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Are interactions among Ponto-Caspian invaders driving amphipod species replacement in the St. Lawrence River?

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ABSTRACT

In Lake Erie and Lake Ontario, the Ponto-Caspian amphipod *Echinogammarus ischnus* has replaced the native amphipod *Gammarus fasciatus* on rocky substrates colonized by dreissenid mussels, which provide interstitial refugia for small invertebrates. Based on the premise that an invader's vulnerability to predation is influenced by its evolutionary experience with the predator and its ability to compete for refugia, we hypothesized that amphipod species replacement is facilitated through selective predation by the round goby *Neogobius melanostomus*, a Ponto-Caspian fish that invaded the Great Lakes in the early 1990s and is now colonizing the St. Lawrence River. In laboratory experiments, we determined if *E. ischnus* excludes *G. fasciatus* from mussel patches, and if the vulnerability of *G. fasciatus* to predation by gobies is increased in the presence of the invasive amphipod. *E. ischnus* and *G. fasciatus* did not differ in their use of mussel patches, either when alone or in each other's presence. Both species were equally vulnerable to predation by the round goby. In field experiments, we determined if the round goby exerts a stronger impact than native predators on the relative abundance of amphipod species. Our results suggest that *E. ischnus* is more vulnerable to native predators, but the round goby does not have a differential impact on the native amphipod. We conclude that competition with *E. ischnus* does not increase the vulnerability of *G. fasciatus* to goby predation, and that the round goby does not promote the replacement of *G. fasciatus* by *E. ischnus* in the St. Lawrence River. The outcome of antagonistic interactions between exotic and native amphipods is mediated more by abiotic factors than by shared evolutionary history with other co-occurring exotic species.

Introduction

The abundance and impact of an exotic species can vary greatly across its invaded range. This variation is largely attributable to heterogeneity in the physico-chemical environment (Alcaraz and Garcia-Berthou, 2007; Berezina and Panov, 2004; Palmer and Ricciardi, 2004) and the composition of the invaded community, particularly the presence of predators (Reusch, 1998; Crooks, 2002; Hunt and Yamada, 2003), competitors (Jensen et al., 2002; van Riel et al., 2007) and facilitators (Ricciardi, 2001, 2005). Vulnerability to a shared predator may be mediated by competition between the invader and native species for refugia (Jensen et al., 2002; Balshine et al., 2005; van Riel et al., 2007; van Riel, 2008), and selective predation on either species may influence the invader's success and impact (Dudas et al., 2005; Bollache et al., 2006; Kinzler and Maier, 2006). The invader's vulnerability to predation is in many cases influenced by its evolutionary experience (Cox and Lima, 2006; Parker et al., 2006; Banks and Dickman, 2007). If the predator originates from the invader's native range, their shared evolutionary history may promote interactions that yield a net mutual benefit for both invading species (Simberloff and Von Holle, 1999; Ricciardi, 2001, 2005) and confer an advantage against native competitors. Alternatively, vulnerability of the invader to predation might depend more on the specific traits of resident predators (e.g. physiological tolerances, foraging behaviour) than on the evolutionary experience of the species involved.

In this study, we examine the relative abundance of competing native and exotic crustaceans, the North American amphipod *Gammarus fasciatus* and the Ponto-Caspian amphipod *Echinogammarus ischnus*, in the presence of other Ponto-Caspian species in the St. Lawrence River. The latter include a benthivorous fish (the round goby, *Neogobius melanostomus*) and dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*), whose colonies provide interstitial refugia for amphipods (Ricciardi et al., 1997; Gonzalez and Downing, 1999) and are commonly inhabited by *E. ischnus* in its native range (Köhn and Waterstraat, 1990). *E. ischnus* was discovered in the Great Lakes in the early 1990s (Witt et al., 1997), and by 1998 it had colonized the St. Lawrence River as far downstream as Montreal (Palmer and Ricciardi, 2004). It has increased its biomass more than 20-fold in the presence of *Dreissena* in western Lake Erie (Stewart et al., 1998a). *E. ischnus* appears to have a higher affinity for *Dreissena* patches than the native species *G. fasciatus*, and has replaced *G. fasciatus* as the dominant amphipod on substrates fouled by dreissenids in Lake Erie and Lake Ontario (Dermott et al., 1998; Van

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Overdijk et al., 2003; Haynes et al., 2005). Although it is assumed to have excluded G. *fasciatus* from mussel patches in the lower Great Lakes (Dermott et al., 1998; Van Overdijk et al., 2003), the mechanisms behind this species replacement are not fully understood (Gonzalez and Burkart, 2004; Limen et al., 2005). They may involve selective predation by fish (Gonzalez and Burkart, 2004; Palmer and Ricciardi, 2005) or intraguild predation, with *E. ischnus* being the dominant predator in water with high concentrations of dissolved ions (Kestrup and Ricciardi, in press). However, no studies have determined if competition for dreissenid-covered substrate with *E. ischnus* increases the vulnerability of *G. fasciatus* to fish predation, which has been implicated as a driver of species replacement among other crustaceans (DiDonato and Lodge, 1993; van Riel, 2008). Although intraguild predation is recognized as an important mechanism of species replacement (Dick and Platvoet, 1996; MacNeil and Platvoet, 2005), its importance relative to other mechanisms such as predation from higher trophic levels has not been tested (Dick, 2008).

The round goby forms dense populations locally in its introduced range (Corkum et al., 2004) and can have a strong impact on the abundance of benthic invertebrates (Kuhns and Berg, 1999; Barton et al., 2005; Lederer et al., 2006). Among its most important prey items are gammarid amphipods (Simonovic et al., 2001; Diggins et al., 2002; Barton et al., 2005). The round goby was already abundant in Lake Erie and Lake Ontario during the 1990s, when *E. ischnus* became dominant (Barton et al., 2005). By contrast, the round goby has only recently become abundant at some sites in the upper St. Lawrence River (Å. Kestrup, personal observation).

If the exclusion of *G. fasciatus* from *Dreissena* patches is caused by increased vulnerability of *G. fasciatus* to predation by gobies, it seems plausible that the rapid species replacement previously observed in the Great Lakes has failed to occur in the St. Lawrence River thus far because of the time delay in the goby's invasion. We hypothesize that predation by the round goby facilitates the replacement of *G. fasciatus* by *E. ischnus* on substrates densely colonized by dreissenids, consistent with the “invasional meltdown” model that predicts increased facilitation amongst invaders with a shared evolutionary history (Simberloff and Von Holle, 1999; Ricciardi 2001, 2005). Alternatively, despite its evolutionary history, *E. ischnus* may not be better adapted to using *Dreissena* patches or may be equally or more vulnerable to round goby predation than *G. fasciatus*. We tested whether (1) the presence of *E. ischnus* alters the use of dreissenid patches by *G. fasciatus*; (2) the round goby selects *G. fasciatus* over *E. ischnus* as prey; (3) the vulnerability of *G. fasciatus* to round goby predation is increased in the presence of *E. ischnus*; and (4) the round goby has a stronger negative impact than native benthivorous fish on the abundance of native amphipods.

Methods

Collection and treatment before lab experiments

The abundances of *E. ischnus* and the round goby are highly variable in the upper St. Lawrence River (Palmer and Ricciardi, 2004; Å. Kestrup and R. Kipp, unpublished data). The round goby has rapidly expanded its populations in the river in recent years. Its distribution is still highly scattered such that sites where it is abundant are in close proximity (<1 km) to sites where it is scarce or absent (Å. Kestrup, personal observation). Exotic and native amphipods used in our laboratory experiments were collected continuously throughout the study at Pointe-du-Moulin on Ile Perrot (an island in the St. Lawrence River adjacent to Montreal), which was not yet colonized by the round goby. Amphipods were collected from dreissenid-covered rocks while wading and snorkelling, and were transported within 3 h to the lab, where they were placed in aerated aquaria containing river water (conductivity 280–300 μS), cobble, sand, dreissenid shells, macrophytes and catfish pellets. All aquaria were kept in the same temperature-controlled chamber at 19 °C in a light regime appropriate for the time of the year (15:9 h light:dark). Round gobies were captured using minnow traps in Lake Saint-François, a fluvial lake in the St. Lawrence River. During an acclimatization period of at least 1 week, fish were stored in aerated 40-L aquaria (L 50 × 27 × 30 cm) with filtered river water, gravel and rocks and were fed frozen chironomid larvae and both species of amphipods. They were exposed to the same temperature and light regime as the amphipods.

Habitat choice experiment

Laboratory experiments were conducted in 54-L aquaria (62 × 31 × 31 cm) filled to 18 cm depth with filtered water of high conductivity (280–300 μS) from the St. Lawrence River. The bottom of each aquarium was covered with a 1-cm thick layer of washed aquarium sand. Placed on the sand were two dreissenid patches, consisting of a monolayer of empty mussel shells attached to 7 × 7 cm transparent plexiglass sheets with nontoxic silicone glue to achieve an average mussel density of 4600 m^{-2} (total area of both patches was 0.0098 m^2 or 5% of the bottom surface area of the aquarium) and weighted down by a stainless-steel plate. The shells were glued at their base with their valves closed and were placed in contact with each other to mimic a single-layered dreissenid colony. To examine if habitat choice was density dependent, we added to the aquarium either a low or high abundance of adult amphipods of both sexes (20 or 40 individuals, equivalent to 104 and 208 individuals m^{-2}, respectively, which is within the range of natural densities in the river; Palmer and Ricciardi, 2004). In both high- and low-density experiments, single species treatments involved either *E. ischnus* or *G. fasciatus*, whereas mixed species treatments consisted of both species in equal ratios. In mixed species treatments, *G. fasciatus* were introduced first and allowed to settle for 5 min before *E. ischnus* were added to the aquaria. After 24 h, the mussel patches were retrieved by covering them with a plastic container that was sealed with a plastic sheet before being lifted out of the aquarium. Amphipods were removed from the mussel patches and counted in a sorting tray. The aquaria were emptied of water and sand and the remaining amphipods were located and counted. Individuals that had been consumed or died were recorded as mortality. No individuals were used in more than one experiment. All experiments had 10 replicates — with the exception of the low-density treatment with single *G. fasciatus*, which had 11 replicates. The low-density experiment was run July 12–August 19, 2007, and the high-density experiment was run September 13–17, 2007. We determined whether the results were influenced by differences in mortality among treatments, by comparing the proportions (arcsine transformed) of surviving amphipods on mussel patches.

Goby predation: lab experiment

The experimental design and procedure were similar to the habitat choice experiment. Aquaria were divided into two compartments of equal size by transparent plexiglass sheets, and the walls of the aquaria were covered with opaque paper to minimize disturbance. A goby was placed into one of the compartments 24 h prior to an experiment and received no food during this time. A total of 40 amphipods (single or mixed species) were added to the other compartment containing two mussel patches. In the single species treatments, the amphipods were allowed to settle for 5 min , whereas in the mixed species treatment *G. fasciatus* individuals were added 5 min prior to the addition of *E. ischnus*. Thereafter, both species were allowed to settle for another 5 min before the divider was removed. The goby was then allowed to forage for 24 h. At the end of the experiment, the mussel patches were retrieved, the fish removed using a hand net, and the remaining amphipods counted. Individual amphipods that had been consumed or died were recorded as mortality. All experiments had 7 replicates and were run August 23–September 6, 2007. To determine if mussels served as a refuge from predation, the proportions of surviving amphipods in mussel beds with and without predation from round gobies were compared in a two-way ANOVA with amphipod species (single *E. ischnus*, single *G. fasciatus*, mixed species) and goby predation (with, without) as fixed factors. Fish of similar size were used in each experiment (57–75 mm TL, average 66.1 mm ± 1.2 SE). During the experiment, the round gobies did not disrupt the dreissenid colonies with their feeding activities, as the total number of mussels per colony was the same at the onset and the end of each experiment.

Goby predation: field experiment

We tested the effect of fish predation on the relative abundance of both amphipod species at two sites in the St. Lawrence River west of Montreal. At one site, an island near Coteau Landing (45°15'11N, 74°12'26W), round gobies were found in high abundance. At another site, Pointe-du-Moulin (54°21'57N, 73°51'06W), situated 30 km downstream, gobies were found in very low abundance. They began to colonize this site in detectable numbers during the month preceding the experiment and were observed for the first time on September 9, 2007, when 5 individuals of <5 cm length were encountered while snorkelling (Å. Kestrup and R. Kipp, personal observation). Both sites, henceforth referred to as the “High Goby” and “Low Goby” sites, are similar in terms of substrate (rocks, boulders and dreissenid colonies) and exposure (facing the main channel of the river), and receive well-oxygenated (8.7–11.5 mg/L, 91–114%) and highly mineralized water (conductance 290–302 µS) from the Great Lakes. Both sites also have a similar composition of native fishes (A. Ricciardi, personal observation). The presence of small (<7 cm) and large (>7 cm) individual gobies at the High Goby site was confirmed on August 9 by two SCUBA divers surveying two 10 m transects, 1 m wide, at 2 m depth. Each transect was surveyed by both divers, and the average of both observations was used as an estimate of the goby abundance along that transect. The abundance of gobies varied between 1.2–4.5 small individuals/m^2 and 0.4–1.8 large individuals/m^2, with means of 2.8 small and 1.1 large individuals/m^2. Experimental treatments consisted of predator-exclusion cages and artificial substrates (cement bricks 19.1 × 9.1 × 5.7 cm) covered with a monolayer of empty dreissenid shells (2.5–3.0 cm shell length). Shells were glued at their base with their valves closed to resemble a natural dreissenid colony, attached to the bricks with nontoxic aquarium silicone. The average number of mussels per brick was 53.8 ± 0.7 SE. Predator-exclusion cages (29.5 × 19.5 × 18 cm) were constructed of stainless-steel wire (mesh size 0.64 cm) and their sides were connected with plastic cable ties. Preliminary trials revealed that small gobies (<7 cm) could easily enter cages with a mesh size of 1.27 cm, but were excluded by the smaller mesh size. In early September 2007, 20 bricks were deployed haphazardly at least 1 m apart at a depth of 0.5–0.8 m at each site. Ten of these bricks were placed individually inside predator-exclusion cages, while another ten bricks remained uncaged and thus served as a predator-access treatment. Bricks were retrieved after 38 and 40 days at the Low Goby and High Goby sites, respectively. Cages were cut open under water and bricks were gently lifted and enveloped within double plastic bags. In the lab, amphipods were removed from the bricks with forceps, and the water in each bag was filtered through a 500 µm mesh sieve. Amphipods were preserved in 70% ethanol and identified to species using a Hund Wetzlar SM33 microscope. Amphipods that were unidentifiable due to the loss of uropods were not included in the analyses.

All analyses were done using SPSS 12.0 for Windows (SPSS Inc. 2003). Statistical tests included independent sample *t*-tests (single species treatments), paired samples *t*-test (mixed species treatments) and one-way ANOVAs. Variances were equal unless otherwise indicated. Prior to analysis, numbers were $\log_{10}$-transformed and proportions were transformed using $\sin^{-1}(x^{0.5})$, where necessary, to meet with the assumption of normality.

Results

Habitat choice experiment

Single species treatment

Individuals of either species were rarely seen swimming in the water column of the aquarium unless disturbed, but instead swam close to the bottom or hid amongst mussel shells. Both species strongly preferred to occupy mussel patches, with densities on the patches more than 5× higher than on sand (paired *t*-tests, $p \leq 0.001$). At low abundances (Fig. 1a), both species showed a similar preference for mussel patches in single species treatments ($t = 1.336$, $p = 0.197$) and their mortality did not differ (*E. ischnus* 0.5 ± 0.2 SE, *G. fasciatus* 1.6 ± 0.5 SE, $t = -1.994$, $p = 0.066$, unequal variances). At high abundances (Fig. 1a), *E. ischnus* showed a stronger preference for mussel patches ($t = 2.369$, $p = 0.029$) and its mortality was higher than that of *G. fasciatus* (*E. ischnus* 1.7 ± 0.4 SE, *G. fasciatus* 0.4 ± 0.2 SE, $t = 2.867$, $p = 0.015$, unequal variances). The final abundance of *E. ischnus* on mussel patches did not differ between high and low abundance treatments ($t = 0.44$, $p = 0.66$), whereas the final abundance of *G. fasciatus* on mussel patches was lower in the high abundance treatment ($t = 2.15$, $p = 0.045$). Similar results were obtained using proportions instead of absolute numbers.

Mixed species treatment

In mixed species treatments, both species preferred to occupy mussel patches over sand at both high and low abundances (paired

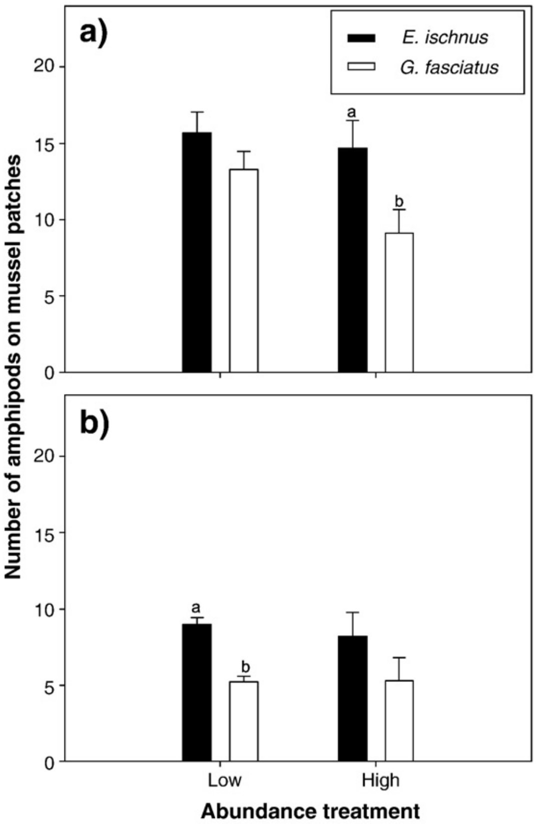

Fig. 1. Number of amphipods on mussel patches of constant size in single species treatments at (a) low and (b) high abundances of amphipods. Error bars denote 1 standard error. Different letters above the bars indicate significant differences ($p < 0.03$).

t-tests, $p \leq 0.018$). In the low abundance treatment (Fig. 1b), *E. ischnus* was found in higher densities on mussel patches than was *G. fasciatus* ($t = -6.626$, $p < 0.001$). There was no difference in the level of mortality for both species (*E. ischnus* 0.4 ± 0.3 SE, *G. fasciatus* 0.7 ± 0.3 SE, $t = 1.406$, $p = 0.193$). In the high abundance treatment (Fig. 1b), there was no significant difference in the number of individuals found among mussel patches ($t = -1.665$, $p = 0.130$) or in the level of mortality (*E. ischnus* 0.4 ± 0.3 SE, *G. fasciatus* 0.7 ± 0.3 SE, $t = 0.605$, $p = 0.560$). Similar results were obtained using proportions instead of absolute numbers. The average number of amphipods found on mussel patches across all replicates was 13.4 (±0.7 SE), and the total number did not differ significantly between treatments (one-way ANOVA, $F_{5,55} = 0.003$, $p = 0.093$).

Goby predation: lab experiment

Both amphipod species were equally vulnerable to predation from gobies in single species treatments ($t = 0.289$, $p = 0.778$; Fig. 2a) and in mixed species treatments ($t = 0.881$, $p = 0.412$; Fig. 2b). Mortality of these species did not vary between single and mixed species treatments (*E. ischnus* $t = 0.26$, $p = 0.80$, *G. fasciatus* $t = -0.13$, $p = 0.90$). Furthermore, total mortality in the mixed species treatment did not differ from that of the single species treatments (one-way ANOVA, $F_{2,18} = 0.057$, $p = 0.95$). A higher proportion of surviving amphipods was found on mussel patches after exposure to predation from round gobies than before predation (two-way ANOVA, $p < 0.001$, $F_{1,51} = 38.361$; Fig. 3). There was no significant effect of species treatment, nor any significant interaction between species and predator treatments.

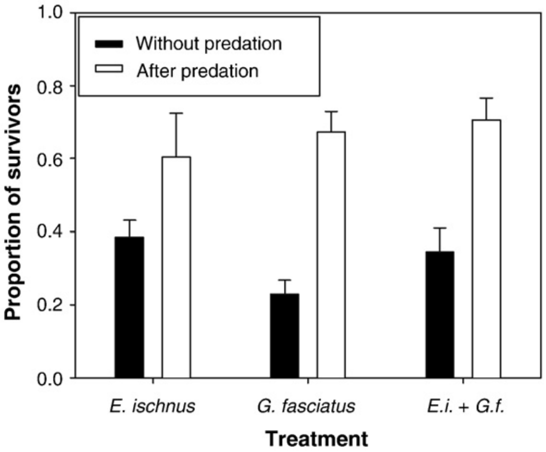

Fig. 3. Proportions of surviving amphipods found on mussel patches in single and mixed species treatments after round goby predation compared with treatments without goby predation. Error bars denote 1 standard error.

Goby predation: field experiment

All bricks were retrieved from the Low Goby site, whereas 5 bricks were lost at the High Goby site (4 caged bricks and 1 uncaged brick). The total abundance of amphipods in the predator-access treatment was higher than in the predator-exclusion treatment at the Low Goby site (224.5 ± 19.1 SE and 154.9 ± 18.7 SE respectively, $t = 2.608$, $p_{2\text{-tailed}} = 0.018$; Fig. 4a), but it did not differ between

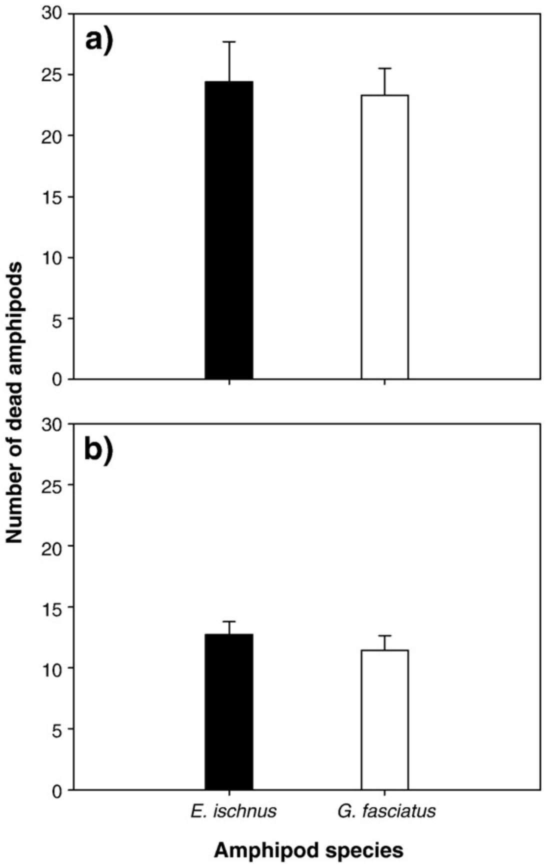

Fig. 2. Total amphipod mortality in single (a) and mixed (b) species treatments after exposure to round goby predation. Error bars denote 1 standard error.

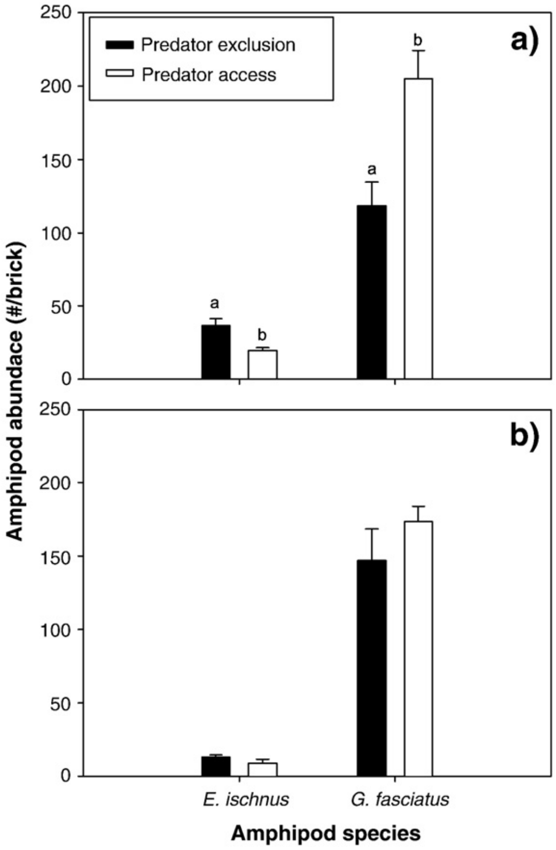

Fig. 4. Amphipod abundance on bricks in predation experiments at field sites with (a) low and (b) high abundances of the round goby. Error bars denote 1 standard error. Different letters above the bars indicate significant differences ($p \leq 0.002$).

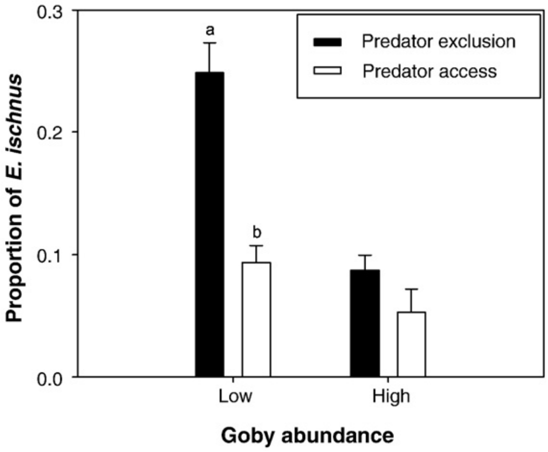

Fig. 5. Proportion of *E. ischnus* on bricks in predation experiments at field sites with low and high abundances of round gobies. Different letters above the bars indicate significant differences ($p < 0.001$, based on transformed data).

treatments at the High Goby site (182.6 ± 9.2 SE and 160.2 ± 22.3 SE respectively, $t = 1.057$, $p_{2\text{-tailed}} = 0.310$, Fig. 4b). At both sites, *G. fasciatus* outnumbered *E. ischnus* in predator-exclusion and predator-access treatments (paired samples *t*-tests, $p \leq 0.001$). However, fish predation did not have the same effect on the relative abundance of *E. ischnus* at both sites. At the Low Goby site, *E. ischnus* comprised a higher proportion of amphipods in the predator-exclusion treatment than in the predator-access treatment (0.25 ± 0.03 versus 0.09 ± 0.01, respectively, $t = -5.871$, $p < 0.001$, arcsine transformed data; Fig. 5). Also in absolute numbers, the number of *E. ischnus* was higher in the predator-exclusion treatment (36.8 ± 4.2 versus 19.6 ± 2.2; $t = -3.60$, $p = 0.002$), while the number of *G. fasciatus* was lower in the predator-exclusion treatment (118.1 ± 16.4 versus 204.9 ± 19.0; $t = 3.46$, $p = 0.003$) (Fig. 4a). At the High Goby site, the relative abundance of *E. ischnus* was similar in the two treatments (0.09 ± 0.01 and 0.05 ± 0.02, respectively; $t = -1.73$, $p = 0.11$, arcsine transformed data; Fig. 5). In absolute numbers, the abundance of *E. ischnus* was also similar in the two treatments (8.9 ± 2.6 and 13.0 ± 1.8, respectively; $t = -1.16$, $p = 0.268$), as was the abundance of *G. fasciatus* (147.2 ± 21.5 and 173.7 ± 10.3; $t = 1.24$, $p > 0.2$) (Fig. 4b).

Discussion

Habitat choice experiment

Despite having evolutionary experience with *Dreissena*, *E. ischnus* does not appear to be better adapted than *G. fasciatus* to using mussel patches as habitat. Both species occupied mussel patches more frequently than surrounding sand. There was no increased mortality in mixed species treatments, suggesting that interspecific predation among amphipods may not be significant at time scales as short as our experiment. In the low abundance treatment, the low numbers of *G. fasciatus* on mussel patches suggested that *E. ischnus* might exclude *G. fasciatus* from dreissenid colonies, but this pattern was not repeated in the high abundance treatment. Therefore, the hypothesis that *E. ischnus* alters the habitat choice of *G. fasciatus* is not supported, even though *E. ischnus* is a dominant intraguild predator in water of high conductivity (Kestrup and Ricciardi, in press). Although the relative abundance of amphipods on mussel patches in mixed species treatments was variable, the total abundance was constant, suggesting that a limited number of amphipods can inhabit a discrete mussel patch regardless of their species composition. However, few studies have shown evidence for competition for habitat among amphipods (Dick, 2008). Where it has been shown, competitive ability appears to be mediated by size, with the larger species excluding the smaller species (van Riel et al., 2007; van Riel, 2008).

Goby predation experiments

Surprisingly, *E. ischnus* and *G. fasciatus* were equally susceptible to goby predation in the presence of mussel patches, despite differences in their evolutionary experience with the round goby and dreissenid mussels. Gobies can reduce total amphipod abundance, but although some previous studies have indicated lower vulnerability of *E. ischnus* compared to other gammarid species in the presence of fish predators (Palmer and Ricciardi, 2005; Kinzler and Maier, 2006), we found no evidence that gobies are selective in their consumption of amphipods or that *G. fasciatus* is more vulnerable to fish predation in the presence of *E. ischnus*. *E. ischnus* is generally more active than *G. fasciatus* (Pennuto and Keppler, 2008; Å. Kestrup, personal observation), yet both species respond to the scent of round gobies similarly by spending more time immobile and moving shorter distances. In prolonged exposure to round goby scent, *E. ischnus* tends to increase its avoidance behaviour while *G. fasciatus* acts oppositely (Pennuto and Keppler, 2008), but our study shows that these behavioural differences do not affect their vulnerability to predation. Apparently, predator recognition does not overcome the risk posed by the efficient hunting tactics of round gobies (Banks and Dickman, 2007), which, being an ambush predator that spends most of its time in close proximity to bottom sediments, may be better at detecting small prey than actively foraging visual predators. The complex interstitial habitat provided by dreissenid mussels may serve as a refuge for amphipods from fish predation (Dermott et al., 1998; Gonzalez and Downing, 1999; Mayer et al., 2001), but whether any particular species is favored depends on the specific behaviour of the predator species. An unpublished study found that a native benthivore, rock bass *Ambloplites rupestris*, preferentially selected *G. fasciatus* over *E. ischnus* (C.M. Mayer, Department of Environmental Sciences, University of Toledo, personal communication). Kolar et al. (2002) found similar results when exposing the North American amphipod *Gammarus pseudolimnaeus* to predation from a benthic ambush predator with a well developed sensory system – the Eurasian ruffe (*Gymnocephalus cernuus*), and a visual predator – the North American yellow perch (*Perca flavescens*); amphipods reduced their activity more in the presence of ruffe, but nevertheless suffered more intense predation from the ruffe.

An appropriate question is whether the use of live mussels instead of intact shells would have produced different results in our experiments by making the mussel patches more attractive to amphipods and gobies. Previous studies showed that both *G. fasciatus* and *E. ischnus* respond primarily to the physical structure of the *Dreissena* patch, rather than to the characteristics of live mussels (Ricciardi et al., 1997; Stewart et al., 1998a,b). Moreover, round gobies of the size used in our lab experiment strongly prefer amphipods over mussels as a prey item (Diggins et al., 2002). Therefore, it seems unlikely that the use of live mussels would have altered the results.

Selective predation by the fish community as a whole may account for the lower relative and absolute abundance of *E. ischnus* in predator-access treatments during the field experiment. Indeed, a previous study found evidence that *E. ischnus* was more vulnerable than *G. fasciatus* to native predators in the St. Lawrence River (Palmer and Ricciardi, 2005). Owing to the small mesh size required to exclude small gobies, there may have been a cage effect that reduced the colonization of bricks by amphipods at both sites. However, such an effect would not explain the higher abundance of *E. ischnus* in the predator-exclusion treatment at the Low Goby site; we would expect reduced flow to negatively affect *E. ischnus*, which prefers habitats with at least moderate current (Palmer and Ricciardi, 2004). At the High Goby site, the total abundances of amphipods in the predator-access and predator-exclusion treatments were not significantly different, perhaps indicating that predation pressure from gobies in predator-access treatments is high enough to compensate for a negative cage effect in the predator-exclusion treatment.

Conclusions

The growing frequency of invasions in aquatic systems worldwide has increased the likelihood that species with shared evolutionary histories will be reunited in new regions (e.g. Adams et al., 2003). Positive interactions are common among such invaders (Simberloff and Von Holle, 1999; Ricciardi, 2001) and can augment their ecological impact (Ricciardi, 2001, 2005). For example, co-adaptation may reduce the intensity of predator–prey interactions and confer a competitive advantage to an exotic prey introduced with its predator over predator-naïve enemies in the invaded community (Case and Bolger, 1991; Adams et al., 2003). Co-adapted relationships that are re-established through multiple invasions in a new region, as is occurring in the Great Lakes, may thus have synergistic effects on native species (Ricciardi, 2005).

However, as we have shown here, the co-occurrence of exotic species with shared evolutionary histories does not guarantee that one or more of them will have a competitive advantage over native species. The exotic and native gammarid amphipods in our study are quite similar morphologically and ecologically, which might account for their similar use of *Dreissena* patches and the lack of selective predation by the round goby. Moreover, in general, species interactions are highly context-dependent and can vary across space and time (Bruno et al., 2003), particularly across physically heterogeneous environments (e.g. Alcaraz and Garcia-Berthou, 2007). We conclude that the outcome of antagonistic interactions among these amphipods in the St. Lawrence River is mediated more by their relative tolerance to local physico-chemical conditions (particularly calcium concentration and conductivity; Kestrup and Ricciardi, in press) than by the presence of other Ponto-Caspian species.

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