



Original research article

High trophic similarity between non-native common carp and gibel carp in Turkish freshwaters: Implications for management

Sadi Aksu^a, Özgür Emiroğlu^b, Paride Balzani^c, J. Robert Britton^d, Esengül Köse^e,
Irmak Kurtul^{d,f}, Sercan Başkurt^b, Oğuzcan Mol^b, Emre Çınar^b, Phillip J. Haubrock^{c,g,h},
Pinar Oztopcu-Vatan^b, Ali Serhan Tarkan^{d,i,j,*}

^a Vocational School of Health Services, Eskişehir Osmangazi University, Eskişehir, Turkey

^b Department of Biology, Faculty of Science, Eskişehir Osmangazi University, Eskişehir, Turkey

^c Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in České Budějovice, Zátěš 728/II, 389 25, Vodňany, Czech Republic

^d Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, Dorset, UK

^e Department of Environmental Protection Technologies, Eskişehir Vocational School, Eskişehir Osmangazi University, Eskişehir, Turkey

^f Marine and Inland Waters Sciences and Technology Department, Faculty of Fisheries, Ege University, İzmir, Turkey

^g Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany

^h Center for Applied Mathematics and Bioinformatics, CAMB, Gulf University for Science and Technology, Al-Abdullah, Kuwait

ⁱ Department of Basic Sciences, Faculty of Fisheries, Muğla Sıtkı Koçman University, Menteşe, Muğla, Turkey

^j Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Łódź, Łódź, Poland

ARTICLE INFO

Keywords:

Stable isotopes
Niche overlap
Cyprinus carpio
Carassius gibelio
Stocking
Invasion

ABSTRACT

Although the detrimental ecological and economic effects of introducing freshwater fish species have been extensively documented, non-native freshwater fishes continue to be introduced in large numbers globally to enhance fisheries and aquaculture. In Turkey, stocking of common carp *Cyprinus carpio* is practised to provide food security for people and job security for artisanal fishers, resulting in a country-wide distribution. These stockings, however, increase the risk of accidental introductions and have led to introductions and subsequent invasions of gibel carp *Carassius gibelio*, a globally invasive and highly detrimental fish species. Here, we assessed the growth types, body conditions and trophic interactions via bulk carbon and nitrogen stable isotope analysis of common and gibel carp in both natural and artificial water bodies in Turkey. The results indicated that common and gibel carp express similar growth types and body conditions in all waters and have similar trophic ecologies. This leads to substantial trophic niche overlaps in waters where they co-occur, with the potential for strong interspecific competition. Considering the ongoing stocking of common carp for fishery enhancement, we recommend to specifically target these stockings in waters where gibel carp has already become invasive. Our findings, indeed, suggest that common carp releases have the potential to hamper invasive gibel carp populations by increasing the competitive interactions between the two species.

1. Introduction

Freshwater fish communities are particularly vulnerable to the impacts of introduced fish species, which have a high potential to cause ecological impacts through increased competition and predation pressure, genetic introgression, and the transmission of non-native pathogens (Britton, 2023; Britton et al., 2023). Despite this, both non-native and native (usually hatchery reared) freshwater fishes are frequently introduced to enhance both recreational and commercial fisheries

around the world (Cowx, 1994) with approximately 90 million fish having been stocked into inland waters in e.g. France in 2013 (Chucherousset et al., 2021).

To increase inland fish production, some countries introduced legislation that promoted the use of non-native species (e.g. Brazil; Forneck et al., 2021; Garcia et al., 2022) through their deliberate release (e.g. Kenya; Hickley et al., 2015; Britton et al., 2023). In Turkey, the widespread stocking of the common carp *Cyprinus carpio* to enhance fishery yields in reservoirs (Vilizzi et al., 2015) is practised as a response

* Corresponding author. Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, Dorset, UK.

E-mail address: serhantarkan@gmail.com (A.S. Tarkan).

<https://doi.org/10.1016/j.aaf.2023.08.003>

Received 22 March 2023; Received in revised form 4 August 2023; Accepted 10 August 2023

2468-550X/© 2023 Shanghai Ocean University. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

to the demand of artisanal fishers for the compensation of economic losses resulting from private land encroachment due to reservoir construction (Gaygusuz et al., 2015). Although the common carp is native to several areas of Turkey (Thrace, Northern Anatolia, Western Transcaucasia and Upper Tigris & Euphrates; Memiş & Kohlmann, 2006), it has been intensively translocated since the 1960s, resulting in it attaining a widespread distribution particularly in Anatolia (Innal & Erk'anan, 2006). Indeed, the stocking of hatchery-reared age-0 common carp into numerous reservoirs for growing-on and subsequent exploitation has occurred annually since 1996, with approximately 100 million fish having been stocked between 2002 and 2019 by the Republic of Turkey's Ministry of Food, Agriculture and Livestock (BSGM, 2021). This is despite common carp being recognised as a globally invasive, high-impact species (Vilizzi et al., 2015), and risk assessments have highlighted it as being of high invasion and impact risk in Turkey (Tarkan et al., 2017; Vilizzi et al., 2021). However, its socio-economic value, long introduction history, and wide spatial distribution means that management programs do not consider common carp as either non-native or invasive (Vilizzi, 2012).

Intentional fish introductions can also result in accidental introductions of other species (Gozlan, Britton, et al., 2010), for example, when batches of fish moved between countries or river basins are contaminated with smaller fishes that are then accidentally released into new areas through 'stepping-stone' introduction events (Gozlan et al., 2010b). In Turkey, common carp stockings have resulted in accidental releases of other non-native cyprinid species, such as the trophically analogous gibel carp *Carassius gibelio* which has been able to obtain a wide distribution via this pathway (Gaygusuz et al., 2015). Gibel carp is now the most abundant invasive introduced species in Turkey, establishing populations in lentic water bodies such as reservoirs, lakes, and ponds (Tarkan, Copp, et al., 2012). This is concerning, as gibel carp can cause considerable ecological impacts in invaded freshwaters, including the significant decline of native cyprinid populations and economically viable common carp populations through reproductive interference and competition (e.g., Emiroğlu et al., 2011; Tarkan, Gaygusuz, et al., 2012). Given the potential ecological impacts that gibel carp may have on Turkish aquatic fauna and not being a demanded fish species except for local fisherman in some regions, management programmes are needed to control and contain their populations (Tarkan et al., 2021; Britton et al., 2023). However, other than fish removal-based pilot projects to control abundant populations by high fishing exploitation, there is currently no management of these non-native populations (Emiroğlu, 2019).

In freshwaters, the resident fish assemblage can provide some biotic resistance against introduced species (Alofs & Jackson, 2014). This resistance can be mediated through a higher, more natural species richness or the presence of certain (i.e., competitive or predatory) species, limiting the establishment and invasion of non-native species through biotic resistance (Henriksson et al., 2015). In Turkish reservoirs invaded by gibel carp, the presence of common carp potentially provides some competitive resistance, given the high functional similarity between these two species in terms of trophic level, habitat use, and the resulting niche overlap (Yalçın Özdişek et al., 2019). Consequently, in this work, we test the growth type, body condition, and trophic interactions of common carp and gibel carp in a series of natural and artificial water bodies in Turkey using a bulk carbon and nitrogen stable isotope analysis (SIA) approach ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). We posit that (i) sympatric common carp and gibel carp express similar growth types and body conditions in both artificial and natural water bodies, despite (ii) common and gibel carp being trophically similar and expressing a high overlap in their trophic niche when in sympatry. The results are then evaluated through comparisons between their populations in natural waters versus reservoirs, and whether fishery enhancement schemes to increase carp production can concomitantly increase the biotic resistance to gibel carp invasion.

2. Materials and methods

2.1. Study areas

Gibel carp and common carp were collected from seven water bodies in Turkey, four of which were reservoirs established in the Afyonkarahisar Province in southwestern Anatolia for irrigation purposes, with surface areas ranging from 2 to 6 km² and average maximum depths of approximately 10 m (Table S1) (Fig. 1). The other study sites were natural lakes of various sizes ranging from 5.6 to 308 km² (Table S1). Lake İznik is a large and deep lake (approximately 60 m) located in the Marmara region in north-western Anatolia, while Gala and Sığircı are shallow alluvial lakes completely covered with reeds, located in Thrace in the European part of Turkey. They have a rich fish diversity (Tarkan, Copp, et al., 2012). All these lakes have undergone ecological succession over several decades and have become meso-eutrophic. Among the sampled sites, perch *Perca fluviatilis* was the dominant piscivore, being present in Bayat, Gala, Seyitler and Sığircı, followed by European catfish *Silurus glanis*, which was present in Gala and İznik, and pikeperch *Sander lucioperca* was present in Gala and Sığircı (Table S1). In all sites, both gibel carp and common carp were present, except Bayat and Seyitler South, where only gibel carp was present.

2.2. Ethical approval for research involving animal

This study does not contain any experiments conducted on animals by any of the authors. The legal permission for collecting fish was provided by the Republic of Türkiye Ministry of Agriculture and Forestry (E-67852565-140.03.03-1800883). All care and use of animals were complied with animal welfare international/national laws, guidelines, and policies (<https://www.resmigazete.gov.tr/eskiler/2014/02/20140215-6.htm>). Some fish were obtained from the fishermen with their consent.

2.3. Sampling process and sample analysis

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 their capture, fish were transported to the laboratory on an ice water slurry. Also, samples of 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 identified to the species level, and measured (total length and weight, nearest [mm] and [g], respectively).

2.4. Stable isotope analysis

For SIA, a sample of dorsal muscle tissue was taken from the area between lateral line and dorsal fin of each individual fish sampled. White muscle tissue has lower variability in nitrogen isotopic signature compared to other tissues and does not require acidification to remove inorganic carbonates (Pinnegar and Polunin, 1999). 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 are depleted in ¹³C compared with the whole organism (Post et al., 2007), lipids were extracted from all animal tissues using a 2:1 chloroform:methanol solution. The plants and invertebrate samples were processed without any chemical treatment. SIA was 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: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. samples were analysed in duplicates and the average standard errors were 0.03‰ for $\delta^{13}\text{C}$ and 0.11‰ for $\delta^{15}\text{N}$.

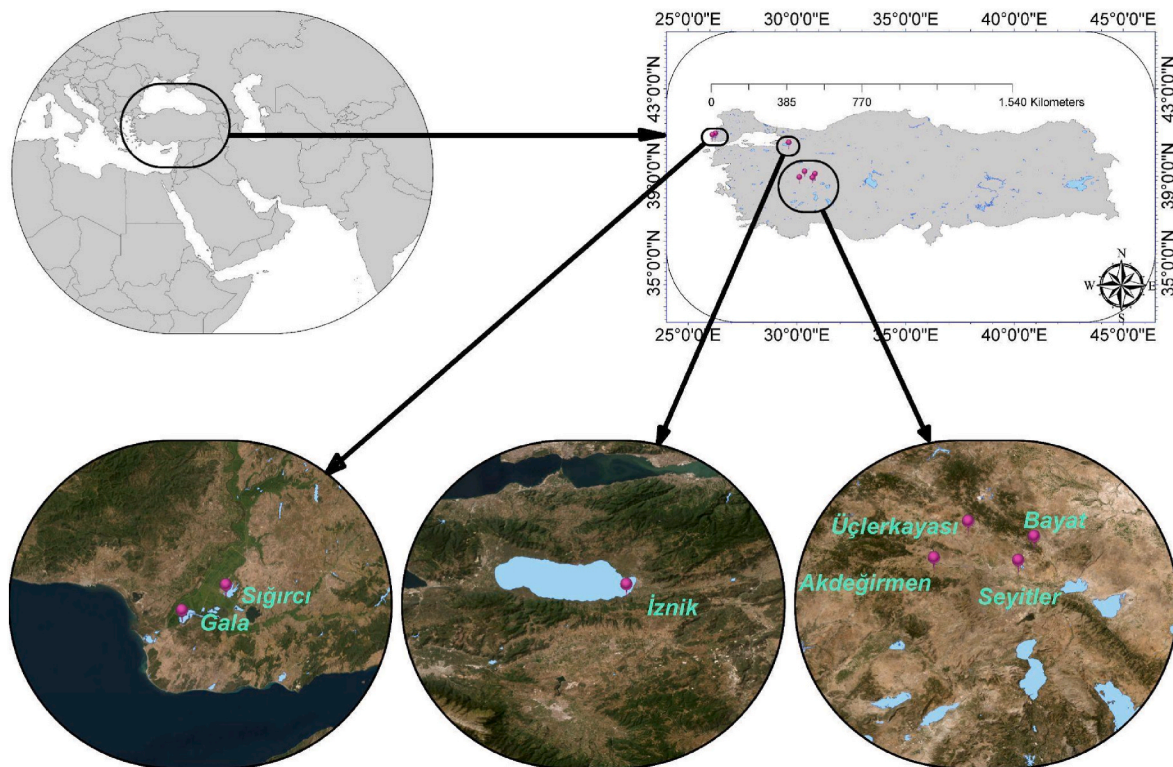


Fig. 1. The sampling sites in western Anatolia, Turkey.

2.5. Statistical analyses

To assess for species-specific differences in their respective growth, a linear model was applied at each site, where in the model, log-transformed weight was response variable and log-transformed total length, species and their interaction were predictors. All linear models, including the interaction term, were tested with type III ANOVA; when the interaction term was not significant, the model was run again without the interaction term using type II ANOVA. Growth was defined using the slope (b) of the linear regression models; if $b > 3$ then growth was hyper-allometric (fish growth is faster in weight than length), if $b < 3$ then growth was hypo-allometric (fish grow faster in length than weight), and if $b = 3.0$ then growth is isometric (Karachle & Stergiou, 2012).

Fish body condition was evaluated by Fulton's condition coefficient (KF; Le Cren, 1951) calculated as $KF = 100,000 \times W/TL^3$, where: W = total body weight [g], TL = total length [mm], and was compared within sites between the two species and within the same species among different sites using a permutational analysis of variance (PERANOVA, with Bray-Curtis dissimilarity index and 9,999 permutations), using the *adonis2* function implemented in the R package *vegan* (Oksanen et al., 2019). A linear mixed effect model, with the KF of gibel carp as response variable and carp presence (yes/no), predator presence (yes/no) and system type (natural lake/reservoir) as predictors, was built with the R package *lme4* (Bates et al., 2015) using the site as random effect, and the results were drawn using the package *sjPlot* (Lüdtke, 2023).

To describe intra-specific niche width, Layman's metrics (Layman et al., 2007) and corrected standard ellipse area (SEAc, Jackson et al., 2016) considering 40% of central data points were calculated using the R package *SIBER* (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2016). The $\delta^{15}N$ and $\delta^{13}C$ ranges (NR and CR), the mean distance to the centroid (CD), as well as the total area encompassing all individual measures (TA), are all indices of the species niche width. The mean nearest neighbour distance (MNND) and the standard deviation of the nearest neighbour distance (SDNND) relate to the distance among

individuals and indicate the degree of trophic redundancy (i.e. the inter-individual competition). SEAc is a measure of the niche width that is less affected by extreme values than TA. Additionally, the Bayesian standard ellipse area (SEAB), was calculated using the R package *SIBER* (Jackson et al., 2016).

To assess the overlap between the isotopic niches of the two species, we used three complementary approaches. First, we identified if the occupied trophic niches were significantly different using a PERMANOVA on the $\delta^{15}N$ and $\delta^{13}C$ of the two species, followed by PERANOVA as post hoc tests, with Euclidean distance and 9,999 permutations using the *adonis2* function implemented in the R package *vegan* (Oksanen et al., 2019). Then, the ratio between the overlap area and the sum of both niche areas for the 95% (maximum likelihood and Bayesian ellipses-SEAB) and 40% (SEAc) standard ellipse areas (SEA) were calculated using the R package *SIBER* (Jackson et al., 2016). Finally, the directional probability of an individual of a species to occur within the niche of the other species (considered as the 95% and 40% standard ellipse area) was estimated applying a Monte Carlo estimation (chain-length: 10,000 steps) using the R package *nicheROVER* (Swanson et al., 2015).

To check for consistent patterns in the niche width of gibel carp, we used linear mixed effect models with SEAc and SEAB of gibel carp as response variables, and carp presence (yes/no), predator presence (yes/no) and system type (natural lake/reservoir) as predictors were built with the R package *lme4* using the site as random effect. The same predictors without carp presence were used in linear models with the proportion of overlap for SEAc and SEAB, as well as the overlap probability of gibel carp into the niche of common carp for the 95% and 40% ellipses as response variables, to check for consistent patterns in the overlap between the two species' niches. Finally, to assess the similarity in diet between the two species, stable isotopes mixing models were run using the R package *simmr* (Govan et al., 2023), using no priors and using the trophic discrimination factors (TDFs) proposed by Post (2002), namely 1.0 for $\delta^{13}C$ and 3.4 for $\delta^{15}N$.

3. Results

Across the 7 sites, 120 specimens were sampled (Akdeg: 10 *C. carpio* and 10 *C. gibelio*; Bayat: 6 *C. gibelio*; Gala: 10 *C. carpio* and 10 *C. gibelio*; Iznik: 4 *C. carpio* and 10 *C. gibelio*; Seyitler North: 4 *C. carpio* and 4 *C. gibelio*; Seyitler South: 10 *C. gibelio*; Sigirci: 13 *C. carpio* and 11 *C. gibelio*; Uclerkayasi: 8 *C. carpio* and 10 *C. gibelio*). The weight to total length relationships were similar between the two species in all sites, as indicated by the non-significant interaction terms (Table S2). Moreover, in some sites (Akdeg, Gala, and Uclerkayasi), the species had a significant effect (Table S2), with gibel carp showing a higher weight than common carp for the same value of total length (Fig. 2). The growth type was hyper-allometric for both species in most sites (Table S3).

The Fulton index of gibel carp did not vary among sites (pseudoF_{7,63} = 1.85, $P = 0.09$), but did for common carp (pseudoF_{5,43} = 2.76, $P < 0.05$). In almost all sites, KF was higher in gibel carp than common carp (Akdeg: pseudoF_{1,18} = 4.12, $P < 0.05$; Gala: pseudoF_{1,18} = 22.04, $P < 0.001$; Iznik: pseudoF_{1,12} = 8.81, $P < 0.01$; Uclerkayasi: pseudoF_{1,16} = 10.37, $P < 0.01$), except in Sigirci (pseudoF_{1,22} = 1.42, $P = 0.24$) and Seyitler North (pseudoF_{1,6} = 7.85, $P = 0.06$; Fig. 3). The linear mixed effect model indicated no significant effect of any of the selected predictors (Fig. S1).

The stable isotope metrics indicated high variability in the isotopic niche width across the sites (Fig. 4), with only a few consistent patterns detected: in reservoirs gibel carp had a greater NR than common carp, and in natural lakes gibel carp had a smaller CD compared with common carp (Table 1). The isotopic niches of gibel carp and common carp were not statistically differentiated in any sites except for Gala and Uclerkayasi (Table 2). In the sites where the niches were segregated, they were differentiated for both stable isotopes values (Gala: pseudoF_{1,18} = 26.29, $P < 0.001$ for $\delta^{13}\text{C}$ and pseudoF_{1,18} = 12.14, $P < 0.01$ for $\delta^{15}\text{N}$; Uclerkayasi: pseudoF_{1,16} = 18.68, $P < 0.001$ for $\delta^{13}\text{C}$ and pseudoF_{1,16} = 5.15, $P < 0.05$ for $\delta^{15}\text{N}$). Similarly, there was high variability in the degree of isotopic niche overlap between the sites (Table 2). No significant relationships were found with any of the selected predictors for both the niche width of gibel carp and the niches' overlap between the two species (Fig. S2).

The stable isotope mixing models showed a high similarity in the diet composition of common carp and gibel carp, with a few sites indicating asymmetries (Fig. 5). In Iznik, gibel carp consumed less zooplankton compared to common carp; in Gala, the common carp was more generalist, while gibel carp was more specialised on macrophytes and phytoplankton; in Uclerkayasi, gibel carp consumed less algae and more zooplankton compared to common carp. No clear differences in the diet

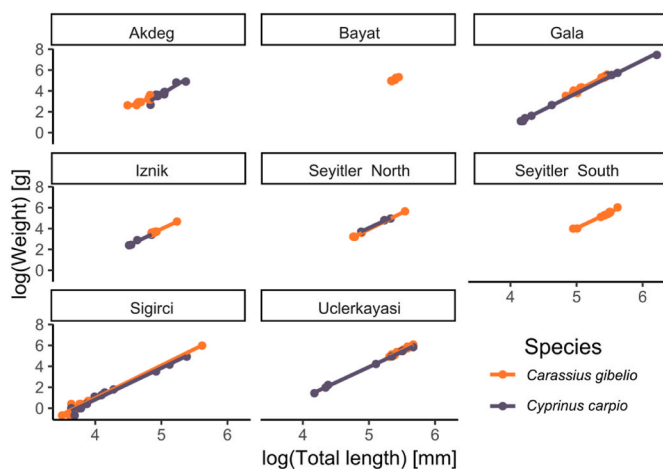


Fig. 2. Regression lines of the log-transformed weight (W) in function of the log-transformed total length (TL) of *Carassius gibelio* and *Cyprinus carpio* in the different sampling sites.

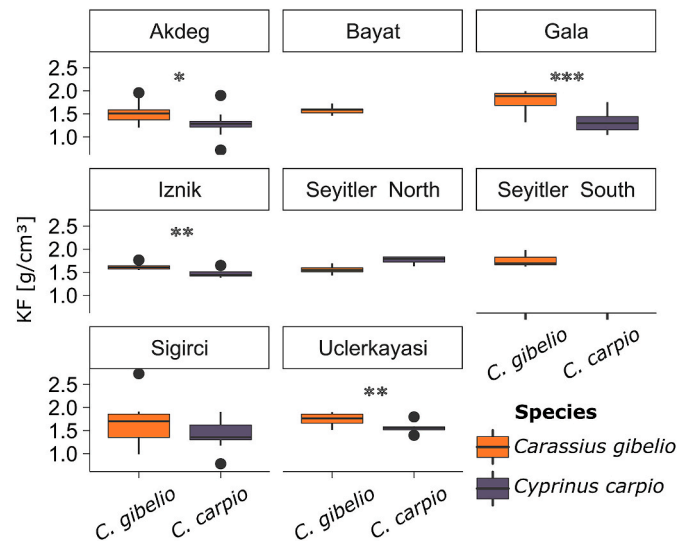


Fig. 3. Fulton condition factor (KF) of *Carassius gibelio* and *Cyprinus carpio* in the different sampling sites. Asterisks indicate the statistical significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

of gibel carp between the sites with common carp and those without were found.

4. Discussion

Interactions among species are complex and, in many cases, unpredictable (Britton et al., 2018). Understanding how interactions can affect the competitiveness or impact of non-native species in freshwater ecosystems remains a crucial subject in invasion biology (Haubrock et al., 2020; Bissattini et al., 2021; Balzani & Haubrock, 2022). Overall, our results revealed that gibel carp had similar weight gain but higher body condition than common carp, although common carp usually grow faster and reach larger sizes than gibel carp (Vilizzi, 2012). Moreover, we found similar features of the trophic niche and diet composition between the two species, regardless of the presence of common carp or predators or the ecosystem type.

The niche width of gibel carp was highly variable, probably due to differences in resources availability in the study sites. Some niche metrics consistently showed that gibel carp had a greater reliance on food sources from multiple trophic levels than common carp in reservoirs, suggesting a higher adaptability to altered habitats and a higher trophic specialisation (with higher intra-specific similarities) than common carp in natural lakes, suggesting a better ability to exploit profitable resources. We also found a high degree of trophic niche overlap between the species, indicating feeding on similar food sources, thereby confirming a previous mesocosm study on common carp and the congeneric goldfish *Carassius auratus*, also being a global invader (Busst & Britton, 2017). Only in two sites (Gala and Uclerkayasi) the trophic niches of the species segregated and their diet compositions differed, which was likely caused by broad prey availability and high productivity in Lake Gala and low fish abundance in the Uclerkayasi reservoir. These results partly corroborate our hypothesis on both species showing similar growth types and body conditions as well as high trophic niche overlap. However, contrary to our predictions, they indicated no effect of site, predator, or common carp presence on the biological and ecological features of gibel carp. Whilst additional or alternative drivers may have led to the observed outcomes, our results are the first indications of trophic interactions among gibel and common carp under natural conditions, limiting our ability to draw further inferences through comparisons to other studies.

Based on invasion ecology theory, invaders can out-compete trophically analogous native competitors by suppressing their niche

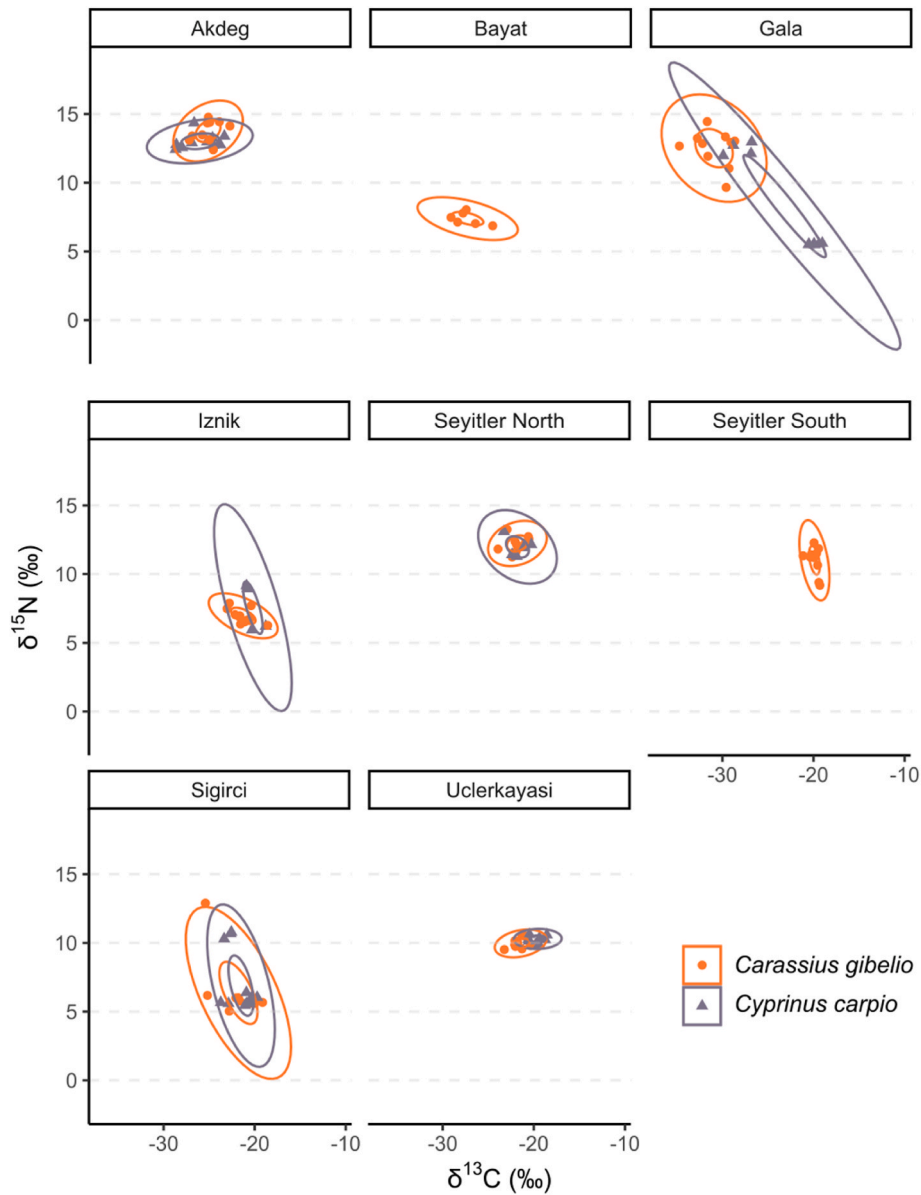


Fig. 4. Biplot of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic niche of *Carassius gibelio* and *Cyprinus carpio* in the different sampling sites. Ellipses represent 95% and 40% of the data.

Table 1

Layman metrics, corrected standard ellipse area (SEAc) and mean Bayesian standard ellipse area (SEAB) of *Carassius gibelio* and *Cyprinus carpio* in the different sampling sites. Type (Reservoir = R; Natural lake = N).

Site (type)	Species (sample N)	NR	CR	TA	CD	NND	SDNND	SEAc	SEAB (mean)
Akdeg (R)	<i>C. carpio</i> (10)	1.92	5.34	5.91	1.84	0.72	0.34	3.74	3.30
	<i>C. gibelio</i> (10)	2.37	4.46	5.59	1.28	0.66	0.34	3.30	3.71
Bayat (R)	<i>C. gibelio</i> (6)	1.17	4.57	2.35	1.33	0.96	0.59	2.50	2.53
	<i>C. carpio</i> (10)	7.48	10.87	21.29	5.19	0.53	0.52	14.77	26.93
Gala (N)	<i>C. gibelio</i> (10)	4.79	6.08	14.93	2.12	1.06	0.56	9.00	9.00
	<i>C. carpio</i> (4)	3.21	2.11	2.52	1.71	0.89	0.75	5.40	5.89
Iznik (N)	<i>C. gibelio</i> (10)	1.61	4.45	4.17	1.12	0.63	0.51	2.10	2.18
	<i>C. carpio</i> (5)	1.80	3.02	2.42	1.12	0.94	0.57	3.31	3.16
Seyitler North (R)	<i>C. gibelio</i> (10)	2.00	3.39	3.87	1.03	0.52	0.52	2.14	2.13
	<i>C. carpio</i> (10)	3.09	1.85	2.81	0.94	0.42	0.22	1.80	1.81
Seyitler South (R)	<i>C. gibelio</i> (10)	3.09	1.85	2.81	0.94	0.42	0.22	1.80	1.81
	<i>C. carpio</i> (13)	5.33	3.99	12.72	2.17	0.39	0.31	8.17	8.32
Sigirci (N)	<i>C. gibelio</i> (11)	7.86	6.27	23.08	2.09	1.20	1.98	11.99	12.50
	<i>C. carpio</i> (8)	0.74	2.01	1.05	0.78	0.25	0.20	0.74	0.72
Uclerkayasi (R)	<i>C. gibelio</i> (10)	1.03	3.51	1.81	0.83	0.48	0.33	1.15	1.14

Table 2

Results of the Permutational Multivariate Analysis of Variance (PERMANOVA, with Euclidean distance and 9,999 permutations) on the ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of *Carassius gibelio* and *Cyprinus carpio*, together with the proportion of niche overlap considering the 95% maximum likelihood (95% SEA), the mean Bayesian (95% SEAB), and the 40% (SEAc) standard ellipse areas (SEA). The last two columns indicate the directional probability of niche overlap for either species. Only sites where both species co-occurred are shown.

Site	PERMANOVA	95% SEA	95% SEAB (mean)	SEAc (40%)	<i>C. carpio</i> - > <i>C. gibelio</i> (95%, mean)	<i>C. carpio</i> - > <i>C. gibelio</i> (40%, mean)	<i>C. gibelio</i> - > <i>C. carpio</i> (95%, mean)	<i>C. gibelio</i> - > <i>C. carpio</i> (40%, mean)
Akdeg (R)	pseudoF _{1,18} = 2.11, <i>P</i> = 0.15	48%	40%	19%	68%	17%	68%	22%
Gala (N)	pseudoF _{1,18} = 20.77, <i>P</i> < 0.001	21%	16%	0%	17%	2%	33%	2%
Iznik (N)	pseudoF _{1,13} = 1.71, <i>P</i> = 0.19	22%	21%	7%	36%	6%	43%	11%
Seyitler North (R)	pseudoF _{1,13} = 0.13, <i>P</i> = 0.86	59%	46%	53%	75%	27%	80%	30%
Sigirci (N)	pseudoF _{1,22} = 0.29, <i>P</i> = 0.72	61%	55%	49%	89%	39%	75%	25%
Uclerkayasi (R)	pseudoF _{1,16} = 17.34, <i>P</i> < 0.001	30%	20%	0%	53%	6%	30%	4%

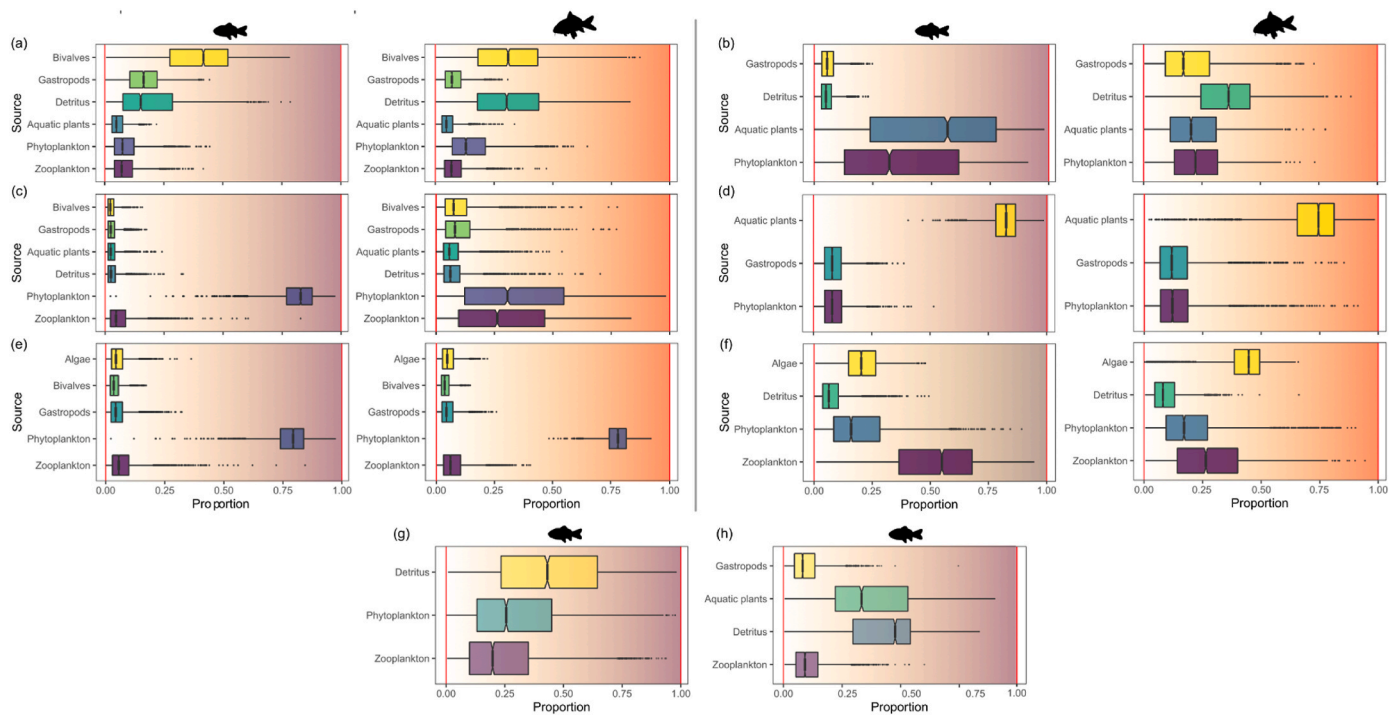


Fig. 5. Results of the stable isotope mixing models for *Carassius gibelio* and *Cyprinus carpio* for each site: (a) Akdeg, (b) Gala, (c) Iznik, (d) Seyitler North, (e) Sigirci, (f) Uclerkayasi, (h) Bayat, (i) Seyitler South. In Acigol, Bayat and Seyitler South, only *Carassius gibelio* was present.

size (niche reduction), leading to specialisation or, eventually, displacement from their original trophic niche (Jackson et al., 2016). Gibel carp are known to affect native and in particular endemic fish species through processes that include reproductive competition (Tarkan, Gaygusuz, et al., 2012) and strong competitive abilities through their occupation of lower trophic positions than other fishes (Yalçın-Özdilek & Jones, 2014) and their faster growth rates (Tapkır et al., 2022). Gibel carp also express a particular case of gynogenesis. Female triploids have been experimentally shown to be sperm parasites that can utilise sperm from common carp, goldfish, crucian carp, roach *Rutilus rutilus*, ide *Leuciscus idus*, and bream *Abramis brama* (Paschos et al., 2004) to trigger embryogenesis (typical gynogenesis). It is possible that gibel carp, distributed in western Turkey, use the sperm of other Cyprinidae species as a reproductive strategy. However, since the specific reproductive mode of gibel carp populations in the current study is unknown, this reproductive feature of the species was not accounted for. It should however be acknowledged that the stocking of common carp

can facilitate the spread of gibel carp.

Although gibel carp are considered as the most invasive freshwater species in Turkey and are almost ubiquitously distributed (Tarkan, Copp, et al., 2012), the status of common carp is less clear, despite having a similar distribution (Vilizzi, 2012). Despite the country-wide intense stocking campaigns, common carp is not one of the main components of the local ichthyofauna, with previous studies on the species in Anatolia indicating relatively slow somatic growth rates in both the native and introduced ranges of Turkey, likely due to the long history of domestication (Vilizzi et al., 2013, 2014). This is in contrast to other countries, where the common carp is recognised as a globally invasive, high-impact invader (Weber & Brown, 2009) that can cause substantial ecological impacts on invaded freshwater ecosystems (Vilizzi et al., 2015), including the suppression of native and other non-native species of e.g. the *Carassius* genus (Bust & Britton, 2017).

Similar to gibel carp, common carp have a high potential to be highly plastic in their trophic niches between different contexts (Britton et al.,

2018). It is worth stressing that niche overlap of the two species, when in sympatry, would only lead to competitive interactions when their shared resources were limited and switching to alternative resources was not possible (Jackson et al., 2016; Tran et al., 2015). In our study, inter-specific differences in their growth and body conditions were negligible, suggesting that their food resources were not limiting or were at least sufficient to maintain their respective growth rates and body condition. A similar observation has been made for two other invasive cyprinid species, the common bleak *Alburnus alburnus* and the topmouth gudgeon *Pseudorasbora parva*, which showed no evidence of suffering competition despite their considerable trophic niche overlap in a site where they co-occurred in Italy (Balzani et al., 2020). A large-scale work on gibel carp in Turkey revealed that in reservoirs (but not lakes), gibel carp are more successful invaders in terms of higher growth rates and reproductive capacities (Tarkan, Copp, et al., 2012). Our results here did not, however, show any significant impact of ecosystem type on either growth, body condition, or interspecific trophic niche interactions. Even though there are numerous varieties of common carp and gibel carp, these are not pertinent to our study populations. The genetic origin of common carp in our study populations can be traced back to two main hatcheries in Turkey (Gaygusuz et al., 2015). Similarly, gibel carp in our study areas has been introduced solely from the north (Thrace) and south (Mediterranean region) of the country (Ağdamar & Tarkan, 2019). Similarly, the present study revealed no significant effect of predator presence, although this factor has been documented as an important driver of crucian carp invasion success (Brönmark & Miner, 1992; Domenici, 2002) and gibel carp feeding and morphology (Tarkan et al., 2023). These differences might relate to the relatively low number of sites for each combination (e.g. natural lakes with and without common carp, reservoirs with and without common carp). Also, the data from the invaded communities have the caveat that they were non-replicated field samples that were only sampled once, thus subject to uncontrolled environmental conditions (e.g., fish abundance, food availability) and so some context dependencies. Therefore, this study should be considered preliminary and should provide an incentive for further research.

4.1. Management implications

Given the wide spatial distribution of both common and gibel carp in invaded regions (Tarkan, Copp, et al., 2012; Gaygusuz et al., 2015; Tapkir et al., 2022), these two species could have synergistic impacts on invaded ecosystems (e.g. habitat modification and ecosystem engineering) or limit each other through competition. Although the impacts of either species to other components of the fish communities were not assessed here, understanding how invasive gibel carp interacts with non-native common carp is critical to developing appropriate management actions that are commensurate with the level of ecological risk. Therefore, this study provides the first, important information on trophic interactions between these two non-native fish species. As strict governmental policy in Turkey, common carp continue to be stocked intensely in Turkey, inevitably facilitating the further dispersal of gibel carp across the country. Unlike gibel carp, common carp is a highly demanded and economically important species, providing food security for local people, and job security and poverty alleviation for artisanal fishers, particularly in Anatolia.

As both species occupy the same niche space and their introduction shows similar ecological consequences (which are not affected by ecosystem type and predator presence), we strongly recommend that common carp stockings should be focused on locations where both fishery benefits can accrue and gibel carp populations are already established. These stockings should be done with great care, such as through auditing fish releases (Davies et al., 2013), to minimise the risk of increasing local abundances of gibel carp even further.

Author contributions

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. Ali Serhan Tarkan: Conceptualization, Methodology, Writing – original draft, review & editing

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships which have or could be perceived to have influenced the work reported in this article.

Acknowledgements

This work has been supported by Eskişehir Osmangazi University Scientific Research Projects Coordination Unit under grant number FBA-2021-2227 and FCD-2021-2146. We thank the TÜBİTAK BİDEB (2219 Program), which supported the authors both Irmak KURTUL and Ali Serhan TARKAN with one-year scholarships during their post doc studies at Bournemouth University, the United Kingdom.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aaf.2023.08.003>.

References

- Ağdamar, S., & Tarkan, A. S. (2019). High genetic diversity in an invasive freshwater fish species, *Carassius gibelio*, suggests establishment success at the frontier between native and invasive ranges. *Zoologischer Anzeiger*, 283, 192–200.
- Alofs, K. M., & Jackson, D. A. (2014). Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. *Ecology*, 95, 3259–3270.
- Balzani, P., Gozlan, R. E., & Haubrock, P. J. (2020). Overlapping niches between two co-occurring invasive fish: The topmouth gudgeon *Pseudorasbora parva* and the common bleak *Alburnus alburnus*. *Journal of Fish Biology*, 97, 1385–1392.
- Balzani, P., & Haubrock, P. J. (2022). Expanding the invasion toolbox: Including stable isotope analysis in risk assessment. *NeoBiota*, 76, 191–210.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bissattini, A. M., Haubrock, P. J., Buono, V., Balzani, P., Borgianni, N., Stellati, L., ... & Vignoli, L. (2021). Trophic structure of a pond community dominated by an invasive alien species: Insights from stomach content and stable isotope analyses. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31, 948–963.
- Britton, J. R. (2023). Contemporary perspectives on the ecological impacts of invasive freshwater fishes. *Journal of Fish Biology*. <https://doi.org/10.1111/jfb.15240>
- Britton, J. R., Lynch, A. J., Bardal, H., Bradbeer, S. J., Coetzee, J. A., Coughlan, N. E., Dalu, T., Tricarico, E., Gallardo, B., Lintermans, M., Lucy, F., Liu, C., Olden, J. D., Raghavan, R., & Pritchard, E. G. (2023). Preventing and controlling non-native species invasions to bend the curve of global freshwater biodiversity loss. *Environmental Reviews*, 31, 310–326.
- Britton, J. R., Ruiz-Navarro, A., Verreycken, H., & Amat-Trigo, F. (2018). Trophic consequences of introduced species: Comparative impacts of increased interspecific versus intraspecific competitive interactions. *Functional Ecology*, 32, 486–495.
- Brönmark, C., & Miner, J. G. (1992). Predator-induced phenotypic change in body morphology in crucian carp. *Science*, 258, 1348–1350.
- BSGM. <https://www.tarimorman.gov.tr/SGB/Belgeler/SagMenuVeriler/BSGM.pdf>, (2021).
- Busst, G. M. A., & Britton, J. R. (2017). Comparative trophic impacts of two globally invasive cyprinid fishes reveal species-specific invasion consequences for a threatened native fish. *Freshwater Biology*, 62, 1587–1595.
- Cowx, I. G. (1994). Stocking strategies. *Fisheries Management and Ecology*, 1, 15–30.
- Cucherousset, J., Lassus, R., Riepe, C., Millet, P., Santoul, F., Arlinghaus, R., & Buoro, M. (2021). Quantitative estimates of freshwater fish stocking practices by recreational angling clubs in France. *Fisheries Management and Ecology*, 28, 295–304.
- Davies, G. D., Gozlan, R. E., & Robert Britton, J. (2013). Can accidental introductions of non-native species be prevented by fish stocking audits? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 366–373.

- Domenici, P. (2002). The visually-mediated escape response in fish: Predicting prey responsiveness and the locomotor behaviour of predators and prey. *Marine and Freshwater Behaviour and Physiology*, 35, 87–110.
- Emiroğlu, Ö. (2019). *Enhancing native fish populations through the suppression of invasive freshwater fish species in the Sakarbaşı in Çifteler*. Osmangazi University Research Fund Project Report.
- Forneck, S. C., Dutra, F. M., de Camargo, M. P., Vitule, J. R. S., & Cunico, A. M. (2021). Aquaculture facilities drive the introduction and establishment of non-native *Oreochromis niloticus* populations in Neotropical streams. *Hydrobiologia*, 848, 1955–1966.
- Garcia, D. A., Occhi, T. V., Agostinho, A., Alves, G. H., Brito, M. F., Casimiro, A. C., Couto, T. B., Cunico, A. M., Jarduli, L. R., Lima-Junior, D. P., & Magalhães, A. L. (2022). More of the same: new policies continue fostering the use of non-native fish in Brazil. *Environmental Conservation*, 49, 4–7.
- Gaygusuz, Ö., Tarkan, A. S., 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. *Turkish Journal of Fisheries and Aquatic Sciences*, 15, 833–840.
- Govan, E., Jackson, A. L., Inger, R., Bearhop, S., & Parnell, A. C. (2023). *simmr: A package for fitting Stable Isotope Mixing Models in R*. arXiv preprint arXiv:2306.07817. ISO 690.
- Gozlan, R. E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Caiola, N., Cakic, P., Djikanovic, V., Esmaili, H. R., Falka, I., Golicher, D., Harka, A., Jeney, G., Kováč, V., Musil, J., Nocita, A., Povz, M., Poulet, N., ... Britton, J. R. (2010). Pancontinental invasion of *Pseudorasbora parva*: Towards a better understanding of freshwater fish invasions. *Fish and Fisheries*, 11, 315–340.
- Gozlan, R. E., Britton, J. R., Cowx, I., & Copp, G. H. (2010a). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*, 76, 751–786.
- Haubrock, P. J., Balzani, P., Britton, J. R., & Haase, P. (2020). Using stable isotopes to analyse extinction risks and reintroduction opportunities of native species in invaded ecosystems. *Scientific Reports*, 10, 1–11.
- Henriksson, A., Yu, J., Wardle, D. A., & Englund, G. (2015). Biotic resistance in freshwater fish communities: Species richness, saturation or species identity? *Oikos*, 124, 1058–1064.
- Hickley, P., Britton, J. R., Macharia, S., Muchiri, S. M., & Boar, R. R. (2015). The introduced species fishery of lake Naivasha, Kenya: Ecological impact vs socio-economic benefits. *Fisheries Management and Ecology*, 22, 326–336.
- Innal, D., & Erk'anan, F. (2006). Effects of exotic and translocated fish species in the inland waters of Turkey. *Reviews in Fish Biology and Fisheries*, 16, 39–50.
- Jackson, M. C., Britton, J. R., Cucherousset, J., Guo, Z., Stakenas, S., Gozlan, R. E., Godard, M. G., Roussel, J. M., & Copp, G. H. (2016). Do non-native pumpkinseed *Lepomis gibbosus* affect the growth, diet and trophic niche breadth of native brown trout *Salmo trutta*? *Hydrobiologia*, 772, 63–75.
- Lüdecke, D. **sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.14**. <https://CRAN.R-project.org/package=sjPlot>.
- Memiş, D., & Kohlmann, K. (2006). Genetic characterization of wild common carp (*Cyprinus carpio* L.) from Turkey. *Aquaculture*, 258, 257–262.
- Paschos, I., Nathanailides, C., Tsoumani, M., Perdicaris, C., Gouva, E., & Leonardos, I. (2004). Intra- and inter-specific mating options for gynogenetic reproduction of *Carassius gibelio* (Bloch, 1783) in Lake Pamvotis (NW Greece). *Belgian Journal of Zoology*, 134, 55–60.
- Tapkir, S., Boukal, D., Kalous, L., Bartoň, D., Souza, A. T., Kolar, V., ... Šmejkal, M. (2022). Invasive gibel carp (*Carassius gibelio*) outperforms threatened native crucian carp (*Carassius carassius*) in growth rate and effectiveness of resource use: Field and experimental evidence. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32, 1901–1912.
- Tarkan, A. S., Copp, G. H., Top, N., Özdemir, N., Önsoy, B., Bilge, G., Filiz, H., Yapıcı, S., Ekmekçi, G., Kirankaya, 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 Management and Ecology*, 19, 178–187.
- Tarkan, A. S., Gaygusuz, Ö., Gürsoy Gaygusuz, Ç., Saç, G., & Copp, G. (2012b). Circumstantial evidence for gibel carp *Carassius gibelio* reproductive competition exerted on native fish species in a mesotrophic reservoir. *Fisheries Management and Ecology*, 19, 167–177.
- Tarkan, A. S., Mol, O., Aksu, S., Köse, E., Kurtul, I., Başkurt, S., ... Emiroğlu, Ö. (2023). Phenotypic responses to piscivory in invasive gibel carp populations. *Aquatic Science*, 85, 75.
- Tarkan, A. S., Tricarico, E., Vilizzi, L., Bilge, G., Ekmekçi, F. G., Filiz, H., ... Copp, G. H. (2021). Risk of invasiveness of non-native aquatic species in the eastern Mediterranean region under current and projected climate conditions. *The European Zoological Journal*, 88, 1130–1143.
- Tarkan, A. S., Vilizzi, L., Top, N., Ekmekçi, F. G., Stebbing, P. D., & Copp, G. H. (2017). Identification of potentially invasive freshwater fishes, including translocated species, in Turkey using the Aquatic Species Invasiveness Screening Kit (AS-ISK). *International Review of Hydrobiology*, 102, 47–56.
- Tran, T. N. Q., Jackson, M. C., Sheath, D., Verreycken, H., & Britton, J. R. (2015). Patterns of trophic niche divergence between invasive and native fishes in wild communities are predictable from mesocosm studies. *Journal of Animal Ecology*, 84, 1071–1080.
- Vilizzi, L. (2012). The common carp, *Cyprinus carpio*, in the Mediterranean region: Origin, distribution, economic benefits, impacts and management. *Fisheries Management and Ecology*, 19, 93–110.
- Vilizzi, L., Copp, G. H., Hill, J. E., Adamovich, B., Aislabie, L., Akin, D., ... Clarke, S. (2021). A global-scale screening of non-native aquatic organisms to identify potentially invasive species under current and future climate conditions. *Science of the Total Environment*, 788, Article 147868.
- Vilizzi, L., Ekmekçi, F. G., Tarkan, A. S., & Jackson, Z. (2014). Growth of common carp *Cyprinus carpio* in Anatolia (Turkey), with a comparison to native and invasive areas worldwide. *Ecology of Freshwater Fish*, 24, 165–180.
- Vilizzi, L., Tarkan, A. S., & Copp, G. (2015). Experimental evidence from causal criteria analysis for the effects of common carp *Cyprinus carpio* on freshwater ecosystems: A global perspective. *Reviews in Fisheries Science & Aquaculture*, 23, 253–290.
- Vilizzi, L., Tarkan, A. S., & Ekmekçi, F. G. (2013). Stock characteristics and management insights for common carp (*Cyprinus carpio*) in Anatolia: A review of weight-length relationships and condition factors. *Turkish Journal of Fisheries and Aquatic Sciences*, 13, 759–775.
- Weber, M. J., & Brown, M. L. (2009). Effects of common carp on aquatic ecosystems 80 years after "carp as a dominant": Ecological insights for fisheries management. *Reviews in Fisheries Science*, 17, 524–537.
- Yalçın Özdişek, Ş., Partal, N., & Jones, R. I. (2019). An invasive species, *Carassius gibelio*, alters the native fish community through trophic niche competition. *Aquatic Sciences*, 81, 29.