

Research Article

Population trends of invasive alien gobies in the upper Danube River: 10 years after first detection of the globally invasive round goby (*Neogobius melanostomus*)

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Abstract

Invasive alien species are a major threat to aquatic biodiversity. Europe's second largest river, the Danube, is affected by several invasions, including those by four closely related Ponto-Caspian goby species. To investigate population dynamics of invasive alien gobies, we surveyed population trends of all goby species, from absence until full establishment of the round goby (*Neogobius melanostomus*), along a 248 Km river section of the upper Danube River. Distribution and abundance of non-native gobies was highly species-specific and varied with both time (year) and space (location). Gobies strongly dominated the fish community along the entire sampled study area, comprising 76% of all caught individuals, whereas abundances of typical native species such as chub (5%), barbel (4%) and ide (3%) were low. Ten years after its first introduction, round goby is most successful in terms of abundance, tubenose goby is most successful in terms of range expansion and persistence, whereas bighead goby seemingly lost the race. While being decoupled from industrial shipping, goby invasion success strongly appears to be triggered by man-made ecosystem alterations and community changes.

Key words: non-native gobies, bighead goby, tubenose goby, aquatic invasive alien species, ecosystem shift

Introduction

Invasive alien species (IAS) are considered a major threat to global biodiversity (Dudgeon et al. 2006), especially in freshwater ecosystems (Geist 2014). IAS strongly contribute to global homogenisation of flora and fauna, within a few years or decades after introduction (Mooney and Cleland 2001). Nevertheless, from a scientific perspective, IAS represent dynamic and replicated semi-natural model systems. Invasion processes can be subdivided into four phases: (i) introduction and (ii) establishment into a new ecosystem, (iii) dispersal into adjacent areas, and (iv) impact on native biota (Kolar and Lodge 2002; Strayer et al. 2006). For these different phases, parti-

cular species-specific characteristics seem to be crucial, such as (rapid) adaptability of the geno- (Sax et al. 2007) and phenotype (Cerwenka et al. 2014a), specific life history traits (García-Berthou 2007), elevated levels of phenotypic plasticity (Wright et al. 2010; Davidson et al. 2011), and good migration and dispersal abilities (Brandner et al. 2015). In addition, single individuals with alternative life-history traits, i.e. traits of potential adaptive value, may be the most important drivers of invasion processes (Cerwenka et al. 2017).

Gobiid fishes of the genera *Neogobius*, *Ponticola*, *Proterorhinus* and *Babka* (all: Teleostei: Gobiidae), native to the Ponto-Caspian region, have recently invaded different types of freshwater ecosystems around

the world. These small-growing fishes have highly restricted natural migration abilities (Brandner et al. 2015) and relatively small home ranges (Brownscombe and Fox 2012). However, within less than 10 years, some gobiid species have colonised most of the navigable parts of the German large rivers, including the Danube River (Harka and Bíró 2007; Haertl et al. 2012; Brandner et al. 2013a, b; Cerwenka et al. 2017). With over 2,800 kilometres in length, the Danube River is the second largest river in Europe. With its opening in 1992, the Rhine-Main-Danube canal (RMD-canal) connected the formerly separated major drainage systems of the rivers Rhine-Main and Danube, providing an artificial corridor for the migration of aquatic species. Taking advantage of the RMD-canal as an entrance point, several Ponto-Caspian goby species quickly colonised the rivers Main and Rhine from their danubian stepping stones. Their limited migration skills, in combination with a sympatric distribution range, thus render these closely related species as ideal models to investigate biological invasions (Ricciardi and Maclsaac 2000; Corkum et al. 2004; Leuven et al. 2009; Borcherdig et al. 2011; Gertzen et al. 2016; Piria et al. 2016; van Kessel et al. 2016; Kornis et al. 2017).

The tubenose goby, *Proterorhinus semilunaris* (Heckel, 1837), was the first non-native postglacial gobiid immigrant to be found in the ~ 600 Km section of the German Danube River, where it is present since, at least, 1985 (Bless et al. 1994). In 1999, the bighead goby *Ponticola kessleri* (Günther, 1861) was first recorded close to the city of Straubing (river-Km: 2,309; Seifert and Hartmann 2000), where it rapidly reached high abundances. Kováč et al. (2009) suggested the bighead goby to be more successful than other invasive alien Ponto-Caspian goby species, if considered over long time periods. In 2004, specimens of the round goby *Neogobius melanostomus* (Pallas, 1814) were first recorded close to the cities of Straubing (river-Km: 2,309) and Passau (river-Km: 2,226, Paintner and Seifert 2006). Soon after its establishment, this species reached very high densities and was found upstream of industrial shipping routes (Brandner et al. 2013a, b, c). In 2011, the racer goby *Babka gymnotrachelus* (Kessler, 1857) was detected close to the cities of Mariaposching (river-Km: 2,292) and Regensburg (river-Km: 2,373) (Haertl et al. 2012). However, this species is infrequent in the main river channel, as it mainly inhabits backwater habitats (Haertl et al. 2012).

Detailed information on the distribution of IAS and their secondary dispersal pathways (without anthropogenic support) is crucial for understanding factors and mechanisms that influence invasion

processes. Furthermore, such information is essential for developing and implementing management strategies (Geist 2011), e.g. to understand and possibly limit further range expansions. Using the upper Danube River as an example, the sympatric invasion of four non-native gobiid fishes enabled a close observation of their population dynamics. The objectives of this study were to analyse the abundance and spatial distribution of invasive gobies, their population dynamics, trends, and secondary dispersal.

Material and methods

Study area and sampling

Eleven representatively distributed rip-rap river stretches were sampled along a 248 Km section of the Danube River between the cities of Engelhartzell (river-Km 2,196) and upstream of Vohburg (river-Km 2,444, Figure 1), in 2010, 2011 and 2015 (Supplementary material Table S1). River stretches were separated by at least 5 river-Km and consisted of a 290 m sampling site at each river side. River stretches 1–10 were sampled in 2010 and 2011. In addition, river stretches 2, 8, 10 and 11 were sampled in 2015 (Table S1). Following Brandner et al. (2013c), at each sampling site, 30-point abundance sampling (PAS) points, with a distance of 10 m in between, were targeted. For that, electrofishing was performed during daylight hours in ~ 60 cm water depth from shorelines, with 10 s of direct current applied at each PAS point with a ring-shaped anode (diameter 31 cm), powered by a mobile 3.0 kW electrofishing generator (ELT62-IID; Grassl GmbH, Berchtesgaden, Germany). All stunned fish were caught by a second person using a round dip net (diameter: 48 cm, mesh size: 5 mm). Every sampling session was carried out by the same persons (JB and AFC), in order to avoid the introduction of a sampling bias.

Data analysis

All fish species captured were identified to the species level and all invasive gobies were weighed to the nearest 0.2 g (Total mass = M_T), measured to the nearest millimetre (Total length = L_T) and their Fulton's condition factor ($CF = 100 \times M_T / L_T^3$ [g/cm^3]) was calculated. All gobies < 50 mm were recorded as juveniles. All adult gobies were sexed according to the morphology of the urogenital papilla (Kornis et al. 2012). Specimens of native fish species were released immediately after measuring, whereas non-native ones were killed according to the German fishing regulations.

Goby population characteristics were analysed for each river stretch and each year and summarised for

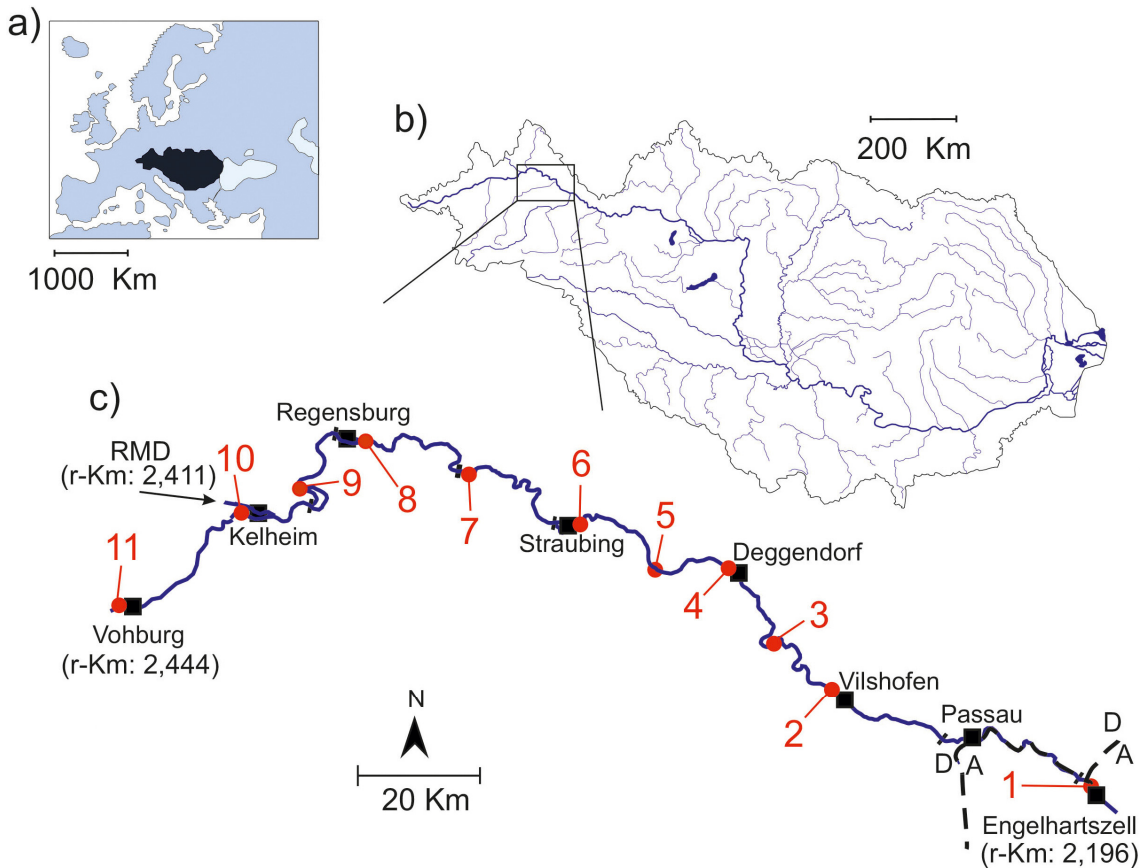


Figure 1. Sampling area along the Danube River. a) Europe, with Danube drainage area highlighted, b) Danube drainage area and c) upper Danube River sampled area. In figure c, the dotted black line indicates the country border between Germany (D) and Austria (A). River kilometres (r-Km) are indicated for the upper, the lowermost sampling stretches and the mouth of the Rhine-Main-Danube canal (RMD-canal). Sampling stretches are indicated by red numbers (1–11), parallel straight lines across the river represent dams and black squares indicate cities.

each annual growth period, i.e. March–October, as suggested by previous studies (Brandner et al. 2013a, c). Specifically, we compared (i) spatial distribution, (ii) relative abundance (gobies caught per PAS, measured by the catch per unit effort (CPUE = number of specimens / number of PAS-points [PAS^{-1}])), (iii) size distribution (measured by L_T), (iv) condition or “health” (estimated by CF) and (v) distribution of sexes (sex ratio = number of females / number of males). To compare goby population characteristics (abundance, sex ratio, L_T and CF) across sampling stretches from each sampling year, for each of the variables we first conducted non-parametric Kruskal-Wallis tests and, in case of significance, then used Mann Whitney U-tests applying a Bonferroni correction to account for multiple comparisons. A comparison of CPUE between sampling done early and late in the year revealed no significant seasonal influence on this variable for any of the invasive goby species (Kruskal-Wallis test: *N. melanostomus*: $n = 24$, $H = 5.38$, $df = 2$, $P > 0.05$; *P. kessleri*: $n = 24$, $H = 5.959$,

$df = 2$; $P > 0.05$; *P. semilunaris*: $n = 24$, $H = 4.594$, $df = 2$; $P > 0.05$), thus data were combined for different months of each year. Data analysis was computed using the free available statistics software PAST 3.06 (Hammer et al. 2001).

Results

In total, 10,408 fish were caught: 3,663 in 2010, 5,230 in 2011 and 1,515 in 2015. The most abundant native species for all years were chub *Squalius cephalus* (Linnaeus, 1758) ($n = 503$), barbel *Barbus barbus* (Linnaeus, 1758) ($n = 426$) and ide *Leuciscus idus* (Linnaeus, 1758) ($n = 337$). Three non-native goby species were caught (tubenose goby *Proterorhinus semilunaris*, bighead goby *Ponticola kessleri* and round goby *Neogobius melanostomus*), with different frequencies (tubenose goby $n = 113$; bighead goby $n = 172$; round goby $n = 7,647$) and varying spatial distribution patterns (Tables 1 and S1). Gobies were present at all

Table 1. Number of sampled invasive adult Ponto-Caspian tubenose, bighead and round gobies and their sex ratios at 11 rip-rap river stretches along the upper Danube River in 2010, 2011 and 2015.

| Sampling year | stretch | Tubenose goby (<i>P. semilunaris</i>) | | | Round goby (<i>N. melanostomus</i>) | | | Bighead goby (<i>P. kessleri</i>) | | |
|---------------|---------|---|--------------|--------------------|---------------------------------------|--------------|--------------------|-------------------------------------|--------------|--------------------|
| | | females [n] | males [n] | sex ratio (f:m) | females [n] | males [n] | sex ratio (f:m) | females [n] | males [n] | sex ratio (f:m) |
| 2010 | 1 | 0 | 0 | – | 76 | 45 | 1.69 | 0 | 0 | – |
| 2011 | 1 | 0 | 0 | – | 100 | 96 | 1.04 | 3 | 0 | – |
| 2010 | 2 | 0 | 0 | – | 372 | 345 | 1.08 | 2 | 1 | 2.00 |
| 2011 | 2 | 1 | 0 | – | 527 | 582 | 0.91 | 6 | 5 | 1.20 |
| 2015 | 2 | 1 | 0 | – | 133 | 120 | 1.11 | 0 | 1 | – |
| 2010 | 3 | 1 | 1 | 1.00 | 61 | 52 | 1.17 | 13 | 12 | 1.08 |
| 2011 | 3 | 1 | 0 | – | 161 | 167 | 0.96 | 7 | 6 | 1.17 |
| 2010 | 4 | 0 | 0 | – | 30 | 30 | 1.00 | 2 | 1 | 2.00 |
| 2011 | 4 | 0 | 0 | – | 102 | 143 | 0.71 | 6 | 4 | 1.50 |
| 2010 | 5 | 0 | 0 | – | 30 | 35 | 0.86 | 0 | 2 | – |
| 2011 | 5 | 0 | 0 | – | 44 | 46 | 0.96 | 2 | 4 | 0.50 |
| 2010 | 6 | 0 | 0 | – | 24 | 44 | 0.55 | 1 | 1 | 1.00 |
| 2011 | 6 | 0 | 0 | – | 134 | 112 | 1.20 | 3 | 1 | 3.00 |
| 2010 | 7 | 0 | 0 | – | 58 | 41 | 1.41 | 6 | 3 | 2.00 |
| 2011 | 7 | 7 | 5 | 1.40 | 208 | 185 | 1.12 | 8 | 3 | 2.67 |
| 2010 | 8 | 1 | 0 | – | 457 | 323 | 1.41 | 5 | 6 | 0.83 |
| 2011 | 8 | 5 | 5 | 1.00 | 428 | 305 | 1.40 | 7 | 7 | 1.00 |
| 2015 | 8 | 3 | 2 | 1.50 | 95 | 80 | 1.19 | 1 | 1 | 1.00 |
| 2010 | 9 | 1 | 0 | – | 89 | 39 | 2.28 | 9 | 13 | 0.69 |
| 2011 | 9 | 11 | 5 | 2.20 | 229 | 193 | 1.19 | 5 | 5 | 1.00 |
| 2010 | 10 | 9 | 1 | 9.00 | 4 | 1 | 4.00 | 0 | 0 | – |
| 2011 | 10 | 4 | 2 | 2.00 | 56 | 47 | 1.19 | 1 | 1 | 1.00 |
| 2015 | 10 | 4 | 2 | 2.00 | 238 | 137 | 1.74 | 0 | 0 | – |
| 2015 | 11 | 0 | 0 | – | 11 | 13 | 0.85 | 0 | 0 | – |

eleven river-stretches and comprised 76% of the total catch. However, we did not find bighead gobies at stretch 11, nor tubenose gobies at stretches 1, 4, 5, 6 and 11 during all sampling campaigns. The highest CPUE of all goby species (10.77 PAS^{-1}) was found at stretch number 2, close to the city of Vilshofen, in 2015, and the lowest (0.13 PAS^{-1}) at stretch 10, close to the city of Kelheim, in 2010 (Table S1).

Proterorhinus semilunaris (Tubenose goby)

The tubenose goby was rarely found in this survey (median CPUE = 0.07 PAS^{-1} , $n = 24$; SE = 0.03). Median CPUE did not differ significantly between years (Kruskal-Wallis test; $H = 4.594$; $df = 2$; $P > 0.1$), but it was higher both in 2011 (0.01 PAS^{-1}) and 2015 (0.28 PAS^{-1}) than in 2010 (0 PAS^{-1}). This goby species was predominantly detected at the lowermost (stretches 2 and 3) and the uppermost sampling sites (stretches 7–9). The stretch-specific highest CPUE for this species was recorded in 2015 at stretches 8 (0.47 PAS^{-1}) and 10 (0.40 PAS^{-1}), where no other gobies were found until 2010 (Brandner et al. 2013b). Total length significantly decreased with sampling time (Kruskal-Wallis test; $H = 39.34$; $df = 2$; $P < 0.001$; Figure 2). No significant differences were detected

between 2010 ($n = 16$, 44–80 mm, median = 61 mm) and 2011 ($n = 54$, 35–106 mm, median = 54 mm), whereas L_T significantly decreased from both 2010 and 2011 to 2015 ($n = 43$, 24–69 mm, median = 40 mm; Mann-Whitney-U, Bonferroni corrected: $P < 0.001$).

Tubenose goby CF also significantly decreased with sampling time (Kruskal-Wallis test; $H = 21.91$; $df = 2$; $P < 0.001$; Figure 3), specifically from 2010 ($n = 16$, $0.94\text{--}1.99 \text{ g/cm}^3$, median = 1.49 g/cm^3) to 2011 ($n = 54$, $0.44\text{--}1.61 \text{ g/cm}^3$, median = 1.17 g/cm^3) and 2015 ($n = 43$, $0.51\text{--}1.71 \text{ g/cm}^3$, median = 1.02 g/cm^3 ; Mann-Whitney-U, Bonferroni corrected: $P < 0.001$). No significant difference was observed between 2011 and 2015. The pooled sex ratio of this species was female dominated during all sampling years (2010: 6.00, 2011: 1.71, 2015: 2.00; stretch specific data Table 1).

Ponticola kessleri (Bighead goby)

Median CPUE of bighead goby was 0.07 PAS^{-1} ($n = 24$; SE = 0.02). For 2010 and 2011 together, CPUE was 0.09 PAS^{-1} ($n = 20$, SE = 0.02) and declined remarkably, but not significantly, in 2015 (0.02 PAS^{-1} , $n = 4$, SE = 0.02) (Kruskal-Wallis test; $H = 6$; $df = 2$; $P = 0.051$). This species was found throughout the

Figure 2. Total length (L_T) of tubenose (*Proterorhinus semilunaris*), bighead (*Ponticola kessleri*) and round goby (*Neogobius melanostomus*) along the upper Danube River in 2010, 2011 and 2015. The centre line denotes the median value, the box encloses the inner two quartiles, the whiskers are drawn up to data points < 1.5 times the box height and circles indicate outliers.

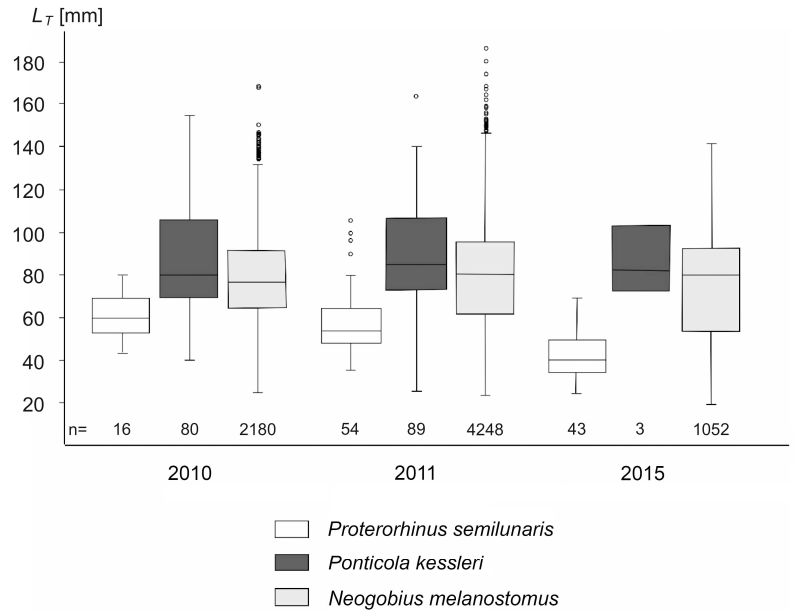
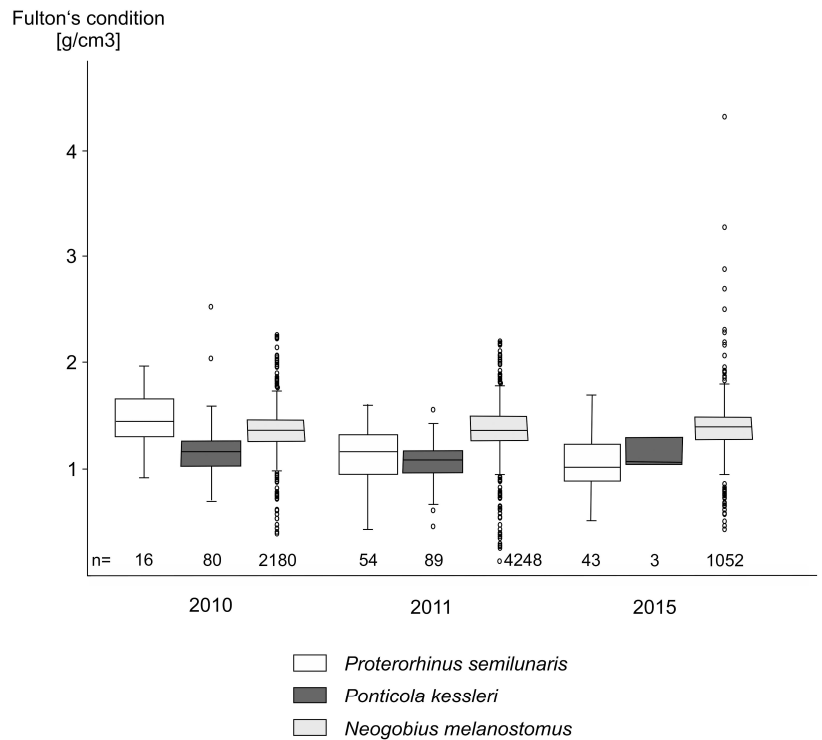


Figure 3. Fulton's condition factor of tubenose (*Proterorhinus semilunaris*), bighead (*Ponticola kessleri*) and round goby (*Neogobius melanostomus*) along the upper Danube River in 2010, 2011 and 2015. The centre line denotes the median value, the box encloses the inner two quartiles, the whiskers are drawn up to data points < 1.5 times the box height and circles indicate outliers.



entire sampling area, but its abundance was low in the uppermost part of the river (stretch 10, CPUE = 0.006 PAS⁻¹). Median L_T did not differ significantly between sampling years (Kruskal-Wallis test; $H = 0.19$; $p = 0.9$; Figure 2). It ranged between 41 and 155 mm ($n = 80$, median = 81 mm) in 2010, between

25–164 mm ($n = 89$, median = 85 mm) in 2011, and between 72–103 mm ($n = 3$, median = 82 mm) in 2015. However, there were significant differences in CF of different years (Kruskal-Wallis test; $H = 10.43$; $df = 2$; $P < 0.05$). Bighead gobies had a significantly higher CF in 2010 ($n = 80$, 0.70–2.52 g/cm³; median

= 1.17 g/cm³) than in 2011 (n = 89, 0.47–1.56 g/cm³, median = 1.09 g/cm³; Mann-Whitney-U, Bonferroni corrected: P < 0.01; Figure 3). Sex ratio was balanced (0.97) in 2010, female dominated (1.3) in 2011 and male dominated (0.5) in 2015 (Table 1).

Neogobius melanostomus (Round goby)

Round goby was the most frequently detected fish species along the upper Danube River, with a median CPUE of 2.44 PAS⁻¹ (n = 24; SE = 0.66), revealing no significant differences among sampling years (2010: 1.11 PAS⁻¹, 2011: 3.98 PAS⁻¹, 2015: 7.50 PAS⁻¹; Kruskal-Wallis test; H = 0.38; df = 2; P = 0.068). The highest relative abundance was found at stretch number 2 in 2015 (CPUE = 10.57 PAS⁻¹, Table S1, Figure 4), close to the location where this species was first detected in Germany, a decade before this study (Paintner and Seifert 2006). In 2010, round goby occurred at low densities in the uppermost part of the sampling area (stretch 10, CPUE = 0.04 PAS⁻¹) where it was first detected in September. This goby species reached stretch 11 only four years later.

Round goby L_T varied significantly between years (Kruskal-Wallis ANOVA; H = 18,04; df = 2; P < 0.001), ranging from 20 mm to 187 mm. Round gobies were significantly smaller in 2010 (n = 2,180, 25–169 mm, median = 78 mm) than in 2011 (n = 4,248, 24–187 mm, median = 81 mm; Mann-Whitney-U, Bonferroni corrected: P < 0.01), and significantly larger in 2011 than in 2015 (n = 1,052, 20–142 mm, median = 81 mm; Mann-Whitney-U, Bonferroni corrected: P < 0.001; Figure 2). Round goby CF ranged between 0.14 and 4.32 g/cm³, and varied significantly between years (Kruskal-Wallis ANOVA; H = 10,02; df = 2; P < 0.01; Figure 3). CF was significantly lower in 2010 (n = 2,180, 0.39–2.28 g/cm³, median = 1.36 g/cm³) than in 2011 (n = 4,248, 0.14–2.19 g/cm³, median = 1.37 g/cm³; Mann-Whitney-U, Bonferroni corrected: P < 0.05) and significantly higher in 2015 (n = 1,052, 0.47–4.32 g/cm³, median = 1.39 g/cm³) than in 2010 (Mann-Whitney-U, Bonferroni corrected: P < 0.05). Sex ratio for the entire upper Danube River was female-biased in every sampling campaign (2010: 1.3; 2011: 1.1; 2015: 1.4; Table 1).

Discussion

Invasive alien gobies have become prime model species in invasion biology (Neilson and Stepien 2009; Cerwenka et al. 2014a, b; Cerwenka et al. 2017; Brandner et al. 2018), but few studies have yet analysed long-term population trends of sympatric goby species from the same habitat, to draw conclusions on their performance and interactions. In contrast, this

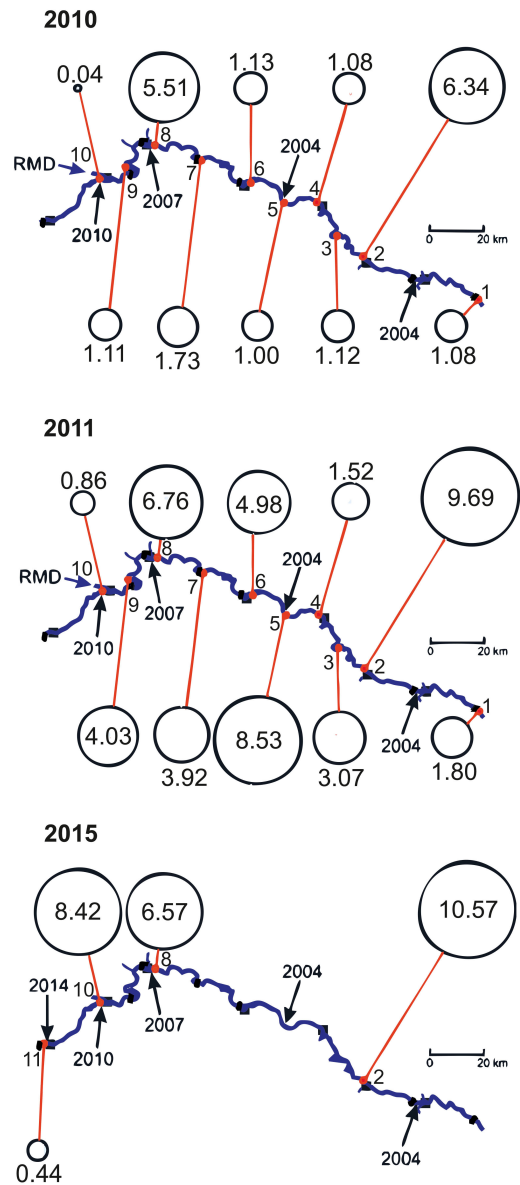


Figure 4. Round goby (*Neogobius melanostomus*) abundances along the upper Danube River (stretches 1–11). Arrows indexed with year dates mark the locality and year of the corresponding first record (2004: Paintner and Seifert 2006; 2007: Brandner et al. 2013a; 2010: Brandner et al. 2013a; 2014: Brandner et al. 2018) and the arrow indexed with RMD shows the mouth of the Rhine-Main-Danube canal. Areas of circles refer relative catch per unit effort (CPUE) in 2010, 2011 and 2015. Absolute numbers of CPUE are presented within the circles.

study for the first time provides a long-term spatio-temporal survey of all co-existing goby species in a 248 river-Km section of the upper Danube River in Germany. Here, the invasive Ponto-Caspian gobies round goby, bighead goby and tubenose goby are currently up to 20 times more abundant than the formerly characteristic native species chub, barbel and

ide (Brandner et al. 2013b). They currently comprise up to two thirds of the total fish biomass, at least in the man-made shoreline habitats. These local findings for the Danube match the general observation of the formation of novel fish community structures in southern Germany, with declines of many specialised native species and range expansions of non-native generalist fishes (Mueller et al. 2018). The data suggest that tubenose goby are most successful in terms of range expansion and persistence, whereas round goby are most successful in terms of abundance. This is true both for the upper Danube River investigated here, as well as on a global scale (Kornis et al. 2012; Mombaerts et al. 2014).

Round goby is considered one of the most successful IAS worldwide. The results of this study underline its supreme global invasive potential by focusing on an important local perspective. Within only about one decade after its first introduction, round goby has rapidly become the dominant fish species, in terms of abundance, within the upper Danube River. Although reaching peak abundances in longer established areas up to 18 PAS⁻¹, median round goby abundance levelled at a CPUE of about 4 PAS⁻¹, which seems to represent the carrying capacity of this species in this habitat. Obviously, an overwhelming propagule pressure, fast spread rates and high reproductive success enabled round goby a fast establishment within the entire invaded ecosystem with a range expansion that is still ongoing (Brandner et al. 2018). Here, the speed of range expansion seems to be driven by the ability to establish populations over very short time-spans (Brandner et al. 2013c), in combination with a long-distance dispersal of single pioneering individuals that reveal upstream directed migration rates of up to 17 river-Km/year (Brandner et al. 2013b). Our data provide evidence for mean dispersal rates of about 10 river-Km/year without the help of anthropogenic transportation vectors. Šlapanský et al. (2017) also found a contiguous range expansion along two connected non-navigable rivers, although with lower dispersal rates, ranging from 1.2 to 3.2 Km/year. Most probably, gaps between newly introduced (sub-)populations were then closed by a continuous downstream-directed short distance dispersal of drifting juveniles (Janáč et al. 2013). Moreover, round goby invasion success has also been demonstrated to be related to its high phenotypic plasticity (Cerwenka et al. 2014a) and genetic adaptability (Cerwenka et al. 2014b) which, in turn, are associated with several other intrinsic factors: (i) a broad trophic niche (Brandner et al. 2013a), (ii) high fecundity and fast reproductive cycles (L'avrincikova et al. 2007) and (iii) modest requirements for the quality of nesting sites (Sapota et al.

2004). For round goby, the “bigger is better” and the “individual trait utility” hypotheses have already been confirmed to explain its invasion success (Brandner et al. 2018). In this context, pioneering invaders with their greater exploratory behaviour, highly adaptive phenotypic plasticity and increased competitive ability seem to act as prime emperors of new habitats, strongly following and benefiting from man-made river-bank structures.

The “bigger is better” hypothesis postulated for invasion success in round goby does not seem to hold true for the comparison among sympatrically occurring gobies analysed in this study. Specifically, the biggest-growing species, bighead goby, revealed a decreasing population trend over time, whereas the smallest-sized tubenose goby revealed an increasing population trend, despite a decrease in total length and Fulton's condition factor. Thus, on the level of competition among species, different factors such as habitat and food preference seem to be of greatest importance for determining performance and invasion success (see also Adrian-Kalchhauser et al. 2017; Nagelkerke et al. 2018).

Bighead goby invasion apparently slowed down or has even stopped, given that this species has not yet been reported far upstream from the point where the upper Danube River main course becomes non-navigable. A scarce survival in ballast water and low upstream migration ability may limit its invasion range, similarly to what happens for round goby (Roche et al. 2013). However, recently, Simonović et al. (2017) found an ongoing invasion of this species in the non-navigable Sava River, a conflux to the middle Danube River in Slovenia. This species strongly depends on a continuous availability of amphipods as a superior prey resource throughout the year (Brandner et al. 2013a) and reveals low interspecific competitive performance (Števove and Kováč 2013). Both factors may explain the limited invasion success in situations with sympatric occurrence with other gobies. In the upper Danube River, bighead goby experienced a boom-phase shortly after first introduction (Paintner and Seifert 2006): both abundance and invasion range rapidly increased. However, the boom-phase was followed by a population crash (“bust”) shortly after the invasion of round goby in 2004. This boom and bust pattern has also been reported in River Rhine (Adrian-Kalchhauser et al. 2016; Borcharding et al. 2016), River Meuse (van Kessel et al. 2016) and the Danube River (Cerwenka et al. 2014a; Janáč et al. 2018). Apparently, a “competition battle” between round and bighead goby began at this point in time, with bighead goby losing the race. In contrast to what Kováč et al. (2009) found, round goby has seemingly outcompeted bighead

goby in terms of numbers and densities. This is particularly remarkable because bighead goby grows larger than round goby, and round goby is its most consumed fish prey (Brandner et al. 2013a). The sympatric Ponto-Caspian gobies in the upper Danube River may be an ideal study case for better understanding the frequency and importance of boom and bust dynamics, which requires empirical studies of large, representative, long-term data sets that use clear definitions of boom-bust, appropriate analytical methods, and careful interpretation (Strayer et al. 2017).

Although in relatively low densities, tubenose goby was consistently found along almost the entire upper Danube River during this five-year investigation period, making it the most successful gobiid invader from a perspective of range coverage. Because this species has the longest invasion history of all gobies in this river section (Ahnelt et al. 1998), it can also be classified as the most persistent goby species there. However, findings of this study indicate that tubenose goby seems to face a distinct suppression by bighead goby: strong intraguild predation (Brandner et al. 2013a) may explain its low CPUE in 2010, when a 2.4-fold higher CPUE of bighead goby was observed. Tubenose goby populations recovered in 2015, with a 16-fold higher CPUE than bighead goby, after the bighead goby population breakdown.

Tubenose goby may profit from low interspecific competition with other non-native goby species, given that it occurred at relatively high abundance at sites where other species were absent or only present in low densities. In addition, tubenose goby seems to benefit from the elevating “competition battle” between sympatric populations of round goby and bighead goby, by mitigating its predatory pressure. Tubenose goby may have been relieved from its strongest (intraguild) predator due to decreasing population density of bighead goby. However, this is not in line with Šlapanský et al. (2017) who reported tubenose goby abundance to be negatively influenced by round goby establishment, while no impact on native fish could be observed. Jakovlić et al. (2015) reported a restriction of round goby to the navigable Sava reaches in the middle Danube area, although its distribution range still seems to be expanding there. Both these studies and the results presented herein indicate that there is no correlation between current goby distribution – at least after secondary spreading – and navigability of rivers, which makes prediction of future invasions and ongoing range expansions difficult.

No further goby species have been detected in this study. Racer goby preferentially inhabits backwater habitats (Haertl et al. 2012) and may not be invasive in the main river channel or, alternatively, may still be in the invasion lag-phase, as defined by Strayer et

al. (2017). Still, the presence of other alien goby species within the Danube River cannot be excluded. The monkey goby (*Neogobius fluviatilis*) is already invasive in the Hungarian section of the Danube River (Molnár 2006), in the River Rhine (van Kessel et al. 2009; Borcherding et al. 2011), in the Vistula River (Grabowska et al. 2010) and in several other riverine freshwater habitats, and may thus already inhabit the upper Danube River.

Population dynamics of IAS depend on: (i) intrinsic species-specific factors, (ii) extrinsic environmental-specific factors, including human habitat alteration, (iii) and invasion-specific features, such as propagule pressure (introduction frequency and number of introduced individuals) and time elapsed since first introduction (Donaldson et al. 2014). Thus, an unambiguous generalisation and forecast of invasion success remains difficult and requires large comparative datasets. Invasive gobies are no exception: their increasing invasive success is apparently determined multifactorially (Brandner et al. 2013a; Cerwenka et al. 2014a; Hirsch et al. 2016), it is species-specific (Cerwenka et al. 2014b), highly dynamic (Brandner et al. 2013c) and may even depend on single individuals (Cerwenka et al. 2017). Presently, the following population dynamics may best characterise invasion histories of invasive alien gobies in the upper Danube River: “boom and bust” in tubenose and bighead goby and “equilibrium” in round goby. Racer goby may still be in the “lag-phase”, although it remains unclear if it will become invasive.

However, population dynamics are not necessarily stable and may rather change over short time periods. In this context, interactions with other (invasive) species may alter population dynamics directly or indirectly. Interspecific competition between round and bighead goby may not only influence the abundance of the involved species, but also indirectly the one of a third party, here the tubenose goby. Another example of such a synergistic impact is the “killer shrimp” *Dikerogammarus villosus* (Sowinsky, 1894): this invasive alien Ponto-Caspian amphipod may have contributed to the creation of a novel ecosystem in two different ways. First, it may have contributed to round goby invasion success as a major food resource of invasive round goby (Brandner et al. 2013a), and second, as a driver of native amphipod decline by a synergistic impact on native amphipods together with round goby (Beggel et al. 2016).

Introduction and dispersal of Ponto-Caspian gobies are globally associated with industrial shipping (Danube River: Wiesner 2005; River Rhine: Kalchauer et al. 2013; Hirsch et al. 2016; Baltic Sea: Leppäkoski and Olenin 2000; North American Great Lakes: Corkum et al. 2004). Hence, industrial harbours may

act as key inoculation points and distinct propagation step-stones (Wiesner 2005; Kalchhauser et al. 2016), supporting a genetic admixture of different source populations eventually changing species invasiveness (Cerwenka et al. 2014b). However, but in line with our data, recent publications report ongoing (self)dispersal and secondary invasions of Ponto-Caspian gobies into headwater habitats decoupled from (industrial) shipping (Jakovlić et al. 2015; Šlapanský et al. 2017). Because in the Danube there is no industrial shipping upstream of the city of Kelheim, new propagules cannot arrive there using this vector. Besides industrial transportation and natural migration, anthropogenic ecosystem alteration may also favour dispersal and success of IAS (Pander et al. 2016). Artificially reinforced shoreline structures, such as rip-rap habitats – a highly frequent intervention in the Danube River, but also in numerous other altered fluvial ecosystems and canals – may greatly support aquatic invasions. Such man-made habitats may support establishment and can thus facilitate secondary range expansion of IAS (Brandner et al. 2015). Given the high preference of gobies for man-made microhabitat structures, in particular *N. melanostomus*, this may also explain the pronounced differences in CPUE among neighbouring sampling sections. However, such environmental stressors resulting from habitat modifications are unlikely to be the sole explanation of invasion success (Fedorenkova et al. 2013; Cerwenka et al. 2017). Multiple (environmental) factors and (species-specific) traits may interact with each other and make every invasion unique. Thus, general predictions are difficult or even impossible. In our case, this is clearly exemplified by highly differential success of non-native Ponto-Caspian gobies within one stream. For managing aquatic ecosystems, evidence-based knowledge on population trends and performance indicators of both invasive and native species is most crucial (Geist 2015; Geist and Hawkins 2016). The data presented in this study suggest that a systematic inter-calibrated sampling programme, along with cross-border monitoring strategies, should urgently be implemented.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Sampling details of the 11 rip-rap river stretches along the upper Danube River.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Cerwenka_et al_Table_S1.xlsx