



## 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.

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### 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  $\mu\text{S}$ ), 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  $\mu\text{S}$ ) 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  $\text{m}^{-2}$  (total area of both patches was 0.0098  $\text{m}^2$  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  $\text{m}^{-2}$ , 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

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