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Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean

Åsa M. Kestrup · Anthony Ricciardi

Abstract The impacts of an exotic species may vary along environmental gradients. We tested the hypothesis that site-specific heterogeneity in the physico–chemical environment alters the dominance of two competing amphipods: *Gammarus fasciatus*, the dominant native species in the upper St. Lawrence River, and *Echinogammarus ischnus*, a euryhaline Ponto-Caspian species that invaded the river in the late 1990s. *E. ischnus* has replaced *G. fasciatus* as the dominant amphipod at some sites, while remaining inferior at other sites—even several years after invasion. We tested the effect of water chemistry (conductivity) on the outcome of interactions between these two species in the laboratory and in the river in 2006 and 2007. Field experiments involved transplanting both species to different sites along a gradient of conductivity within the river, whereas the laboratory experiments examined interspecific predation in water collected from these sites. The laboratory experiments revealed that these species are mutual predators and their rate of predation on each other varies with conductivity; *E. ischnus* is the dominant predator at higher conductivity, while *G. fasciatus* dominates at lower conductivity. The field experiments showed interannual variation, but supported the lab results at high conductivity in 2006 and at low conductivity in 2007. *E. ischnus* was more sensitive than *G. fasciatus* to variation in conductivity, which apparently mediates this invader's ability to replace or dominate the native species in a heterogeneous environment.

Keywords Amphipod · Competition · Conductivity · *Echinogammarus* · *Gammarus* · Intraguild predation · Invasive species · Species replacement

Å. M. Kestrup · A. Ricciardi (✉)
Redpath Museum, McGill University, 859 Sherbrooke St.
West, Montreal, QC H3A 2K6, Canada
e-mail: tony.ricciardi@mcgill.ca

Å. M. Kestrup
e-mail: asa.kestrup@mcgill.ca

Introduction

There can be substantial spatial variation in the establishment success and population growth of an introduced species (Hunt and Yamada 2003; Jones and Ricciardi 2005; deRivera et al. 2005) and in its impact on native species populations (MacNeil et al. 2001; Ricciardi 2003; Melbourne et al. 2007). This site-specific dependence is driven largely by the physiological tolerance of the invader to local conditions, which can affect the outcome of its interactions with other species in the invaded range (Dunson and Travis 1991; Moyle and Light 1996; Von Holle 2005). Thus, an invader that is a superior competitor at one site may be an inferior competitor at other sites, depending on whether the physico–

chemical conditions optimal to the invader differ from those optimal to its competitors (Dunson and Travis 1991; Hunt and Yamada 2003; deRivera et al. 2005). For example, water quality parameters such as conductivity (specific conductance) have been recently shown to mediate the outcome of invasions by freshwater crustaceans in Europe (Dick and Platvoet 1996; MacNeil et al. 2003, 2004).

The aim of our study is to examine the influence of conductivity on the interactions between an invasive amphipod crustacean of Ponto-Caspian origin, *Echinogammarus ischnus*, and a North American amphipod, *Gammarus fasciatus*. *E. ischnus* is a successful invader of fresh and brackish waters in Europe (bij de Vaate et al. 2002; Kinzler and Maier 2003) and more recently in the North American Great Lakes, where it became established in the early 1990s (Witt et al. 1997; Dermott et al. 1998; Van Overdijk et al. 2003). By 1998, it had colonized the upper St. Lawrence River between Lake Ontario and the Island of Montreal (Palmer and Ricciardi 2004). In the Great Lakes, *E. ischnus* has replaced the previously dominant amphipod, *G. fasciatus*, on rocky substrate colonized by other Ponto-Caspian species: dreissenid mussels *Dreissena polymorpha* and *D. bugensis* (Dermott et al. 1998; Van Overdijk et al. 2003; Gonzalez and Burkart 2004; Haynes et al. 2005). By contrast, a decade after its discovery in the St. Lawrence River, *E. ischnus* rarely dominates amphipod communities even on mussel covered substrate (Palmer and Ricciardi 2004, 2005; Å.K. personal observation).

The hypothesized mechanisms of this species replacement include resource competition, interspecific (intraguild) predation and interspecific aggression (Gonzalez and Burkart 2004; Limén et al. 2005). Many species of amphipods engage in cannibalism and interspecific predation (Conlan 1994; MacNeil et al. 1997, 1999; MacNeil and Platvoet 2005). An individual is particularly vulnerable to predation during moulting (Dick et al. 1999); this vulnerability can be influenced by abiotic conditions that deviate from the conditions to which the species is optimally adapted (Dick and Platvoet 1996). However, there is contrasting evidence regarding the mechanisms of dominance and species replacement involving *E. ischnus* and *G. fasciatus* (Dermott et al. 1998; Van Overdijk et al. 2003; Limén et al. 2005), and thusfar no studies have examined the influence of conductivity on *E. ischnus* dominance. Although both amphipods have a freshwater ancestry (Barnard and Barnard 1983), *E. ischnus* is a euryhaline species adapted to fresh and brackish water environments with high conductivity and calcium concentration (Cristescu et al. 2004) and its activity is reduced in ion-poor water (Wijnhoven et al. 2003), whereas *G. fasciatus* is a strictly freshwater species (Clemens 1950; Holsinger 1972).

We evaluated the hypothesis that water chemistry mediates the impact of *E. ischnus* on *G. fasciatus*, and tested whether (1) interspecific predation is a mechanism by which *E. ischnus* dominates amphipod communities in the St. Lawrence River, (2) the magnitude and direction of interspecific predation between *E. ischnus* and *G. fasciatus* is influenced by conductivity, and (3) the mean body size and survivorship of both species varies across a conductivity gradient in the river.

Methods

A series of experiments was performed in the laboratory and at field sites in Lake St. Louis, a fluvial lake situated at the Island of Montreal where the Ottawa River joins the St. Lawrence River. The lake is chemically heterogenous because of the mixing of these two water masses (Ottawa River: conductivity 80 μS cm^{-1}; St Lawrence River: conductivity 300 μS cm^{-1}) (Centre St-Laurent 2003). We selected three
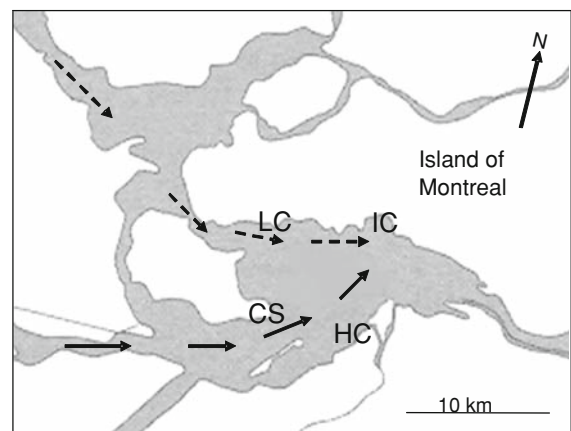

Fig. 1 *Map* of Lac St Louis showing the collection site (CS) at PDM and the experimental sites with low (LC), intermediate (IC), and high conductivity (HC). The *dashed arrows* indicate low conductivity water flow from the Ottawa River and the *full arrows* indicate high conductivity water flow from the St. Lawrence River

sites (Fig. 1) that had bottom substrate suitable for amphipods (cobble, sand, and rocks with *Dreissena* colonies) and which also differed in conductivity (Table 1) and in the relative abundance of the two amphipod species (Palmer and Ricciardi 2004); henceforth, these sites are referred to as the low (LC), intermediate (IC) and high conductivity (HC) sites. The LC site receives water mainly from the Ottawa River, the HC site receives water from the St. Lawrence River, whereas the water at the IC site is a mixture of water from both rivers. Water chemistry was sampled repeatedly at all sites to account for fluctuations in conductivity. The water was collected just above the river bottom in clean plastic bottles, and stored at 4°C in a refrigerator until analysed <3 days later (LaMotte Model PHT-CM-DR-LT). Water chemistry variables (pH, O_2, conductivity, temperature) were measured in situ with an electronic meter (YSI# 85-25-FT). All amphipods used in the experiments were collected from Point-du-Moulin (PDM) at the southern end of Ile Perrot, an island immediately west of Lac St. Louis, where both species were found in high abundance (Fig. 1); thus, we avoided using individuals that may have adapted to different microenvironments.

Individuals were identified to species and sex, using the criteria of Witt et al. (1997), Holsinger (1972) and Clemens (1950). We measured the total straight length (i.e. from the base of the antennae to the tip of the telson) of a separate group of individuals from each site, to avoid exposing the experimental animals to additional stress. Our study was performed at sites not yet invaded by the round goby (*Neogobius melanostomus*), a Ponto-Caspian fish with a potentially strong predatory impact on amphipod abundance (Barton et al. 2005).

Survey of the relative abundance of the two amphipod species

The abundance of amphipods on rocky substrate at each site was estimated from samples of 10 *Dreissena*-covered rocks collected by snorkeling. This was done to identify natural patterns of the relative abundance of the two amphipods in relation to conductivity. Rocks were collected randomly from 1 m depth on 26–30 July 2007, placed individually in double plastic bags while under water, stored in coolers and transported to the lab within 3 h. In the lab, all organisms were removed from the rocks. Amphipods were collected using a sieve with a mesh size of 0.5 mm, preserved in 70% ethanol, and later identified to species. Small juveniles that passed through the sieve were therefore not included, resulting

Table 1 Average (A) and range (R) of the values of the physico–chemical properties measured at the sites with low conductivity (LC), intermediate conductivity (IC) and high conductivity (HC) and the collection site (PDM)

Site	Year	Conductivity (μS cm^{-1})	Ca^{2+} (mg l^{-1})	Temp (°C)	O_2 (%)	O_2 (mg l^{-1})	pH
PDM	2006	A: 273 (9)	A: 37.5 (5)	A: 25.3 (9)	A: 139 (7)	A: 9.1 (7)	A: 9.1 (7)
		R: 253–295	R: 32–42	R: 23.9–26.2	R: 115–155	R: 7.4–12.6	R: 8.8–9.4
	2007	–	–	–	–	–	–
LC	2006	A: 98 (10)	A: 13.9 (7)	A: 26.0 (10)	A: 119 (9)	A: 9.5 (9)	A: 8.8 (8)
		R: 87–107	R: 13–15	R: 22.7–27.5	R: 101–128	R: 7.6–12.9	R: 8.4–9.2
	2007	A: 110 (4)	A: 15.8 (2)	A: 24.3 (4)	A: 110 (4)	A: 9.2 (4)	–
		R: 83–113	R: 13–18	R: 19.9–27.0	R: 88–132	R: 8.2–10.3	–
IC	2006	A: 149 (8)	A: 23.1 (7)	A: 25.5 (8)	A: 109 (7)	A: 9.1 (7)	A: 8.4 (6)
		R: 121–175	R: 20–27	R: 21.9–27.3	R: 89–126	R: 8.2–11.2	R: 7.9–8.7
	2007	A: 203 (4)	A: 26.9 (2)	A: 24.4 (4)	A: 134 (4)	A: 11.2 (4)	–
		R: 177–215	R: 21–33	R: 19.6–27.5	R: 82–153	R: 7.5–12.6	–
HC	2006	A: 286 (8)	A: 34.5 (7)	A: 24.0 (8)	A: 116 (8)	A: 9.8 (8)	A: 8.8 (6)
		R: 276–294	R: 32–35	R: 19.8–27.5	R: 94–135	R: 8.5–11.4	R: 8.5–8.9
	2007	A: 281 (4)	A: 34.2 (2)	A: 24.3 (4)	A: 127 (4)	A: 10.7 (4)	–
		R: 280–284	R: 33–35	R: 21.3–26.1	R: 109–150	R: 9.0–12.5	–

The number in brackets represents the number of sampling occasions. In 2007, pH was not measured at any site, and conductivity was not measured at PDM

in an underestimate of amphipod abundance. However, newly hatched juveniles are very difficult to distinguish as species, and including them would increase the risk of misidentification. The surface area of the rock was estimated from its three orthogonal dimensions (length, width, breadth) by an equation that determines the area of an ellipsoidal shape (Dall 1979):

$$\text{Surface area} = \pi/3(\text{length} \times \text{width} + \text{length} \times \text{breadth} + \text{width} \times \text{breadth})$$

Given that amphipod abundance is correlated with *Dreissena* and macrophyte biomass (Palmer and Ricciardi 2004), both parameters were measured. Using an electronic balance, the wet weight of *Dreissena* was measured to the nearest 0.1 g, and the dry weight of *Cladophora* was determined after drying samples in an oven for 12 h at 60°C. One-way ANOVAs with Tukey multiple comparisons post-hoc tests were performed to identify differences in abundance between sites. The data were $\log_{10}$-transformed prior to analysis to meet with assumptions of normality.

Laboratory experiment: interspecific predation on females

Rates of inter- and intraspecific predation on females were examined in experimental arenas using water collected from the three sites. Preliminary experiments showed that the rate of intra- and interspecific predation among males was very low, while inter- and intraspecific predation by males on females was frequent; therefore only predation rates on females were examined in subsequent experiments. Experiments took place in August 2006 using only healthy, sexually mature males and non-gravid females found in precopula pairs collected at PDM (Fig. 1). Prior to the experiment, animals were stored in well-aerated tanks with source water and gravel from the collection site for >24 h provided with food in excess (*Vallisneria americana* and catfish pellets). Experiments were conducted in an environmental chamber (Lab-Line Environette) at a constant temperature (24°C) and with a cycle of 12 h light:12 h darkness, appropriate for the time of the year. Experimental arenas consisted of glass vials (6 cm Ø), with 2 ceramic filter tubes (1 cm long, 0.6 cm Ø) per vial serving as shelters, filled with 50 ml of source water (LC, IC or HC). Water used in the experiment was allowed to stand in the lab for 1 h prior to the onset of the experiment to ensure acclimation to room temperature. Food was not added to the experimental arenas. The observation time was limited to 12 h during the light cycle. The mortality of single females was used as controls (25 replicates per species) to account for mortality due to stressors other than predation. Treatments (25 replicates per treatment) consisted of one female in combination with one male (native or exotic) or two males (1 native + 1 exotic). Any acts of ongoing cannibalism or predation and unobserved deaths were recorded at 30 min, 1, 2, 4 and 12 h after the initial introduction of amphipods. However, as both species were predators and scavengers, the different causes of mortality are treated as total mortality. Statistical comparisons of raw data were done with the Fisher Exact test (one-tailed).

Field experiment: interspecific predation along a conductivity gradient

To examine if the results from the lab experiment could be extrapolated to the field, field transplants were performed in 2006 and 2007. These involved single-species treatments with either 12 *E. ischnus* or 12 *G. fasciatus*, and mixed-species treatments with six individuals of each species (six replicates per treatment). Single-species treatments were used to assess differences in the tolerance to abiotic conditions, mortality and the occurrence of cannibalism, while mixed-species treatments were used to examine the rate of interspecific predation. Bioassay tubes (18 in total per site) containing individuals collected at PDM were deployed at 1 m depth at each of the three field sites. In 2006, the experiments were started on July 25–27 and ran for 7 days, whereas in 2007 they were started on July 19–20 and ran for 4 days. Individuals were collected at PDM 1 day prior to the onset of the experiment and stored overnight in well-aerated aquaria with source water and food in excess. Only healthy, sexually mature males and non-gravid females were used. The proportion of females and males was random in 2006, whereas equal sex ratios were used in 2007. Bioassay tubes were PVC pipes (length 20 cm, Ø 5 cm) with a single terminal opening covered with two layers of nylon mesh of 1 mm pore size; the opposite opening was sealed with a PVC screw cap. Pre-trials indicated that two layers of mesh of this size were required to prevent amphipods from escaping, but still allowed the free movement of water and prevented clogging by silt and debris. Each tube contained two

catfish food pellets and two 20 cm strands of eelgrass (*Vallisneria americana*). Triplets of tubes (one with each treatment) secured to two bricks were placed randomly within 1 m of each other throughout each site. Survival of native and exotic species in single-species tubes at the different sites was compared in one-way ANOVAs and Tukey multiple comparisons post-hoc tests. Survival in mixed-species tubes was compared in paired *t*-tests with equal variances assumed, as was survival of natives and exotics in single-species tubes within a site.

Size measurement of males

Ion-poor water is more stressful to some species than others (Wijnhoven et al. 2003). To determine whether differences in mean body size influences which species is more vulnerable to predation in suboptimal conductivities, length measurements were made of individuals of *E. ischnus* and *G. fasciatus* from all three sites in late July 2007. Only males were measured, because they are responsible for predation (MacNeil et al. 1997; Å.K. personal observations). The body length, i.e. the base of the antennae to the tip of the telson when straightening the back of the animal, was measured to the nearest 0.5 mm using a ruler under a dissection microscope. Males were identified according to Witt et al. (1997) and Clemens (1950). The samples from the IC site contained too few male *E. ischnus* to obtain significant results in July, therefore amphipods of both species were collected again from the three sites on October 22, 2007. The size of *G. fasciatus* at the different sites was compared in one-way ANOVAs with a Tukey multiple comparisons post-hoc test, whereas the size of *E. ischnus* was compared across different sites and with co-occurring *G. fasciatus* in independent-samples *t*-tests with equal variances assumed, unless otherwise indicated.

All analyses were done using SPSS 12.0 for Windows statistical software (release 12.0.0).

Results

Relative abundance of the amphipod species in relation to conductivity

The native amphipod *G. fasciatus* was more abundant at the IC and HC sites than at the LC site

($F_{2,27} = 20.7$, $P < 0.001$; Fig. 2). By contrast, *E. ischnus* was abundant only at the HC site, and insignificant or absent at the other sites ($F_{2,27} = 16.3$, $P < 0.001$). The low abundance of *E. ischnus* at the IC site was not driven by either low *Dreissena* biomass or overgrowth of *Cladophora*, as *Dreissena* was most abundant at this site ($F_{2,27} = 6.7$, $P = 0.004$; Fig. 3) and *Cladophora* was absent ($F_{2,27} = 58.2$, $P < 0.001$; Fig. 4). Furthermore, *E. ischnus* was found at high abundances at the HC site, despite lower *Dreissena* biomass and overgrowth of *Cladophora*.

Laboratory experiment: interspecific predation on females

In August 2006, the total lengths of *G. fasciatus* males and females that were collected at PDM and used in the experiments were 7.2–9.0 and 5.7–7.8 mm, respectively. *E. ischnus* males and females were 8.0–9.1 and 5.5–7.5 mm in length, respectively. In the controls, the mortality of single *E. ischnus* females was higher than the mortality of *G. fasciatus* females only in HC water ($P < 0.001$; Fig. 5). Both
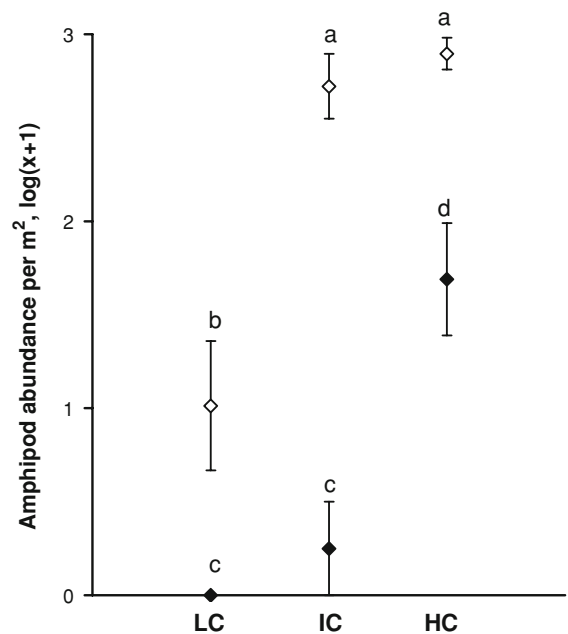

Fig. 2 Abundance of *G. fasciatus* (*open diamonds*) and *E. ischnus* (*solid diamonds*) at the three experimental sites in late July. *Error bars* denote 1 standard error. *Different letters* above the bars indicate statistical differences ($P < 0.001$)
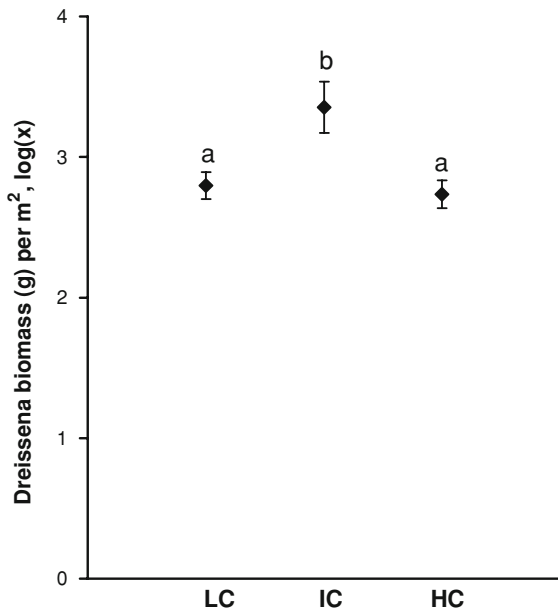
Fig. 3 *Dreissena* biomass (g) per m². *Error bars* denote 1 standard error. *Different letters* above the bars indicate statistical differences ($P < 0.02$)
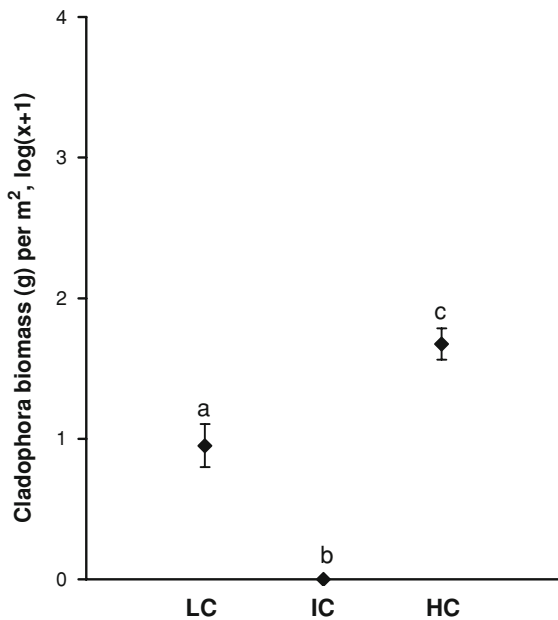

Fig. 4 *Cladophora* biomass (g) per m². *Error bars* denote 1 standard error. *Different letters* above the bars indicate statistical differences ($P < 0.001$)

species acted as cannibals, interspecific predators and scavengers—as indicated by our observations of amphipods attacking carcasses of individuals that
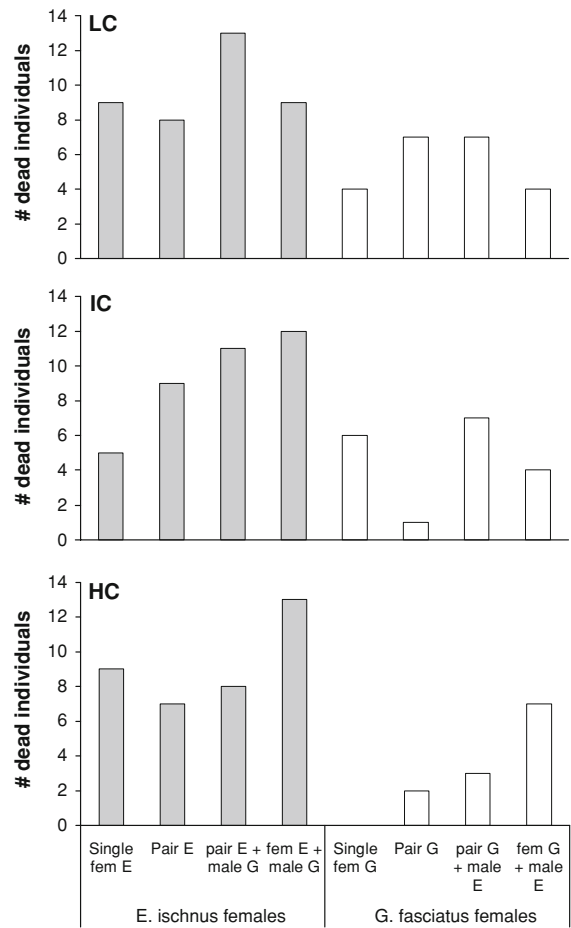

Fig. 5 Mortality of females in combination with 0, 1 or 2 males in experimental treatments. *E. ischnus* mortality is represented by *grey bars* and *G. fasciatus* mortality by *white bars*

had died from causes other than predation. Missing bodies could therefore not be interpreted as being the result of predation only. Instead, death rate due to predation was measured indirectly as an increase in death rate compared to single-species treatments. In IC water, there was an increase in the mortality of exotic females in the presence of native males ($P = 0.037$), but not of native females (Fig. 5; Table 2). In HC water, the pattern was reversed and the mortality of native females was increased in the presence of *E. ischnus* males ($P = 0.0048$). At low conductivity, there was no evidence of increased mortality of females of either species in the presence of males. Neither of the observed increases were significant at the Bonferroni-corrected alpha level of 0.003.

Table 2 Statistical comparisons of mortality of females in controls and treatments at the low conductivity (LC), intermediate conductivity (IC) and high conductivity (HC) sites

Site	E. ischnus female +	P	G. fasciatus female +	P
LC	E male	NS	G male	NS
	E + G male	NS	E + G male	NS
	G male	NS	E male	NS
IC	E male	NS	G male	NS
	E + G male	NS	E + G male	NS
	G male	0.037	E male	NS
HC	E male	NS	G male	NS
	E + G male	NS	E + G male	NS
	G male	NS	E male	0.0048

P probability value from Fisher Exact test

NS not significant

Field experiment: interspecific predation along a conductivity gradient

In 2006, we retrieved all but one replicate of the single-species treatment of each species at the HC site and all but one replicate of the mixed-species treatment at the IC site. In single-species treatments, survival of *E. ischnus* was lower at the LC site than at the IC and HC sites, whereas there was no difference between IC and HC sites ($F_{2,14} = 8.7$, $P = 0.004$; Fig. 6a). The native amphipod *G. fasciatus* survived equally well at all sites ($F_{2,14} = 0.8$, $P = 0.5$). The survival of both species was similar at the IC and HC sites, and differed only at the LC site ($t = 4.5$, $P = 0.001$). In mixed-species treatments, survival of *G. fasciatus* was lower at the HC site ($t = -5.5$, $P = 0.003$; Fig. 6b). At the IC and LC sites, there was no indication of increased mortality due to interspecific predation (*t*-tests, $P > 0.2$).

In the second series of experiments, performed in July 2007, all replicates were recovered. *E. ischnus* survival varied across sites in single-species treatments ($F_{2,15} = 6.2$, $P = 0.011$; Fig. 7a); however, survival differed only between the HC and the LC sites. Again, there was no difference in *G. fasciatus* survival across sites ($F_{2,15} = 0.587$, $P = 0.568$), but the survival of *G. fasciatus* was lower than that of *E. ischnus* at the HC site ($t = 0.8$, $P = 0.042$). In mixed-species treatments, survival of *E. ischnus* was lower than that of *G. fasciatus* at the LC site
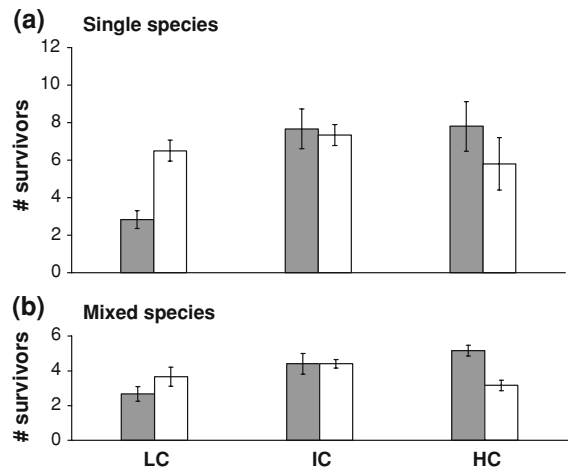
Fig. 6 Number of survivors in field transplants in 2006 for **a** single-species and **b** mixed-species treatments. *E. ischnus* survival is represented by *grey bars* and *G. fasciatus* survival by *white bars*. In single-species treatments, survival of *E. ischnus* was lower at the LC than at the IC ($P = 0.007$) and HC ($P = 0.009$) sites, while survival of the native species did not differ among sites. In mixed-species treatments, survival of the native species was lower than that of the exotic only at the HC site. *Error bars* denote 1 standard error
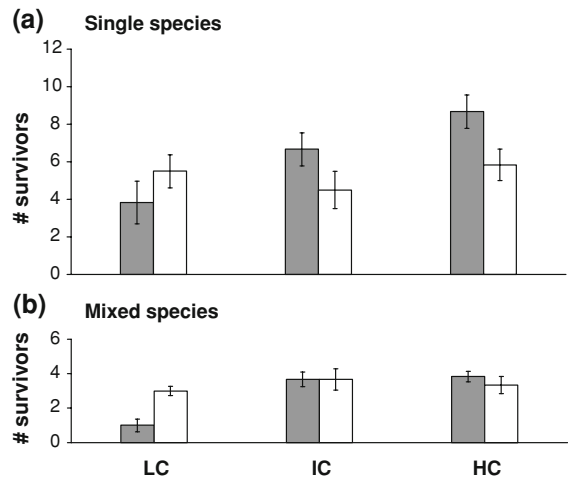
Fig. 7 Number of survivors in field transplants in 2007 for **a** single-species and **b** mixed-species treatments. *E. ischnus* survival is represented by *grey bars* and *G. fasciatus* survival by *white bars*. In single-species treatments, survival of *E. ischnus* was higher at the HC than at the LC site ($P = 0.008$). In mixed-species treatments, survival of *E. ischnus* was lower than that of *G. fasciatus* at the LC site ($P = 0.007$). *Error bars* denote 1 standard error

($t = -4.5$, $P = 0.007$; Fig. 7b). There was no difference in survival between species at the IC and HC sites (*t*-tests, $P > 0.4$).

Relative size of male amphipods

In July, *G. fasciatus* males were larger at the IC site than at the LC site, but there was no difference in size between the HC and the other sites ($F_{2.77} = 3.0$, $P = 0.056$; Fig. 8a). There were too few male *E. ischnus* to perform a similar comparison.
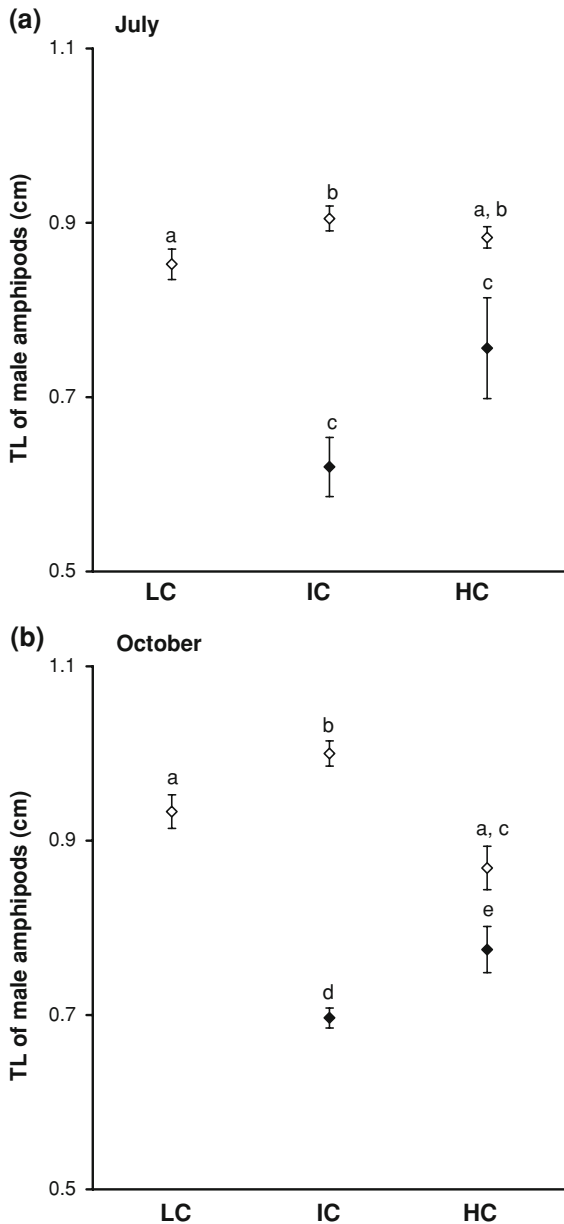

(a) July

(b) October

Fig. 8 Average size of male *G. fasciatus* (*open diamonds*) and *E. ischnus* (*solid diamonds*) in **a** late July and **b** late October. *Error bars* denote 1 standard error. *Different letters* above the bars indicate statistical differences of $P < 0.05$

In late October, the size of both *G. fasciatus* and *E. ischnus* differed among sites ($F_{2.54} = 8.9$, $P < 0.001$, and $t = -5.9$, $P < 0.001$, Fig. 8b). *G. fasciatus* achieved its largest size at the IC site. *E. ischnus* was largest at the HC site ($t = 4.5$, $P < 0.001$). *E. ischnus* was larger than *G. fasciatus* at both sites in which they co-occurred (IC: $t = 14.7$, $P < 0.001$, HC: $t = 2.4$, $P = 0.025$).

Discussion

In our lab experiments, the rate and direction of interspecific predation varied with conductivity. Consistent with previous studies, males of the dominant species preyed almost exclusively on females of the inferior species and mortality was reduced in females guarded by a conspecific male (Dick et al. 1999; MacNeil et al. 1999). However, the contrasts are not very strong, and we found an increase in mortality only when comparing the survival of single females and females together with males. Male *E. ischnus* were more predaceous at high conductivity, whereas male *G. fasciatus* were more predaceous at low conductivity. Other studies have similarly found that the vulnerability of an individual to predation is influenced by suboptimal abiotic conditions (Dick and Platvoet 1996; MacNeil et al. 2003). However, to our knowledge, this is the first observation of a native crustacean replacing an invader as the superior predator along an environmental gradient. In previous studies of predatory interactions between native and exotic crustaceans, the impact of the superior species on the inferior species was reduced in unfavourable abiotic conditions, but the predator-prey relationship was not reversed (Dick and Platvoet 1996; Hunt and Yamada 2003; MacNeil et al. 2003; deRivera et al. 2005).

In both years of our field experiment, survival of *E. ischnus* increased with conductivity in the absence of interspecific interactions, while survival of the native species did not change. This finding is consistent with the predominant occurrence of *E. ischnus* in ion-rich waters within its native range (Wijnhoven et al. 2003; Cristescu et al. 2004). Although both species tolerate fresh water, the conductivities at our IC and LC sites could be at the lower tolerance limit of the invader. In our field and laboratory experiments, the presence of

E. ischnus increased the mortality of *G. fasciatus* at high conductivity. In contrast to the laboratory results, *G. fasciatus* had no negative influence on *E. ischnus* survival at the IC site. However, the native species had an antagonistic effect that resulted in a reduction in the survival of *E. ischnus* at low conductivity. There was interannual variation in the outcome of interspecific interactions; we found a negative effect of the exotic on the native amphipod only in 2006 and a negative effect of the native on the exotic amphipod only in 2007, suggesting that other external variables (e.g. temperature, oxygen) might contribute to the relative competitiveness of a species and its vulnerability to predation (Wijnhoven et al. 2003; MacNeil et al. 2004).

The native amphipod occurred at all three field sites, but was found in lower abundances at the site with low conductivity. At this site, *E. ischnus* was absent; its abundance increased with conductivity at the other two sites. *E. ischnus* abundance is strongly influenced by both *Dreissena* and *Cladophora* biomass (Palmer and Ricciardi 2004). Although both species of amphipods can use *Cladophora* as food, *E. ischnus* is more susceptible to predation from fish on this substrate because of its conspicuous coloration (Gonzalez and Burkart 2004). Selective predation therefore excludes *E. ischnus* from becoming abundant on plants. However, despite more favourable conditions at the IC site regarding *Cladophora* and *Dreissena* biomass, *E. ischnus* was found in low abundance at this site, suggesting that these two variables are not driving the patterns found in our field survey.

At sites where the two species co-occurred, the native males were generally larger than the exotic males, but exotic males became larger with increasing conductivity. The reduction in size of *E. ischnus* in ion-poor water may be due to increased physiological stress that limits their growth (Wijnhoven et al. 2003), possibly also affecting their predatory activities.

The impact of *E. ischnus* in North America is similar to that in its introduced range in Western Europe, where it is a superior predator on other gammarid amphipods (Kinzler and Maier 2003). However, the negative impact of *E. ischnus* on *G. fasicatus* in the Great Lakes-St. Lawrence River system apparently occurs only in water of high conductivity. Low conductivity limits the range of environments that *E. ischnus* could potentially invade, but even where it becomes established its dominance may be further limited by interactions with *G. fasciatus* in areas where the physico–chemical environment is suboptimal to the invader.

Our results reveal the importance of considering physiological tolerances and variation in water quality when examining antagonistic interactions between native and exotic species. They support the hypothesis that increasing environmental heterogeneity facilitates species coexistence (Chesson and Huntly 1997; Chesson 2000)—a concept applicable to species invasions. A spatially heterogenous environment offers closely spaced habitats suitable for either native or exotic species, or both, and is therefore more invasible than homogenous environments (Davies et al. 2005). Furthermore, heterogenous environments provide refugia for competitively inferior species in the presence of a dominant native or exotic species (Hunt and Yamada 2003; deRivera et al. 2005). Indeed, there is an increasing understanding of the role of habitat heterogeneity and biotic interactions on invasion success and impact (Davies et al. 2005; Mitchell et al. 2006; Melbourne et al. 2007), with examples that include bivalves and their various enemies (Reusch 1998; Reusch and Williams 1999; Byers 2002; Hunt and Yamada 2003; deRivera et al. 2005), fishes (Alcaraz et al. 2008), ants (Holway et al. 2002), and terrestrial plants (Von Holle 2005).

To our knowledge, this is the first experimental study in North America to test the role of water chemistry in regulating the impact of an aquatic invader. Our findings suggest that conductivity mediates the rate and direction of interspecific predation between the invasive amphipod *E. ischnus* and the native amphipod *G. fasciatus* in the St. Lawrence River. We conclude that interspecific predation is at least one mechanism by which *E. ischnus* is replacing *G. fasciatus* in the Great Lakes basin, but via this mechanism either amphipod may dominate, depending on local water chemistry.

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