

Research Article

Spread of invasive Ponto-Caspian gobies and their effect on native fish species in the Neckar River (South Germany)

Julia Gaye-Siessegger^{1,*}, Steffen Bader¹, Ralf Haberbosch² and Alexander Brinker^{1,3}

¹Fisheries Research Station Baden-Württemberg, LAZBW, Argenweg 50/1, 88085 Langenargen, Germany

²Freshwater Biologist (Freelancer), 88069 Tettnang, Germany

³University of Konstanz, 78457 Konstanz, Germany

*Corresponding author

E-mail: julia.gaye-siessegger@lazbw.bwl.de

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Abstract

Fish assemblages in the Neckar River were investigated by electrofishing under the Water Framework Directive 2000/60/EC (WFD) to assess the ecological status of rivers. This monitoring program also provides information on the distribution of invasive Ponto-Caspian gobies along the Neckar River in Germany, a tributary of the Rhine River. The western tubenose goby *Proterorhinus semilunaris* was first recorded on the Neckar River in 2007, followed by bighead goby *Ponticola kessleri* and round goby *Neogobius melanostomus* in 2009 and 2012, respectively. The current distribution boundary for Ponto-Caspian gobies coincides with the navigation limit for cargo ships at the river port of Plochingen (about 200 km up-stream of the city of Mannheim). Marked differences in fish assemblages took place following invasion of the round goby, with average CPUE of native stone loach *Barbatula barbatula* and gudgeon *Gobio gobio* declining from 19.6 and 21.5 individuals per 100 m, respectively, to fewer than one. Bighead gobies failed to build up a stable stock after round goby invasion but have still been caught in small numbers at most sampling sections. The earlier-arriving western tubenose goby could not be detected any longer. The results indicate a strong impact of the round goby on native fish assemblages in the Neckar River which will hamper efforts to improve the ecological quality of the river. Further investigations are needed to assess long term effects of round goby invasion and find solutions for achieving the mandatory European Water Framework Directive (WFD) target of “good ecological status” of the river.

Key words: biodiversity, gudgeon, invasive alien species, round goby, stone loach

Introduction

Aquatic species are threatened by many factors worldwide, including climate change, habitat loss, pollution, exploitation and, to an increasing extent, invasive alien species (IAS) (Arthington et al. 2016). Spread of IAS is driven primarily by an increased shipping activity and the climate change (Meyerson and Mooney 2007; Keller et al. 2011; Early et al. 2016). The introduction of invasive species to an environment often brings irreversible ecological change (Chucholl 2016; Magliozzi et al. 2020; Sala et al. 2000), for example as a result of new diseases and parasites, and as a result of new competitors or predators, causing disruption to food chain effects and even

whole ecosystems (Chucholl 2016; Pyšek et al. 2020). The extent and variety of known impacts is increasing continuously. For example, since the 1990s, the Great Lakes of North America have undergone massive ecological changes due to the introduction of numerous IAS. These include e.g. the zebra mussel *Dreissena polymorpha* (Pallas, 1771), the quagga mussel *D. rostriformis* (Andrusov, 1897), the sea lamprey *Petromyzon marinus* Linnaeus, 1758, the Eurasian ruffe *Gymnocephalus cernua* (Linnaeus, 1758) as well as Ponto-Caspian gobies (Griffiths et al. 1991; Jude et al. 1992; Mills et al. 1994; Ricciardi and MacIsaac 2000). As the variety and severity of IAS impacts increased, European regulations aiming to prevent and manage the introduction and spread of IAS were published in 2014 (European Union 2014) and 2016 (European Union 2016), but their efficacy is questionable. Pyšek et al. (2020) stated that the European list of aliens with highest impacts includes 149 species from all taxonomic groups but only 66 species are listed as IAS of EU concern so far. The round goby *Neogobius melanostomus* (Pallas, 1814), now known as one of the most wide-ranging invasive fish species (Kornis et al. 2012), is not listed because it is native to some EU member states and native species are excluded from listing as IAS of EU concern.

By 1995, few individuals of the genera *Dikerogammarus* and *Corbicula* were observed in the southern federal state of Baden-Wuerttemberg/Germany (Leuven et al. 2009), and the ensuing years saw a rapid change of biocenosis in the Rhine and Neckar systems (Baur and Schmidlin 2007). Following the opening of the Rhine-Main-Danube Canal in 1992, invasion of aquatic species native to the Ponto-Caspian Region in German rivers was facilitated (Baur and Schmidlin 2007; Nagelkerke et al. 2018). Among fish, the greatest impact had several closely related Ponto-Caspian gobies (family Gobiidae) (Kornis et al. 2012; Roche et al. 2013; Cerwenka et al. 2018). The first, western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837), was recorded in the German Danube in the mid-1980s (Bless et al. 1994), followed by the bighead goby *Ponticola kessleri* (Günther, 1861) fourteen years later (Seifert and Hartmann 2000) and by the round goby in 2004 (Paintner and Seifert 2006). Although Ponto-Caspian gobies have restricted natural migration abilities (Brandner et al. 2015) and relatively small home ranges (Ray and Corkum 2001; Brownscombe and Fox 2012), some gobiid species colonized most navigable parts of the German river system in less than 10 years (Cerwenka et al. 2018). One of these species, the round goby, is among the most widespread invasive fishes (Kornis et al. 2012). The fast spread of this species is due in part to its diverse diet, aggressive behavior, high tolerance for a wide range of environmental conditions, ability to spawn repeatedly in a given season, parental care by males and large body size compared to other species with a similar benthic lifestyle (Charlebois et al. 2001; Ray and Corkum 2001; Taraborelli et al. 2009; Kornis et al. 2012; Perello et al. 2015). Kornis et al. (2012) already

stated that round goby will probably continue to spread worldwide, especially via ballast water, accidental bait release and natural dispersal. Moreover, increasing water temperatures due to climate change will most likely enhance the species expansion, increasing its impact still further in future. However, other possible ways of spreading have so far received little attention, e.g. Bussmann et al. (2022) investigated the role of motor cooling water of recreational boats as translocation vector for AIS. Although they detected only one goby larva, the authors saw this as an important proof of invasive goby translocation by small watercraft via motor cooling systems.

In Baden-Württemberg, the western tubenose and the bighead gobies were first detected in the Main River in 2006, the round goby in the Upper Rhine River in 2010. Within a short timeframe, all three species reached the Neckar River, a tributary of the Rhine River. The impacts of Ponto-Caspian gobies on native fish species are well studied and effects on native species are often found to be serious, with the genus *Cottus* appearing to suffer particularly badly (e.g. Janssen and Jude 2001; Van Kessel et al. 2016; Baer et al. 2017). However, results are not wholly consistent, and some studies did not find a significant impact (Janáč et al. 2016). A fish monitoring program established under the European Water Framework Directive (European Community 2000) along about 500 sections of rivers in the federal state of Baden-Wuerttemberg/Germany includes eleven sections of the Neckar River, of which eight are located on the navigable part. The present study used data from the WFD monitoring program to 1) describe the spread of three non-native gobies in the Neckar River since their first record and 2) to compare present and pre-invasion native fish species abundance.

Materials and methods

Study area

The Neckar River is a tributary of the Rhine River in southern Germany, with a length of 367 km and a catchment area of 13,928 km² (Haag 2006; Kunz 2011). Substrates were dominated by hard stony structures, mainly coarse gravel (> 20 mm) as well as varying proportions of sand (< 2 mm), gravel (> 2 mm), stones (> 63 mm) and mud. It rises from the Black Forest in the Schwarzwald-Baar-Kreis district of Baden-Württemberg and passes through several large towns, including Tübingen, Plochingen, Esslingen, Stuttgart, Ludwigsburg, Heilbronn, Heidelberg and Mannheim. Average discharge into the Rhine River at Mannheim is about 145 m³/s. Since 1968, the Neckar River has been navigable by cargo ships for about 200 km, up to the river port of Plochingen. The river descends 161 m between Plochingen and Mannheim and is used to commercial power hydroelectric schemes and to supply cooling water for coal and nuclear power plants.

Fish data

Investigations of fish assemblages were conducted as part of monitoring under the WFD. Eight sections of the lower, navigable Neckar River and

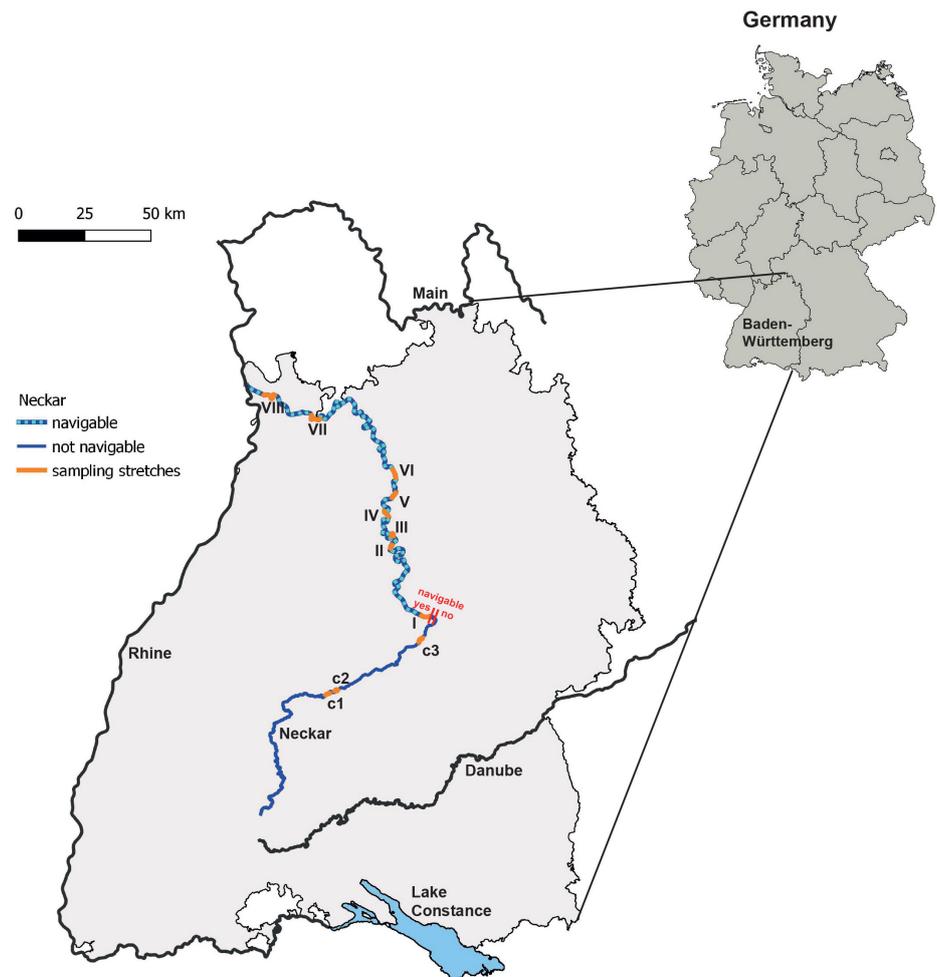


Figure 1. Study area along the Neckar River. Sampling sections are indicated by black numbers (c1–c3: not navigable; I–VIII: navigable).

three sections further upstream were sampled at least six times each between 2007 and 2020 (Figure 1, Supplementary material Table S1). Sampling was conducted from a boat using a single anode, 600 V DC electrofishing gear (EFKO Elektrofischfängergeräte GmbH). All surveys met the strict requirements of the WFD, including fixed periods for investigation (August 1st to October 15th), minimum section length (depending on river width) and minimum number of individuals to be sampled (> 30-fold of the number of species of the reference fish community) (Dussling 2009). All captured fish were identified, allocated to a 5 cm length class, counted and released.

Data analysis and statistics

Catch per unit effort (CPUE) was estimated as the number of fish per 100 m of river in each section. CPUE in the eight sections of the navigable part of the Neckar River were compared by Mann-Whitney non-parametric U-test before and after invasion of round goby. Community composition (based on CPUE) was contrasted between periods using a one-way analysis of similarity (ANOSIM, 9999 permutations). The ordination method was

based on $\log(x+1)$ -transformed data using a Bray-Curtis similarity matrix. For the visualization of differences in community composition between periods, non-metric multidimensional scaling (NMDS) was used. Fish species primarily responsible for the differences in community composition between periods were subsequently determined by similarity percentages (SIMPER, Bray-Curtis similarity measure) (Bray and Curtis 1957; Clarke 1993). Spearman's rank correlation coefficient (r_s) was used to examine correlations between CPUE of round goby and the species that differed most in the SIMPER analyses as well as for the two other goby species. Analyses were performed using PAST Version 4.05 (Hammer et al. 2001). Nominal logistic regression analysis was used to test whether there was an effect of sampling year on the relationships found in the correlation analyses, and was performed in JMP Pro 15.0.0 (SAS Institute Inc., Cary, NC, USA).

Ecological status assessment under the Water Framework Directive

For the assessment of the ecological status of rivers in Germany, the German fish assessment method (fiBS) is used (Dussling 2009). Reference fish communities were reconstructed by combined use of historical information (e.g. Baldner (1666) as the oldest work), recent sampling data and expert judgement, taking into account zoogeographical and regional aspects as well as the longitudinal zonation of the river/river section. Fish are grouped into Guiding Species ($\geq 5\%$), Typespecific Species ($\geq 1\%$) or Accompanying Species ($< 1\%$) depending on their percentage in the references. For the assessment, the actual fish assemblages caught at the sampling sections are compared to these references. Here abundance and age structure of Guiding Species are of great significance.

Results

Spread of Ponto-Caspian gobies

Up to 2020, three goby species have been caught in the federal state Baden-Wuerttemberg/Germany (Figure 1, Table S2). Western tubenose gobies were first detected in the Neckar River in 2007, and had reached the navigable limit of the river at Plochingen (about 200 km upstream) by 2010. For bighead gobies the same spread was achieved between 2009 and 2014 (with two individuals caught near sampling section VIII outside the monitoring program) and for round gobies it was between 2012 and 2016. Until 2020, no Ponto-Caspian gobies have been caught upstream of Plochingen.

Effect of round goby invasion on fish species

CPUE of fish species for sampling sections are shown in Table S2. Mean fish CPUE differed significantly before and after round goby invasion (132.0 and 392.2 individuals/100 m, respectively; Mann-Whitney U-test: $U = 144$, $P < 0.001$). A significant difference in community composition before

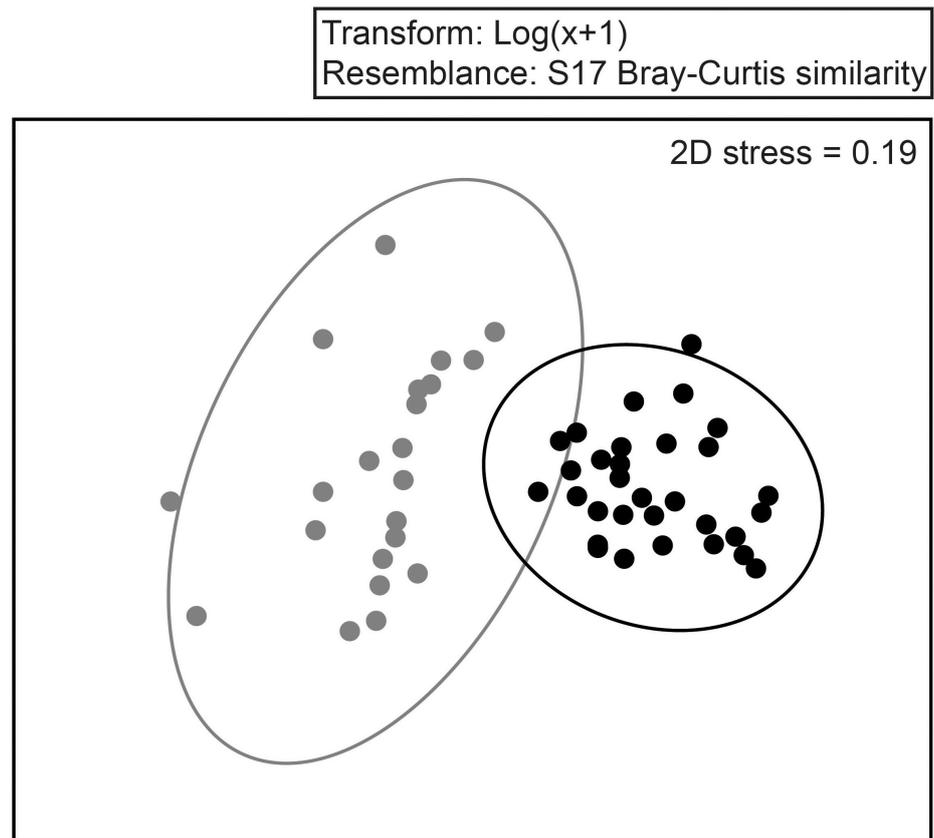


Figure 2. Non-metric multidimensional scaling (NMDS) plot of fish community composition (sampling sections I–VIII) before (grey dots) and after round goby invasion (black squares). Lines indicate similar grouping.

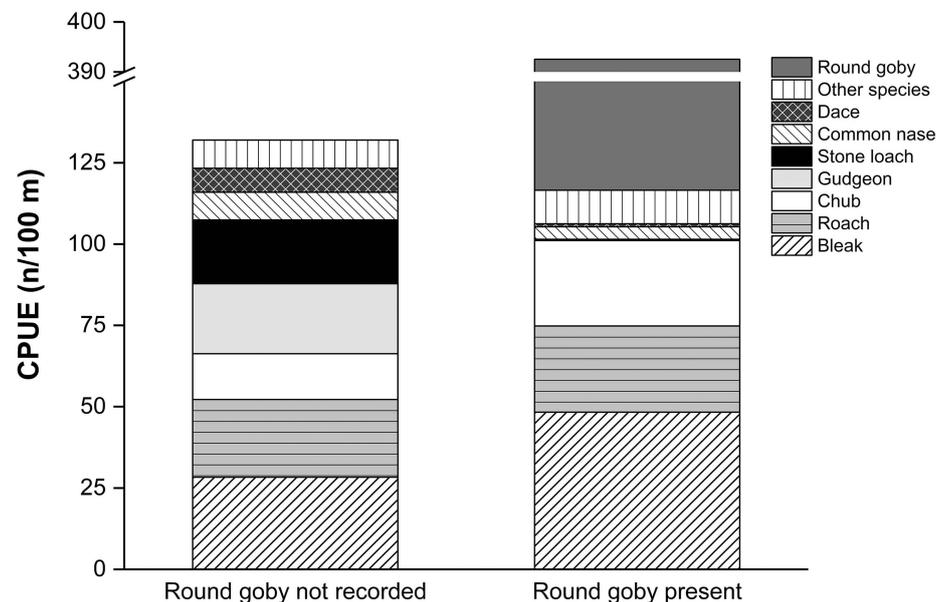


Figure 3. Species contributing most to dissimilarity of fish communities between periods before and after round goby invasion according to similarity percentage analysis (SIMPER).

and after invasion was found (ANOSIM: $R = 0.82$, $P < 0.001$). The NMDS analysis also revealed a clear separation of fish communities before and after invasion (Figure 2). The SIMPER analysis identified the species contributing most to variation in fish community composition between periods (Figure 3;

Table 1. Spearman's rank correlation coefficient values to evaluate possible relationships between CPUE of round goby and other fish species.

Species	Spearman's rs	P
Stone loach	-0.78	<0.001
Gudgeon	-0.72	<0.001
Bighead goby	0.49	<0.001
Western tubenose goby	-0.34	<0.05
Dace	-0.30	<0.05
Chub	0.25	>0.05
Bleak	0.05	>0.05
Schneider	-0.03	>0.05
Common nase	-0.03	>0.05
Roach	0.02	>0.05

Table 2. Results of nominal regression.

Species	Chi square	df	Prob > Chi square	Effects	Estimate	L-R Chi square	Prob > Chi square
Stone loach	31.71	3	< 0.001	Round goby CPUE	-0.14	9.26	< 0.01
				Year	-4.32	1.59	> 0.05
				Round goby CPUE*Year	-0.03	1.80	> 0.05
Gudgeon	35.54	3	< 0.001	Round goby CPUE	-0.02	3.89	< 0.05
				Year	-0.02	0.00	> 0.05
				Round goby CPUE*Year	0.00	5.30	< 0.05
Bighead goby	8.97	3	< 0.05	Round goby CPUE	0.02	6.37	< 0.05
				Year	-1.07	5.06	< 0.05
				Round goby CPUE*Year	-0.01	8.26	< 0.01
Dace	3.84	3	> 0.05	Round goby CPUE	-0.01	1.92	> 0.05
				Year	0.15	0.28	> 0.05
				Round goby CPUE*Year	0.00	1.41	> 0.05
Western tubenose goby	5.81	3	> 0.05	Round goby CPUE	-1.19	84.03	< 0.001
				Year	6.19	0.00	> 0.05
				Round goby CPUE*Year	0.03	0.00	> 0.05

Number of observations = 53.

average dissimilarity 82.95%): round goby (49.78%), bleak *Alburnus alburnus* (Linnaeus, 1758) (14.89%), roach *Rutilus rutilus* (Linnaeus, 1758) (8.38%), chub *Squalius cephalus* (Linnaeus, 1758) (7.53%), gudgeon *Gobio gobio* (Linnaeus, 1758) (5.57%), stone loach *Barbatula barbatula* (Linnaeus, 1758) (5.10%), common nase *Chondrostoma nasus* (Linnaeus, 1758) (2.80%), dace *Leuciscus leuciscus* (Linnaeus, 1758) (1.80%) and schneider *Alburnoides bipunctatus* (Bloch, 1782) (0.90%). Significant correlations were found between CPUE of round goby and those of stone loach, gudgeon, bighead goby, western tubenose goby and dace (Table 1). Also in the nominal logistic regression analysis (Table 2), round goby CPUE was significantly negatively related to the presence of stone loach and gudgeon and significantly positively related to the presence of bighead goby. Sampling year was found to interact significantly with these relationships for the data of gudgeon (positive) and bighead goby (negative). Average CPUE of stone loach and gudgeon declined from 19.6 and 21.5 to less than one individual per 100 m at sites colonized by round goby.

Table 3. Assessment of the ecological status of sampling sections with original data and with 30 individuals (10 individuals of age-0 fish) of gudgeon and stone loach added to the original data using the German assessment tool fIBS (classes according to the WFD > 3.75: high, > 2.50–3.75: good, > 2.00–2.50: moderate, > 1.50–2.00: poor, ≤ 1.50: bad).

Sampling section		Score original data		Score gudgeon/loach added	
I	Esslingen	2.49	moderate	2.71	good
II	Pleidelsheim	2.25	moderate	2.49	moderate
III	Mundelsheim	1.66	poor	2.05	moderate
IV	Lauffen	2.27	moderate	2.38	moderate
V	Heilbronn	2.22	moderate	2.27	moderate
VI	Neckarsulm	2.63	good	2.85	good
VII	Neckargemünd	2.13	moderate	2.32	moderate
VIII	Ilvesheim	2.00	poor	2.19	moderate

Ecological status of sampling sections

Only one of the eight sample sections achieved the good ecological status (Table 3). Adding 30 individuals of gudgeons and loaches, as well as 10 individuals 0+ each, to the catch result improves the score at all sampling sections and the classification of the ecological status at three sections.

Discussion

The Danube-Rhine corridor is an important long-distance dispersal route for aquatic IAS, including several species of Ponto-Caspian gobies, which have spread along it since the 1960s (Roche et al. 2013). This paper documents rapid spread of three Ponto-Caspian gobies in the Neckar River, a tributary of the Rhine River. The WFD monitoring data collated here highlight significant differences in fish community composition in the navigable part of the Neckar River before and after the invasion of round goby, with native stone loach and gudgeon disappearing almost completely, with just a few records of gudgeon from nearby tributaries and overall fish CPUE increasing threefold after invasion due to the sheer number of round gobies. Significant correlations were found between CPUE of round goby and those of stone loach, gudgeon and bighead goby. Sampling year was found to interact significantly with these relationships for the data of gudgeon (positive) and bighead goby (negative). For gudgeon this might be explained with a time lag between round goby invasion and effect on gudgeon presence over the sampling years (Gallardo et al. 2016). For bighead goby this can be explained by the initial positive related increase in both species, while at the end of the period the bighead goby started to decrease in the area whereas the round goby remained abundant.

The rapid expansion of the round goby and its significant impact on native species and ecosystems have driven extensive research, but the results are not consistent. Jurajda et al. (2005) stated that the invasion of *Neogobius* species coincided with a decline in native benthic fishes in the Slovak Danube, including stone loach, bullhead *Cottus gobio* Linnaeus, 1758 and white-finned gudgeon *Romanogobio albipinnatus* (Lukasch, 1933). Analyses undertaken by Piria et al. (2016) indicated a potentially positive

impact of round and bighead gobies on Balkan golden loach *Sabanejewia balcanica* (Karaman, 1922) and a negative impact on chub and zingel *Zingel zingel* (Linnaeus, 1766) in the Croatian Danube. Błońska et al. (2017) found a negative effect of male western tubenose goby presence on stone loach under laboratory conditions, suggesting that male western tubenose gobies would force stone loach individuals away from a shelter, especially in their reproductive season (late spring and early summer). In the upper Elbe, the introduction of round gobies appears to have had negative effects on native 0+ fish abundance and species richness (Janáč et al. 2019). Effects on fish older than 1+ were more diverse, with the increase in round goby abundance correlating with a significant decline in chub abundance and a significant increase in European eels *Anguilla anguilla* (Linnaeus, 1758). The authors assumed higher survival of juvenile eels or a concentration of eels along the nearshore zone because eels most likely feed on gobies. Although they perceived a relatively high potential risk to benthic species, such as barbel *Barbus barbus* (Linnaeus, 1758) and gudgeon, only barbel exhibited a (close to significant) decline in the upper Elbe. Bullhead abundance was low even before round goby introduction. These results were interpreted as a validation for case-specificity in round goby impact on original fish fauna. Janáč et al. (2016) investigated the effect of round goby colonization on abundance and habitat utilization in young-of-the-year (YOY) native fish and on previously established western tubenose goby in a medium-sized European river. Niche use by YOY round and western tubenose gobies overlapped significantly, but the authors did not find a significant effect on native species in the study area and attributed this to lack of niche overlap and/or surplus resources. Van Kessel et al. (2011) conducted habitat choice experiments between two native benthic species (river bullhead *Cottus perifretum* Freyhof, Kottelat and Nolte, 2005 and stone loach) and four invasive gobiid species. They found negative effects of western tubenose and bighead gobies only on river bullhead which moved from the available shelter place to less preferred habitat types. Additionally, they did not find negative effects of round goby on the habitat choice of both native species. The study was conducted outside the spawning season of the investigated species and the authors suggested that reproductive behavior could increase territorial behavior and subsequent competition for shelter.

Before round goby invasion, single specimens of bullhead were caught at the sampling sections I, VII and VIII, while none were recorded after invasion. This is in line with numerous other studies demonstrating significant impacts of round goby invasion on species of *Cottus* (family Cottidae). In southern Lake Michigan, populations of mottled sculpin *Cottus bairdi* Girard, 1850 decreased rapidly after the first round gobies were detected in the area in 1994 (Janssen and Jude 2001), with suggested mechanisms for the disappearance in 1998 including competition for food

at small sizes, for space at medium sizes, and for spawning grounds at large sizes. In the Meuse River in The Netherlands, the protected river bullhead declined rapidly from an average density of 20 individuals per 100 m² to one in the years following the arrival of the round goby (Van Kessel et al. 2016). River bullhead density also declined at sites colonised by western tubenose and/or bighead gobies, but remained relatively high compared to sites where round goby was present. Between 2011 and 2014, Baer et al. (2017) investigated the occurrence of three gobiids in the Rhine River/Baden-Württemberg in the cooling water intake of a nuclear power plant. They found negative effects only for the bullhead, *C. gobio*. In 2011, 57 bullheads were recorded, but with the appearance of Ponto-Caspian gobiids numbers decreased to four individuals in 2012, none in 2013 and one in 2014. Meanwhile, Janáč et al. (2018) found no negative impact of four non-native gobiids species on *C. gobio* abundance along a 1,200 m section of rip-rap placed in the Austrian Danube. They evaluated eight years of electrofishing and caught 26 fish species in total. Most native species were caught only occasionally whereas bullhead and the gobiids were caught regularly. The authors suggested potential region-specific effects.

The invasion of Ponto-Caspian gobies has previously shown to change food chains through selected predation of aquatic invertebrate species and by serving as a new food source for native predatory fish (Kornis et al. 2012). In both rivers, the Rhine and the Neckar, abundances of native invertebrate species have strongly decreased since the arrival of Ponto-Caspian Region invasive species via the Rhine-Main-Danube-Canal in 1992 (Tittizer et al. 2000; Baur and Schmidlin 2007; Leuven et al. 2009). These declines have continued in recent years, including for example the caddisfly *Tinodes waeneri* (Linnaeus, 1758) and species of *Caenis* mayfly (personal communication, Renate Semmler-Elpers, June 2021, LUBW Landesanstalt für Umwelt Baden-Württemberg). The river limpet *Ancylus fluviatilis* Müller, 1774 disappeared completely from the Neckar River after 2012. WFD monitoring of the benthic invertebrate fauna in the Neckar River in 2017 suggested that only sponges, dipterans and worms were maintaining abundances with acceptable changes from the type-specific communities. The most likely causes of these declines are assumed to be IAS, principally the amphipod crustacean *Dikerogammarus villosus* (Sowinski, 1894) and the Ponto-Caspian gobies (personal communication, Renate Semmler-Elpers, June 2021, LUBW). Mikl et al. (2017a) investigated the influence of western tubenose and round gobies on macroinvertebrates in the Dyje River of the Czech Republic. Both species were found to exert a significant negative impact on aquatic invertebrate density and community composition. Krakowiak and Pennuto (2008) examined invertebrate and fish communities in New York tributaries of Lake Erie. Streams with round gobies had reduced diversity values, reduced species richness of Ephemeroptera, Plecoptera and Trichoptera (EPT), reduced EPT/chironomid ratios and increased macroinvertebrate density compared to goby-free streams.

Meanwhile, fish community metrics did not differ significantly between goby-present and goby-free streams but all metrics were lower in streams containing gobies.

The prey of Ponto-Caspian gobies may differ between waterbodies and even within the same waterbody, reflecting their ability to exploit a wide variety of foods (Kornis et al. 2012). Nagelkerke et al. (2018) used a food-fish model (FFM) to determine the trophic profile of five Ponto-Caspian and four native benthic fish species. They found roughly three groups. The first group with monkey goby *Neogobius fluviatilis* (Pallas, 1814) as well as round and western tubenose gobies has the most generalized trophic profile and shows a relatively large capacity to feed on benthic resources such as insect larvae, mollusks, detritus, and crustaceans. The second group with the native stone loach and gudgeon and the alien *Romanogobio belingi* (Slastenenko, 1934) has a higher capacity for feeding on sessile algae, phytoplankton and zooplankton, and a smaller capacity to feed on fish and insects. The third group with the two native *Cottus* species and the alien bighead goby has a greater capacity to feed on fish and a smaller capacity for benthic resources, plankton and sessile algae. Bighead goby overlapped with the two native *Cottus* species, whereas round and western tubenose gobies overlapped with each other and with stone loach and gudgeon, indicating potential trophic competition. Brandner et al. (2013a) investigated the trophic niche differentiation between round goby and bighead goby, their food preferences as well as the role of invasive versus native prey in their invasive success in the upper Danube River. Both species were found to be predacious omnivores with high dietary overlap and a generalistic feeding strategy, but feeding on benthic invertebrates was not completely random, as amphipods were the most important and commonly preferred prey. During the growth period, intraguild predation and cannibalism increased in bighead goby and molluscivory in round goby. Both gobies fed mainly on other non-native species (~ 92% of gut contents) and are likely to benefit from previously invaded species such as *Dikerogammarus villosus*. Beggel et al. (2016) found synergistic effects of *D. villosus* and round goby on the native amphipod *Gammarus pulex* (Linnaeus, 1758). When shelter was available, predation of round goby on *G. pulex* was threefold higher in the presence of *D. villosus* compared to a single expose of *G. pulex*. Therefore, previous invasions of *D. villosus* likely facilitate the rapid range expansion of round goby.

Invasive gobies have become an increasingly important food source for many native piscivorous fish. Recreational fishermen at the Neckar River reported predator stomachs were full of gobies, but scientific evaluation remains to be done. Meanwhile long-term data from Lakes Erie and Ontario have been used to model mass-length relationships for native predators, and estimates of changes in mass-at-length following invasion used to compare the effects of round goby on predator body condition

(Crane et al. 2015). The body condition of smallmouth bass *Micropterus dolomieu* Lacepède, 1802 increased after goby invasion, but the changes were not uniform among size classes or between lakes. The body condition of yellow perch *Perca flavescens* (Mitchill, 1814) changed variably in direction and magnitude, that of walleye *Sander vitreus* (Mitchill, 1818) increased in Lake Ontario but only for larger specimens, while in burbot *Lota lota* (Linnaeus, 1758), minor increases were recorded only for the smallest length class. The authors appealed for further research investigating the implications of these condition changes on growth, age at maturity, fecundity and survival of native predators. Mikl et al. (2017b) investigated stomach contents from native species of a European lowland river, the Dyje. Species closely associated with the artificial rip-rap bank (burbot, perch *Perca fluviatilis* Linnaeus, 1758 and European catfish *Silurus glanis* Linnaeus, 1758) had a higher percentage of non-native Ponto-Caspian gobies in their diet than species feeding more in open water (pike *Esox lucius* Linnaeus, 1758 and Volga pikeperch *Sander volgensis* (Gmelin, 1789)) because gobies in this stretch rarely leave the rip-rap bank.

As well as affecting native species, Ponto-Caspian goby species also interact with each other. In 2007, 22 individuals of western tubenose goby were found in the Neckar River about 35 km upstream of the Rhine confluence. In the subsequent years only 19 individuals were caught at three sampling sections in the navigable part of the Neckar River. From 2009 the bighead goby was caught at all sampling sections, sometimes in large numbers (maximum 574 individuals). But neither species built up large stocks, presumably because of the strong spread of the round goby few years later. This is in line with the results of other studies. In the 1990s, when western tubenose and round gobies invaded the Great Lakes (Charlebois et al. 2001), round goby proliferated and spread farther than the western tubenose goby. By 2001, the round goby had spread to all the Great Lakes and several of their tributaries as well as many other inland rivers, and populations increased to a level where they affected the trophic dynamics of the entire Great Lakes system (Charlebois et al. 2001; Janssen and Jude 2001; Kornis et al. 2012). Borcharding et al. (2013) assumed a high level of competition for food resources between three goby species coexisting in the Lower Rhine (monkey, round and bighead gobies), because they exhibit the same sedentary life style. Cartwright et al. (2019) conducted laboratory experiments to investigate competition mechanisms that are responsible for the spread of round gobies in localities previously invaded by western tubenose gobies. As both species have broad diets, the authors attributed the difference in the invasive success to competition for shelter and the higher aggression of the round goby. Van Kessel et al. (2011) suggested that competition for shelter between bighead and western tubenose gobies is likely to occur at sites where shelter is limited. Cerwenka et al. (2018) characterised the biological invasion of invasive gobies in the

upper Danube River as boom and bust for western tubenose and bighead goby and equilibrial for round goby. A comparable pattern can be seen on the Neckar River.

Although electrofishing is the sampling method officially recommended for river fish by the WFD and is considered to be the most appropriate method for effective fish sampling in different habitats, efficiency is influenced by many factors, e.g. characteristics of fish species, individual fish, stream size, depth and conductivity (Meador et al. 2003; De Leeuw et al. 2007; Mueller et al. 2017). Brandner et al. (2013b) identified point abundance sampling electrofishing as a suitable method to assess fish communities in rip-rap bank habitats of large rivers. In deeper rivers such as the Neckar River, electric fishing is considered only suitable to sample the shallow, littoral zone (De Leeuw et al. 2007). Species that are found mainly in the middle of rivers are caught at lower frequencies, making the impact of gobies on these species difficult to assess in our study, e.g. a potential beneficial effect on larger predatory fish.

Less than 10 years after first detection of round goby in the lowest sampling section of the Neckar River, the species has become an important part of the aquatic food web, as both a predator of aquatic invertebrates and as prey to predators. The Neckar River was dammed up at 27 locks and thereby had become a heavy shipping waterway up to Plochingen (Haag 2006). It was mostly straightened to prevent flooding and to gain areas for the industry. So far, Ponto-Caspian gobies have only been caught in the navigable part of the river. In their recent spread in the Neckar River, round gobies have probably been heavily supported by ship traffic, other IAS as well as a high tolerance for varying environmental conditions (Kornis et al. 2012; Roche et al. 2013; Beggel et al. 2016). Whether or when the gobies make the leap into the non-navigable Neckar River cannot yet be estimated. High predation by native fish species may limit goby abundance in the navigable Neckar River compared to, for example the St. Clair River / Michigan (Burkett and Jude 2015). Nevertheless, their strong impact on the ecology of the waterbody runs counter to the goals of the WFD. Van Kessel et al. (2016) have already pointed out that losses of native fish species in areas invaded by the round goby may render the ecological status objectives of two major European Directives (European Community 1992; European Community 2000) unachievable. For species and habitats, the overall percentage in favorable condition is higher in terrestrial ecosystems than in freshwater and marine ecosystems (EEA 2015). The present study demonstrates the negative effect of round gobies on gudgeon and stone loach in the navigable part of the Neckar River. Other factors, such as climate change and increasing abundance of cormorants (*Phalacrocorax carbo* (Linnaeus, 1758)) in the study area may be at play but are not sufficient to explain the decline in abundance for these two species. The fact that both native species continued to be caught in the non-navigable part of the Neckar, where no gobies have been found

so far, supports the results found in our study. Both species are ecologically important with the gudgeon identified as a Guiding Species in the study area and the stone loach in the upper third of the river. Table 3 highlights differences in the ecological status of sampling sections when 30 individuals of these species are added to the original data. The disappearance of the native species amounts to a deterioration of river status despite strong efforts made by the federal state Baden-Württemberg/Germany to improve the quality of structure and functioning of the aquatic ecosystem. Geist and Hawkins (2016) indicated the need for habitat recovery and restoration of freshwater bodies across Europe but in relation to the above, success in aquatic restoration can be hampered by IAS.

Conclusions

Ponto-Caspian gobies were first detected in the federal state Baden-Württemberg/Germany in 2006. Over the ensuing years, they spread along the navigable parts of the Rhine and Neckar as well as the lower sections of tributaries such as Schutter, Acher, Kinzig and Jagst. Western tubenose and bighead gobies invaded the Rhine and Neckar first, but the round goby has spread quickly since 2010 and of the three gobiid species it is currently almost exclusively present and recorded in high densities. With the expansion of the round goby, native stone loach and gudgeon have almost disappeared in the navigable part of the Neckar River. But long-term studies are still required in order to show whether the impacts of IAS on native species are long-lasting, as in many cases populations have recovered to pre-invasion levels after a certain time period (Bruno et al. 2005; Goodenough 2010).

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Authors' contribution

JG-S and RH conceptualized the study. JG-S, AB, SB analysed the data. JG-S wrote the manuscript and all authors participated in editing and finalising the manuscript.

References

- Arthington AH, Dulvy NK, Gladstone W, Winfield IJ (2016) Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 838–857, <https://doi.org/10.1002/aqc.2712>
- Baer J, Hartmann F, Brinker A (2017) Invasion strategy and abiotic activity triggers for non-native gobiids of the River Rhine. *PLoS ONE* 12: e0183769, <https://doi.org/10.1371/journal.pone.0183769>
- Baldner L (1666) Vogel-, Fisch- und Thierbuch. Straßburg, 279 pp, <https://orka.bibliothek.uni-kassel.de/viewer/image/1343227732549/1/>
- Baur B, Schmidlin S (2007) Effects of invasive non-native species on the native biodiversity in the river Rhine. In: Nentwig W (ed), *Biological Invasions*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 257–273, https://doi.org/10.1007/978-3-540-36920-2_15

- Beggel S, Brandner J, Cerwenka AF, Geist J (2016) Synergistic impacts by an invasive amphipod and an invasive fish explain native gammarid extinction. *BMC Ecology* 16: 32, <https://doi.org/10.1186/s12898-016-0088-6>
- Bless R, Lelek A, Waterstraat A (1994) Rote Liste und Artenverzeichnis der in Deutschland in Binnengewässern vorkommenden Rundmäuler und Fische (Cyclostomata and Pisces). *Schriftenreihe für Landschaftspflege und Naturschutz* 42: 137–156
- Błońska D, Kobak J, Grabowska J (2017) Shelter competition between the invasive western tubenose goby and the native stone loach is mediated by sex. *Journal of Limnology* 76: 221–229, <https://doi.org/10.4081/jlimnol.2016.1557>
- Borcherding J, Dolina M, Heermann L, Knutzen P, Krüger S, Matern S, Treeck R van, Gertzen S (2013) Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. *Limnologica* 43: 49–58, <https://doi.org/10.1016/j.limno.2012.08.003>
- Brandner J, Auerswald K, Cerwenka AF, Schliewen UK, Geist J (2013a) Comparative feeding ecology of invasive Ponto-Caspian gobies. *Hydrobiologia* 703: 113–131, <https://doi.org/10.1007/s10750-012-1349-9>
- Brandner J, Pander J, Mueller M, Cerwenka AF, Geist J (2013b) Effects of sampling techniques on population assessment of invasive round goby *Neogobius melanostomus*. *Journal of Fish Biology* 82: 2063–2079, <https://doi.org/10.1111/jfb.12137>
- Brandner J, Auerswald K, Schäufele R, Cerwenka AF, Geist J (2015) Isotope evidence for preferential dispersal of fast-spreading invasive gobies along man-made river bank structures. *Isotopes in Environmental and Health Studies* 51: 80–92, <https://doi.org/10.1080/10256016.2014.993978>
- Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349, <https://doi.org/10.2307/1942268>
- Brownscombe JW, Fox M (2012) Range expansion dynamics of the invasive round goby (*Neogobius melanostomus*) in a river system. *Aquatic Ecology* 46: 175–189, <https://doi.org/10.1007/s10452-012-9390-3>
- Bruno JF, Fridley JD, Bromberg KD, Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: Sax DF, Stachowicz JJ, Gaines SD (eds), *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer Associates, Sunderland, Massachusetts, pp 13–40
- Burkett EM, Jude DJ (2015) Long-term impacts of invasive round goby *Neogobius melanostomus* on fish community diversity and diets in the St. Clair River, Michigan. *Journal of Great Lakes Research* 41: 862–872, <https://doi.org/10.1016/j.jglr.2015.05.004>
- Bussmann K, Hirsch PE, Burkhardt-Holm P (2022) Invasive goby larvae: first evidence as stowaways in small watercraft motors. *Management of Biological Invasions* 13: 191–203, <https://doi.org/10.3391/mbi.2022.13.1.11>
- Cartwright A, Gebauer R, Vanina T, Stejskal V, Drozd B (2019) Shelter competition between mature non-indigenous western tubenose goby (*Proterorhinus semilunaris*) and immature invasive round goby (*Neogobius melanostomus*) for plants and rocks. *Biological Invasions* 21: 2723–2734, <https://doi.org/10.1007/s10530-019-02006-9>
- Cerwenka AF, Brandner J, Schliewen UK, Geist J (2018) Population trends of invasive alien gobies in the upper Danube River: 10 years after first detection of the globally invasive round goby (*Neogobius melanostomus*). *Aquatic Invasions* 13: 525–535, <https://doi.org/10.3391/ai.2018.13.4.10>
- Charlebois PM, Corkum LD, Jude DJ, Knight C (2001) The Round Goby (*Neogobius melanostomus*) Invasion: Current Research and Future Needs. *Journal of Great Lakes Research* 27: 263–266, [https://doi.org/10.1016/S0380-1330\(01\)70641-7](https://doi.org/10.1016/S0380-1330(01)70641-7)
- Chucholl C (2016) The bad and the super-bad: prioritising the threat of six invasive alien to three imperilled native crayfishes. *Biological Invasions* 18: 1967–1988, <https://doi.org/10.1007/s10530-016-1141-2>
- Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18: 117–143, <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Crane D, Farrell J, Einhouse D, Lantry J, Markham J (2015) Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. *Freshwater Biology* 60: 111–124, <https://doi.org/10.1111/fwb.12473>
- De Leeuw JJ, Buijse AD, Haidvogel G, Lapinska M, Noble R, Repecka R, Virbickas T, Wiśniewski W, Wolter C (2007) Challenges in developing fish-based ecological assessment methods for large floodplain rivers. *Fisheries Management and Ecology* 14: 483–494, <https://doi.org/10.1111/j.1365-2400.2007.00576.x>
- Dussling U (2009) Handbuch zu fiBS. - Schriftenreihe des Verbandes Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler e.V., Heft 15, 72 pp, https://lazbw.landwirtschaft-bw.de/pb/site/pbs-bw-new/get/documents/MLR.LEL/PBSDocuments/lazbw_2017/lazbw_ffs/Dokumente_ffs/WRRL/Handbuch_fiBS.pdf
- Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Gonzalez P, Grosholz ED, Ibañez I, Miller LP, Sorte CJB, Tatem AJ (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7: 12485, <https://doi.org/10.1038/ncomms12485>

- EEA (2015) The European environment - state and outlook 2015: synthesis report. European Environment Agency, Copenhagen, 205 pp, <https://doi.org/10.2800/944899>
- European Community (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities* L206: 7–50
- European Community (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities* L327: 1–72
- European Union (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. *Official Journal of the European Union* L317: 35–55
- European Union (2016) Commission Implementing Regulation (EU) 2016/1141 of 13 July 2016 adopting a list of invasive alien species of Union concern pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council. *Official Journal of the European Union* L189: 4–8
- Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22: 151–163, <https://doi.org/10.1111/gcb.13004>
- Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. *Community Ecology* 11: 13–21, <https://doi.org/10.1556/ComEc.11.2010.1.3>
- Griffiths RW, Schloesser DW, Leach JH, Kovalak WP (1991) Distribution and Dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1381–1388, <https://doi.org/10.1139/f91-165>
- Haag I (2006) A basic water quality model for the River Neckar: Part 1 - model development, parameter sensitivity and identifiability, calibration and validation. *Acta hydrochimica et hydrobiologica* 34: 533–548, <https://doi.org/10.1002/ahch.200400652>
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 4, http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- Janáč M, Valová Z, Roche K, Jurajda P (2016) No effect of round goby *Neogobius melanostomus* colonisation on young-of-the-year fish density or microhabitat use. *Biological Invasions* 18: 2333–2347, <https://doi.org/10.1007/s10530-016-1165-7>
- Janáč M, Roche K, Šlapanský L, Polačik M, Jurajda P (2018) Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. *Hydrobiologia* 807: 263–275, <https://doi.org/10.1007/s10750-017-3398-6>
- Janáč M, Jurajdová Z, Roche K, Šlapanský L, Jurajda P (2019) An isolated round goby population in the upper Elbe: population characteristics and short-term impacts on the native fish assemblage. *Aquatic Invasions* 14: 738–757, <https://doi.org/10.3391/ai.2019.14.4.12>
- Janssen J, Jude DJ (2001) Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Research* 27: 319–328, [https://doi.org/10.1016/S0380-1330\(01\)70647-8](https://doi.org/10.1016/S0380-1330(01)70647-8)
- Jude DJ, Reider RH, Smith GR (1992) Establishment of Gobiidae in the Great Lakes Basin. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 416–421, <https://doi.org/10.1139/f92-047>
- Jurajda P, Černý J, Polačik M, Valová Z, Janáč M, Blažek R, Ondračková M (2005) The recent distribution and abundance of non-native *Neogobius* fishes in the Slovak section of the River Danube. *Journal of Applied Ichthyology* 21: 319–323, <https://doi.org/10.1111/j.1439-0426.2005.00688.x>
- Keller RP, Drake JM, Drew MB, Lodge DM (2011) Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Diversity and Distributions* 17: 93–102, <https://doi.org/10.1111/j.1472-4642.2010.00696.x>
- Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* 80: 235–285, <https://doi.org/10.1111/j.1095-8649.2011.03157.x>
- Krakowiak PJ, Pennuto CM (2008) Fish and macroinvertebrate communities in tributary streams of Eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). *Journal of Great Lakes Research* 34: 675–689, [https://doi.org/10.1016/S0380-1330\(08\)71610-1](https://doi.org/10.1016/S0380-1330(08)71610-1)
- Kunz C (2011) Standardisation of shiplock elongations on the River Neckar. In: Van Shel L (ed), PIANC Yearbook 2010, pp 135–140
- Leuven RSEW, van der Velde G, Baijens I, Snijders J, van der Zwart C, Lenders HJR, bij de Vaate A (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions* 11: 1989–2008, <https://doi.org/10.1007/s10530-009-9491-7>
- Magliozzi C, Tsiamis K, Vigiak O, Deriu I, Gervasini E, Cardoso AC (2020) Assessing invasive alien species in European catchments: Distribution and impacts. *Science of The Total Environment* 732: 138677, <https://doi.org/10.1016/j.scitotenv.2020.138677>
- Meador MR, McIntyre JP, Pollock K (2003) Assessing the efficacy of single-pass backpack electrofishing to characterize fish community structure. *Transactions of the American Fisheries Society* 132: 39–46, [https://doi.org/10.1577/1548-8659\(2003\)132<0039:ATEOSP>2.0.CO;2](https://doi.org/10.1577/1548-8659(2003)132<0039:ATEOSP>2.0.CO;2)

- Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment* 5: 199–208, [https://doi.org/10.1890/1540-9295\(2007\)5\[199:IASIAE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[199:IASIAE]2.0.CO;2)
- Mikl L, Adámek Z, Všetičková L, Janáč M, Roche K, Šlapanský L, Jurajda P (2017a) Response of benthic macroinvertebrate assemblages to round (*Neogobius melanostomus*, Pallas 1814) and tubenose (*Proterorhinus semilunaris*, Heckel 1837) goby predation pressure. *Hydrobiologia* 785: 219–232, <https://doi.org/10.1007/s10750-016-2927-z>
- Mikl L, Adámek Z, Roche K, Všetičková L, Šlapanský L, Jurajda P (2017b) Invasive Ponto-Caspian gobies in the diet of piscivorous fish in a European lowland river. *Fundamental and Applied Limnology* 190: 157–171, <https://doi.org/10.1127/fal/2017/1024>
- Mills EL, Leach JH, Carlton JT, Secor CL (1994) Exotic Species and the Integrity of the Great Lakes: Lessons from the past. *BioScience* 44: 666–676, <https://doi.org/10.2307/1312510>
- Mueller M, Pander J, Knott J, Geist J (2017) Comparison of nine different methods to assess fish communities in lentic flood-plain habitats. *Journal of Fish Biology* 91: 144–174, <https://doi.org/10.1111/jfb.13333>
- Nagelkerke LAJ, van Onselen E, van Kessel N, Leuven RSEW (2018) Functional feeding traits as predictors of invasive success of alien freshwater fish species using a food-fish model. *PLoS ONE* 13: e0197636, <https://doi.org/10.1371/journal.pone.0197636>
- Paintner S, Seifert K (2006) First record of the round goby, *Neogobius melanostomus* (Gobiidae), in the German Danube. *Lauterbornia* 58: 101–107
- Perello MM, Simon TP, Thompson HA, Kane DD (2015) Feeding ecology of the invasive round goby, *Neogobius melanostomus* (Pallas, 1814), based on laboratory size preference and field diet in different habitats in the western basin of Lake Erie. *Aquatic Invasions* 10: 463–474, <https://doi.org/10.3391/ai.2015.10.4.09>
- Pirja M, Jakšić G, Jakovčić I, Treer T (2016) Dietary habits of invasive Ponto-Caspian gobies in the Croatian part of the Danube River basin and their potential impact on benthic fish communities. *Science of The Total Environment* 540: 386–395, <https://doi.org/10.1016/j.scitotenv.2015.05.125>
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M van, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews* 95: 1511–1534, <https://doi.org/10.1111/brv.12627>
- Ray WJ, Corkum LD (2001) Habitat and site affinity of the round goby. *Journal of Great Lakes Research* 27: 329–334, [https://doi.org/10.1016/S0380-1330\(01\)70648-X](https://doi.org/10.1016/S0380-1330(01)70648-X)
- Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology & Evolution* 15: 62–65, [https://doi.org/10.1016/S0169-5347\(99\)01745-0](https://doi.org/10.1016/S0169-5347(99)01745-0)
- Roche KF, Janač M, Jurajda P (2013) A review of Gobiid expansion along the Danube-Rhine corridor - geopolitical change as a driver for invasion. *Knowledge and Management of Aquatic Ecosystems* 411: 01, <https://doi.org/10.1051/kmae/2013066>
- Sala OE, Stuart Chapin F, III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770, <https://doi.org/10.1126/science.287.5459.1770>
- Seifert K, Hartmann F (2000) Die Kesslergrundel (*Neogobius kessleri* Günther 1861), eine neue Fischart in der deutschen Donau. *Lauterbornia* 38: 105–108
- Taraborelli AC, Fox MG, Schaner T, Johnson TB (2009) Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. *Journal of Great Lakes Research* 35: 266–271, <https://doi.org/10.1016/j.jglr.2008.12.004>
- Tittizer T, Schöll F, Banning M, Haybach A, Schleuter M (2000) Aquatische Neozoen im Makrozoobenthos der Binnenwasserstraßen Deutschlands. *Lauterbornia* 39: 1–72. https://www.zobodat.at/pdf/Lauterbornia_2000_39_0001-0072.pdf
- Van Kessel N, Dorenbosch M, De Boer MRM, Leuven RSEW, Van Der Velde G (2011) Competition for shelter between four invasive gobiids and two native benthic fish species. *Current Zoology* 57: 844–851, <https://doi.org/10.1093/czoolo/57.6.844>
- Van Kessel N, Dorenbosch M, Kranenbarg J, Van der Velde G, Leuven RSEW (2016) Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. *Aquatic Invasions* 11: 179–188, <https://doi.org/10.3391/ai.2016.11.2.07>

Supplementary material

The following supplementary material is available for this article:

Table S1. Sampling sections along the Neckar River and year of sampling between 2007 and 2020.

Table S2. CPUE of fish species recorded in eight sections of the navigable Neckar River (I–VIII) and three sections upstream of the navigation limit (c1–c3) between 2007 and 2020 (light grey areas: round goby not recorded, dark grey areas: round goby present).

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Gaye-Siessegger_et_al_SupplementaryMaterial.xlsx