 h at 60 °C and homogenized into a fine powder with an agate mortar and pestle. A 1 mg sample of homogenized tissue from each fish and invertebrate material and 2 mg of plant material were weighed accurately and put into individual 5 × 9 mm tin cups using an ultra-microbalance (Sartorius MSA3.6P-000-DM Cubis Micro Balance). Samples were analysed with an elemental analyser (Flash EA, 1,112 series, Thermo-Finnigang) coupled with a continuous flow isotope ratio mass spectrometer (Finnigan MAT DeltaPlus, Thermo-Finnigang at Davis, University of California). Stable carbon and nitrogen isotope compositions were expressed as ‰ with the δ notation based on δ13C or δ15N = [((Rsample/Rstandard) – 1) × 1,000], where R is 13C/12C or 15N/14N ratios. Results were referenced to Vienna Pee Dee Belemnite for carbon and to atmospheric N_2 for nitrogen as secondary standards with known relation to international standards (Atomic Energy Agency (IAEA) international standards: N1, N2 and USGS25 for nitrogen and CH6, CH7 and USGS24 for carbon).

To quantify intraspecific niche width, Layman's metrics (Layman et al. 2007) and corrected standard ellipse area (SEA_c, Jackson et al. 2011) were calculated using the R package "SIBER" (version 2.1.6, Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011). The total area (TA) encompassing all individual measures indicates a species' trophic niche diversity (Layman et al. 2007), whereas SEA_c is a bivariate estimate of the core isotopic niche width considering 40% of central data points, and is thus less sensitive to extreme values than TA. The R package, SIBER was also used for calculation the 95% probability Bayesian standard ellipse area (SEA_b) (Jackson et al. 2011).

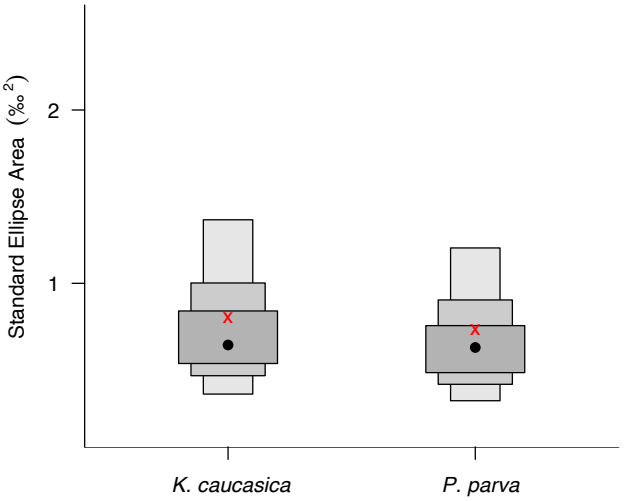

Fig. 1. Posterior probability distributions of estimated Bayesian standard ellipse area for *Knipowitschia caucasica* and *Pseudorasbora parva*. The black dot represents the mean, whereas dark, intermediate and light grey boxes represent the 40%, 75% and 95% credibility intervals, respectively.

The Kernel isotope niche (R package "rKIN", Eckrich et al. 2020) was used for a spatial analysis using isotopic coordinates in a bivariate normal Kernel utilization density estimator (estKIN) to calculate "estimated isotopic homing ranges" (40%, 75% and 95%) of each species. This provided estimates of the Kernel utilization density (UD), ellipse and minimum convex polygon overlap between both species (confidence contours, calcOverlap).

The contribution of food sources to the isotopic signatures of both species under study were

Table 1. Mean TL (mm), W (g), δ13C, δ15N of *Knipowitschia caucasica* and *Pseudorasbora parva*.

	K. caucasica	*P. parva*	F#	*P*#
TL (mm)	35.7 ± 0.3	42.8 ± 0.7	8.798	0.0097
W (g)	0.4 ± 0.1	0.6 ± 0.3	3.295	0.0799
δ13C	–22.2 ± 0.9	–20.2 ± 0.5	13.906	0.0002
δ15N	12.9 ± 0.3	11.8 ± 0.5	21.265	0.0001

#permutational

examined by Stable Isotope Mixing Models. These were supplemented with previously available stomach content data (percentage of prey occurrence) as priors and trophic discrimination factors (TDFs) (R package "simmr", Parnell & Inger 2016). Results are presented as the average percentage with standard deviation.

A permutational univariate analysis of variance (PERANOVA) was used to test the significance of differences of standard length, weight, δ13C and δ15N between species using PERMANOVA 1.0.1. + add-in to PRIMER version 6.1.11 (PRIMER-E Ltd., Plymouth, UK, Anderson et al. 2008). This procedure was performed with Type III sums of squares following normalization of the data and was based on a Euclidian distance matrix and 9999 permutations of the residuals under a reduced model.

Results

In total, 20 specimens of each species were collected for SIA. Mean fish length, but not weight, of topmouth gudgeon was significantly higher than that of the Caucasian dwarf goby, whereas mean δ13C and δ15N of the Caucasian dwarf goby were significantly greater than topmouth gudgeon (Table 1). No significant relationships were found with the linear models employed between δ13C or δ15N and total length for both species (*P*s > 0.05) except for the Caucasian dwarf goby with δ13C (F = 13.31, *P* = 0.007).

The Caucasian dwarf goby expressed a wider niche space than topmouth gudgeon, as indicated by the larger TA and SEA_c (Table 2). In parallel, SEA_b was greater in the Caucasian dwarf goby than topmouth gudgeon (Fig. 1). However, no niche overlap between the species was observed, which were fully supported by the results of the estimated home ranges for either Kernel UD, ellipse and polygon area (Fig. 2; Table 2, Table S1).

Results from mixing models indicated that, according to the proportions of dietary items for topmouth gudgeon macrobenthos and submerged macrophyte were the most abundant food component, whereas it was zooplankton and macrobenthos for the Caucasian dwarf goby (Fig. 3).

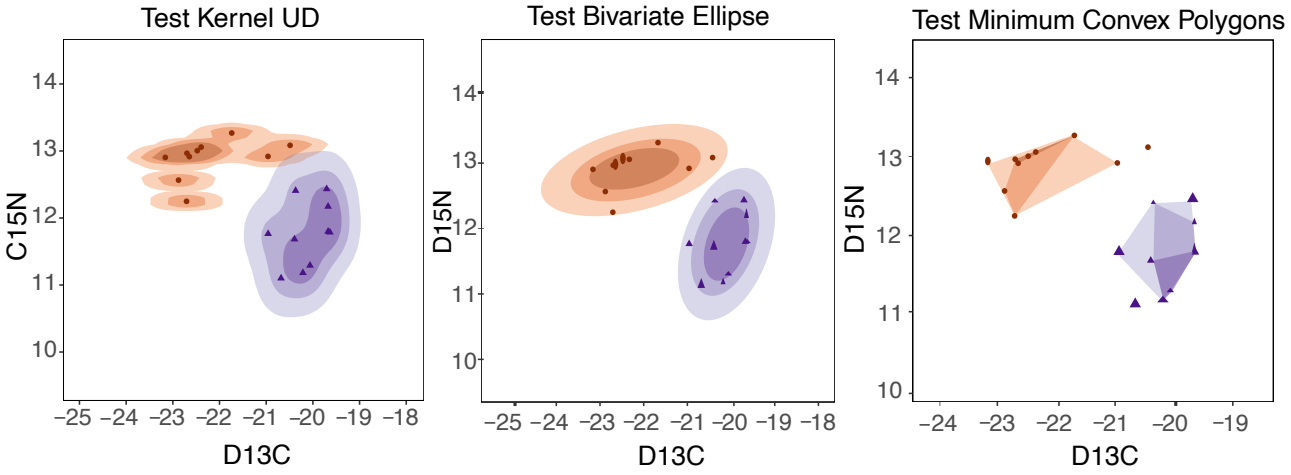

Fig. 2. Isotopic homing areas based on isotopic coordinates of *Knipowitschia caucasica* (red) and *Pseudorasbora parva* (purple) and the relative overlap between both according to a) Kernel utilization density, b) bivariate ellipses and c) minimum convex polygons. Dark, intermediate and light colours represent the percentage of data utilized for the estimations (40%, 75% and 95%, respectively). (●) *K. caucasica*; (▲) *P. parva*; (■) *K. caucasica* 40; (■) *K. caucasica* 75; (■) *K. caucasica* 95; (■) *P. parva* 40; (■) *P. parva* 75; (■) *P. parva* 95.

Table 2. Convex hull area (TA), corrected standard ellipse area (SEAc), Kernel utilization density (KUD), bivariate ellipse (BE) and minimum convex polygon (MCP) home ranges considering 40%, 75% and 95% of the data of *Knipowitschia caucasica* and *Pseudorasbora parva*.

	TA	SEAc	KUD (40%)	KUD (75%)	KUD (95%)	BE (40%)	BE (75%)	BE (95%)	MCP (40%)	MCP (75%)	MCP (95%)
K. caucasica	1.27	0.77	0.32	NA	2.79	NA	1.98	4.29	NA	0.41	1.11
P. parva	1.20	0.67	1.04	NA	4.70	NA	1.80	3.89	NA	0.62	1.05

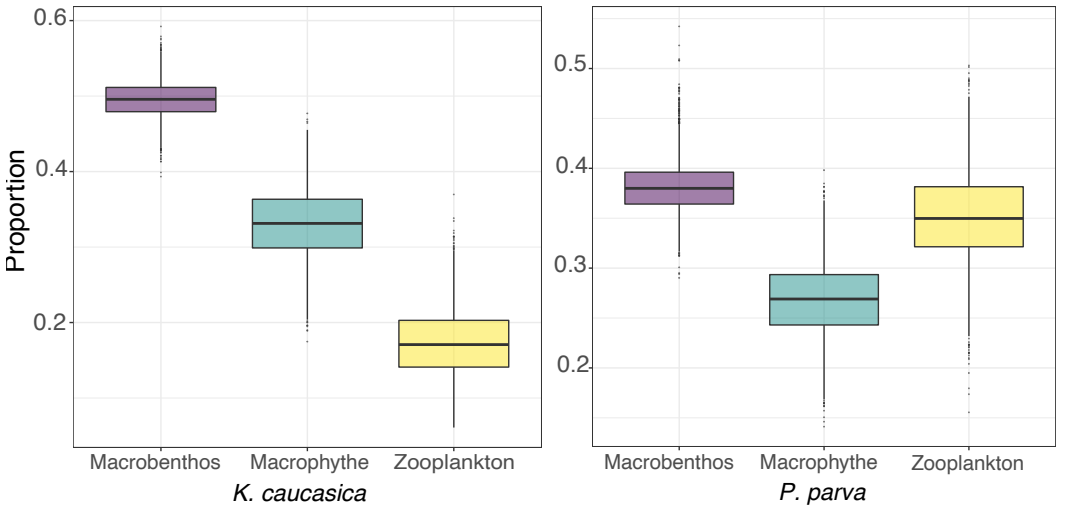

Fig. 3. Results of Stable Isotope Mixing Models for *Knipowitschia caucasica* and *Pseudorasbora parva* based on diet priors and trophic discrimination factors.

Discussion

The results of the present study clearly indicated that there was no isotopic niche overlap between the Caucasian dwarf goby and topmouth gudgeon (i.e. trophic niche divergence) based on stable isotope analysis (Fig. 2). The Caucasian dwarf goby showed wider niche space than topmouth gudgeon suggesting more opportunistic feeding in the former than the latter species in Lake Manyas. Our sampling and observations have confirmed that both species were abundant in the lake and seemingly co-exist at a local scale, though no temporal data are available on their abundance. However, this finding should be considered as questionable due to the short lifespan of both species (i.e. three years for topmouth gudgeon, Kottelat & Freyhof 2007 and two years for Caucasian dwarf goby, Froese & Pauly 2021) and as such might be expected to show an unstable population structure, i.e. fluctuations in abundance depending on environmental conditions (Didenko et al. 2020).

The trophic niches of the species under study indicated the potential for the diet of the Caucasian dwarf goby and topmouth gudgeon to overlap substantially. Although it is a generally benthic feeder, postlarvae of the Caucasian dwarf goby are pelagic (Froese & Pauly 2021), which might relate to habitat overlap with topmouth gudgeon. In addition, their feeding strategy changes as a function of ontogenetic differences and seasonal variations (Güçlü & Erdoğan 2017, Didenko et al. 2020). The present study was completed in winter (early January) and the Caucasian dwarf goby was reported to feed on zooplankton in winter and spring, while they feed on benthos in summer and autumn (Güçlü & Erdoğan 2017). Our study partly supports this result with zooplankton and macrobenthos the most preferred food component of the Caucasian dwarf goby in Lake Manyas. Similarly, our SIA results revealed that topmouth gudgeon seem to feed predominantly on macrobenthos, submerged macrophyte and less on zooplankton in Lake Manyas. The species has been described as an omnivore and generally feeding on zooplankton (Gozlan et al. 2010, Yalçın-Özdilek et al. 2012).

Due to niche shifts of both species when in sympatry, niche divergence was apparent. Patterns of trophic niche divergence detected between the Caucasian dwarf goby and topmouth gudgeon were generally consistent, with patterns observed for the latter species in mesocosms and natural ponds with a greater number of co-occurring native fish species (i.e. up to nine species, Tran et al. 2015). This finding is in line with the general patterns of trophic niche divergence that are detected between invasive and native species at small and larger spatial scales, especially in systems of increased species diversity (e.g. Tarkan et al. 2018). In the case of topmouth gudgeon, our results are in agreement with some previous studies that found similar patterns of trophic niche divergence between topmouth gudgeon, *C. carpio* and *Pacifastacus leniusculus* across six established small ponds in southern England (Jackson & Britton 2014), and *Tinca tinca* and *Gasterosteus aculeatus* in mesocosm experiments (Tran et al. 2015). However, the findings are contradicted by a SIA study on resource sharing between topmouth

gudgeon, *R. rutilus* and *C. carpio* in an invaded fishing lake in England (Britton et al. 2010). In the latter study, the main reason for isotopic niche overlap was thought to be due to high topmouth gudgeon abundance, suggesting that trophic niche overlap and competitive processes could be attributed to the situations where highly abundant topmouth gudgeon populations have been able to develop (Jackson et al. 2014).

Divergence between the niches of topmouth gudgeon and the Caucasian dwarf goby could partly be due to trophic position, which was generally lower in topmouth gudgeon. In mesocosm experiments where topmouth gudgeon was in sympatry with other species, Tran et al. (2015) found that trophic niche sizes of topmouth gudgeon were reduced compared with their allopatric treatment, suggesting greater diet specialization. This outcome was also apparent in the present study, though at an earlier stage of the invasion, with topmouth gudgeon found to have a lower trophic position than the co-occurring native Caucasian dwarf goby. Although this finding challenges the paradigm of fish invasion ecology, which suggests that an adverse impact often develops through increased interspecific competition for food resources between invasive and sympatric native fishes (Gozlan et al. 2010, Cucherousset et al. 2012), it is well recognised that topmouth gudgeon is able to shift its diet in response to changed environmental conditions (Rolla et al. 2020). In the present case, the preference for vegetation could be a result of exploiting underutilised resources (in this case submerged macrophytes, Fig. 3) and this suggests that the invaders tend to use more specialized diets at a population level, with this enabling their coexistence with native fishes in small systems where resources could otherwise have been limiting (Chesson 2000, Kylafis & Loreau 2011). This result could explain the high invasion success of the species, as well as their wide ecological tolerance (Britton et al. 2007) and generalized opportunistic feeding behaviour (Xie et al. 2000, Yalçın-Özdilek et al. 2012) reflecting an adaptive evolutionary response to harsh conditions (Ding et al. 2019). The same might be also true for the Caucasian dwarf goby that it is invasive in northern Asia, with the diet of invading populations characterized by a greater variety of prey (Didenko et al. 2020). Thus, our results from Lake Manyas may indicate that the Caucasian dwarf goby is a robust and adaptable competitor.

These results were contrary to predictions that topmouth gudgeon would have relatively large niches with high overlap with native species (Jackson & Britton 2013). Indeed, the observed difference for the isotopic niches of both species suggest the Caucasian dwarf goby express greater trophic plasticity and less intraspecific competition than topmouth gudgeon, which contradicts the findings in some other studies on SIA showing topmouth gudgeon niche can overlap with that of other cyprinid species (i.e. *C. carpio*, *R. rutilus* and *S. erythropthalmus*, *Alburnus alburnus*, Britton et al. 2010, Jackson & Britton 2013, Balzani et al. 2020). In both species examined in the present study, although similar in their feeding preferences, a general pattern was divergence in their isotopic niches that suggests they might integrate into new fish communities via exploitation of resources that are either underexploited by other species or will initially share resources before their niches diverge. This finding implies the latter mechanism might be important as it could potentially lead to competitive displacement. However, in Lake Manyas this mechanism seems not to be the case since we found niche partitioning instead of overlap at an early stage of the introduction of non-native topmouth gudgeon. There may be some context dependency in the present study, as abundant food availability in hypereutrophic Lake Manyas might be a factor in the occupation of different trophic niches by both species, whereas other studies showing niche overlap were conducted in different ecological systems (i.e. river or pond), with outcomes potentially context dependent (Britton et al. 2010, Jackson & Britton 2013, Balzani et al. 2020). Nonetheless, our findings add to an increasing literature on how introduced and invasive freshwater fishes can trophically integrate into new communities.

In summary, given a recent increase in the spread of topmouth gudgeon, especially in its introduced range in Anatolia, it is likely that it can co-exist with native or endemic freshwater fish populations. Impacts of topmouth gudgeon appear to vary across regions and understanding its interactions with recipient species and how these can affect recipient environments is of crucial importance to mitigate its impacts. However, it should be acknowledged that isotopic analyses were performed only in one season (i.e. early winter reflecting feeding interactions in autumn). Hence, results obtained from the present study must be considered in this context when extrapolating results to other sites.

In this regard, spatio-temporal studies on trophic interactions of topmouth gudgeon (e.g. Haubrock et al. 2021), as well as prevention of further multiple introductions of the species, are recommended. This study provides important baseline information on the trophic interactions of native Caucasian dwarf goby and non-native topmouth gudgeon that can be useful for understanding their consequences in their non-native range. Both species might have a consistent pattern of niche divergence, rather than simply being strongly competitive, which could facilitate their establishment and coexistence with other species in their expanded range.

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Supplementary online material

Table S1. Overlap between *Pseudorasbora parva* and *Knipowitschia caucasica* isotopic niches as estimated according to Kernel utilization density (UD), bivariate ellipse and minimum convex polygon home ranges considering 40%, 75% and 95% of the data (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-4-2021-TOP-KARAKUS-et-al.-Tables-S1.pdf).