

Research Article

An isolated round goby population in the upper Elbe: population characteristics and short-term impacts on the native fish assemblage

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Abstract

The round goby *Neogobius melanostomus* is a small invasive benthic fish that has caused multiple and variable impacts in freshwaters. One of the most recent round goby introductions occurred in the upper Elbe in 2015. In this case, the new population was isolated from other populations both by land and by at least 600 river km. Monitoring of this population has provided a unique opportunity to describe the characteristics of round gobies naturally spreading from a single introduction point and to examine its effects on native fish. Passive downstream dispersal of early life stages has played a central role in population spread, with the proportion of small fish increasing downstream and decreasing with time. The sex ratio of the novel population was strongly female-biased and with no apparent spatial structure. Round goby introduction appears to have had a negative impact on native 0+ fish abundance and species richness. Relationships with $\geq 1+$ fish were more diverse, ranging from a significant decrease in chub *Squalius cephalus* abundance to a significant increase in European eel *Anguilla anguilla* abundance as goby abundance increased. As no impacts on these species have been reported before, the study appears to provide further evidence for case-specificity in round goby impact.

Key words: biological invasions, case-specific impact, Ponto-Caspian gobiids, shipping, drift, biotic resistance

Introduction

The severity of threat from biological invasions on native ecosystems and economies has been well documented and acknowledged, at least among the scientific community (Simberloff et al. 2013). While identification of potential invaders and predictions of their possible establishment and spread in novel areas is now relatively well developed (Ricciardi et al. 2013), predicting invader impacts represents one of the major challenges facing invasion biology today. Unreliable impact predictions may represent a significant problem as regards both management practice and future studies searching for general impact patterns across species and ecosystems. Impacts of many species are now known to be case specific (Ricciardi and Kipp 2008; Pyšek et al. 2012; Ricciardi et al. 2013); hence, there is an urgent need for further impact case studies that would allow more precise impact predictions.

The round goby *Neogobius melanostomus* (Pallas, 1814), a small Ponto-Caspian gobiid species, has become invasive in both Europe and North America, with earliest records of expansion coming from the early 1990s (Kornis et al. 2012). In both continents, a combination of transfer by marine and inland shipping and active swimming has contributed to rapid long-range dispersal of the species (Hensler and Jude 2007; Roche et al. 2013), with anthropogenically modified habitats such as navigable rivers with rip-rap banks typically facilitating successful establishment of new populations (Ray and Corkum 2001; Janáč et al. 2016). A combination of efficient reproductive strategy (high fecundity, batch-spawning, parental care; MacInnis and Corkum 2000; Meunier et al. 2009; Konečná et al. 2016), phenotypic plasticity (Hôrková and Kováč 2014, 2015; Cerwenka et al. 2014) and wide environmental tolerance (Charlebois et al. 2001) have been key factors in the successful establishment and rapid population explosion of many of the invasive goby populations (Marsden and Jude 1995; van Kessel et al. 2016; Šlapanský et al. 2017). Once abundant, these populations have the potential to affect recipient systems in a number of ways (see e.g. Kornis et al. 2012 for review), with impacts on the local fish assemblage commonly at the centre of attention for both scientists and the general public.

Round goby impacts on native fish assemblages are strongly case-specific (i.e. context-dependent, varying both between species and within the same species between invaded ecosystems; Janáč, *in prep.*). Studies on Danubian tributaries, for example, suggested no effect on native fish assemblages, possibly due to a lack of species with niches overlapping that of round goby and related competition relaxation (Janáč et al. 2016; Šlapanský et al. 2017). On the other hand, competition has been implicated in the decline of juvenile turbot *Psetta maxima* (Linnaeus, 1758) abundance near the Latvian coast of the Baltic Sea (Ustupš et al. 2016), and perhaps the decimation of river bullhead *Cottus perifretum* (Freyhof, Kottelat and Nolte, 2005) populations recorded in the River Meuse (van Kessel et al. 2016). Note, however, that populations of its close relative, the European bullhead *Cottus gobio* Linnaeus, 1758, appear to have flourished in the middle Danube near Vienna, despite round goby being present for over a decade (Janáč et al. 2018). Similar disparities have also been noted in North American impact studies. While several studies convincingly documented population failures in several benthic species following round goby introduction to the Great Lakes (Janssen and Jude 2001; Lauer et al. 2004; Riley et al. 2008), others found contradictory results (Kornis et al. 2013; Leino and Mensinger 2016), and several studies have documented concurrent negative, neutral and positive effects on species within the same assemblage (Raab et al. 2018; Morissette et al. 2018). Despite the general case-specificity, there is an apparent trend regarding highest risk of negative impacts on small benthic fishes displaying niche overlap with round goby, e.g. gobiids, cottids and darters (Hirsch et al. 2016; Janáč, *in prep.*).

In 2015, a new isolated round goby population was detected in the upper River Elbe near the inland port of Ústí nad Labem (Buřič et al. 2015). Given that the population was restricted to the proximity of the port, with the nearest Elbe population found 600 km downstream in the lower Elbe near Hamburg (Hempel and Thiel 2013), commercial shipping was determined as the most probable vector. The upper Elbe population was morphometrically distant from the Danubian populations (Roche et al. 2015), later confirmed genetically by Janáč et al. (2017), suggesting that the population originated through admixture of several source populations. Since this first observation, the fish assemblage in the Czech part of the Elbe has been continuously monitored. As monitoring has been based on four distantly placed main sites, each representing different stages of population development (see Roche et al. 2015), the data covers a wide range of round goby abundance. Given that the main effects of round goby on native fish abundance commonly occur as early as four years since first occurrence (Janáč, *in prep.*), and in some cases even earlier (see Janssen and Jude 2001; van Kessel et al. 2016), data from 2016–2018 monitoring theoretically provides sufficient material for describing short-term impacts of round goby on the native fish assemblage. Furthermore, these data provide a unique picture of round goby population expansion downstream from a single introduction point (movement being limited upstream by a weir near the introduction point). The main aim of this study, therefore, was to describe (i) population characteristics of a newly established round goby population and (ii) impacts of the population on the native fish assemblage.

Materials and methods

Data sampling

This study took place along a 35 km stretch of the navigable Czech section of the River Elbe, between Dolní Žleb (river km 363) and Ústí nad Labem (river km 328; Figure 1). Channel width ranges from 100 m to 130 m and annual mean discharge ranges from 293 m³s⁻¹ at Ústí nad Labem to 311 m³s⁻¹ at the state border near Dolní Žleb. The river banks along the whole study section have been stabilised with stony rip-rap (10–50 cm), while the river bottom comprises sections of natural stony substrate, partly supplemented by sand-gravel beaches. Sampling of the round goby population was carried out between 2016 and 2018, with four sites (A–D) sampled biannually in spring (May–June) and autumn (September–October; Table 1; Figure 1). Sampling always took place during the day (9:00–16:00). Conditions at each sampling site remained relatively stable between years, with no substantial variation in discharge between sampling occasions. Fish were captured by electrofishing using portable backpack electrofishing gear (SEN f. Bednář, Czech Republic, maximum output 225/300V, frequency

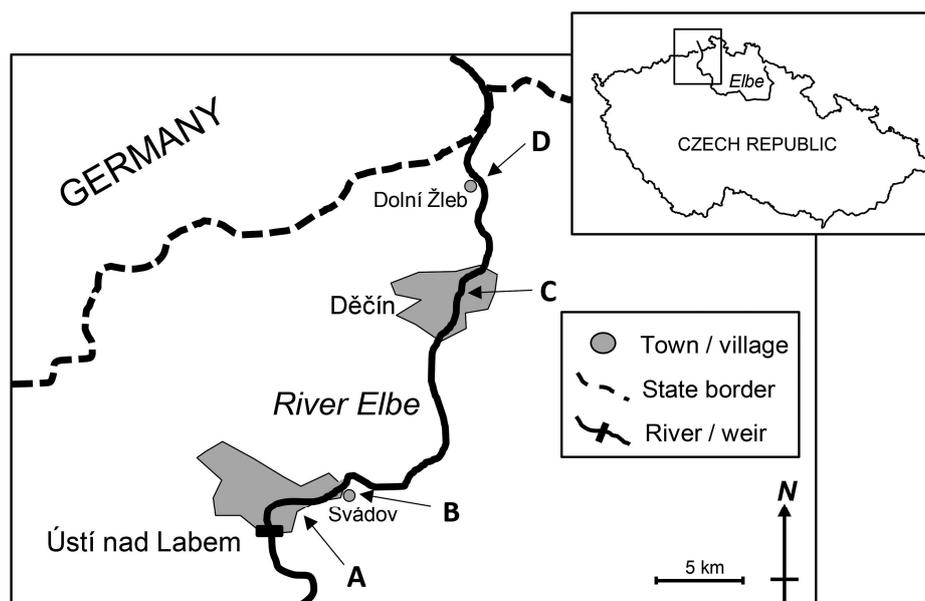


Figure 1. Map of the upper section of the Elbe. Sampling sites are marked by capital letters.

Table 1. Sampling site location and sampling dates (year/month/day) for round goby monitoring surveys in the Elbe.

Site	A	B	C	D
Name	Ústí nad Labem	Svádov	Děčín	Dolní Žleb
Latitude	50.6490639	50.6661258	50.7819181	50.8427964
Longitude	14.0450797	14.1007403	14.2074183	14.2192544
River Km	328	333	353	363
≥1+ Fish Sampling Dates				
2016/05/17	x	x	x	x
2016/10/19	x	x	x	x
2017/06/08	x	x	x	x
2017/09/21	x	x	x	x
2018/06/07	x	x	x	x
2018/09/19	x	x	x	x
Total	6	6	6	6
0+ Fish Sampling Dates				
2006/08/08	x			
2010/09/22				x
2013/09/05	x		x	x
2015/08/26			x	x
2016/10/19	x		x	x
2017/09/21	x		x	x
2018/09/19	x		x	x
Total	5	0	5	6

75–85 Hz) fitted with an elliptical stainless steel anode (250 × 150 mm) with 4 mm mesh netting. Each sample site consisted of 100 m of rip-rap shoreline, with electrofishing conducted by wading in an upstream direction. As the nearshore zone was relatively shallow (0.7 m), we were able to sample the whole rip-rap zone up to a distance of 2 m from the bank. All fish sampled were identified and measured to the nearest millimetre (standard length, SL) on the bankside. Round goby sex was determined in the field by urogenital papillae (Kornis et al. 2012). All measured fish (native and non-native) were immediately returned back to the river.

Data analysis

On each sampling occasion, sex-ratio deviance from parity was tested using Chi-square tests. Although not originally hypothesised, a high proportion of females (see Results) prompted us to search for spatial or temporal patterns in sex-ratio, i.e. whether the proportion of females increased downstream and with year (see Discussion for the rationale behind this test). Similarly, we searched for changes in fish size along the same gradients in order to confirm whether the novel population spread mainly via passive downstream dispersal (see Janáč et al. 2013a, b), i.e. drift causing size to decrease downstream and increase with year. In this case, sampling year was expressed as the number of years from first occurrence of round goby (1–3), with sites ranked in downstream order (1–4, corresponding to sites A–D). Fish size would naturally be expected to differ between spring and autumn, due to both growth increments during the year and to the occurrence of young-of-the-year fish in autumn. Similarly, sex-ratio could potentially change between spring and autumn as intersex differences in goby movement patterns may vary between seasons (Šlapanský et al., *in prep.*). Both fish size and sex-ratio, therefore, were visualised separately and time of year (spring, autumn) was included in the analysis as a random factor. The effect of year and site on fish size was tested, therefore, using linear mixed models (LMM), while their effect on proportion of females in the population of fish with determined sex (non-juvenile population) was tested using generalised linear mixed model (GLMM, Bernoulli distribution). LMMs were validated using a visual check of model residuals (normality, lack of patterns).

Round goby impact on the native fish assemblage was tested using two different datasets. Effect on $\geq 1+$ fish was analysed using a dataset comprising both spring and autumn samples from 2016–2018 at the four sampling sites. The dataset for testing effect on 0+ fish comprised (i) samples from routine 0+ fish monitoring from the period before round goby occurrence (2006–2015; conducted in the same habitats and the same months as our autumn 2016–2018 samples; data available for three of the four sampling sites), and (ii) autumn samples from 2016–2018 for the same three sites (Table 1).

Impact on species richness and abundance of the most common native species was tested using GLMM (Poisson distribution detected in all cases). All these GLMMs contained round goby abundance as the single fixed effect and sampling occasion and site as random effects; individual-level random effects were added to those models that displayed over-dispersion.

We also analysed impact on structure of the native fish assemblage by searching for possible round goby abundance effects on similarity between native fish assemblage samples. These similarities were expressed as distance matrices based on (i) binary Jaccard distance, and (ii) quantitative Bray-Curtis

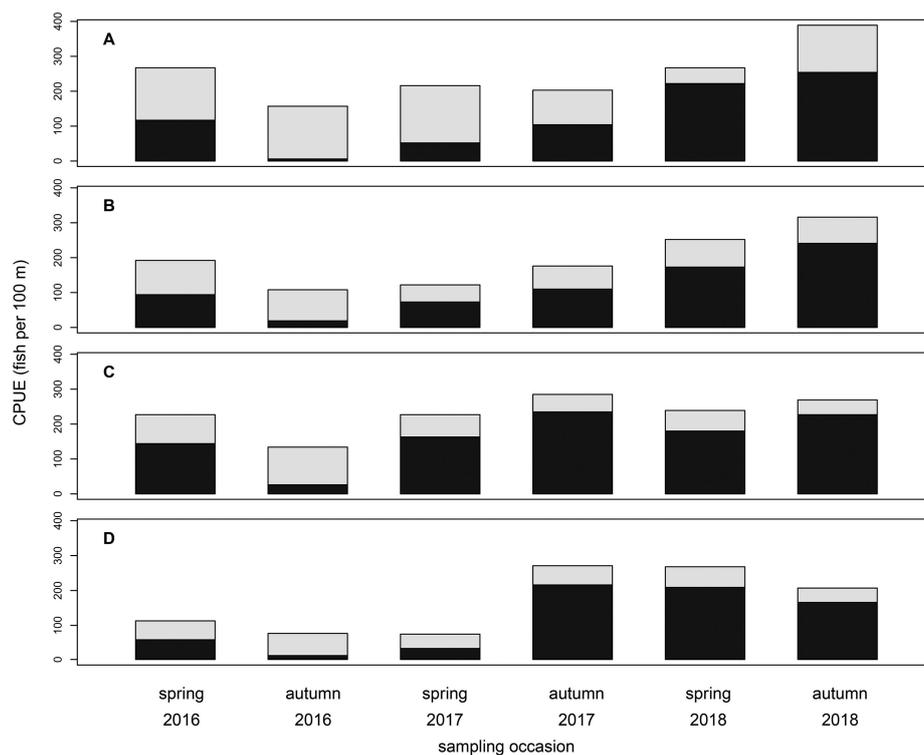


Figure 2. Abundance of round goby (dark) and other fish species (light) captured along the nearshore zone of the upper Elbe between 2016 and 2018. See Table 1 for site codes (A–D).

distance (data were fourth-square root transformed for Bray-Curtis distance in order to down-weight rare species). Projection of these matrices onto a two-dimensional space was conducted using non-metric multidimensional scaling (NMDS). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to test for the effect of goby abundance on these distance matrices, with the effect of goby being controlled for by placing sampling occasion and site in front of goby abundance in the model formula. As round goby abundance was highly correlated with sampling occasion (Figure 2), we also used variance partitioning to determine the proportion of variability in distance matrices explained solely by round goby abundance. Based on a series of partial distance-based redundancy analyses (db-RDA) conducted on a combination of three predictors expected to affect assemblage structure (sampling occasion, site, round goby abundance), variance partitioning isolated the proportion of variance explained solely by these predictors and that explained by their joint effect (Oksanen et al. 2015).

All analyses were conducted in R version 3.5.2. (R Core Team 2015), using the packages *nlme* (Pinheiro et al. 2017), *lme4* (Bates et al. 2015) and *vegan* (Oksanen et al. 2015).

Results

Population characteristics

A total of 4167 $\geq 1+$ fish (2659 round gobies) and 1622 0+ fish (375 round gobies) were captured (Appendix 1). Since their first detection in 2015, round

Table 2. Results of mixed models for predicting the effect of space (sites ranked in downstream order) and time (years) on round goby size (using LMM) and sex ratio (proportion of females in the non-juvenile population; using GLMM). Significant P values in bold.

Response	Predictor	Estimate	SE	t (z)	P
Fish size (SL, in mm)	Intercept	56.15	1.41	39.86	< 0.001
	Space	-3.273	0.317	-10.32	< 0.001
	Time	4.263	0.451	9.44	< 0.001
Sex ratio	Intercept	-0.830	0.259	-3.20	0.001
	Space	0.049	0.048	1.02	0.306
	Time	0.039	0.072	0.54	0.586

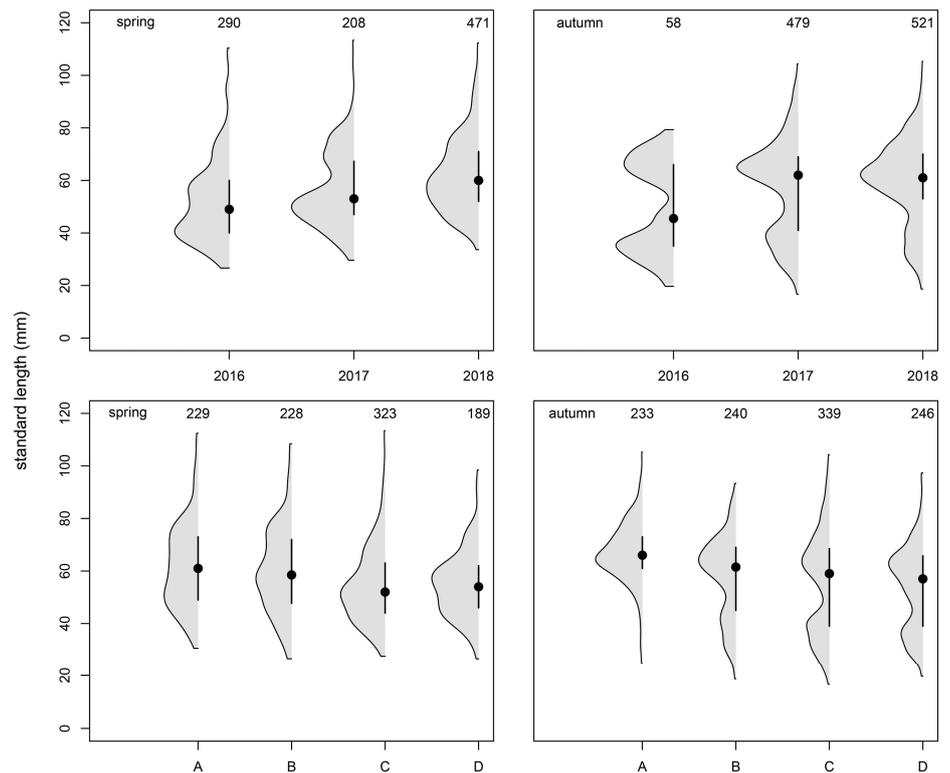


Figure 3. Change in round goby size along gradients of time (upper panels; years) and space (lower panels; sites) in spring (left panels) and autumn (right panels). Size distribution is depicted by the grey areas, the median by full points and inter-quartile ranges by solid lines. Sample size is indicated above each plot. See Table 1 for site codes (A–D).

gobies rapidly came to dominate samples at all sites, increasing from an average dominance of 52 and 14% in spring and autumn of 2016 to 76 and 77% in spring and autumn of 2018 (Figure 2). Chub *Squalius cephalus* (Linnaeus, 1758), European eel *Anguilla anguilla* (Linnaeus, 1758), roach *Rutilus rutilus* (Linnaeus, 1758), and gudgeon *Gobio gobio* (Linnaeus, 1758) dominated the native $\geq 1+$ fish assemblage, while chub, roach, European perch *Perca fluviatilis* Linnaeus 1758 and barbel *Barbus barbus* (Linnaeus, 1758) dominated the native 0+ fish assemblage.

Round goby size increased significantly with time (from 2016 to 2018) and decreased in a downstream direction (LMM, $n = 2027$, $P < 0.001$ for both terms; Table 2). Original small-sized, juvenile-dominated populations were replaced with larger fish with a more even size distribution over time (Figure 3; Appendix 2). Sex ratio did not change significantly along gradients

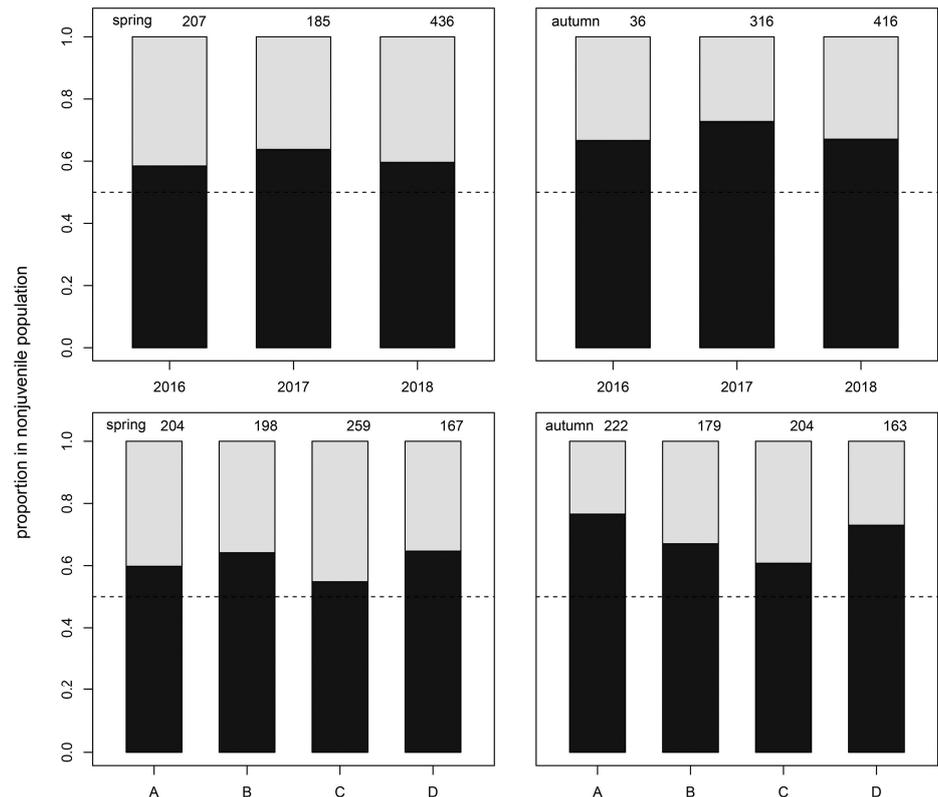


Figure 4. Proportion of females (dark) and males (light) in the round goby non-juvenile population and their variation along gradients of time (upper panels; years) and space (lower panels; sites) in spring (left panels) and autumn (right panels). Sample size is indicated above each plot. Dashed lines mark parity. See Table 1 for site codes (A–D).

of time or space (GLMM, $n = 1596$, $P = 0.306$ and 0.586 for space and time, respectively; Table 2). On all sampling occasions, the sex ratio was significantly female-biased (Chi-square tests, all $P < 0.05$; Appendix 2), with females ranging from 58 to 73% of the non-juvenile population (Figure 4; Appendix 2).

Impact

While abundance of $\geq 1+$ chub decreased significantly with increasing round goby abundance (GLMM, $n = 24$, $P < 0.001$), abundance of $\geq 1+$ European eel increased significantly (GLMM, $n = 24$, $P = 0.007$; Table 3a, Figure 5). No significant effect on $\geq 1+$ native species richness was observed, or on the abundance of other $\geq 1+$ native species (GLMM, all $n = 24$ and $P > 0.05$; Table 3a), though decreasing trends in $\geq 1+$ barbel and European perch were close to significance (Table 3a, Figure 5). On the other hand, round goby had a significant negative effect on $0+$ species richness (GLMM, $n = 16$, $P = 0.014$), as well as the abundance of $0+$ chub and roach (GLMM, both $n = 16$, $P < 0.001$ and $P = 0.013$), with no significant effects on other $0+$ fish (GLMM, all $n = 16$ and $P > 0.05$, Table 3b; Figure 6).

Fish assemblage structure appeared to change over a gradient of round goby abundance when projected onto two-dimensional space (significant linear fits to the first-two NMDS axis coordinates, all $P < 0.05$; Figure 7). On the other hand, goby abundance explained only a very small amount of

Table 3. Results of generalised linear mixed models used for testing the effect of round goby abundance on the abundance and richness of $\geq 1+$ (a) and $0+$ (b) native species. Models in which individual-level random effects were used to cope with over-dispersion are marked with ILRE.

a) $\geq 1+$ fish					
Response	Predictor	Estimate	SE	z	P
<i>Anguilla anguilla</i>	Intercept	3.84	0.34	11.33	< 0.001
ILRE	Round goby	-0.01	0.00	-2.69	0.007
<i>Squalius cephalus</i>	Intercept	0.84	0.47	1.78	0.075
ILRE	Round goby	0.01	0.00	4.40	< 0.001
<i>Rutilus rutilus</i>	Intercept	1.58	0.59	2.69	0.007
ILRE	Round goby	0.00	0.00	-0.75	0.455
<i>Gobio gobio</i>	Intercept	0.51	1.46	0.35	0.727
ILRE	Round goby	-0.01	0.01	-0.66	0.509
<i>Perca fluviatilis</i>	Intercept	1.42	0.66	2.17	0.030
	Round goby	-0.01	0.00	-1.90	0.057
<i>Gymnocephalus cernua</i>	Intercept	0.31	0.70	0.45	0.655
	Round goby	0.00	0.00	0.51	0.607
<i>Barbus barbus</i>	Intercept	-1.33	3.24	-0.41	0.681
	Round goby	-0.02	0.01	-1.90	0.057
Species richness	Intercept	1.79	0.16	11.07	< 2e-16
	Round goby	0.00	0.00	0.06	0.951
b) $0+$ fish					
Response	Predictor	Estimate	SE	z	P
<i>Squalius cephalus</i>	Intercept	3.45	0.37	9.23	<0.001
ILRE	Round goby	-0.01	0.00	-3.64	< 0.001
<i>Rutilus rutilus</i>	Intercept	2.28	0.00	550.02	<0.001
ILRE	Round goby	-0.01	0.00	-2.48	0.013
<i>Perca fluviatilis</i>	Intercept	1.09	0.69	1.57	0.117
ILRE	Round goby	0.00	0.00	0.66	0.512
<i>Barbus barbus</i>	Intercept	1.15	0.76	1.51	0.131
ILRE	Round goby	-0.01	0.01	-1.52	0.129
<i>Leuciscus idus</i>	Intercept	1.12	0.62	1.80	0.072
ILRE	Round goby	-0.01	0.00	-1.46	0.144
Species richness	Intercept	1.97	0.12	16.38	<0.001
	Round goby	0.00	0.00	-2.46	0.014

variability in both $\geq 1+$ and $0+$ native fish composition when controlled for by site and year, with the term “goby abundance” being marginally significant when analysing Bray-Curtis distances of $0+$ fish assemblage samples and non-significant in the other three cases (Table 4). Variance partitioning revealed that the lack of effect was most likely due to a high proportion of assemblage structure variability attributable to goby abundance being explained by sampling occasion (Table 5). While a proportion of $0+$ assemblage structure similarity was explained by round goby abundance, this was only the case for very little (Bray-Curtis similarity) or none (Jaccard similarity) of the $\geq 1+$ fish assemblage structure variability (Table 5).

Discussion

The novel round goby population introduced to the upper Elbe now appears to have successfully established itself, growing in both numbers and area colonised. With probable introduction between 2013 and 2015 (Roche et al. 2015), it took gobies just 2–4 years to become the dominant fish caught during nearshore fish surveys along our 35 km river stretch. While

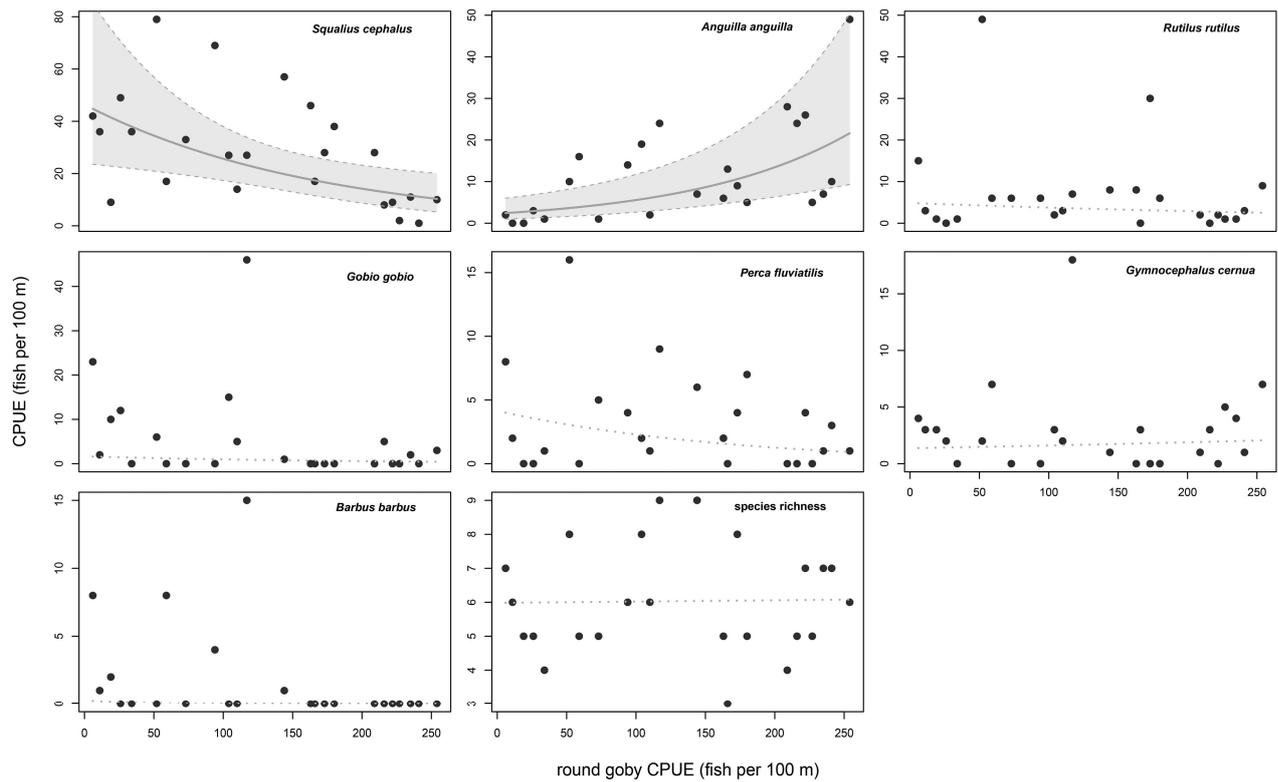


Figure 5. Relationship between round goby abundance and abundance of the most common $\geq 1+$ fish species and native species richness (based on 24 samplings in all cases). Significant effects (according to GLMM) are depicted by predicted curves (solid lines) and their 95% confidence interval bands (grey areas), while non-significant trends are depicted by dotted curves.

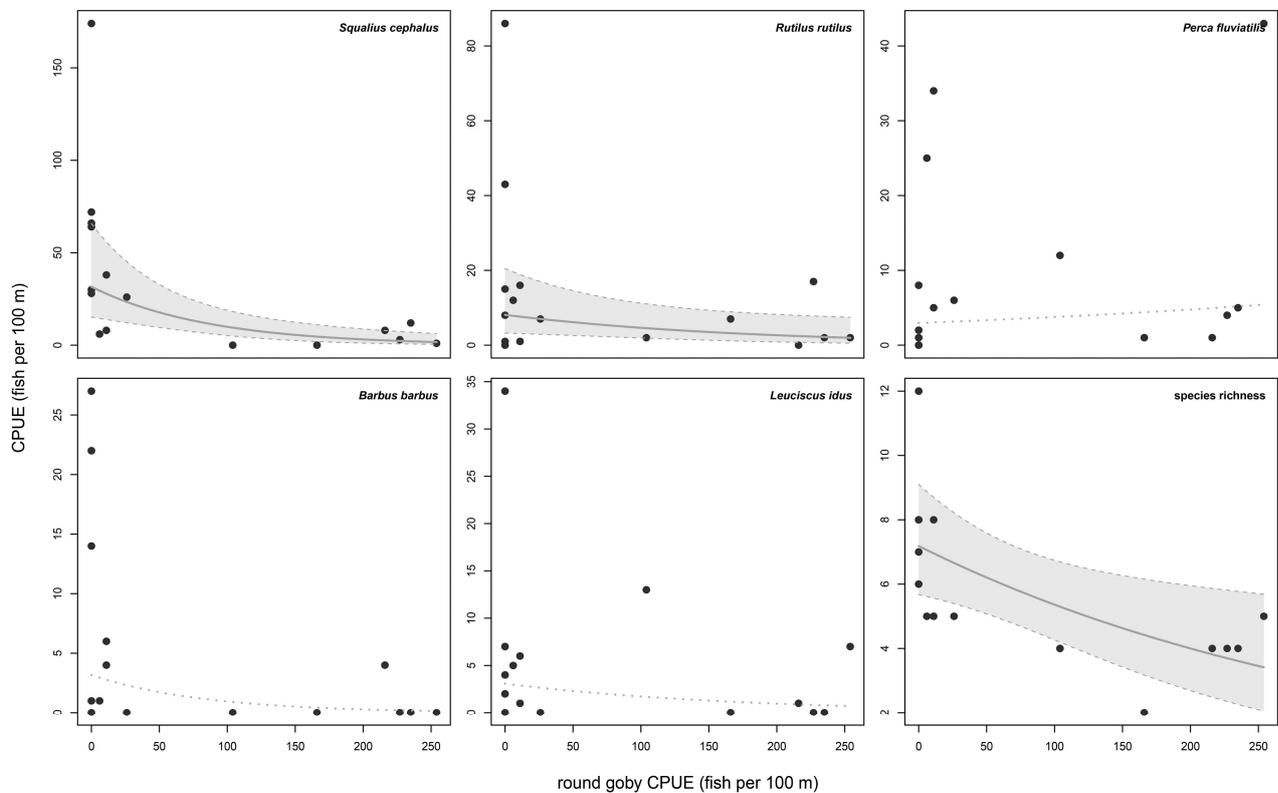


Figure 6. Relationship between round goby abundance and abundance of the most common $0+$ fish species and native species richness (based on 16 samplings in all cases). Significant effects (according to GLMM) are depicted by predicted curves (solid lines) and their 95% confidence interval bands (grey areas), while non-significant trends are depicted by dotted lines.

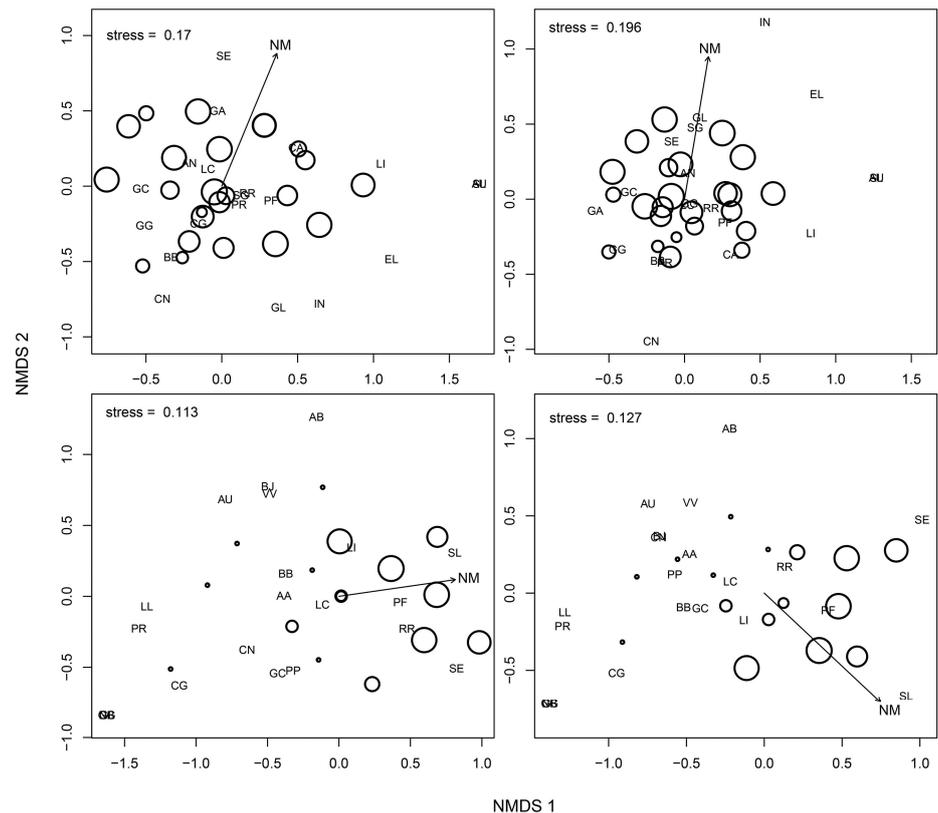


Figure 7. Nonmetric multidimensional scaling ordination of Jaccard (left panels) and Bray-Curtis (right panels) distances between the $\geq 1+$ (upper panels) and $0+$ (lower panels) native fish assemblage samples. Points mark respective samples while point size is relative to round goby abundance. Linear fit of round goby abundance to coordinates of the first two axes is marked by an arrow. The fit of each arrow was significantly different from that for a randomised coordinate position, with $P < 0.05$ in all four cases. See Appendix 1 for species codes.

just a few gobies were caught in the stretch in 2015 (Roche et al. 2015), the year of first report, they comprised more than half of the catch the next spring and, despite an apparent decrease over autumn 2016, more than three-quarters of the catch in 2018. Similarly rapid goby domination has been reported at many other sites, including the Laurentian Great Lakes (e.g. Marsden and Jude 1995) and European rivers (e.g. van Kessel et al. 2016; Cerwenka et al. 2018). As with previously reported invasions, one can presume that anthropogenic modifications, i.e. rip-rap embankments and navigation, played a major role in round goby success on the upper Elbe (see Janáč et al. 2016, 2018). Regarding area expansion, the most downstream point of the population shifted from site C (Děčín, r. km 353) in 2015 to the furthest downstream sampling site at Dolní Žleb in 2016 (r. km 363, site D), with individuals recorded in the German stretch near the town of Schmilka (r. km 369) the same year (Völker and Gause 2017). These records would suggest rapid downstream dispersal at a rate of at least 16 km per year (using this rate, one could estimate the original introduction of round goby at Ústí nad Labem at around 2013; though such back-calculations only serve as an exercise). It is highly unlikely that non-juvenile gobies would contribute substantially to such rapid downstream dispersal as

Table 4. Results of PERMANOVA based on Jaccard distance (a,c) or Bray-Curtis distance (b,d) matrices of $\geq 1+$ (a,b) and $0+$ (c,d) native fish assemblage samples. Significant terms in bold.

 a) Jaccard distance, $\geq 1+$ fish

Predictor	Df	F	R ²	P
Sampling occasion	5	2.92	0.393	0.001
Site	3	2.63	0.212	0.001
Round goby	1	0.68	0.018	0.698
Residuals	14		0.377	

 b) Bray-Curtis distance, $\geq 1+$ fish

predictor	Df	F	R ²	P
Sampling occasion	5	4.41	0.467	0.001
Site	3	3.38	0.215	0.001
Round goby	1	1.02	0.021	0.419
Residuals	14		0.297	

 c) Jaccard distance, $0+$ fish

predictor	Df	F	R ²	P
Sampling occasion	6	2.45	0.594	0.001
Site	2	1.27	0.103	0.273
Round goby	1	1.47	0.059	0.173
Residuals	6		0.377	

 d) Bray-Curtis distance, $0+$ fish

predictor	Df	F	R ²	P
Sampling occasion	6	3.61	0.626	0.002
Site	2	2.21	0.128	0.044
Round goby	1	2.51	0.072	0.047
Residuals	6		0.297	

Table 5. Results of db-RDA based partitioning of native fish assemblage structure variance between round goby abundance, sampling occasion and sampling site. Proportion of variance in native fish assemblage structure explained exclusively by the predictors, shared variance (X) and unexplained (residual) variance. Analyses were conducted on Jaccard distance and Bray-Curtis distance based matrices of the native $\geq 1+$ fish and $0+$ fish assemblages.

	Jaccard $\geq 1+$	Bray-Curtis $\geq 1+$	Jaccard $0+$	Bray-Curtis $0+$
Sampling occasion	0.294	0.292	0.256	0.362
Site	0.166	0.203	0.048	0.150
Round goby		0.001	0.041	0.094
Sampling occasion X Site				
Sampling occasion X Round goby	0.052	0.123	0.098	0.089
Site X Round Goby				
Sampling occasion X Site X Round goby	0.004		0.010	0.035
Residual	0.619	0.487	0.607	0.434

they are more geared toward upstream movement (Brownscombe and Fox 2012; Šlapanský et al., *in prep.*); hence, the rapidity of downstream spread is most likely the result of goby early life stage drift (Janáč et al. 2013a; Borchering et al. 2016; Ramler et al. 2016). While no rates of downstream drift-aided dispersal have yet been reported for round goby, a similar rate of 20 km/year has been documented for tubenose goby *Proterorhinus semilunaris*, another Ponto-Caspian gobiid invader (Janáč et al. 2012). An even faster downstream spreading rate is suggested by unofficially published round goby catches from 2017 downstream of Dresden, suggesting it had spread a further 70 km (<https://www.saechsische.de/grundel-macht-sich-in->

[der-elbe-breit-3734779.html](#)), though facilitation by anthropogenic means cannot be excluded in such cases.

Downstream drift-facilitated dispersal contributed to a number of unusual characteristics in the novel population. Small-sized, juvenile fishes were the main proponents of dispersal, representing the majority of the novel population. This is in sharp contrast to those populations spreading upstream, as demonstrated by the geographically closest population to the Elbe in the River Dyje, a secondary tributary of the River Danube (Šlapanský et al. 2017). In that part of the population actively spreading upstream, juveniles were mostly rare in the earliest years of invasion, with their proportion slowly increasing over time (Šlapanský et al. 2017). Similarly, a high proportion of females was only observed on the Dyje after several years. The reasons for a female-dominated population on the Elbe are obscure and beyond the scope of this paper, though one explanation may lie in sexually-biased goby dispersal. Providing that females are more stationary than males (Marentette et al. 2011; Žák et al. 2018; Šlapanský et al., *in prep.*), and that upstream movement typically prevails over the non-juvenile population (Šlapanský et al., *in prep.*; see also Brownscombe and Fox 2012), one might expect that males migrating upstream would shift the sex-ratio of novel downstream populations toward a female bias. On the other hand, this would result in a male-biased sex-ratio and higher competition at the already densely populated upstream introduction-point, where further upstream movement has been prevented by an impassable weir, and an increasing proportion of females in the downstream direction. However, no such patterns were observed in our study (Figure 4, Appendix 2). Moreover, while such behavioural patterns would result in a male-biased sex-ratio at the upstream invasion front, pioneer sex-ratios have tended to vary greatly between invasions (Gutowsky and Fox 2011; Brownscombe and Fox 2012; Brandner et al. 2013a, 2018; Šlapanský et al. 2017).

Round goby abundance appeared to be a significant predictor, explaining changes in several components of the native fish assemblage in the upper Elbe. As we sampled nearshore areas only, our results are likely to be restricted to fishes that inhabit these areas during the daylight hours (excluding, for example large specimens of benthic or pelagic fish that typically dwell further from the bank). Nevertheless, such a restriction is typical for most goby impact studies conducted in rivers (see e.g. van Kessel et al. 2018 or Cerwenka et al. 2018) and such a design will still provide representative samples of many fishes vulnerable to goby impact, such as small benthic fish or 0+ fish. It should still be stressed, however, that this study does not provide representative data on goby impact on fishes that occur further from the bank, such as large individuals of barbel or nase or some larger predators.

Round goby appear to have had negative effects mostly on 0+ fish along our study stretch. Such an impact is somewhat intuitive as the 0+ group is

most likely to (i) show an immediate impact from egg/juvenile predation and spawning interference (Janssen and Jude 2001), and (ii) be outcompeted for food or shelter due to their small size. On the other hand, predation on the eggs or juveniles of native species has yet to be documented in European rivers (Števo ve and Kováč 2013; Brandner et al. 2013b; Vašek et al. 2014; Všetická et al. 2015), suggesting that impacts from round goby presence are most probably realised through competition. Thanks to its wide diet range and opportunistic feeding behaviour, there is the potential for diet niche overlap with native 0+ fish, with competition over chironomids being most likely (Brush et al. 2012; Brandner et al. 2013b; Števo ve and Kováč 2016; Mikl et al. 2017a). Likewise, the more aggressive round goby may force native 0+ out of their shelters (e.g. see Ray and Corkum 2001) and expose them to higher predation pressure by native predators. However, these suggestions contradict the findings of the only study to date focusing on round goby effects on 0+ fish assemblages in European rivers, in which Janáč et al. (2016) observed no effect on either abundance or niche shift of native 0+ fish in the River Dyje. A possible reason for these contrasting results may lie in the differing bank morphology of the two rivers, with the Dyje providing a larger range of refuge habitats for native 0+ fish, e.g. aquatic vegetation and beaches, compared with the faster flowing Elbe where an homogenous cover of boulders provides less suitable shelter for 0+ fish and attracts large numbers of gobies as potential competitors. A further explanation may lie in our sampling design. The observed effect of round goby on 0+ fish was mostly attributable to a relatively high abundance of native 0+ fish in samples taken before round goby introduction (Figure 6); however, these samples were mostly obtained several (up to nine) years before the introduction, thus increasing the chances that any round goby effect may have been confounded with some other environmental change occurring in those years and not considered in this study.

If round goby impacts were realised through effects on 0+ fish only (i.e. predation or competition with juveniles), the effects would become visible in $\geq 1+$ fish after a time lag. The direct relationship recorded here between round goby abundance and that of chub and European eel raises the question of whether the relationships are really causal, i.e. whether species abundance was correlated to some confounding factor not included in our study. However, the inclusion of sampling occasion and site as random effects in our models should have encompassed the majority of possible environmental variability, thus the significant relationships are more likely to have been caused by direct interactions between round goby and the $\geq 1+$ populations of these species.

Round gobies are expected to negatively affect the abundance of small benthic fishes showing a substantial niche overlap, e.g. cottids (Janssen and Jude 2001; Lauer et al. 2004; van Kessel et al. 2016), gobiids (Valová et al.

2015; Šlapanský et al. 2017; Janáč et al. 2018) or darters (Lauer et al. 2004; Reid and Mandrak 2008; Stauffer et al. 2016). Of these, only the European bullhead is found in the Elbe. Just four specimens of European bullhead were captured during this study, and these were randomly distributed along the gradient of round goby abundance. As far as we can judge from its rare occurrence in 0+ fish samples from before goby introduction and the sporadic capture of adult bullheads during these surveys, the species would appear to have been rare in the upper Elbe, even before round goby introduction. As such, it was not possible to determine any effect of round goby on this species. Other benthic species, such as barbel or gudgeon, have a relatively high potential risk of experiencing a negative impact; however, only barbel abundance showed a (close to significant) decrease (Table 3, Figure 5). In the light of the apparent lack of effect on benthic species, the unexpected decrease in benthopelagic chub abundance is even more enigmatic. Diet competition may be a possible mechanism whereby round goby affect chub, similar to 0+ fishes. The severe impact on 0+ chub suggests that any impact on older specimens of the same species may not be coincidental. The majority of the chub population comprises small-sized fish of < 130 mm SL (corresponding to the 1+ and 2+ cohorts; Appendix 3), which may contribute to their vulnerability. Logically, smaller chub will be more easily outcompeted than larger specimens; consequently, any effects on 0+ fish will be rapidly revealed in the 1+ and 2+ cohorts. On the other hand, this would hold true for almost all native species, and yet no such effect was observed in these cases. As such, this study provides further evidence of round goby impact being case-specific (Hirsch et al. 2016; Janáč, *in prep.*), emphasising the difficulties of predicting invader impact in general (Ricciardi et al. 2013).

European eel abundance was positively correlated with that of round goby, suggesting a possible causal relationship, most likely related to eels preying on round gobies. The majority of the eel catch comprised juvenile eels of < 350 mm SL (Appendix 3), most probably representing non-stocked upstream migrants (eel is not stocked along the stretch we studied; T. Kava, Czech Angling Union, *pers. comm.*). Our study design did not allow us to distinguish whether the increase in eel abundance was due to gobies supporting survival of juvenile eels (i.e. through diet) or whether eels already present in the river were attracted to gobies along the nearshore zone (i.e. population concentration). In each case, however, juvenile eels are likely to feed on gobies, a phenomenon as yet unreported in the literature. Thanks to the eel's morphology, it is easily able to access gobies in the interstitial spaces between rip-rap, making them an attractive prey. A similar situation has previously been documented as regards the similarly shaped burbot *Lota lota* (Crane et al. 2015; Hares et al. 2015; Mikl et al. 2017b). While round goby have been shown to serve as prey for many native predators, effects on predator abundance, condition and growth

differ between invaded ecosystems (see Hirsch et al. 2016 for a review). Similar variability was also observed in our study as regards European perch abundance. While previous studies tend to show an increase in perch abundance following round goby invasion (e.g. Jůza et al. 2018), our own study indicated a non-significant negative relationship with goby abundance. Overall, the final effect of round goby presence on native predator abundance will be determined through interactions between (i) any net increase in prey abundance (increase in round goby abundance, goby-related decrease in native prey abundance), (ii) differences in energetic value, manipulative costs and accessibility between round goby and native prey, and (iii) other factors such as negative effects of round goby on predator early life stages (see e.g. Houghton and Janssen 2015).

Despite the significant relationships between abundances of round goby and several 0+ and $\geq 1+$ fish species, PERMANOVA showed no significant effect on the structure of native fish assemblages. This lack of effect was probably caused by marginal changes at the assemblage structure level (compared to the effects on some other species) and by a relatively strong correlation between round goby abundance and sampling occasion, which meant that sampling occasion explained a large proportion of variance otherwise explainable by round goby abundance (Figure 7, Table 5). Variance partitioning demonstrated that just a small proportion of the $\geq 1+$ assemblage structure variability measured by Bray-Curtis distance was explained by round goby abundance, and none when measured by Jaccard distance. Clearly, the short-term effect of round goby was not great enough to extirpate some $\geq 1+$ native species, and observed changes in abundance caused only marginal shifts in the overall assemblage structure. On the other hand, changes in the 0+ fish assemblage were more pronounced (Figure 7, Table 5), with apparent shifts in the proportion of some species (as suggested by Bray-Curtis distance based analysis) and possibly even effects on the presence of some species (as suggested by Jaccard distance based analysis), the latter also being supported by a significant effect on 0+ native species richness.

It is important to note here that round goby impacts on recipient systems go beyond direct effects on native fish assemblages. Predation on benthic invertebrates, for example, may cause shifts in their assemblage structure (Lederer et al. 2008; Kipp and Ricciardi 2012; Mikl et al. 2017a), with possible consequences for exploiting prey resources and increased competition with native fish. Round goby introduction also has the potential to cause alterations in host-parasite relationships, such as parasite spill-over (Ondračková et al. 2015; Šlapanský et al. 2016) or dilution effects (Poos et al. 2010; Gendron and Marcogliese 2017). Further, round goby dietary preference in combination with goby consumption by native predators could alter nutrient flows through the food web, increasing the risks of contaminant accumulation in higher trophic levels (Marentette et

al. 2010; Polačik et al. 2015). All the aforementioned impacts will have consequences for other ecosystem components and, in the long run, will affect the native ichthyofauna. Hence, it is vital that long-term monitoring of round goby impacts on invaded systems takes place, going beyond the short-term effects presented in this study.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Species list

Table S1. Numbers of $\geq 1+$ and $0+$ fish species captured on the upper Elbe during sampling in 2016–2018 ($\geq 1+$ fish) and 2010–2018 ($0+$ fish).

Appendix 2. Sex-ratio and fish size

Table S2. Number of round goby males and females captured, sex-ratio (number of males per female), proportion of females in the non-juvenile population, results of Chi-square tests for sex parity and sex-ratio (sr) at each of the four sites.

Figure S1. Site- and year-specific visualisation of patterns in fish size (points = medians, solid lines = interquartile range, grey areas = size distribution) in the upper Elbe round goby population.

Figure S2. Year and site-specific visualisation of patterns in fish size (points = medians, solid lines = interquartile range, grey areas = size distribution) in the upper Elbe round goby population.

Figure S3. Site- and year-specific visualisation of patterns in sex-ratio (proportion of females [dark] and males [light] in the non-juvenile population) in the upper Elbe round goby population.

Figure S4. Year- and site-specific visualisation of patterns in sex-ratio (proportion of females [dark] and males [light] in the non-juvenile population) in the upper Elbe round goby population.

Appendix 3. Length-size distributions

Figure S5. Length-frequency distribution of native $\geq 1+$ chub (*Squalius cephalus*) and European eel (*Anguilla anguilla*) captured along the upper Elbe in 2016–2018.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2019/Supplements/AI_2019_Janac_etal_Appendix_1.pdf

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