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RESEARCH ARTICLE

An invasive species, *Carassius gibelio*, alters the native fish community through trophic niche competition

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Abstract

Carbon and nitrogen stable isotope analyses were used to determine isotopic niche width of the invasive fish species *Carassius gibelio* to help assess the niche overlap and potential impact of this species on the native fish fauna in the Karamenderes River, northwest Turkey. *C. gibelio* had the highest niche area of the coexisting species. The greatest overlap of isotopic niche was between *C. gibelio* and *Mugil cephalus* in the river mouth. The freshwater species displayed similar patterns when taking into consideration their relative abundance and isotopic overlap. While *C. gibelio* is likely to outcompete some species at some localities, the species was found co-occurring with others by maximum tolerable overlap degree and apparently utilised vacant niche space at some stations. Overall our results indicate that *C. gibelio* has extensive niche overlap with the native fish species making it a strong competitor, and because of its high abundance and high niche width this invasive species represents a serious threat to the native fish fauna, particularly in the river mouth.

Keywords Feeding ecology · Fish · Stable isotopes · Invasive

Introduction

Niche width of a species is affected by several abiotic and biotic factors such as resource density and diversity, population density, competitors and predators (Fox 1981; Bearhop et al. 2004; Olsson et al. 2009). The relation between niche widths and abundance of species was formalized by early ecologists as a spatial model of the niche concept (Hutchinson 1957; Levins 1968; MacArthur 1968). Although a negative correlation between species abundance and niche width of a species in a community has been discussed by some authors (Seagle and Mccracken 1986), the general consensus is for a positive correlation between the abundance and the niche width of species which is explained by an increase in the variety of resources consumed and increased tolerance to environmental conditions (Rocha et al. 2018). Successful invaders tend to have wider niches with high abundance and higher plasticity in resource use than non-invasive species (Correia 2002), thus increasing their competitive capabilities (Blossey and Nötzold 1995; Tilman 1999). There are several hypotheses about the wide niche area of a species. For example; expansion of niche width has been explained as a result of decreased interspecific competition in order to maintain energy requirements (Robinson and Wilson 1994; Svanbäck and Persson 2004). As a superior competitor, an invasive species can compete for particular resources used by native species and cause competitive exclusion of that native species (Britton et al. 2018). On the other hand, co-existence of an invasive species with other species might be explained by availability of sufficient resources for all species and resource partitioning. In that respect, the degree of virtual and actual niche width of species (Colwell and Futuyma 1971), The maximum tolerable overlap among species in a community (Pianka 1974), is a useful tool to understand competition and the potential impact of an invasive species. Successful invaders may also occupy previously vacant niche space (Karlson et al. 2015). Therefore, the abundance of invasive fish species and degree of niche overlap with the native populations is a good indicator of possible impacts

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on a fish community. The impact of an invasive species with the abundance and overlap degree were documented recently for some fish species (Sakai et al. 2001; Ayala et al. 2007; Carey and Wahl 2010). However, revealing the quantitative ecological impacts of invasive species is challenging due to the complexity of ecological interactions (Miranda and Perissinotto 2012), and there are still gaps in the empirical examples of the impact of an invasive species in terms of community dynamics.

The Gibel carp, *Carasius gibelio* (Bloch 1782), with its rapid dispersion and high establishment success in both lentic and lotic inland waters is considered a nuisance species in Turkey and Europe (Özcan 2007; Özuluğ et al. 2004). The community-based impact of this species has only been reported to a limited extent (Crivelli 1995; Gaygusuz et al. 2007; Specziár and Rezsu 2009; Tarkan et al. 2012; Yalçın Özdilek and Jones 2014). Therefore studies of the spatio-temporal variation of niche width together with the niche overlap with native species along a river will improve understanding of community dynamics and potential impact for this invasive species.

Stable isotope analysis (SIA) offers an effective tool for understanding trophic niche widths of fish (Layman et al. 2007b; Schmidt et al. 2007; Syväranta and Jones 2008; Fink et al. 2012; Syväranta et al. 2013), the dietary overlap of species in a fish guild (DeNiro and Epstein 1978; Bootsma et al. 1996) and also the impact of invasive species (Vander Zanden et al. 1999; Simon et al. 2004; Yuille et al. 2015; Britton et al. 2018). We therefore used trophic (isotopic) niche width to understand the impact of invasive *C. gibelio* and the extent of dietary overlap with native species in the Karamenderes River in northwest Turkey. To explain the impact of this invasive species we tested the hypotheses that invasive *C. gibelio* have wider isotopic niche than co-existing species. *C. gibelio* may outcompete some co-existing species or may be found together by maximum tolerable overlap degree of co-existing species. In addition, invasive *C. gibelio* may occupy vacant niche space by having minor dietary overlap with co-existing species.

Materials and methods

Study area and sampling

The Karamenderes River, which rises in the Ağı and Kaz Mountains and flows into the Çanakkale strait near the ancient city of Troy, is located in northwest Turkey (Fig. 1). The river is about 110 km long with discharge from 60 to 70 m^3 to 1530 m^3 per second throughout the year and is one of the biggest rivers in the Biga Peninsula (Sarı et al. 1999; Baba et al. 2007). The river flow is regulated by two reservoirs at Bayramiç and Pınarbaşı. The first record of invasive *C. gibelio* from this river was in a 2007 survey at Pınarbaşı station (Yalçın Özdilek 2008) after field studies performed in the Biga Peninsula in 2000 and 2001 (Sarı et al. 2006). The Karamenderes river has regional endemic species such as *Salmo* cf. *coruhensis, Squalius cii* (Richardson, 1857), *Alburnus cf attalus, Barbus oligolepis* Battalgil, 1941, *Cobitis fahirae* Erk'akan, Atalay-Ekmekçi-Nalbant, 1998. *Cyprinus carpio* has been introduced to reservoirs by aquaculture activities. Another introduced species *Gambusia holbrooki*

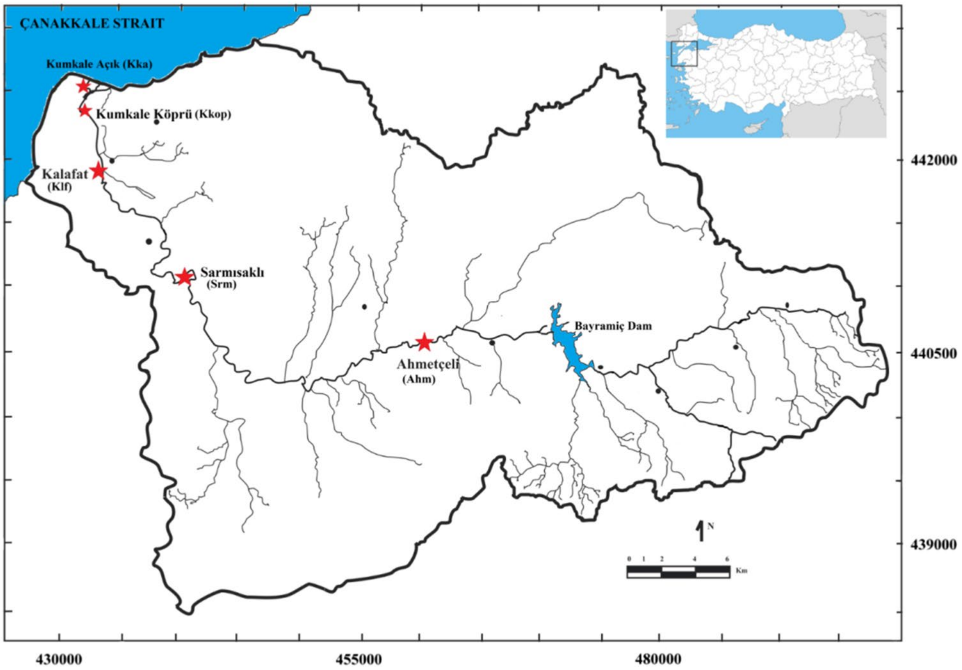

Fig. 1 The study area showing the Karamenderes River and the sampling stations (Changed from Partal and Yalçın Özdilek 2017)

Girard, 1859 had not been recorded from this river before this field study. *Gobio kovatschevi* Chichkoff, 1937 is also a regional endemic and is listed by the IUCN (International Union of Conservation of Nature) as vulnerable (Freyhof and Kottelat 2008). *Anguilla anguilla* (L., 1758) has a wide distribution, but the population of this species is decreasing and it is listed by the IUCN as critically endangered (Jacoby and Gollock 2014).

Materials for the study were collected at five locations, Ahmetçeli (Ahm), Sarmısaklı (Srm), Kalafat (Klf), Kumkale Köprü (Kkop), Kumkale açık (Kka), from upstream to downstream along the river in Summer 2012, Fall 2012, and Spring 2013 (Fig. 1). Along the river each station has different characteristics such as depth (30 cm to 5 m) and width (5–30 m). Therefore, the fish sampling was performed using backpack electrofishing (SAMUS 725G) accompanied by cast net (10–16 mm), gill net (18–45 mm), and fyke net to cover all habitat types. The water temperature, (T, °C), dissolved oxygen (DO, mg L^{-1}) and electrical conductivity (C, µS cm^{-1}) were measured by WTW® 340i multimeter in the field. The relative abundance (%N) of each species was calculated as numerical percentage of all specimens collected (Table 1). The sum of relative abundances of all species was assumed to be one hundred for each sampling station. Fork length of each *C. gibelio* individual was recorded and dorsal muscle tissue samples of all fish specimens were taken for stable isotope analysis (SIA).

Stable isotope analyses

For isotopic analysis, muscle samples of all fish specimens were dried at 60 °C for 24 h and homogenized with a microdismembrator-U (2 min at 1500 rpm) into a fine powder. Stable isotope analyses were conducted using a FlashEA 1112 elemental analyser (Thermo Fisher Scientific Corporation, Waltham, MA, U.S.A.) coupled to a Thermo Finnigan DELTA^{plus} at the University of Jyväskylä, Finland. Prior to analysis, 0.500–0.600 mg of homogenized powder from each sample was weighed into tin capsules. Standard delta notations (δ^{13}C and δ^{15}N) were used for stable carbon and nitrogen isotope ratios relative to the international standards for carbon (Vienna PeeDee Belemnite) and nitrogen (atmospheric nitrogen). Pike (*Esox lucius* L.) white muscle tissue with known isotopic composition was used as an internal working standard inserted in each run after every five samples. Standard deviation of the internal standards was less than 0.16‰ for δ^{13}C and 0.12‰ for δ^{15}N in each run. Lipid correction of muscle δ^{13}C values was not performed because the C:N ratios (average = 3.4, range = 3.2–3.8) indicated very low lipid content (Kiljunen et al. 2006; Post et al. 2007).

Data analyses and statistics

The isotopic niche widths of the fish species were calculated from the δ^{13}C or δ^{15}N data as total area (TA), which means the total amount of isotopic niche area occupied, and as the standard ellipse area corrected for sample size (SEAc), which is less sensitive to outliers, using the SIAR package (Stable Isotope Analysis in R; Layman et al. 2007a; Parnell et al. 2010). The overlap between ellipses was calculated using the Bayesian method (SEA.B) and polygons were drawn using the code that underlines the overlap function in the SIBER package (Jackson et al. 2011). Bayesian-based determination of standard elipse area of each species (SEA.B) was used to compare the isotopic niche metrics of species statistically in the same package in R. The mean SEAc values of all specimens in the stations with and without *C. gibelio* were compared using Student t-Test. In the assessment of the degree of niche overlap between species (overlap degree), the fish species were grouped as < 1 and > 1 units of overlap degree. The highest overlap degree of *C. gibelio* with the other species were taken as the maximum tolerable overlap degree. The α value was calculated as $\alpha = 0.05/49 = 0.001$ for multiple comparisons of SEA.B values of species pairs according to Bonferroni correction (Bland and Altman 1995). Statistics were performed using

Table 1 The mean fork length with standard deviation of invasive *C. gibelio* and some habitat characteristics of water along Karamenderes River (N, number of specimens used for SIA analysis; FL, fork length; G, gillnet; C, cast net; F, fykenet; E, electrofishing)

Season	Stations	Gear	Mean FL	±	sd	T, °C	DO, mgL^{-1}	C, µScm^{-1}
Summer 2012	Ahm	C	5.1	±	0.55	20.3	11.6	320
	Srm	F, G	7.6	±	1.8	25.6	6.6	458
	Klf	F, G, E	11.4	±	6.98	24.4	5.8	611
	Kkop	G	18.1	±	2.99	25.7	6.0	871
	KKa	G, F	21.4	±	3.17	25.0	7.2	6730
Fall 2012	Ahm	E	6.3	±	0.5	14.5	8.4	640
	Klf	E	9.9	±	1.74	22.4	8.6	648
	KKop	E, G	7.2	±	1.61	17.7	8.2	647
	KKa	G	17.1	±	3.18	14.0	7.8	1019
Spring 2013	Klf	E	19.0	±	3.86	21.1	8.7	502
	Kkop	E, G	24.2	±	3.86	21.7	7.4	610

R, version 2.1.3 (Jackson et al. 2011) and Microsoft Excel version 2010.

Results

A total of 106 individuals of the invasive *C. gibelio* together with individuals of other species were caught with various nets along the Karamenderes River. *C. gibelio* were caught from all the stations below the Bayramiç reservoir dam along the river. The mean length of *C. gibelio* with the standard deviation and some habitat characteristics for each station are given in Table 1. While small specimens were caught at the upper stations, larger specimens were caught from the river mouth in all three seasons. In the river mouth with the low temperature and high salinity, smaller specimens were found in fall than in the other seasons (Table 1). The relative abundances of *C. gibelio* and of the other species are given Table 2 as N%. *C. gibelio* had highest relative abundance in the river mouth stations in Summer 2012 (Table 2).

The other fish species were categorised into three groups: (1) native freshwater fish species, which were *(A) anguilla, S. cii, (B) oligolepis, (A) cf. attalus, G. kovatschevi, C. fahirae, Rhodeus amarus* (Bloch, 1782); (2) introduced species, which were *C.carpio* and *G. holbrooki;* and (3) marine-freshwater transitional fish species, which were *L. aurata* (Risso, 1810), *Liza ramada* (Risso, 1827), *Chelon saliens* (Risso, 1810), *C. labrossus* (Risso, 1827), *Mugil cephalus* L., 1758, and *Platichthys flesus* (L., 1758) (Table 2). While *C. gibelio* were collected from all stations below the Bayramiç reservoir in summer, they were not sampled at the Srm station in fall and were collected only from the two lower stations, Klf and KKop in spring. *C. gibelio* shared the last two stations KKop and KKa with transitional fish species such as Mugilidae family members and *P. flesus*. Specimens of *S. cii, (B) oligolepis, R. amarus* together with *(C) gibelio* were caught only from Klf and KKop stations in all three seasons (Table 2). *Sparus aurata* with low abundance were recorded only from KKa station in Summer 2012 (7.3%) and Spring 2013 (1.4%). Similarly, *A. anguilla* were recorded from Srm (1.5% in Summer 2012), KKop (10% Spring 2013), KKa (3.3% in Summer 2012 and 12.2% in Spring 2013) stations.

Carassius gibelio exhibited wide variation in δ^{13}C and δ^{15}N values which encompassed the range of values of nearly all the native species (Fig. 2). Total isotopic niche area (TA) of *C. gibelio* varied from 2.2 to 25.7‰ and exceeded that of all the other species. The highest recorded value of TA was for *C. gibelio* in spring at the KKop station, when there were no mugilids at that station. In general, the TA of *C. gibelio* increased downstream, the downstream KKa site having the highest TA (Table 3).

The indigenous freshwater fish species shared similar isotopic niche area with the three most freshwater tolerant transition fish species (Fig. 3). Interestingly, *C. gibelio* appears to occupy a similar isotopic niche area as nearly all the other freshwater and transitional fish species. However, *C. gibelio* occupied a wider isotopic overall niche area than the others, exhibited higher plasticity in isotopic niche width, and occupied a particular isotopic area which was about -26‰ to -27‰ and about 14‰ to 16‰ for δ^{13}C and δ^{15}N values, respectively.

Carassius gibelio had higher values of standard ellipse area than the native fish species except for Mugilidae family members. We compared two ellipses for significant differences in SEA.B to test whether *C. gibelio* isotopic niche area differed from that of other fish groups (Table 3).The SEA.B values for *C. gibelio* showed a much larger area than the other species particularly at the river mouth stations and particularly for native freshwater fish species, but also for other introduced species (Table 3). However, the SEA.B value of *C. gibelio* was not significantly larger than that of the mugilids ($p > 0.05$).

The corrected mean standard ellipse areas (SEAc) of all specimens for the stations with and without *C. gibelio* were 25.1 ± 14.6 and 10.8 ± 5.6 respectively, and there was a significant difference between these mean values ($t = 2.74$; $p < 0.05$). However, at the level of individual species, although SEAc values of *S. cii* (1.7 times) and *B. oligolepis* (1.5 times) were higher in the absence of *C. gibelio*, there were no significant differences between SEAc values of these native fish species, which are the dominant freshwater fish in the Karamenderes River, in the presence and absence of *C. gibelio* ($p > 0.05$).

The niche overlap degrees between species and their significance varied according to season and station (Table 3; Fig. 3). The species which had < 1 overlap degrees any time with *C. gibelio* were *P. flesus, G. holbrooki*, and *C. fahirae. B. oligolepis, G. kovatschevi* and *L. ramada* followed having < 1 overlap degrees with *C. gibelio* on more than 75% of co-occurrences of these species. About 50–60% of co-occurrence of the species of *S. cii, A. cf. attalus, R. amarus, C. carpio, L. aurata* and *M. cephalus* were < 1 overlap degrees with *C. gibelio*. No overlap was observed with *C. labrossus*. Moreover, there were no, or only very low, overlap degrees between *C. gibelio* and other species at KKop and Ahm stations in Summer 2012 and Fall 2012 seasons, respectively (Table 3).

The greatest extent of isotopic niche overlap was between *C. gibelio* and *M. cephalus* at the Kka station in summer and the Kkop station in fall. Despite the low abundance of *M. cephalus*, SEA.B of *C. gibelio* was not larger than *M. cephalus* at these sites ($p > 0.05$; Fig. 4). In addition, there were high overlaps with *L. ramada* at the Kac station in fall and with *B. oligolepis* at the Sar station in summer (Fig. 4).

Table 2 The SEAc and TA of fish species in three seasons along the Karamenderes River (N%: Percentage of abundance of species, N: number of specimens used in analysis)

Station	Species	Summer 2012				Fall 2012				Spring 2013			
		N%	N	SEAc	TA	N%	N	SEAc	TA	N%	N	SEAc	TA
Ahm	*A. cf atalus*	9.1	6	1.3	1.4	1.4				–	7	1.7	2.0
	B. oligolepis	15.2	10	2.5	4.1	9.2	9	7.7	11.2	3.4	7	3.8	4.5
	C. carpio	6.1	4	0.4	0.2	0.7				–			
	C. fahirae	4.6	6	2.4	2.5	29.8	10	1.3	2.2	5.1	7	1.3	1.3
	C. gibelio	18.2	10	4.7	7.3	14.9	10	2.1	3.0	–			
	G. kovatschevi	13.6	6	2.9	3.1	13.5	10	5.8	8.1	35.7	7	1.7	2.0
	R. amarus	3.0				1.4				1.7	2		
	S. cii	30.3	9	2.7	4.3	29.1	10	1.8	3.4	54.0	16	2.8	6.6
Srm	*A. cf attalus*	–				1.4	6	0.5	0.5	5.5	1		
	B. oligolepis	11.9	9	6.8	11.7	12.7	9	5.2	7.3	12.7	7	3.5	4.3
	C. fahirae	3.7	5	0.5	0.5	1.6	7	0.8	1.0	16.4	2		
	C. gibelio	7.4	10	3.5	6.8	0.2				1.8	1		
	G. kovatschevi	14.8	10	3.2	5.2	14.3	10	3.2	5.0	–			
	G. holbrooki	8.2	–			–				–			
	R. amarus	17.0	–			34.4	10	4.1	7.6	7.3			
	S. cii	35.6	10	3.3	5.4	35.3	10	5.2	10.4	56.4	26	3.1	11.3
Klf	*A. cf attalus*	5.0	6	0.3	0.4	14.0	10	2.1	3.5	8.1			
	B. oligolepis	26.1	9	1.6	3.3	3.2	7	1.5	1.9	26.4	18	1.7	4.8
	C. carpio	3.4	4	9.7	8.0	0.5				–			
	C. gibelio	10.1	6	6.0	7.7	3.2	7	12.0	15.1	9.2	8	5.0	6.7
	G. kovatschevi	0.8				2.3	5	1.0	0.7	–			
	G. holbrooki	3.4	4	0.1	0.1	–				–			
	R. amarus	8.4	8	0.8	1.3	57.2	10	4.3	8.2	17.2	12	2.4	4.1
	S. cii	41.2	10	1.2	2.6	19.8	11	1.1	1.7	39.1	10	1.6	2.8
KKop	*A. cf attalus*	–				7.0	10	1.8	2.6	7.0	16	0.3	0.3
	B. oligolepis	13.2	9	0.6	0.8	3.0	6	0.8	0.9	10.0	7	1.9	1.5
	C. fahirae	–				–				1.2			
	C. gibelio	16.7	6	2.3	2.2	6.0	12	9.6	16.6	16.3	6	10.1	25.7
	L. aurata	0.9				12.5				1.2	1		
	L. ramada	6.1	5	8.8	5.9	–	7	5.6	7.4	2.3	1		
	M. cephalus	12.3	5	15.0	10.7	2.5	7	7.0	7.6	3.5	–		
	P. flesus	13.2	10	1.1	2.0	–				–			
	R. amarus	–				52.0	10	1.0	1.7	–			
	S. cii	37.7				17.0	5	2.7	2.1	47.7	5	4.3	4.7
KKa	*A. cf attalus*	–				1.0				–			
	B. oligolepis	–				1.0				–			
	C. gibelio	60.9	21	10.9	13.8	11.5	10	9.0	14.7	4.1			
	C. labrosus	–				14.6	4	2.9	1.8	–			
	M. cephalus	13.3	4	34.7	18.5	16.7	7	14.8	7.0	13.5			
	L. aurata	2.7				1.0	4	12.0	14.6	10.8	9	4.6	7.2
	L. ramada	8.0	7	4.9	15.2	47.9	6	14.5	16.6	8.1			
	C. saliens	–				–				14.9	11	3.2	6.1
	P. flesus	4.6	3			1.0				1.4			
	S. cii	–				5.2	6	0.9	0.7	–			

At these stations the SEA.B value of *C. gibelio* was also statistically lower than those of these other species (Table 3). However, these species were more abundant than *C. gibelio* at those stations.

The relation between abundance and isotopic overlap of particularly freshwater fish species indicated that the species represented similar patterns rather than station (Fig. 4b). For instance, *S. cii* and *R. amarus* were more abundant and had

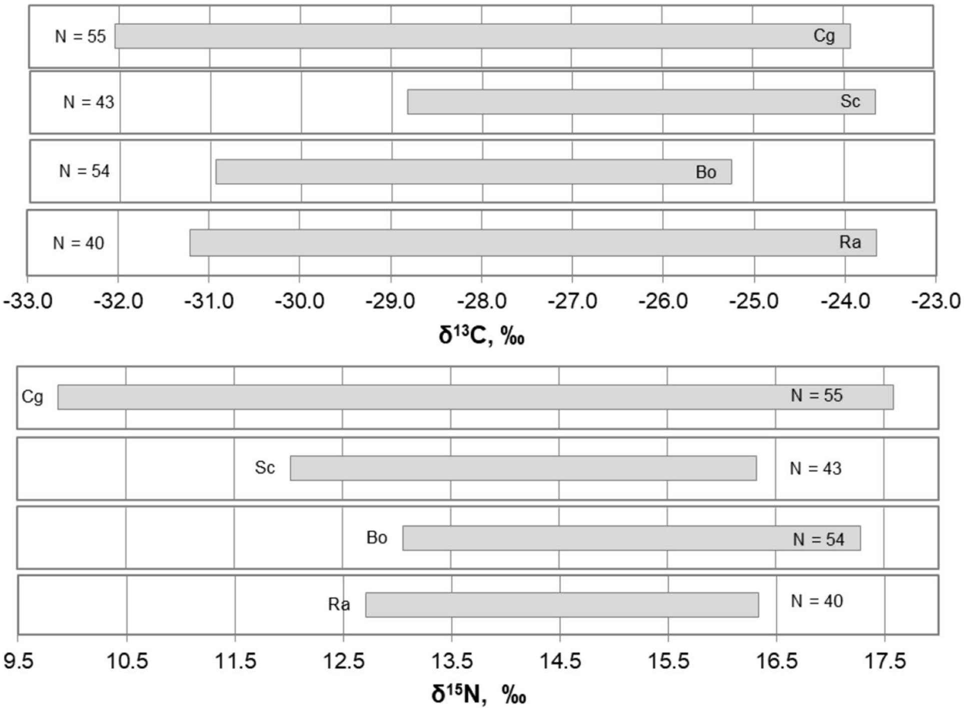

Fig. 2 The range of δ^{13}C and δ^{15}N values of four species collected from Klf and Kkop for three seasons combined (Cg: *C. gibelio*, Sc: *S. cii*, Bo: *B. oligolepis*, Ra: *R. amarus)*

high overlap degree at various stations even under the condition of higher isotopic niche area of *C. gibelio*. These species are freshwater species which had mostly smaller isotopic niche areas than that of *C. gibelio* and the extent of overlap at different stations related to their abundance relative to *C. gibelio*.

Discussion

The isotopic niche concept, which is widely used by ecologists, is a useful tool for indicating the potential impact of invasive species. In a river ecosystem, the dynamics of the fish community is flexible and environmental dependent. Even though the possible consequences of invasive fish introductions to natural ecosystems is well known, the possible effects of invasive species on dynamic stream ecosystems are poorly understood. This study presents some explanatory arguments on the possible impacts of invasive species on native fish species in a dynamic lotic system. The most important findings of this study are that *C. gibelio* has a large niche width and high niche overlap with native fish species. The hypotheses that successful invaders have a large niche width (Elton 1958; Shea and Chesson 2002) is supported by our results. In addition, this invasive species occupies vacant niche space particularly in unfavourable environmental conditions for freshwater fish.

The isotopic niche width and the isotopic niche overlap of coexisting species in the Karamenderes river showed spatial and temporal variation. It is known that interspecific competition is a major factor determining the trophic niche width of coexisting species (MacArthur 1972; Pianka 1974; Cody 1974). According to optimal foraging theory, niche width will increase as the availability of foraging resources decreases (Mac Arthur and Pianka 1966, 2011). Therefore, high niche width with the lower overlap of *C. gibelio* might be explained by a decrease in the optimal prey of *C. gibelio*. These limited resource conditions promote the consumption of a wide range of suboptimal prey types which are shared by all freshwater fish species particularly at the river mouth stations (Klf, Kka and Kkop) in fall and spring, where the maximum tolerable overlap of *C. gibelio* was 2.33, 0.16, 1.63, 0.35, 2.77 for *S. cii, B. oligolepis, A. cf. attalus, G. kovatschevi* and *R. amarus*, respectively. We suggest that *C. gibelio* has a greater advantage in habitat use than the other freshwater fish species, particularly less abundant species like *C. fahirae* and *G. kovatschevi*, and the fact that these rare species were not found from some stations may reflect competitive exclusion. The importance of impact by *C. gibelio* is clear when taking into consideration the vulnerability of *G. kovatschevi*.

The total niche area of fish communities generally increased from upstream to the river mouth except in spring. The fluctuations in the total niche area in that season might be explained by low abundance of *C. gibelio* at the Srm (1.8%) and KKa (4.1%) stations. The dominance of transitional fish species in that season suggests that high salinity (7.44 mS cm^{-1}) might have limited the abundance of *C. gibelio* in the river mouth in Spring 2013. On the other hand, *C. gibelio* appeared to occupy high salinity (6730 µS cm^{-1})

Table 3 The significant values of statistical test results from comparisons of *C. gibelio* SEA.B with the other fish species and the overlap degrees of each species with *C. gibelio* are indicated in parentheses

Season	Station	Native freshwater fish species						Introduced species		Transition fish species				
		Sc	*Bo*	*Cf*	*Acfa*	*Gk*	*Ra*	*Cc*	*Gh*	*Lr*	*La*	*Mc*	*Cl*	*Pf*
Summer - 2012	**Ahm**	0.07 (0.97)	0.05 (1.2)	0.07 (0.18)	0.03 (0.41)	0.18 (0.30)		0.05 (0.24)						
	Sar	0.42 (2.14)	0.86 (3.03)	0.09 (0.07)		0.40 (1.91)								
	Klf	0.01 (0.69)	0.05 (0.29)		0.01 (0.38)		0.02 (0.46)	0.80 (1.60)	0.03 (<0.01)					
	Kkop		0.10 (0.03)							0.93 (0.00)		0.54 (0.00)		0.38 (<0.01)
	Kka									0.71 (0.00)	0.89 (1.21)	1.00 (4.93)		
Fall - 2012	**Ahm**	0.45 (<0.01)	0.99 (0.00)	0.32 (0.00)		0.98 (<0.01)								
	Klf	**<0.001** (0.68)	**<0.001** (0.16)		**<0.001** (1.51)	0.01 (0.35)	0.05 (2.77)							
	Kkop	0.03 (2.33)	**<0.001** (0.63)		**<0.001** (1.63)		**<0.001** (0.37)			0.13 (0.86)		0.28 (3.91)		
	Kka	0.01 (<0.01)								0.78 (3.07)	0.69 (<0.01)	0.66 (<0.01)	0.06 (1.37)	
Spring - 2013	**Klf**	0.05 (1.31)	0.02 (0.29)				0.15 (1.58)							
	Kkop	0.04 (1.91)	0.01 (0.16)		**<0.001** (0.21)									

Sc, S. cii; Bo, B.oligolepis; Acfa, A. cf. attalus; Cc, C. carpio; Gk, G. kovatschevi; Cf, C. fahirae; Ra, R. amarus; Gh, G. holbrooki; Lr, L. ramada; La, L. aurata; Mc, M. cephalus; Cl, C. labrossus; Pf, P. flesus

environmental conditions which other freshwater fish species could not survive at KKa station in Summer 2012. As explained by Hubbell (2001), new individuals cannot enter the community, either by birth or by immigration, unless there is a vacant niche left by individuals. Environmental fluctuation at the river mouth may result in disappearance of freshwater fishes because of intolerance to salinity. Then the vacant niches might be used by *C. gibelio* and transitional fish species under high salinity conditions. The chemistry of a river has dynamic patches through time and space with more fluctuations in the lower reaches than in the headwaters (Sabater et al. 1991). The more time-dependent chemistry of the lower reaches might represent a marked advantage for survival of *C. gibelio*.

The variance in the population stable isotope values of species can be used as an indicator of feeding niche widths (Syväranta and Jones 2008). Bearhop et al. (2004) recommended using SEAc for estimating the niche width from small sample sizes (Bearhop et al. 2004; Jackson et al. 2011). However, even SEAc is still susceptible to sample size effects (Syväranta et al. 2013), and we acknowledge that our sample sizes are small. However, SEA.B, which provides the 95% CI of the ellipse, is used in SIBER when comparing the ellipses of species. Therefore, the statistical test results give unbiased comparison of isotopic niche area of *C. gibelio*. In fact, the highest TA value for *C. gibelio* actually derived from a small sample size (n = 6) in KKop in Spring 2013. Moreover, the rather close clustering of replicate individuals from each species suggests that our calculated SEAc values are unlikely to be overestimates and we are confident that the larger value for *C. gibelio* than for the other species is a true reflection that this species has a wider trophic niche than the native freshwater species.

The isotopic niche width of *C. gibelio* was relatively small compared to other fish species at Ahm and Sar stations. The small niche width at these sites might be explained by less

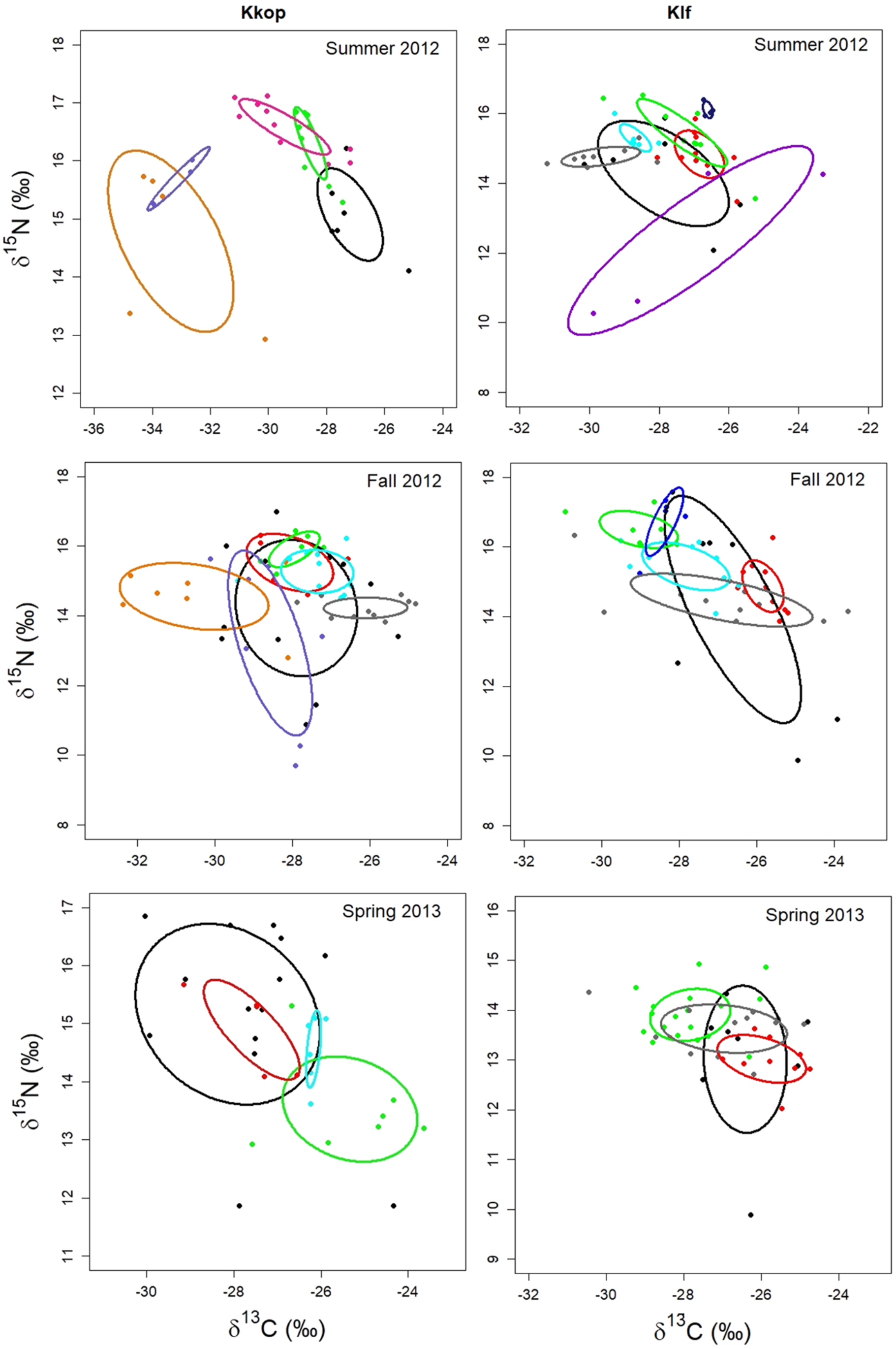

Fig. 3 Trophic niche widths and overlaps of native fish species and invasive *C. gibelio* along the Karamenderes River (black, *C. gibelio*; red, *S. cii*; green, *B. oligolepis*; cyan, *A. cf. attalus*; darkviolet, *C. carpio*; blue, *G. kovatschevi* ; grey, *R. amarus*; midnightblue, *G. holbrooki*; orange, *L. ramada*; slateblue, *M. cephalus*; pink, *P. flesus*)

diverse resources, with species adapting to the availability of the most suitable foods (Gordon and Illius 1989). On the other hand, smaller niche area with a high degree of overlap with sympatric species might be explained by Pianka's maximum tolerable overlap degrees of these species (Pianka 1974). In the Karamenderes river, the smaller and even zero degree of overlap support Pianka's hypothesis that limited resources result in smaller degree of overlap among sympatric species before competitive exclusion occurs. This would suggest that, *C. fahirae* is the most susceptible species in the presence of invasive *C. gibelio*. However, elimination of these vulnerable species because of competitive exclusion should take place slowly for the reasons given by Hubbell (2001) relating to density dependence.

There are different microhabitat characteristics along the river and depending on their adaptations different kinds of fishes respond with greater or lesser foraging niche width and abundance. In general, and despite having a small isotopic niche area than *C. gibelio, S. cii* is abundant probably due to its better adaptability to any particular microhabitat

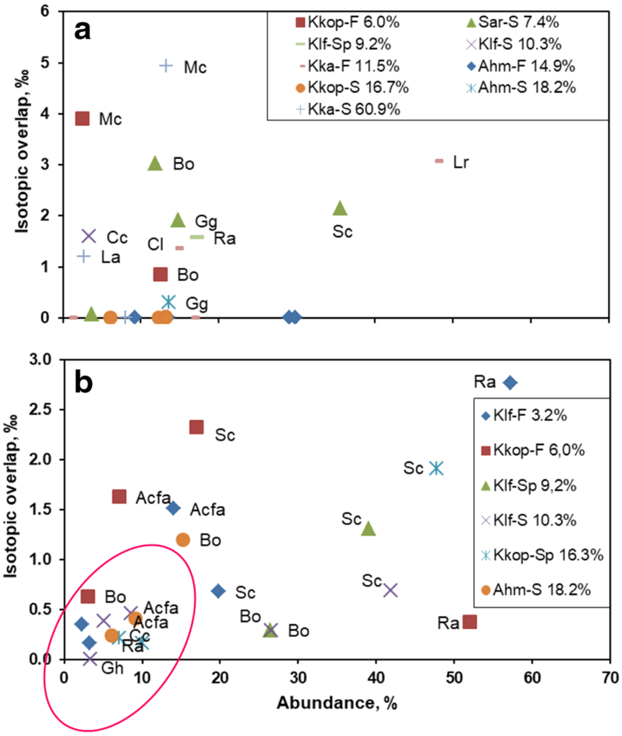

Fig. 4 The abundance and isotopic overlap relationships of fish species at different *C. gibelio* abundances. **a** These species had significantly larger SEA.B values than that of *C. gibelio*. **b** These species had significantly smaller SEA.B values than that of *C. gibelio*. The circle indicates freshwater fish species which have low abundance and low overlap with *C. gibelo*

throughout the river. *S. cii* has a generalist feeding strategy, may outcompete other species under limited resource conditions (Yalçın Özdilek 2017) and is also widespread through the Biga peninsula (Bakaç 2018). *C. gibelio* is also a generalist feeder and mostly utilises similar food items as *S. cii* (Partal and Yalçın Özdilek 2017; Yalçın Özdilek 2017). It was notable that *C. gibelio* mostly covered at least 50% of the SEAc of *S. cii* and the two species compete for some foods. *S. cii* outnumbers *C. gibelio* only at the upper station (Srm). However, *C. gibelio* did not outcompete *S. cii* at any other station or season. Therefore, the competitive pressure of *C. gibelio* on at least the dominant fish species, *S. cii*, is not as large as expected. On the other hand the river provides many suitable microhabitats for both fish species with their high spatial and temporal dietary plasticity.

C. gibelio has a wide diet compared to native species in the Karamenderes river (Partal and Yalçın Özdilek 2017), so some degree of isotopic niche overlap with other freshwater fish is expected. In this study the isotopic overlaps were assessed for fish of all length groups combined and there is a lack of data regarding possible length-based niche overlaps between fish species. However, the degree of overlap may vary according to length groups; Specziar & Rezsu (Specziár and Rezsu 2009) reported that *C. gibelio* diet overlapped only with 41–120 mm *Rutilus rutilus*. Studies of possible size-specific overlap will be required to understand fully the competitive interactions between *C. gibelio* and the native freshwater fish species. *C. carpio* is another species which is regularly introduced into the Bayramiç Dam which is a potential site for entry of *C. gibelio* to the lower sections of the river system. *C. carpio* and *G. holbrooki* are not common in the river system and the abundances of these species were very low (*Cc*, 6.1% in Ahm 3.4% in Klf and *Gh*, 3.4% in Klf). The high isotopic niche area *C. gibelio* with the low degree of overlap might be explained by high competition with these introduced species.

C. gibelio has herbivore-omnivore characteristics and the trophic position of *C. gibelio* is lower than that of the other dominant fish species such as *S. cii, B. oligolepis* and *A. cf attalus* (Yalçın Özdilek and Jones 2014). Therefore, the population of *C. gibelio* might be regulated by piscivore species such as *A. anguilla* at the river mouth stations. The large mean fork length of *C. gibelio* recorded at the KKa and Kkop stations might support this finding being a consequence of size-dependent prey selectivity by piscivore species on small *C. gibelio* species. If we can assume *C. gibelio* is a potential prey for European eel, even though no data in this study can be used to support that assumption, the decreasing trend in *A. anguilla* populations (ICES 2016) might be advantageous for *C. gibelio* particularly at the river mouth.

The introduction of *C. gibelio* is assumed to arise from escapes from reservoirs, and the Ahm station is the station for entrance of C. *gibelio* to the river system. The results indicate that *C. gibelio* has not successfully established at these first two stations but when moving to the lower part of the river they find the most suitable conditions at Klf station where they can establish by resource partitioning with the other dominant fish species such as *S. cii* and *B. oligolepis* according to the maximum tolerable niche overlaps. However, at the river mouth stations, very variable environmental parameters, such as conductivity, restricts survival of the freshwater fish species and the more tolerant *C. gibelio* can occupy the resulting vacant niche space, outcompeting or sharing the resources with the transition fish species in terms of resource partitioning.

In addition to typical advantages for successful invasion, the wide isotopic niche area and competition ability of *C. gibelio* was assessed in this study. Less than a decade from the first introduction into the river system (Yalçın Özdilek 2008) may be too soon to see the full potential impact of this species on the native river fish community in terms of any extinction of species compared to previous data (Sarı et al. 2006). However, it is clear that *C. gibelio* has an important functional role in the community dynamics, having high dominance, high niche area and some degree of niche overlap with many freshwater and transitional fish species, including new introductions. We suggest that the different microhabitat characteristics of the river system should be maintained and long-term monitoring studies are needed for the river management plan.

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References

Ayala JR, Rader RB, Belk MC, Schaalje GB (2007) Ground-truthing the impact of invasive species: spatio-temporal overlap between native least chub and introduced western mosquitofish. Biol Invas 9:857–869. https://doi.org/10.1007/s10530-006-9087-4

Baba A, Deniz O, Gülen O, Gülen O (2007) Effects of mining activities on water around the Çanakkale Plain, Turkey. In: Zaidi MK (ed) Wastewater reuse–risk assessment, decision-making and environmental security. Springer, Netherlands, pp 3–10

Bakaç İ (2018) Assessment of distribution and abundances of freshwater fish in Çanakkale, Turkey. Çanakkale Onsekiz Mart University, Çanakkale

Bearhop S, Adams CE, Waldron S et al (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012. https://doi.org/10.1111/j.0021-8790.2004.00861.x

Bland JM, Altman DG (1995) Multiple significance tests: the Bonferroni method. BMJ 310:170

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis author (s): Bernd Blossey and Rolf Notzold source. J Ecol 83:887–889

Bootsma HA, Hecky RE, Hesslein RH, Turner GF (1996) Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analysis. 77:1286–1290

Britton JR, Ruiz-Navarro A, Verreycken H, Amat-Trigo F (2018) Trophic consequences of introduced species: comparative impacts of increased interspecific versus intraspecific competitive interactions. Funct Ecol 32:486–495. https://doi.org/10.1111/1365-2435.12978

Carey MP, Wahl DH (2010) Native fish diversity alters the effects of an invasive species on food webs. Ecology 91:2965–2974. https://doi.org/10.1890/09-1213.1

Cody ML (1974) Optimization in ecology: natural selection produces optimal results unless constrained by history or by competing goals. Science 183:1156–1164. https://doi.org/10.1126/science.183.4130.1156

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567–576. https://doi.org/10.2307/1934144

Correia AM (2002) Niche breadth and trophic diversity: feeding behaviour of the red swamp cray sh (Procambarus clarkii) towards environmental availability of aquatic macroinvertebrates in a rice eld (Portugal). Acta Oecol 23:421–429

Crivelli A (1995) Are fish introductions a threat to endemic freshwater fishes in the Northern Mediterranean region? Biol Conserv 72:311–319

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

Elton CS (1958) The ecology of invasions by animals and plants, first. Chapman and Hall, London

Fink P, Reichwaldt ES, Harrod C, Rossberg AG (2012) Determining trophic niche width: an experimental test of the stable isotope approach. Oikos 121:1985–1994. https://doi.org/10.1111/j.1600-0706.2012.20185.x

Fox BJ (1981) Niche parameters and species richness. Source Ecol 62:1415–1425

Freyhof J, Kottelat M (2008) Gobio kovatschevi. In: IUCN Red List Threat. Species 2008 e.T135615A4162824. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T135615A4162824.en. Accessed 27 Apr 2018

Gaygusuz Ö, Tarkan AS, Gaygusuz ÇG (2007) Changes in the fish community of the Ömerli Reservoir (Turkey) following the introduction of non-native gibel carp *Carassius gibelio* (Bloch, 1782) and other human impacts. Aquat Invas 2:117–120. https://doi.org/10.3391/ai.2007.2.2.6

Gordon IJ, Illius AW (1989) Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383–389. https://doi.org/10.1007/BF00384318

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, New Jersey

Hutchinson GE (1957) Concluding Remarks. In: Cold Spring Harbor Symposia on Quantitative Biology. pp 415–427

ICES (2016) ICES WGEEL report 2016 report of the working group on Eels WGEEL9. ICES, Cordoba

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jacoby D, Gollock M (2014). *Anguilla anguilla*. The IUCN Red List of Threatened Species 2014:e.T60344A45833138. https://doi.org/10.2305/IUCN.UK.2014-1.RLTS.T60344A45833138.en. Accessed 08 Feb 2019

Karlson AML, Gorokhova E, Elmgren R (2015) Do deposit-feeders compete? Isotopic niche analysis of an invasion in a species-poor system. Sci Rep 5:1–8. https://doi.org/10.1038/srep09715

Kiljunen M, Grey J, Sinisalo T et al (2006) A revised model for lipid-normalizing δ13C values from aquatic organisms, with implications for isotope mixing models. J Appl Ecol 43:1213–1222. https://doi.org/10.1111/j.1365-2664.2006.01224.x

Layman CA, Arrington AD, Montana CG, Post DM (2007a) Can stable isotope ratios provide for community-wide measures of trophic structure ? 88:42–48. https://doi.org/10.1002/jae.1200

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007b) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol Lett 10:937–944. https://doi.org/10.1111/j.1461-0248.2007.01087.x

Levins R (1968) Evolution in changing environments: some theoretical explorations. Princeton University Press, New Jersey

Mac Arthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

MacArthur RH (1968) The theory of the niche. In: Lewontin RC (ed) Population biology and evolution. Syracuse University Press, Syracuse, pp 159–176

MacArthur RH (1972) Patterns in the distribution of species. In: MacArthur RH (ed) Geographycal ecology, first. Princeton University Press, New York

Miranda NAF, Perissinotto R (2012) Stable isotope evidence for dietary overlap between alien and native gastropods in coastal lakes of Northern KwaZulu-Natal, South Africa. PLoS One 7:e31897. https://doi.org/10.1371/journal.pone.0031897

Olsson K, Stenroth P, Nyström P, Graneli W (2009) Invasions and niche width: does niche width of an introduced crayfish differ from a native crayfish? Freshw Biol 54:1731–1740. https://doi.org/10.1111/j.1365-2427.2009.02221.x

Özcan G (2007) Distribution of non-indigenous fish species, Prussian carp *Carassius gibelio* (Bloch, 1782) in the Turkish freshwater systems. Pakistan J Biol Sci 10:4241–4245

Özuluğ M, Meriç N, Freyhof J (2004) The distribution of *Carassius gibelio* (Bloch, 1782) (Teleostei: Cyprinidae) in Thrace (Turkey). Zool Middle East 31:63–66. https://doi.org/10.1080/09397140.2004.10638023

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS One 5:1–5. https://doi.org/10.1371/journal.pone.0009672

Partal N, Yalçın Özdilek Ş (2017) Feeding ecology of invasive *Carassius gibelio* (Bloch, 1782) in Karamenderes Stream, Turkey. Ege J Fish Aquat Sci 34:157–167. https://doi.org/10.12714/egejfas.2017.34.2.07

Pianka ER (1974) Niche overlap and diffuse competition. Proc Nat Acad Sci USA 71:2141–2145

Pianka ER (2011) Evolutionary ecology, vol 486. Eric R. Pianka, Siskiyou County. https://doi.org/10.2307/2257971

Post DM, Layman CA, Arrington DA et al (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189. https://doi.org/10.1007/s00442-006-0630-x

Robinson BW, Wilson DS (1994) Character release and displacement in fishes: a neglected literature. Am Nat 144:596–627. https://doi.org/10.1086/285696

Rocha MP, Bini LM, Siqueira T et al (2018) Predicting occupancy and abundance by niche position, niche breadth and body size in stream organisms. Oecologia 186:205–216. https://doi.org/10.1007/s00442-017-3988-z

Sabater F, Armengol J, Sabater S (1991) Physico-Chemical disturbances associated with spatial and temporal variation in a Mediterranean river. J N Am Benthol Soc 10:2–13. https://doi.org/10.2307/1467759

Sakai AK, Allendorf FW, Holt JS et al (2001) The population biology of invasive specie source: annual review of ecology and systematics. Annu Rev Ecol Syst 32:305–332

Sarı HM, Balık S, Bilecenoğlu M, Türe G (1999) Recent changes in the fish fauna of Lake Bafa, Aegean region of Turkey. Zool Middle East 18:67–76. https://doi.org/10.1080/09397140.1999.10637783

Sarı HM, Balık S, Ustaoğlu R, İlhan A (2006) Distribution and ecology of freshwater ichthyofauna of the Biga Peninsula, North-western Anatolia, Turkey. Zool Turk J 30:35–45

Schmidt SN, Olden JD, Solomon CT, Vander Zanden MJ (2007) Quantitative approaches to the analysis of stable isotope food web data. Ecology 88:2793–2802. https://doi.org/10.1890/06-0937.1

Seagle SW, Mccracken GF (1986) Species abundance, niche position, and niche breadth for five terrestrial animal assemblages. Ecology 67:816–818

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176. https://doi.org/10.1016/s0169-5347(02)02495-3

Simon KS, Townsend CR, Biggs BJF et al (2004) Habitat-specific nitrogen dynamics in New Zealand streams containing native or invasive fish. Ecosystems 7:777–792. https://doi.org/10.1007/s10021-004-0024-z

Specziár A, Rezsu ET (2009) Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. J Fish Biol 75:247–267. https://doi.org/10.1111/j.1095-8649.2009.02283.x

Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. J Anim Ecol 73:973–982. https://doi.org/10.1111/j.0021-8790.2004.00868.x

Syväranta J, Jones RI (2008) Changes in feeding niche widths of perch and roach following biomanipulation, revealed by stable isotope analysis. Freshw Biol 53:425–434. https://doi.org/10.1111/j.1365-2427.2007.01905.x

Syväranta J, Lensu A, Marjomäki TJ et al (2013) An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data an empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche. PLoS One 8:e56094. https://doi.org/10.1371/journal.pone.0056094

Tarkan AS, Gaygusuz O, Gürsoy Gaygusuz C et al (2012) Circumstantial evidence of gibel carp, *Carassius gibelio*, reproductive competition exerted on native fish species in a mesotrophic reservoir. Fish Manag Ecol 19:167–177. https://doi.org/10.1111/j.1365-2400.2011.00839.x

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474. https://doi.org/10.2307/176540

Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467. https://doi.org/10.1038/46762

Yalçın Özdilek Ş (2017) Turkish Journal of Zoology Seasonal and ontogenetic diet shift of two sympatric cyprinid fish species from the temperate Karamenderes River, Çanakkale, Turkey. Turk J Zool 41:67–81. https://doi.org/10.3906/zoo-1603-34

Yalçın Özdilek Ş, Jones RI (2014) The diet composition and trophic position of introduced prussian Carp *Carassius gibelio* (Bloch, 1782) and native fish species in a Turkish River. Turk J Fish Aquat Sci 14:769–776. https://doi.org/10.4194/1303-2712-v14_3_19

Yalçın Özdilek Ş (2008) Karamenderes'in Doğal ve istilaci baliklari. In: Akdemir A, Demircan O, Yılmaz S et al (eds) Ezine değerleri sempozyumu. Olay Matbaası, Çanakkale, pp 129–139

Yuille MJ, Fisk AT, Stewart T, Johnson TB (2015) Evaluation of Lake Ontario salmonid niche space overlap using stable isotopes. J Great Lakes Res 41:934–940. https://doi.org/10.1016/j.jglr.2015.05.011