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ORIGINAL PAPER

Competitive interactions for food resources between invasive racer goby *Babka gymnotrachelus* and native European bullhead *Cottus gobio*

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Abstract Racer goby is one of several Ponto–Caspian gobiids spreading throughout European rivers and concurrent with recent declines in threatened populations of a native species of similar biology, the European bullhead. Although suggestive of competitive interactions, evidence thereof is scarce, so we examined behavioural interactions between racer goby and bullhead (single specimens of each species together, also pairs of each species) under experimental conditions (shared space with two shelters) to determine whether the invader displaces the native species when food resources are limited. Food (live chironomids) was added to a single feeder at rates below satiation levels twice over 24 h (once in light and once in darkness), with fish behaviour (aggressive interactions: attacks and threatening) and feeding activity (time spent near or inside the feeder) recorded using video cameras and infrared illumination. Racer goby exhibited aggressive behaviour towards bullhead (mean = 2.5 aggressive events h^{-1}), but rarely the inverse (threatening only, mean = 0.05 events h^{-1}), significantly limiting bullhead foraging time (by 62 %) and being faster to reach food in the feeding time in 76 % of cases. Gobies were more aggressive during daylight (77 % of all aggressive events occurring in light), and both species spent more time on feeding activities in darkness (88 and 66 % of all time spent in the feeder by bullheads and gobies, respectively). However, the adverse impact of goby on bullhead was independent of light conditions. Our results suggest that under natural conditions, racer goby are likely to displace bullhead during feeding, with potential consequences for foraging efficiency.

Keywords Ponto–Caspian gobiids · Interspecific competition · Aggressive behaviour · Non-native species

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Introduction

Amongst the most impressive fish invasions in European inland waters in recent decades are those of the topmouth gudgeon *Pseudorasbora parva*, which occurred mainly as a contaminant of fish transport (see Copp et al. 2005; Simon et al. 2011), and of the Ponto–Caspian gobies, which colonized new areas mainly by natural dispersal via inter-basin connections, e.g. being transported by river ships (see Grabowska 2005 and Wiesner 2005). So far, six gobiid species have been recorded in Europe as non-native species, including bighead goby *Ponticola kessleri*, Caspian bighead goby *P. gorlap*, monkey goby *Neogobius fluviatilis*, racer goby *Babka gymnotrachelus*, round goby *N. melanostomus* and Western tubenose goby *Proterorhinus semilunaris*. These species have invaded or expanded their range in large European rivers such as the Danube (Ahnelt et al. 1998, 2001; Kautman 2001; Naseka et al. 2005), Rhine (Freyhof 2003; van Kessel et al. 2009), Vistula (Grabowska et al. 2008) and Volga (Copp et al. 2005). The Ponto–Caspian gobies are relatively small (up to 15–20 cm total length), bottom-dwelling species that are usually associated with crevice habitats, though some invading populations have been reported to have established in sandy areas (Sapota 2004). These species are territorial and aggressive, with nest-guarding males (Smirnov 1986; Charlebois et al. 1997; Pinchuk et al. 2003a, b), making them potential competitors to native European species of similar environmental biology, such as Gobiidae in brackish waters (Corkum et al. 2004) and Cottidae in fresh waters. This is particularly relevant to the European bullhead *Cottus gobio*, which is listed in Annex II of the European Habitats and Species Directive (92/43/EEC) because of declines in various parts of its range (e.g. Lelek 1987; Knaepkens et al. 2004). This includes Poland, where the European bullhead is listed as vulnerable (Witkowski et al. 2009). The threat of Ponto–Caspian gobies to native Cottidae has already been demonstrated in the Laurentian Great Lakes, where invasive round goby have been found to out-compete native mottled sculpin *Cottus bairdii* for preferred habitat and to disrupt their reproduction (Dubs and Corkum 1996; Janssen and Jude 2001). Reported declines in European bullhead populations, coinciding with goby invasions of the rivers Danube (Jurajda et al. 2005) and Rhine (Dorenbosch and van der Velde 2009) suggest that Ponto–Caspian gobies are having a similar adverse impact on European as on North American Cottidae. However, studies on the potential impacts of gobies on European bullhead (henceforth simply 'bullhead') are limited to one experimental study (van Kessel et al. 2011), which focused on the potential displacement of bullhead and stone loach *Barbatula barbatula* from their preferred habitats by four gobiid species. However, racer goby was not included in this study.

In Polish inland waters, the gobiid species most likely to have deleterious consequences for the native bullhead is the racer goby, which has established itself in parts of the River Vistula catchment where the bullhead is native (Marszał et al. 2004; T. Kakareko, personal observation). Both species are bottom dwellers of similar size, habitat use (crevices), and reproductive strategy (Tomlinson and Perrow 2003; Pinchuk et al. 2003a) as well as similar dietary preferences, i.e. soft-bodied (non-mollusc) benthic invertebrates, especially chironomid larvae and amphipods (Welton et al. 1991; Grabowska and Grabowski 2005; Kakareko et al. 2005). The bullhead is effectively the European equivalent of the North American cottid, the mottled sculpin *Cottus bairdi*, which in the Great Lakes has been demonstrated to be adversely affected by invading round goby populations (Corkum et al. 2004). There similarities makes the two species very likely competitors for space, spawning grounds, feeding areas and food types.

The aim of the present study was to examine the interactions between these two species under experimental conditions in order to assess whether racer goby (henceforth referred to collectively as 'gobies') has an adverse impact on bullhead feeding behaviour (time and location) when food resources are limited. The working hypothesis was that racer goby would be more aggressive than native bullhead of comparable size, the former being a stronger competitor and displacing the latter from the profitable feeding areas, and this is expected to have adverse consequences for bullhead foraging efficiency and fitness.

Material and methods

European bullhead were collected whilst SCUBA diving in a tributary of the lower River Vistula, the River Brda, near the city of Bydgoszcz (central Poland), where stones were overturned and bullhead specimens were captured by manoeuvring them into an aquarium dip net. Racer gobies were collected by electrofishing (IUP-12, Radet, Poznań, Poland) from the Włocławek Reservoir, which is located in the lower River Vistula, central Poland about 100 km from the River Brda site. Immediately after capture, the fish were transported to the laboratory in aerated plastic 5-L bottles (1.5 h transport time), immediately placed in 80-L tanks (filtered, aerated water at 17–19 °C; 20 % of water exchange per week), with 5–8 specimens per tank (segregated by species) and fed with live chironomid larvae.

During the experiments, fish mean total length (TL) was measured from digital photographs (taken from the top view of the experimental aquaria) using image analysis software (ImageJ v1.40 g freeware by W.S. Rasband, U.S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/i). Fish measurements were taken when the specimen was located in front of an underwater scale situated on the tank bottom near the feeder, so as to ensure a constant measurement distance between the camera and all measured fishes. Fish used in the experiments were not in spawning condition, exhibiting no symptoms such as dark colouration of males or courtships. Mean lengths were 83 mm (min–max: 58–125 mm TL) and 81 mm (60–111 mm TL) for gobies and bullheads, respectively. Capture and use in this study of European bullhead, a legally protected species in Poland, was under permit (no. DOPozgiz-4200/V-20/3068/10/ls), as was the experimental procedure (Statements nos. 6/2010 and 8/ŁB507/2010 of the Local Ethics Committees for Bydgoszcz and Łódź, Poland).

Experiments were undertaken during March–April 2011 in four 40 L tanks filled with settled, aerated tap water with mean, minimum and maximum water quality values monitored (multimeter Multi340i, WTW GmbH, Weilheim, Germany) and maintained at: 25 cm depth, 18 °C (range 17–19 °C), 8.6 mg O_2 L^{-1} (8.5–8.7 mg L^{-1}), 7.9 pH (7.8–8.0) and 544 μS cm^{-1} (534–569 μS cm^{-1}). To reduce handling and disturbance impacts on the fish, all tanks were curtained off on all sides by black foil and/or Styrofoam screens. During night-time experiments, each tank was completely enclosed by isolation screens, and an infrared illuminator (MFL-I/LED5-12, Eneo, Germany) was used to permit the recording of fish behaviour. During daytime experiments, the top screen was partially removed to permit an incandescent lamp to simulate natural photo-period (30 luxes at water surface; measured with a luxometer L-20A, Sonopan Ltd., Białystok, Poland). Each tank (Fig. 1) was fitted with two shelters (PVC half-pipes placed on the bottom) to provide a refuge outside of feeding periods, a CCTV day and night video camera (SDC425P, Samsung, South Korea, suspended ≈ 45 cm above the water level), and at one end a feeder, which consisted of a Petri dish (attached to the tank bottom with silicone glue) and a transparent plastic hose (suspended ≈ 0.5 cm above the dish bottom). Food (30–60 mg of live chironomid larvae depending upon fish size; i.e. 3–4 × below satiation level, as per preliminary observations) was flushed through a hose with a small amount of water into the Petri dish, where they remained until taken by the fish. Fish were allowed to get used to these conditions in separate, segregated aquaria for 2 months prior to the experiments.

Fish were tested in pairs of similar length (≤1 cm difference in TL): (1) two bullheads (10 trials); (2) two gobies (11 trials); and (3) one goby and one bullhead (16 trials; mean TLs not significantly different; Student's t test for dependent samples: $t_{15} = 0.71$, $P = 0.490$). Each pair of fish was tested in two light conditions (30 lux light vs. total darkness) during a single trial, which lasted 24 h. The fish in both experimental tanks and the stock tanks were held under the same light cycle, i.e. 12 h (light)/12 h (darkness), 09:00–21:00. The fish were acclimated to these light conditions for 2 months before the experiments began. At the beginning of each trial, two fish from the stock tanks (of previously unused fish) were placed in the experimental tank 9 h prior to the trial (the acclimation period) so that they could become familiar with the experimental arena. The experimental tank was held in either darkness or daylight, the light conditions alternated between trials to avoid the confounding effects of time of day (of recording behaviour) and the progressive familiarity of the two specimens over the course of a trial. On each occasion, the fish were gently moved from stock tanks into experimental tanks. In darkness low-power led torch was used during the procedure with attention to complete it efficiently to ensure minimal disturbance of the fish. After the 9 h acclimation period, the light conditions were changed (from light to darkness, or from darkness to light), and then after 1 h the video camera was turned on and food was delivered to the feeder. Fish behaviour was recorded for the next 2 h. After a 9 h period (i.e. 21 h after placing the fish in the tank), the light conditions were again changed, with food (same quantity as previously) delivered 1 h later and fish behaviour recorded for another 2 h. The photoperiod maintained in the stock and experimental tanks was identical, so no change in circadian rhythm

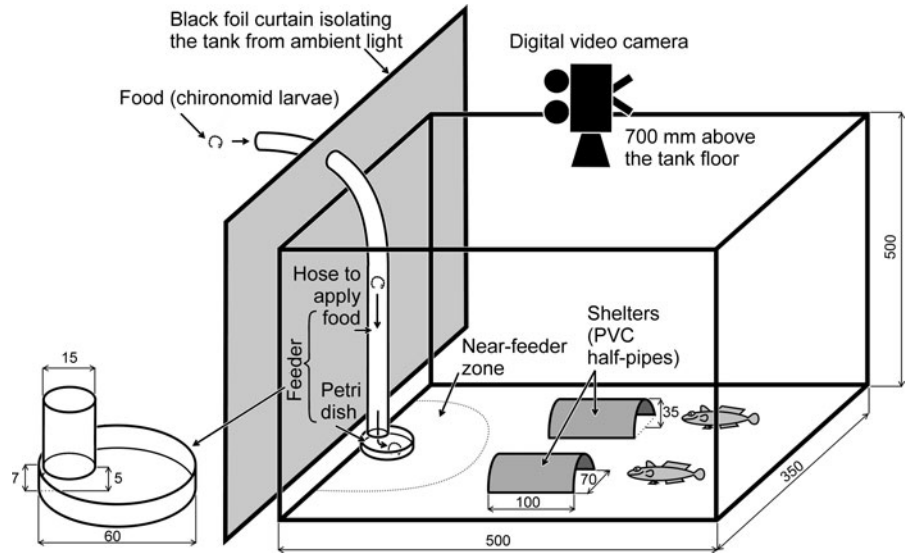

Fig. 1 Experimental setup. Dimensions are given in mm

was experienced by the fish following their introduction into the experimental system. Following each trial, the test fish were moved to aquaria containing previously used specimens (to avoid re-use of specimens) and at the end of the experiments, all racer gobies were disposed of, and all European bullheads were re-released to the wild at the location of capture.

In the data analysis, five response variables were considered, two aggressive interactions and three measures of feeding efficiency: (1) 'Attacks', i.e. aggressive interactions consisting of one fish moving quickly towards the other, and biting and/or chasing it; (2) aggressive interactions in which one fish threatened the other one with stretched fins, but with no chasing nor physical contact between them ('Threatening acts'); (3) Time spent by the fish near the feeder, i.e. within a radius equal to the length of the fish tested (Fig. 1), without feeding ('Time spent near the feeder'); (4) time spent by the fish directly in the feeder ('Feeding time'); and (5) the species identity of the first visitor in the feeder in each interspecific pair (separately in light and darkness), assumed to be the individual benefiting from the richest food source. Although it was difficult to observe the consumption of food by the fish directly, particularly in darkness, the fourth parameter, the time spent by the fish inside the feeder, was assumed to be correlated with food consumption.

To identify differences between both species with regard to the first four response variables (aggressive interactions as well as time spent near the feeder zone and directly in the feeder), mixed model ANOVAs for cross-over designs were carried out as per Díaz-Uriarte (2002) and Jones and Kenward (2003). The following factors were included in the model: (1) 'Species', a within-subject factor (as two specimens were tested together); (2) 'Period', a within-subject factor adjusted for light conditions, indicating the first or second recording made during each trial to show the effect of passing time on fish responses; (3) 'Sequence', a between-subject factor referring to the sequence of periods, light/dark (with the first recording taken in light) or dark/light (with the first recording taken in darkness); and (4) 'Light Conditions' during recording, a within-subject factor adjusted for period.

The factors were coded in the model following Jones and Kenward (2003). The 'Sequence' factor corresponds to the presence of carry-over effects (the effects of particular light conditions persisting after their change and affecting subsequent fish behaviour) or a 'Light' × 'Period' interaction (i.e. the impact of light varying with the passing time), these effects being indistinguishable from each other in a 2 × 2 design like one used in the present study (Díaz-Uriarte 2002; Jones and Kenward 2003). However, the occurrence of carry-over effects seems unlikely in the present design, as light is a natural environmental factor, fish were acquainted with the photoperiod used during the experiments for several months and given 1 h to adapt to changed light conditions before recording their behaviour in each period of the trial. Thus, a significant 'Sequence' effect is more likely to point out to a dependence of fish responses to light on the passing time.

To check whether the aggressive behaviours of gobies against bullheads differed from those exhibited by gobies in the presence of conspecifics, mixed-model ANOVAs were carried out with the same four factors described here above except with the first factor ('Species') replaced by 'Accompanying species', a between-subject factor (a bullhead or goby). As gobies always dominated bullheads in the two-species trials, the results obtained for the dominating goby specimens from each single-species pair were used for this analysis.

Feeding behaviour might differ between species independent of their potential reciprocal impacts on each other. Therefore, to check whether the gobies had an effect on bullhead foraging, the feeding efficiency of bullheads in the presence of gobies was compared with that of bullheads in single-species trials. Bullheads that dominated in their conspecific pairs were used in this comparison—these individuals were assumed to exhibit optimum feeding behaviour and therefore appropriate for determining whether or not feeding was negatively affected by the presence of gobies. The data were analysed using the same model as that described above for the aggressive behaviours of gobies.

For the above analyses, data were square-root transformed to reduce departures from assumptions of homoscedasticity and normality, which were checked using the Levene and Kolmogorov–Smirnov tests, respectively. The frequencies of the individuals of each species being first in the feeder were compared to a uniform proportional distribution (50:50) using a G test of goodness of fit with Williams correction (separately for light and dark conditions).

Results

Virtually all acts of aggression observed during the study were exhibited by gobies, revealing 2.5 aggressive events h^{-1} on average. Bullheads never attacked other fish (Fig. 2a) and very rarely threatened them (only three cases in all trials altogether, 0.05 events h^{-1}, Fig. 2b). Thus, both species differed significantly from each other in the number of attacks (Table 1A) and threatening acts (Table 1B). Moreover, significant 'Sequence' × 'Species' interactions (Tables 1A, B) indicate that the effect of light conditions occurred only for gobies and was stronger in the light/dark sequence trials, with most of aggressive events observed during their first, illuminated period (Fig. 2). The numbers of attacks exhibited by gobies against bullheads did not differ significantly from the numbers of attacks displayed by dominating goby individuals against conspecifics (Fig. 2a; Table 1C). On the other hand, the patterns of threatening acts displayed by gobies towards bullheads and conspecifics differed from each other, resulting in a significant 'Sequence' × 'Accompanying Species' interaction (Table 1D). Threatening directed towards bullheads occurred mainly in the first period of the light/dark sequence trials, whereas threatening events among conspecifics became more common in the second period of the dark/light sequence trials (Fig. 2b). In general, gobies were more aggressive in light than in darkness (Fig. 2), with 77 % of all aggressive events occurring in light.

In the mixed-species feeding trials, gobies spent significantly more time near the feeder and directly in the feeder than bullheads (Fig. 3; Tables 1E, F). The difference between both species in the time spent in the feeder was particularly high in the second period of the trial, independent of the applied sequence of light conditions, resulting in a significant 'Species' × 'Period' interaction (Table 1F). Moreover, bullheads tested in the presence of gobies occupied the feeder zone and the feeder itself significantly less often (by 62 %) than did dominant bullheads in the single-species trials (Tables 1G, H). This observation clearly confirms that bullhead feeding behaviour was affected by goby presence.

The time spent near the feeder by both species was independent of light conditions (Tables 1E, G). On the other hand, the difference in the feeding time between light and darkness was significant for both species (Tables 1F, H), with 88 and 66 % of all time spent in the feeder by bullheads and gobies, respectively, falling on dark hours. The goby was the first visitor in the feeder in 82 % (light) and 71 % (darkness) of cases. This effect was statistically significant in light only ($G_1 = 7.50$, $P = 0.006$ and $G_1 = 2.89$, $P = 0.089$, for light and darkness,

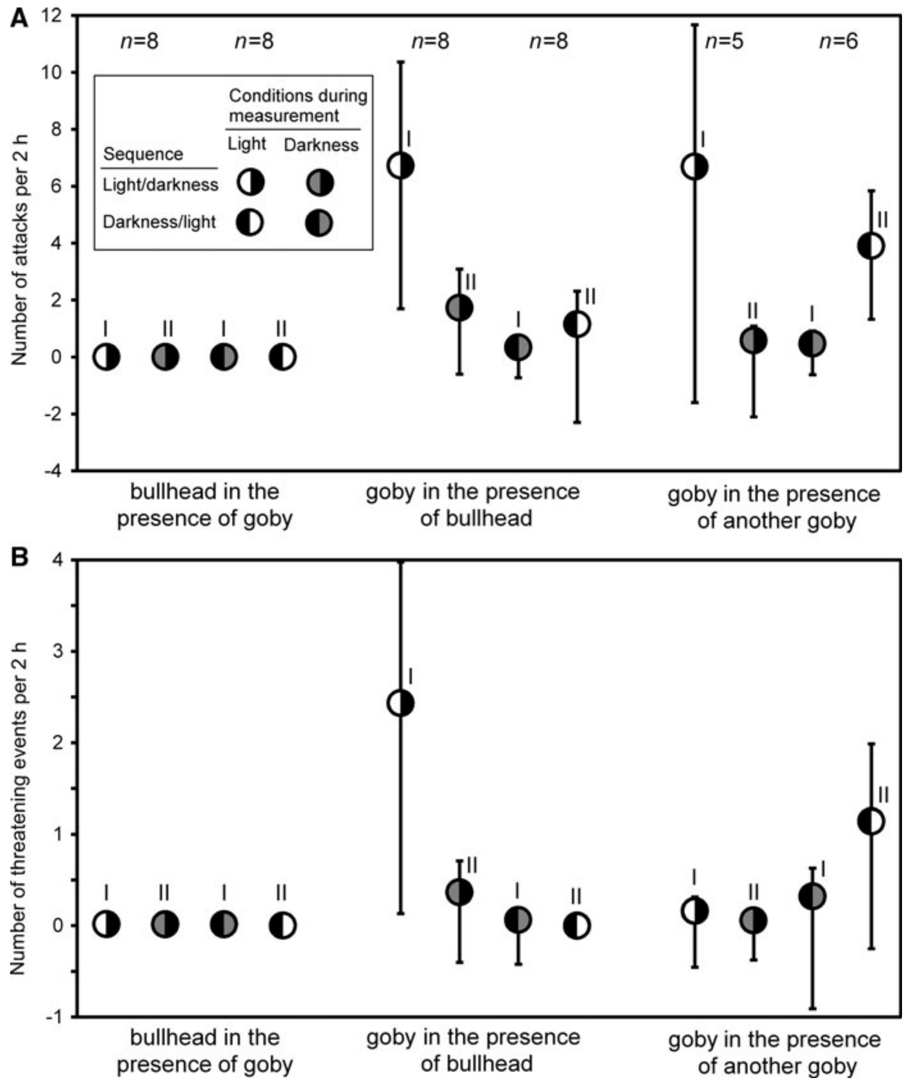

Fig. 2 Number of attacks (**a**) and threatening acts (**b**) (back-transformed means ± 95 % confidence intervals) displayed by racer goby and European bullhead in the two-species and single-species trials (n = number of replicates). *Roman numbers* at the data points indicate the period of a trial (first or second) in which the measurement was made

respectively), but the tendency was the same during the entire period.

Discussion

The present study has clearly confirmed the hypothesis that non-native gobies are much more aggressive fish than are bullheads of comparable size, which were easily displaced from the vicinity of the feeding area and forced to move to another part of the experimental tank. This result is similar to those obtained for invasive round goby in its interactions with the native North American cottid, the mottled sculpin (Jude et al. 1992; Dubs and Corkum 1996) and logperch (Balshine et al. 2005), being more aggressive in defending their territories and more efficient in displacing the other fish from their shelters. Round goby have also been found to be more aggressive than ruffe *Gymnocephalus cernuus*, which is also native to Eurasia but introduced to North America (Leigh 1998). The round and racer gobies (Charlebois et al. 1997; Pinchuk et al. 2003a) as well as European and North American cottids (Becker 1983; Tomlinson and Perrow 2003) are similar with respect to ecological requirements and behaviour. Therefore, we suspect that the aggressive pressure exerted by racer goby on European cottid species would be similar to that reported by Dubs and Corkum (1996) for interactions between round goby and the mottled sculpin. Indeed, compared to racer

Table 1 Results of the mixed model ANOVA on the relationships between the European bullhead and racer goby

	Parameter	Comparison	Effect	*df*	*MS*	*F*	*P*
A	Number of attacks	Goby TS versus bullhead TS	Sequence^{BS}	1	4.6	5.36	0.036
			Error	14	0.8		
			Period^{WS}	1	0.2	0.31	0.585
			Light^{WS}	1	4.4	6.39	0.024
			Error	14	0.7		
			Species^{WS}	1	32.3	37.83	<0.001
			Sequence × species^{WS}	1	4.6	5.36	0.036
			Error	14	0.8		
			Period × species^{WS}	1	0.2	0.31	0.585
			Light × species^{WS}	1	4.4	6.39	0.024
			Error	14	0.7		
B	Number of threatening acts	Goby TS versus bullhead TS	Sequence^{BS}	1	4.2	13.17	0.003
			Error	14	0.3		
			Period^{WS}	1	1.8	5.00	0.042
			Light^{WS}	1	0.3	0.95	0.345
			Error	14	0.4		
			Species^{WS}	1	4.2	26.86	<0.001
			Sequence × species^{WS}	1	3.2	20.68	0.001
			Error	14	0.1		
			Period × species^{WS}	1	1.2	5.10	0.040
			Light × species^{WS}	1	0.7	3.01	0.105
			Error	14	0.2		
C	Number of attacks	Goby TS versus goby SS	Accompanying species^{BS}	1	0.2	0.01	0.922
			Sequence^{BS}	1	115.2	7.12	0.014
			Sequence × acc. species^{BS}	1	0.0	0.00	0.967
			Error	23	16.2		
			Period^{WS}	1	11.9	0.82	0.373
			Period × acc. species^{WS}	1	0.6	0.04	0.836
			Light^{WS}	1	295.5	20.43	<0.001
			Light × acc. species^{WS}	1	0.2	0.01	0.914
			Error	23	14.5		
D	Number of threatening acts	Goby TS versus goby SS	Accompanying species^{BS}	1	0.0	0.00	0.948
			Sequence^{BS}	1	0.5	1.41	0.248
			Sequence × acc. species^{BS}	1	7.3	18.89	<0.001
			Error	23	0.4		
			Period^{WS}	1	0.7	1.55	0.226
			Period × acc. species^{WS}	1	1.7	3.52	0.073
			Light^{WS}	1	1.1	2.35	0.139
			Light × acc. species^{WS}	1	0.0	0.09	0.772
			Error	23	0.5		
E	Time in the feeder zone	Goby TS versus bullhead TS	Sequence^{BS}	1	8.1	1.23	0.286
			Error	14	6.5		
			Period^{WS}	1	1.5	0.87	0.366
			Light^{WS}	1	3.1	1.78	0.203
			Error	14	1.7		
			species^{WS}	1	156.8	13.91	0.002
			Sequence × species^{WS}	1	9.1	0.81	0.384
			Error	14	11.3		
			Period × species^{WS}	1	15.0	3.59	0.079
			Light × species^{WS}	1	0.3	0.07	0.796
			Error	14	4.2		

Table 1 continued

	Parameter	Comparison	Effect	*df*	*MS*	*F*	*P*
F	Feeding time	Goby TS versus bullhead TS	Sequence^{BS}	1	2.7	1.90	0.189
			Error	14	1.4		
			Period^{WS}	1	0.9	0.54	0.475
			Light^{WS}	1	9.1	5.73	0.031
			Error	14	1.6		
			species^{WS}	1	41.5	9.46	0.008
			Sequence × species^{WS}	1	6.9	1.58	0.229
			Error	14	4.4		
			Period × species^{WS}	1	19.3	6.69	0.022
			Light × species^{WS}	1	1.2	0.43	0.522
			Error	14	2.9		
G	Time in the feeder zone	Bullhead TS versus bullhead SS	Accompanying species^{BS}	1	75.0	7.70	0.011
			Sequence^{BS}	1	0.6	0.06	0.812
			Sequence × acc. species^{BS}	1	0.8	0.08	0.774
			Error	22	9.7		
			Period^{WS}	1	8.1	3.20	0.088
			Period × acc. species^{WS}	1	2.7	1.06	0.314
			Light^{WS}	1	0.6	0.24	0.627
			Light × acc. species^{WS}	1	1.5	0.60	0.445
			Error	22	2.5		
H	Feeding time	Bullhead TS versus bullhead SS	Accompanying species^{BS}	1	29.7	8.65	0.007
			Sequence^{BS}	1	2.0	0.59	0.450
			Sequence × acc. species^{BS}	1	5.2	1.51	0.232
			Error	22	3.4		
			Period^{WS}	1	5.6	3.98	0.058
			Period × acc. species^{WS}	1	0.5	0.33	0.570
			Light^{WS}	1	9.9	7.07	0.014
			Light × acc. species^{WS}	1	0.2	0.16	0.692
			Error	22	1.4		

Note that a sequence effect may stand for carry-over effects or a light × period interaction (Jones and Kenward 2003)

TS Two species trials, *SS* single species trials, *BS* between subject factor, *WS* within subject factor

goby, European bullhead never exhibited any attacks towards any other co-existing fishes. The bullhead is known to establish its domination structure using sound and visual threat displays (spreading gill covers and darkening) and rarely resorting to a direct fight (Ladich 1989; Tomlinson and Perrow 2003). This could make them defenceless when confronted by aggressive gobies, which regularly use brute force in their relationships with other individuals, including conspecifics. Van Kessel et al. (2011) have noticed that European bullhead was displaced from their preferred shelter places to less suitable habitats by bighead and tubenose goby, which suggests that these two species might also exert aggressive pressure on the cottid species and force them to use less preferred habitats.

Interspecific competition is said to be rarely stronger than intraspecific competition (Connell 1983; Britton et al. 2010), and competition between species is often avoided by resource partitioning (e.g. Fobert et al. 2011). Accordingly, the present study has shown that Ponto–Caspian gobies do not exert stronger pressure towards native bullheads than against conspecifics. However, in contrast to the results of Dubs and Corkum (1996) and Savino and Riley (2007), who found that round goby showed greater aggression towards conspecifics than towards mottled sculpin and ruffe, respectively, the present study revealed similar

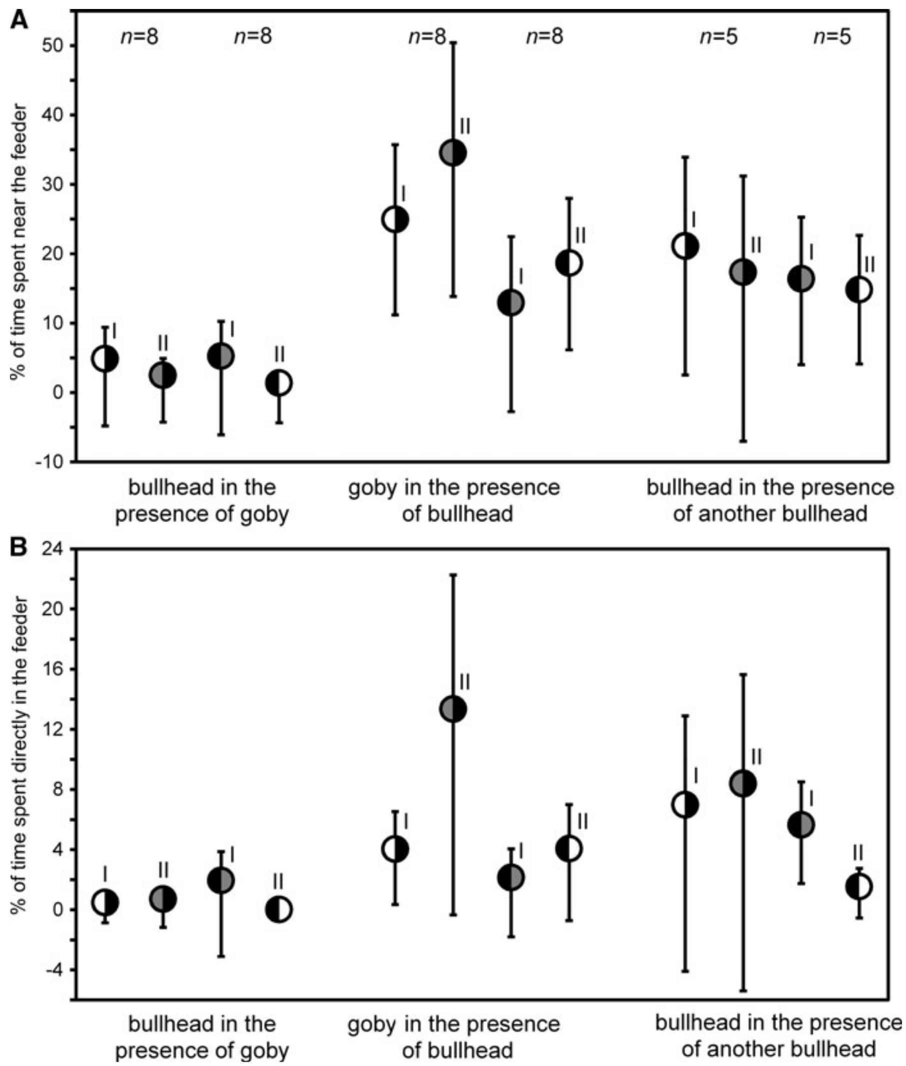

Fig. 3 Percentage of time (100 % = 2 h) spent by gobies and bullheads near the feeder (**a**) and directly in the feeder, i.e. feeding (**b**) (back-transformed means ± 95 % confidence intervals) in the two-species and single-species trials. See Fig. 2 for the meaning of symbols and labels

overall aggression level towards native bullheads and conspecifics. This discrepancy could be accounted for by the scarcity of food in our experiments (much below the satiation level), which probably enhanced goby aggression towards any potential food competitor, regardless of species. Both intra- (Grossman 1980; Gozlan et al. 2003) and inter-specific (Gaudreault and Fitzgerald 1985; Maruyama et al. 2010) aggression will allow a dominant fish to increase its access to limited food resources or spawning sites. Whereas, gobies in the present study did exhibit a different behavioural response towards conspecifics compared to bullheads; gobies were threatened more often in the second period of the test whereas bullheads were subjected to this behaviour mainly during the first period. This could be accounted for by the fact that bullheads seemed to be less active in the second part of the test, having lower feeding times (Fig. 3b) and perhaps therefore being less exposed to goby aggression. In contrast, the aggression of gobies against conspecifics was still apparent in the second part of the test, particularly when the light was on, though the behaviour switched partly from direct attacks to less harmful threatening (Fig. 2).

The feeding activities of individual bullhead were clearly shorter than those shown by coexisting gobies. Nevertheless, it remains possible that bullheads, despite being chased away from the feeding area and threatened by gobies, would be able to fulfil their nutritional needs, for instance by more efficient feeding in periods when gobies are less active, particularly if they could get to the feeder earlier than the invader. However, the negative influence of gobies on bullheads was confirmed by the reduction of bullhead feeding time in the presence of gobies compared to the single-species trials. Moreover, gobies exhibited a tendency to attend the feeder before bullheads, particularly in light. Thus, they were more likely to benefit from getting to the richest food resources. This further supports the evidence for the negative impact of gobies on the foraging efficiency of bullheads. This impact was observed both in light (day) and darkness (night), showing that if any differences in diurnal activity occur between these species, they were not sufficient to reduce the competitive interactions for food. In our study, both fishes spent more time in the feeders in darkness, showing that they are both nocturnal species. Indeed, the bullhead has been reported as a dark-active species (Andreasson 1969; Prenda et al. 2000), and recent research involving goby gut fullness coefficients indicates that the racer goby also feeds primarily at night (Grabowska and Grabowski 2005). The racer goby may possess enhanced sensory systems that facilitate better detection and capture of prey at night compared to the bullhead. The round goby has a well-developed lateral line system (Jude et al. 1995), which is better than that of the mottled sculpin, enabling them to forage efficiently under low or no light conditions. However, an experimental study has revealed that round goby do not possess enhanced visual and lateral line systems compared to slimy sculpin *Cottus cognatus* and spoonhead sculpin *Cottus ricei* (Bergstrom and Mensinger 2009), and thus the alien species does not appear to have any physiological advantage during nocturnal foraging. Although it is unknown whether the same relationship holds for the racer goby and the European bullhead, our results suggest that the bullhead's noctural habits do not appear to protect the species from interference competition presented by the racer goby. Interestingly, the aggressive behaviour of gobies was much more common during daylight, contrary to their nocturnal feeding activity. This might be explained by the fact that light affects aggressor-defender interactions in a similar manner as the relationships between predators and their prey. Light enhances the visual capabilities of predators and therefore increases the risk of predation (Culp 1989; Culp and Scrimgeour 1993; Bradford et al. 2004). Perhaps the same mechanism stimulated aggressive events amongst the fish in our study, but this remains unclear and requires further study. Moreover, a higher aggression level could be expected during the first period of a trial, before the domination structure between the tested fish was fully established. Together with the fact that aggression was stimulated by light, this could account for both the observed peaks in the numbers of aggressive interactions during the first period of the light/dark sequence trials and the greater time-related changes of fish behaviour during these trials (Fig. 2).

Our laboratory observations have shown that racer goby do constitute a real threat for bullhead, providing direct experimental evidence to the hypothesis that the decline of bullhead in European waters could be partially attributed to the recent invasions of the invasive Ponto–Caspian gobiids (Jurajda et al. 2005; Dorenbosch and van der Velde 2009) due to direct competitive and aggressive interactions for space and food resources. Because both species studied are benthic clingers that use similar microhabitats (Brylinska 2000; Pinchuk et al. 2003a, b) and their distributions may overlap (T. Kakareko, pers. observ.), it is probable that racer goby are forcing bullheads to abandon their most profitable habitats and to occupy energetically inferior locations, and may even be eliminating the bullhead from parts of its native European range. There is strong evidence that the interference competition of introduced fishes, which use aggression in their interactions with native species (Connell 1983; Schoener 1983), could be adversely affecting the foraging conditions and growth of the latter (Marchetti 1999; Lawler et al. 1999; Baxter et al. 2007; Blanchet et al. 2007), though this is not always the case (Fobert et al. 2011). European bullheads can survive in small streams with strong water current, unsuitable to racer gobies, which are normally associated mainly with lentic, slowly flowing waters (Smirnov 1986; Pinchuk et al. 2003a). Thus, the total extirpation of one species by the other at a large spatial scale seems unlikely. However, bullhead also occur in larger rivers with lentic habitats and lakes (Tomlinson and Perrow 2003), which can be invaded by racer goby. In such places, gobies could strongly affect bullhead limiting their ranges, decreasing abundances, causing local population extinctions and perhaps also lowering the genetic diversity of the species. Thus, the invasion of racer goby is likely to weaken the condition of the native species considerably and increase their vulnerability to other environmental threats.

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