Community interactions affecting the relative abundances of native and invasive amphipods in the St. Lawrence River

M.E. Palmer and Anthony Ricciardi

Abstract: The Eurasian amphipod *Echinogammarus ischnus* is reportedly replacing the common native amphipod *Gammarus fasciatus* in the Great Lakes – St. Lawrence River system. A potential mechanism for this replacement is competition mediated by resident species. Other Eurasian invaders, dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*), dominate rocky substrates throughout the system and might be promoting the rapid expansion of *E. ischnus* by providing habitat and refugia from predation. Using an in-situ predator-exclusion experiment, we tested the hypothesis that *E. ischnus* is better able than *G. fasciatus* to use *Dreissena* spp. colonies as refugia and thus is less susceptible to predators in the St. Lawrence River. Co-occurring *E. ischnus* and *G. fasciatus* showed similar increases in density in the presence of *Dreissena* spp., in spite of *E. ischnus* having evolutionary experience with *Dreissena* spp. Predators reduced the density of both amphipod species, but *E. ischnus* was more susceptible to predation on dreissenid substrates, which suggests that predation mediates the coexistence of *G. fasciatus* and *E. ischnus* in the river.

Résumé : L'amphipode eurasiatique *Echinogammarus ischnus* est, rapporte-t-on, en train de remplacer l'amphipode indigène commun *Gammarus fasciatus* dans le système des Grands Lacs et du Saint-Laurent. Un mécanisme possible de cette substitution est une compétition par l'intermédiaire des espèces résidantes. D'autres envahisseurs eurasiatiques, les bivalves dreisséniidés (*Dreissena polymorpha* et *Dreissena bugensis*), dominent les substrats rocheux dans tout le système et peuvent peut-être favoriser l'expansion rapide d'*E. ischnus* en fournissant un habitat et des refuges contre la prédation. À l'aide d'une expérience in situ d'exclusion des prédateurs, nous avons éprouvé l'hypothèse selon laquelle, dans le Saint-Laurent, *E. ischnus* est plus habile que *G. fasciatus* à utiliser les colonies de *Dreissena* spp. comme refuges et il est moins vulnérable aux prédateurs. Les *E. ischnus* et les *G. fasciatus* en cohabitation montrent les mêmes accroissements de densité en présence de *Dreissena* spp., bien qu'*E. ischnus* ait une expérience de cohabitation avec *Dreissena* spp. au cours de son évolution. Les prédateurs réduisent la densité des deux espèces, mais *E. ischnus* est plus vulnérable à la prédation sur les substrats de dreisséniidés, ce qui laisse croire que la prédation explique la coexistence de *G. fasciatus* et d'*E. ischnus* dans le fleuve.

[Traduit par la Rédaction]

Introduction

The impact of an introduced exotic species can vary across communities, causing the extirpation of native species at some sites while coexisting with the same species at others (MacNeil et al. 1999, 2001). One explanation for this variance, apart from the influence of abiotic variables, is that the composition of the recipient community determines the effects of a species' introduction (Ricciardi 2003; Ricciardi and Atkinson 2004). The impact of an introduced species is reduced in communities where its abundance is limited by predators (Robinson and Wellborne 1988; Arnott and Vanni 1993), which may promote its coexistence with native species (Celik et al. 2002). Moreover, differential susceptibility to predators may lead to the dominance of one competing species over another (DiDonato and Lodge 1993).

Conversely, some resident species, including previous invaders, can facilitate the establishment and population growth of an introduced species, thereby enhancing its impact within the community (Castellanos et al. 1994; Simberloff and Von Holle 1999; Ricciardi 2005). Facilitative interactions between introduced species appear to be at least as common as antagonistic interactions (Simberloff and Von Holle 1999; Ricciardi 2001). The introduction of an "ecosystem engineer" (Crooks 2002) can increase the frequencies of both direct and indirect facilitative interactions, as has been observed in the Laurentian Great Lakes following the introduction of two Eurasian molluscs, the zebra mussel,

Received 31 March 2004. Accepted 4 December 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 27 May 2005.
J18057

M.E. Palmer. Department of Biology and Redpath Museum, McGill University, Montréal, QC H3A 2K6, Canada.
Anthony Ricciardi.[1] School of Environment and Redpath Museum, McGill University, Montréal, QC H3A 2K6, Canada.

[1] Corresponding author (email: tony.ricciardi@mcgill.ca).

Can. J. Fish. Aquat. Sci. **62**: 1111–1118 (2005) doi: 10.1139/F05-012

Dreissena polymorpha, and the quagga mussel, *Dreissena bugensis* (Ricciardi 2001; hereinafter referred to collectively as *Dreissena*). The proliferation of these macrofouling bivalves has altered substrate quality (by the formation of aggregated mussel colonies) and increased water clarity and sedimentation (by their filtration activities) throughout the system (Vanderploeg et al. 2002). *Dreissena* may have facilitated the invasion of other Eurasian species by providing an abundant food source for the round goby, *Neogobius melanostomus*, increased grazing area and refugia for the faucet snail, *Bithynia tentaculata*, and increased light availability for exotic macrophytes such as watermilfoil, *Myriophyllum spicatum*, and curly pondweed, *Potamogeton crispus* (Ricciardi and MacIsaac 2000; Ricciardi 2001; Vanderploeg et al. 2002).

Dreissena might also be promoting the expansion of the Eurasian amphipod crustacean *Echinogammarus ischnus*, a species native to large rivers in the Black and Caspian seas basin (Jaźdźewski 1980). *Echinogammarus ischnus* was discovered in North America in the Detroit River in 1995 (Witt et al. 1997) and by 2002 it had spread to all of the Great Lakes (Dermott et al. 1998; Nalepa et al. 2001; Grigorovich et al. 2003) and as far downstream in the St. Lawrence River as Québec City (Vanderploeg et al. 2002; M.E. Palmer and A. Ricciardi, unpublished data). Throughout much of this invaded range, *E. ischnus* appears to be replacing a taxonomically and morphologically similar species, the native North American amphipod *Gammarus fasciatus* (Dermott et al. 1998; Stewart et al. 1999; Nalepa et al. 2001). This replacement seems to be particularly prevalent on *Dreissena*-covered substrates (Dermott et al. 1998).

Formed by clumped mussels attached to solid substrate, dreissenid colonies are structurally complex, with a greater surface area and more interstitial spaces than typical bare substrate (Ricciardi et al. 1997). Gammarid amphipods show increased abundance as a result of this enhanced microhabitat complexity (Ricciardi et al. 1997; González and Downing 1999; Ricciardi 2003), which provides small invertebrates with refugia from large predators (Diehl 1992). To a large predator, an amphipod in an interstitial space is less visually apparent and difficult to reach (Ryer 1988). The Great Lakes – St. Lawrence River system contains many predators of amphipods, including yellow perch, *Perca flavescens*, which commonly use *G. fasciatus* as a prey item (Harnois et al. 1992; Pothoven et al. 2000). *Echinogammarus ischnus* occurs naturally in dreissenid colonies in its native range and may be adapted to living in mussel beds (Köhn and Waterstraat 1990). Therefore, *E. ischnus* may be better able than *G. fasciatus* (which has no evolutionary experience with *Dreissena*) to use *Dreissena* colonies as both habitat and refugia from predators. Because mussel colonies are patchy and limited in size, amphipods might compete for interstitial spaces. A weaker ability to use interstitial spaces may render *G. fasciatus* more exposed to predation, and thus disadvantaged in competition with *E. ischnus*.

In this study we use a predator-exclusion experiment to investigate whether *Dreissena* is facilitating the replacement of native amphipods by *E. ischnus*. Specifically, we test the hypotheses that (*i*) *E. ischnus* shows a stronger positive response to *Dreissena* than does *G. fasciatus*, and (*ii*) *E. ischnus* and *G. fasciatus* have differential susceptibilities to large predators (fish and crayfish) in the presence of *Dreissena*.

Methods

Experimental protocol

Experiments were carried out at Pointe-du-Moulin, Île Pérrot, Quebec, which is located within a fluvial lake (Lac St-Louis) on the St. Lawrence River (73°51′01″W, 45°22′0.5″N). Pointe-du-Moulin is a public park where human activities are prohibited near the shore. It is a shallow-water (<3-m depth) site with a substrate of bedrock and a few scattered boulders, and its bottom is covered with abundant patches of *Dreissena* and macrophyte (*Vallisneria americana*) beds. Potential amphipod predators commonly found at the site include yellow perch, rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieu*), American eel (*Anguilla rostrata*), and crayfish (*Orconectes* spp.) (M.E. Palmer, personal observations). The experiment was carried out over 2 years: September–October 2002, July–August 2003, and September–October 2003.

Experimental treatments consisted of a combination of predator-exclusion cages and artificial substrates (cement bricks 19 cm × 9 cm × 5.7 cm) covered with *Dreissena* shells. In 2002, six treatment combinations were used. Reference treatments were uncaged bare bricks and bricks with their top face fully covered with a monolayer of *Dreissena* shells. Experimental treatments consisted of bare bricks and *Dreissena*-covered bricks enclosed by a stainless-steel cage. An additional set of treatment bricks was placed in predator-accessible open cages to control for cage effects. Upon analysis it was determined that the open cages introduced additional variables affecting amphipod abundance and did not provide a direct control for cage effects. Thus, open-cage controls were replaced with low-density (half-covered) *Dreissena* cover bricks in 2003. Ten replicates of each treatment combination (uncaged, open-caged, and caged zero-density (ZD), low-density (LD), and high-density (HD) *Dreissena* cover) were used, resulting in a total sample size of 60 per experimental period and a statistical power of 83% (Eckblad 1991), based on a preliminary survey in August 2002.

Prior to use, all bricks were soaked in St. Lawrence River water for 7 days. Dreissenid mussels (average length 27 mm, standard deviation (SD) 4.3 mm) were collected at the site from a depth of 1–3 m by SCUBA. Mussels were boiled and rinsed to remove all tissue as well as any attached invertebrates. Following a drying period of at least 3 days for both bricks and shells, bricks designated LD and HD were covered with a layer of empty shells. Nontoxic aquarium silicone was used to attach the shells to the upper surface of the bricks (~9.5 cm × 4.5 cm for LD bricks and 19 cm × 9 cm for HD bricks). Mussels were glued at their base so that shell valves remained closed, and they were placed adjoining each other so as to resemble a natural, clumped colony. The average number of mussels per brick was 25 (±5) for LD bricks and 47 (±15) for HD bricks; the former had mussels placed either in the middle or at one end of the brick (determined randomly), leaving the rest of the top face of the brick uncovered.

Cages (29 cm × 20 cm × 19 cm) were constructed of stainless-steel wire (mesh size 1.25 cm) and their sides were connected with plastic cable ties. Predator-access cages (20 cm × 19 cm) had one open side. Bricks were placed centrally in the cages. Bricks were placed at depths of 1.5–2 m;

Table 1. Multivariate analysis of variance for amphipod species in 2002 and 2003.

	Wilks' λ	*F*	df	*p*[a]
2002				
Dreissena	0.1769	120.99	2,52	**<0.0001**
Cage	0.8156	2.79	4,104	**0.0301**
Dreissena × cage	0.8536	2.14	4,104	0.0809
2003				
Season	0.4701	58.05	2,103	**<0.0001**
Dreissena	0.1874	67.46	4,206	**<0.0001**
Cage	0.7840	14.19	2,103	**<0.0001**
Season × *Dreissena*	0.6838	10.78	4,206	**<0.0001**
Season × cage	0.9503	2.69	2,103	0.0724
Dreissena × cage	0.6915	10.43	4,206	**<0.0001**
Season × *Dreissena* × cage	0.9526	1.26	4,206	0.2851

[a] Values in boldface type are significant.

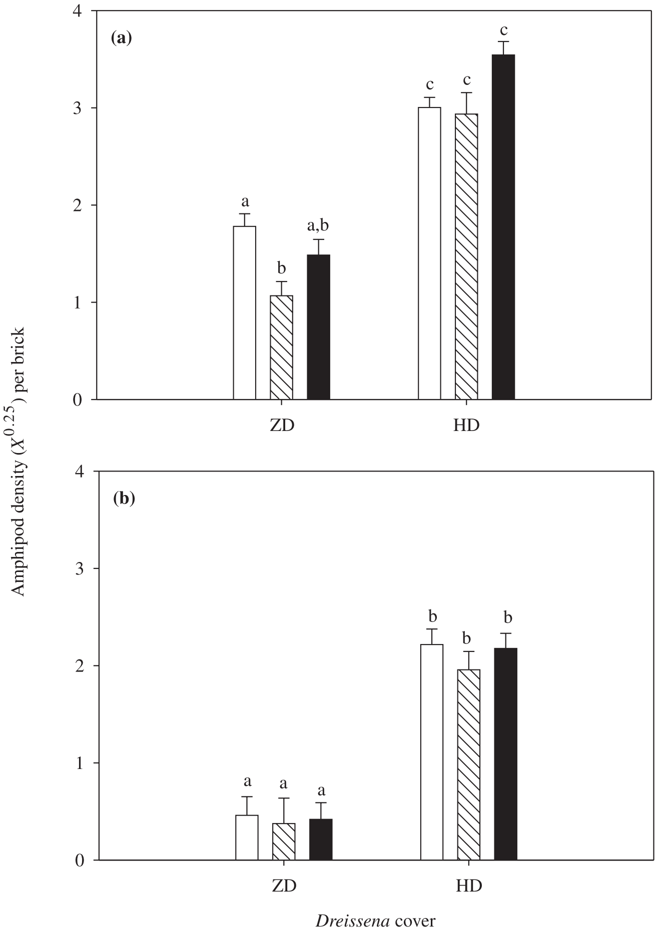
placement and orientation were random except that all bricks were separated by at least 2 m. After 5 weeks, all bricks were collected and placed in labeled plastic bags (doubled to prevent leaks) while under water. Cages were cut open under water and the bricks were removed and transferred into bags with as little disturbance as possible to prevent the escape of amphipods. Bagged bricks were transported back to the laboratory within 2–4 h. Amphipods were collected by filtering the water contained in each bag through a 500 µm mesh sieve and removing all invertebrates from the brick with forceps, as well as by rinsing each brick with water passed through another 500 µm mesh sieve. Amphipods were then preserved in 70% ethanol. A Hund–Wetzlar SM33 stereoscope was used to identify the species of each amphipod using standard morphological features (Witt et al. 1997).

Statistical analysis

The relationship between mean (m) and variance (s^2) for total amphipod density across treatments ($s^2 = 0.38m^{1.46}$; $r^2 = 0.92$, $p < 0.001$) indicated that a fourth-root transformation was required for stabilizing variances (Downing 1979). Multivariate analysis of variance (MANOVA) tests were performed to determine whether amphipod species density varied among treatments in 2002 and 2003. Analysis of variance (ANOVA) tests were then used to identify treatment differences for individual species. *Echinogammarus ischnus* and *G. fasciatus* densities in 2002 were examined using two-fixed-factor (*Dreissena* and cage type) ANOVAs. The 2003 densities were evaluated using three-fixed-factor (season, *Dreissena*, and cage type) ANOVAs. Individual density differences for *E. ischnus* in 2002 and 2003 were detected using the Tukey–Kramer multiple-comparison procedure for factors with significant interactions. The same procedure was used for *G. fasciatus* in 2003, while the Tukey–Kramer multiple comparison for factors without interactions was applied to the 2002 data.

For 2003 data, the strength of the interaction between amphipods and *Dreissena* on uncaged and caged bricks was determined by simple linear regression. The relationships were then compared using analysis of covariance (ANCOVA).

Fig. 1. Densities (mean + standard error) of (*a*) *Echinogammarus ischnus* and (*b*) *Gammarus fasciatus* on bricks with zero-density (ZD) and high-density (HD) *Dreissena* cover in September–October 2002. Open bars represent uncaged reference bricks (n = 10), hatched bars represent open-cage bricks (n = 9), and solid bars represent caged bricks (n = 10). Different letters above the bars indicate statistical differences (α = 0.05).



ANCOVA was also used to compare the relationship between *E. ischnus* density and *G. fasciatus* density as a function of time. As both amphipod densities were subject to measurement error and dimensionless after fourth-root transformation, major axis (model II) regression (Sokal and Rohlf 1995) was used to examine the linear relationship between

Table 2. Analysis of variance for amphipod species in 2002 and 2003.

	MS	*F* test	df	*p*[a]
Echinogammarus ischnus, 2002				
Model	9.48	40.21	5	**<0.0001**
Dreissena	43.37	183.94	1	**<0.0001**
Cage	1.39	5.88	2	**0.0049**
Dreissena × cage	0.95	4.04	2	**0.0232**
Error	0.24		53	
Gammarus fasciatus, 2002				
Model	8.58	23.79	5	**<0.0001**
Dreissena	42.51	117.84	1	**<0.0001**
Cage	0.16	0.43	2	0.651
Dreissena × cage	0.05	0.14	2	0.873
Error	0.36		53	
Echinogammarus ischnus, 2003				
Model	8.65	31.19	11	**<0.0001**
Season	26.56	95.79	1	**<0.0001**
Dreissena	25.00	90.15	2	**<0.0001**
Cage	0.59	2.13	1	0.1474
Season × *Dreissena*	2.84	10.25	2	**<0.0001**
Season × cage	1.31	4.73	1	**0.0320**
Dreissena × cage	6.41	23.11	2	**<0.0001**
Season × *Dreissena* × cage	0.27	0.98	2	0.3791
Error	0.28		104	
Gammarus fasciatus, 2003				
Model	10.49	37.43	11	**<0.0001**
Season	2.02	7.22	1	**0.0084**
Dreissena	47.33	168.87	2	**<0.0001**
Cage	7.97	28.45	1	**<0.0001**
Season × *Dreissena*	4.92	17.54	2	**<0.0001**
Season × cage	0.43	1.54	1	0.2169
Dreissena × cage	0.37	1.33	2	0.2699
Season × *Dreissena* × cage	0.37	1.31	2	0.2732
Error	0.28		104	

[a]Values in boldface type are significant.

E. ischnus and *G. fasciatus*. This was done separately for the 2002, July–August 2003, and September–October 2003 data. All statistical procedures were performed using the SAS statistical package version 8 (SAS Institute Inc. 1999).

Results

All bricks were recollected in 2002. However, a single ZD brick that was found outside its open cage was not included in our statistical analyses. In August 2003, 1 uncaged HD brick was lost. In October 2003, 1 LD and 2 HD caged bricks were lost. These losses were due to poor visibility. At all times of collection, bricks and cages had very low levels of fouling (<10%).

In 2002, multivariate analysis indicated that *Dreissena* and cage type affected amphipod densities ($p < 0.0001$ and 0.0301, respectively; Table 1). *Echinogammarus ischnus* was the dominant amphipod over all treatment combinations (Fig. 1) and 79% of its variance was explained by *Dreissena*, cage type, and their interaction (Table 2). *Echinogammarus ischnus* density was 2.2 times greater on HD bricks than on ZD bricks and was reduced on ZD bricks in open cages compared with uncaged bricks (adjusted $p = 0.027$). *Gammarus fasciatus* density was 5 times higher on HD bricks than on LD bricks and was not affected by predation (Table 2; Fig. 1*b*). Over 69% of its variance was explained by *Dreissena*, cage type, and their interaction.

In 2003, MANOVA indicated that one or more amphipod species was affected by season, *Dreissena*, and cage type ($p < 0.0001$; Table 1). Individual ANOVA found that the combined variables of season, *Dreissena*, cage type, and their interactions explained 77% of variation in *E. ischnus* density (Table 2). *Echinogammarus ischnus* density was 2.1 times higher in September–October than in July–August and increased by a factor of 2.7 and 4 on LD and HD bricks, respectively, compared with ZD bricks. Predation reduced *E. ischnus* density on LD and HD bricks in July–August ($p = 0.007$ and 0.023, respectively). Cage treatments had a negative effect on *E. ischnus* density on ZD bricks. This trend was significant in September–October ($p = 0.027$) but nonsignificant in July–August ($p = 0.084$; Fig. 2*a*).

Gammarus fasciatus was the dominant amphipod in 2003 (Fig. 2). Season, *Dreissena*, cage type, and their interactions explained 80% of the variation in *G. fasciatus* density (Table 2). *Gammarus fasciatus* was 1.1 times more abundant in July–August than in September–October. Densities on LD

Fig. 2. Densities (mean + standard error) of (*a*) *Echinogammarus ischnus* and (*b*) *Gammarus fasciatus* for two seasons in 2003. An asterisk indicates a significant difference between uncaged and caged bricks within *Dreissena*-cover densities (zero density (ZD), low density (LD), and high density (HD)) and seasons ($p \leq 0.05$).

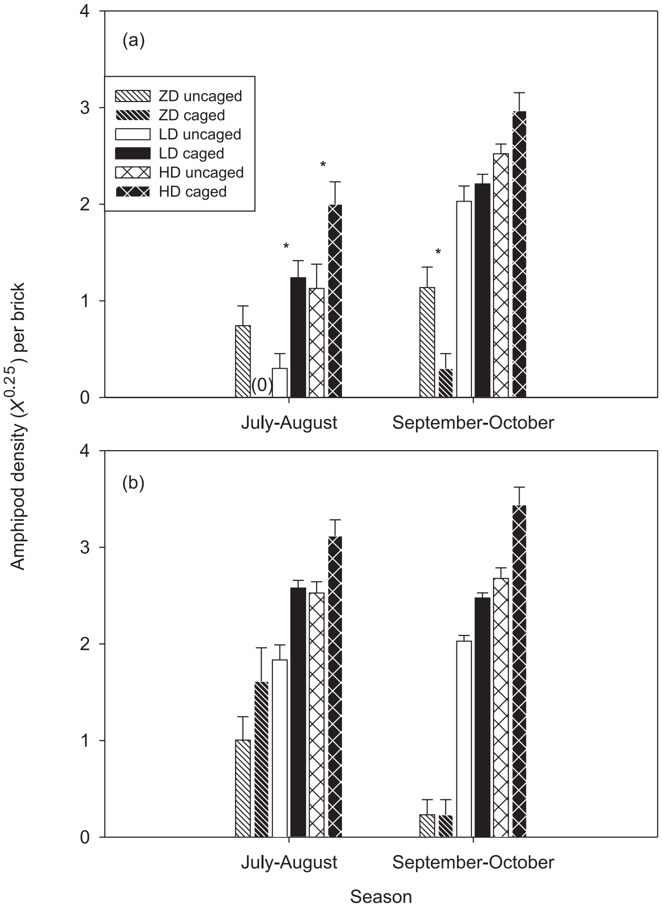
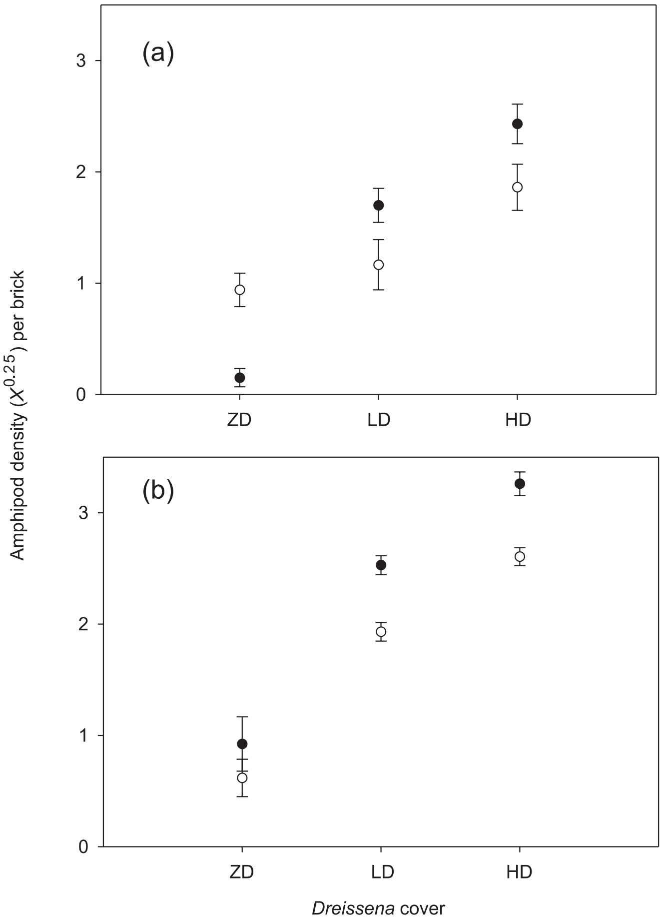


Fig. 3. Densities (mean ± standard error) of (*a*) *Echinogammarus ischnus* and (*b*) *Gammarus fasciatus* on bricks with zero-density (ZD), low-density (LD), and high-density (HD) *Dreissena* cover in 2003. Open circles represent uncaged bricks (n = 59) and solid circles represent caged bricks (n = 57). For both species, amphipod density increased with density of *Dreissena* cover in both caged and uncaged treatments (analysis of variance, $p < 0.0001$, except for the *E. ischnus* uncaged treatment, where $p = 0.002$). Predation weakened the relationship between *E. ischnus* and *Dreissena* (analysis of covariance, $p = 0.0004$) but did not affect the relationship between *G. fasciatus* and *Dreissena* ($p = 0.569$).



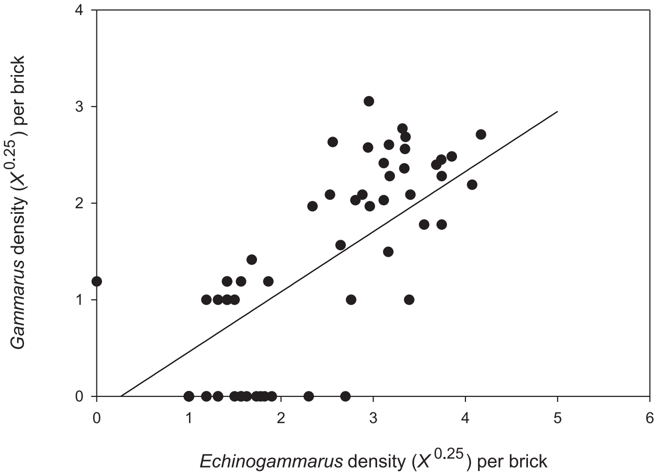
and HD bricks were 2.9 and 3.8 times higher, respectively, than on ZD bricks. *Gammarus fasciatus* was negatively affected by predation, but differences on *Dreissena*-covered bricks were not significant ($p > 0.05$; Fig. 2*b*). Predation weakened the relationship between *E. ischnus* and *Dreissena* (ANCOVA, $p = 0.0004$; Fig. 3*a*), but had no effect on the relationship between *G. fasciatus* and *Dreissena* ($p = 0.569$; Fig. 3*b*).

The relationship between *E. ischnus* and *G. fasciatus* varied among the three experimental periods (ANCOVA, $p < 0.0001$), but was consistently positive, with both species exhibiting high density on the same experimental substrates (model II regression results: 2002 (Fig. 4), $r^2 = 0.59$, $p < 0.0001$; July–August 2003 (Fig. 5*a*), $r^2 = 0.25$, $p < 0.0001$; September–October 2003 (Fig. 5*b*), $r^2 = 0.76$, $p < 0.0001$). These relationships remained significant when zero values were removed.

Discussion

Although both the invasive amphipod *E. ischnus* and the native *G. fasciatus* were present on experimental substrates in 2002, *E. ischnus* was numerically dominant. In the following year, *G. fasciatus* outnumbered *E. ischnus*. These findings contrast with those in the Great Lakes, where *E. ischnus* has progressively become the dominant amphipod at numerous sites (Van Overdijk et al. 2003), often within a year of detection (Dermott et al. 1998). Given that *E. ischnus* has been present in the St. Lawrence River near Montreal since at least 1998 (A. Ricciardi, unpublished data) and specimens collected in 2002 contained reproductive individuals (indicated by the presence of eggs) and three size classes (M.E. Palmer, unpublished data), the species had likely been established at Pointe-du-Moulin for at least a year prior to this experiment; *E. ischnus* reproduces twice per year (Köhn and Waterstraat 1990) and the most recent date of establishment that could produce three size classes was early summer 2001. Unfortunately, past *G. fasciatus* densities at the site are not known and so comparisons of density before and after invasion cannot be made.

Fig. 4. Relationship between *Echinogammarus ischnus* and *Gammarus fasciatus* densities in September–October 2002 (major axis model II regression: $y = 0.6225x - 0.1633$, $r^2 = 0.59$, $p < 0.0001$, $n = 59$). When zeros are removed, $y = 0.6832x + 0.0083$, $r^2 = 0.52$, $p < 0.0001$, $n = 39$.



Because results of short-term experiments may not be representative of natural community responses, it is conceivable that amphipod densities did not have sufficient time to equilibrate during our experiment and thus were not representative of the surrounding community. However, Stewart et al. (1998*c*) concluded that a colonization period of 37 days was long enough for non-mussel macroinvertebrate densities on experimental live *Dreissena* substrates to equal those on surrounding substrates, which suggests that the time frame of our experiment was sufficient to permit amphipod densities to reach equilibrium.

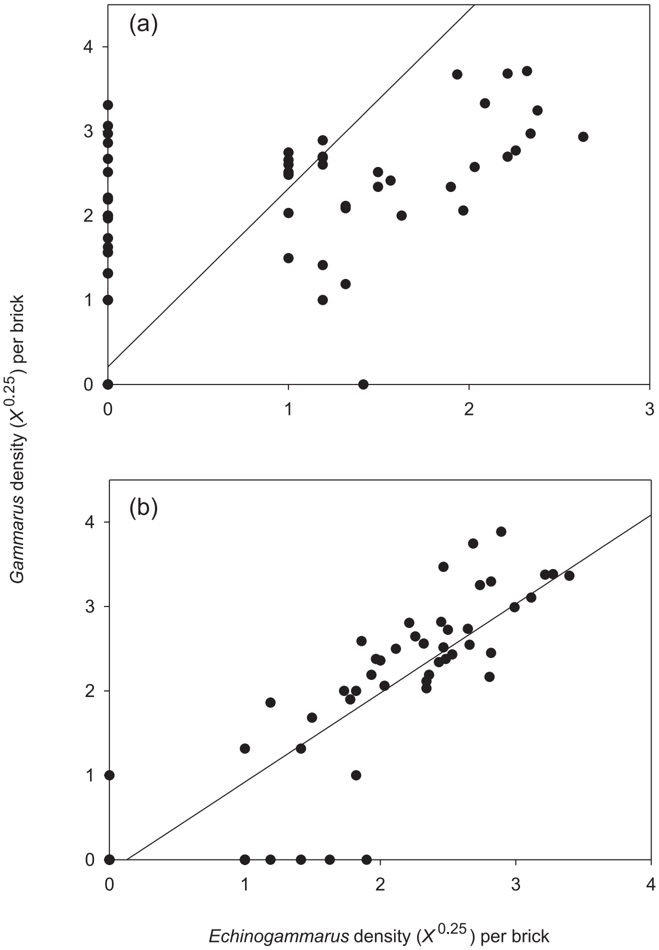
Effect of *Dreissena*

Total amphipod density was enhanced in the presence of *Dreissena*, consistent with previous findings (Ricciardi et al. 1997; Stewart et al. 1998*b*; Van Overdijk et al. 2003). Surprisingly, *G. fasciatus* showed a similar (in 2003) or more rapid increase (in 2002) in density than did *E. ischnus* on *Dreissena*-covered bricks. These results do not support the hypothesis of greater (coevolved) interaction strength between *E. ischnus* and *Dreissena* (Ricciardi and MacIsaac 2000).

Gammarus fasciatus is a substrate generalist and can use a broad range of microhabitats (Dermott et al. 1998), an ability that apparently allows it to thrive within dreissenid colonies. In fact, after *Dreissena* became established in the Great Lakes – St. Lawrence River system, *G. fasciatus* increased in abundance at many sites and was often the dominant non-dreissenid invertebrate present (Stewart and Haynes 1994; Wisendon and Bailey 1995; Ricciardi et al. 1997).

The greater enhancement of *G. fasciatus* in the presence of *Dreissena* may be a result of differing colonization abilities of the two amphipod species. *Gammarus fasciatus* has a higher fecundity and shorter generation time than *E. ischnus* (Dermott et al. 1998). During our experiments, *G. fasciatus* was also more abundant on surrounding natural substrates (M.E. Palmer and A. Ricciardi, unpublished data), perhaps giving it first access to the added experimental substrate.

Fig. 5. Relationship between *Echinogammarus ischnus* and *Gammarus fasciatus* densities in 2003: (*a*) July–August (major axis model II regression: $y = 2.1131x + 0.2082$, $r^2 = 0.25$, $p < 0.0001$, $n = 59$); (*b*) September–October ($y = 1.0553x - 0.1359$, $r^2 = 0.76$, $p < 0.0001$, $n = 57$). Note the difference in *x*-axis scales in *a* and *b*. When zeros are removed, $y = 1.6048x + 0.0082$, $r^2 = 0.28$, $p = 0.0015$, $n = 33$, in *a*, and $y = 1.0827x - 0.0156$, $r^2 = 0.63$, $p < 0.0001$, $n = 40$, in *b*.



However, the proportion of total amphipod density made up by *E. ischnus* was higher on experimental substrates than on natural *Dreissena* and *V. americana* substrates in 2003 (30% and 15%, respectively; M.E. Palmer and A. Ricciardi, unpublished data), which indicates that *E. ischnus* was able to rapidly colonize experimental bricks despite an apparent disadvantage in the size of its local source population. Alternatively, our use of dead *Dreissena* shells, which accumulate less organic matter (i.e., detritus and pseudofeces) than living mussels (Stewart et al. 1998*c*), may have affected amphipod colonization if *E. ischnus* and *G. fasciatus* differ in their foraging ability and resource use. Nevertheless, even when *E. ischnus* was more prevalent on experimental substrates (in 2002), *G. fasciatus* still produced a greater increase in density in the presence of *Dreissena*.

Amphipod densities may have been too low for space competition to occur within the experimental *Dreissena* colonies. High *Dreissena* abundance might reduce competition by adding an abundant resource over which the two amphipod species can segregate. Positive responses by both species to the same extrinsic factors might account for the positive relationship between *E. ischnus* and *G. fasciatus*. Van Overdijk et al. (2003) also found that the two species were positively correlated on experimental scales. Perhaps *E. ischnus* has a competitive advantage when amphipod densities increase and resources become limited, which might be the case for littoral sites in Lake Erie and Lake Ontario, where it dominates amphipod communities (Dermott et al. 1998).

Effect of predation

Predator-access cages

The open-cage treatment was omitted from the 2003 experiments because it was a poor control for cage effects. *Echinogammarus ischnus* density was reduced on bricks in open cages, possibly because the cage structure attracted small fish and crayfish by allowing them to feed while being protected against larger predators; in Lake Erie, Stewart et al. (1999) observed that some predator species were attracted to open cages. *Gammarus fasciatus* did not show this pattern, which implies that *E. ischnus* is more susceptible to small predators — particularly when it is present at higher densities.

Predator-exclusion cages

Amphipod density was apparently reduced by predation. However, predation effects on *G. fasciatus* in the presence of *Dreissena* were not significant, whereas predation reduced *E. ischnus* density on *Dreissena*-covered bricks in July–August. *Echinogammarus ischnus* is more active than *G. fasciatus* (Van Overdijk et al. 2003) and uses its uropods and antennae to move across *Dreissena* shells (Dermott et al. 1998), while *G. fasciatus* tends to burrow into interstitial spaces amongst mussels, where silty detritus accumulates (M.E. Palmer, personal observations). It would be worthwhile to test whether these respective behaviors render *E. ischnus* more susceptible to predation on *Dreissena*-covered substrates, especially as our use of dead shells may have resulted in unusually high levels of *E. ischnus* foraging activity that cause it to be more conspicuous to predators. Predation effects also vary seasonally and were not significant for *E. ischnus* on *Dreissena*-covered bricks in September–October for either year. The reduction in *E. ischnus* density on caged ZD bricks in 2003 suggests that cage structure has a negative effect on *E. ischnus*, perhaps because of impeded water flow. This implies that the positive response of *E. ischnus* to predator exclusion on *Dreissena*-covered bricks is underestimated.

Our findings do not support the hypothesis that predation is mediating the replacement of *G. fasciatus* by *E. ischnus* on *Dreissena*-covered substrate. Rather, predation appears to be contributing to the coexistence of the two species, as large predators had a greater negative effect on *E. ischnus*, preventing it from becoming competitively dominant. Additional support for this conclusion is given by Stewart et al. (1998*a*, 1999), who found that when the species occurred separately, the presence of large predators did not affect *G. fasciatus* biomass but coincided with a decline in *E. ischnus* biomass.

The replacement of *G. fasciatus* by *E. ischnus* that is observed in the Great Lakes has not yet occurred in the upper St. Lawrence River, even though *E. ischnus* has been present since the late 1990s. We suggest that the species replacement reported for the lower Great Lakes is not a result of *E. ischnus* being better able than *G. fasciatus* to use dreissenid colonies as habitat and refugia. The dominance of one species over the other might be determined by differential environmental preferences (M.E. Palmer and A. Ricciardi, unpublished data) as well as direct interactions between the two species. Dermott et al. (1998) found that when *E. ischnus* was present, the number of immature *G. fasciatus* was reduced, possibly as a result of intraguild predation (cf. Dick and Platvoet 1996). Small-scale experiments are needed to examine the interactions of *E. ischnus* and *G. fasciatus* to determine precisely their direct impacts on each other.

Acknowledgements

We thank Dr. Krzysztof Jaźdźewski for confirming our initial *E. ischnus* identifications, and we are grateful to L. Jones, A. Jokela, and S. Atkinson for their field assistance. Several graduate students in the Biology Department of McGill University provided valuable comments on an early draft of the manuscript. This research is supported by a grant from the Natural Sciences and Engineering Research Council of Canada to A.R.

References

Arnott, S.E., and Vanni, M.J. 1993. Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. Ecology, **74**: 2361–2380.

Castellanos, E.M., Figueroa, M.E., and Davy, A.J. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. J. Ecol. **82**: 239–248.

Celik, K., Schlinder, J.E., Foris, W.J., and Knight, J.C. 2002. Predator-mediated coexistence of exotic and native crustaceans in a freshwater lake? Biol. Invasions, **4**: 451–455.

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos, **97**: 153–166.

Dermott, R., Witt, J., Um, Y.M., and Gonzalez, M. 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. J. Gt. Lakes Res. **24**: 442–452.

Dick, J.T.A., and Platvoet, D. 1996. Intraguild predation and species exclusions in amphipods: the interaction of behaviour, physiology and environment. Freshw. Biol. **36**: 375–383.

DiDonato, G.T., and Lodge, D.M. 1993. Species replacements among *Orconectes* crayfishes in Wisconsin lakes: the role of predation by fish. Can. J. Fish. Aquat. Sci. **50**: 1484–1488.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology, **73**: 1646–1661.

Downing, J.A. 1979. Aggregation, transformation, and the design of benthos sampling programs. J. Fish. Res. Board Can. **36**: 1454–1463.

Eckblad, J.W. 1991. How many samples should be taken? BioScience, **41**: 346–348.

González, M.J., and Downing, A. 1999. Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish–amphipod interactions. Can. J. Fish. Aquat. Sci. **56**: 679–685.

Grigorovich, I.A., Gray, D.K., Duggan, I.C., Colautti, R.I., and MacIsaac, H.J. 2003. Lake Superior: an invasion coldspot? Hydrobiologia, **499**: 191–210.

Harnois, E., Couture, R., and Magnan, P. 1992. Variation saisonniére dans la repartition des resources alimentaires entre cinq espèces de poisons en fonction de la disponibilité des proies. Can. J. Zool. **70**: 769–803.

Jaźdźewski, K. 1980. Range extensions of some gammaridean species in European inland waters caused by human activity. Crustaceana, **6**(Suppl.): 84–107.

Köhn, J., and Waterstraat, A. 1990. The amphipod fauna of Lake Kummerow (Mecklenberg, German Democratic Republic) with reference to *Echinogammarus ischnus* Stebbing, 1899. Crustaceana, **58**: 74–82.

MacNeil, C., Elwood, R.W., and Dick, J.T.A. 1999. Differential microdistributions and interspecific interactions in coexisting *Gammarus* and *Crangonyx* amphipods. Ecography, **22**: 415–423.

MacNeil, C., Dick, J.T.A., Elwood, R.W., and Montgomery, W.I. 2001. Coexistence among native and introduced freshwater amphipods (Crustacea): habitat utilization patterns in littoral habitats. Arch. Hydrobiol. **151**: 591–607.

Nalepa, T.F., Schloesser, D.W., Pothoven, S.A., Hondorp, D.W., Fanslow, D.L., Tuchman, M.L., and Fleischer, G.W. 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. J. Gt. Lakes Res. **27**: 384–391.

Pothoven, S.A., Nalepa, T.F., and Brandt, S.B. 2000. Age-0 and age-1 yellow perch diet in southeastern Lake Michigan. J. Gt. Lakes Res. **26**: 235–239.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? Can. J. Fish. Aquat. Sci. **58**: 2513–2525.

Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshw. Biol. **48**: 972–981.

Ricciardi, A. 2005. Facilitation and synergistic interactions among introduced aquatic species. *In* Invasive alien species: a new synthesis. *Edited by* H.A. Mooney, R.N. Mack, J. McNeely, L.E. Neville, P.J. Schei, and J.K. Waage. Island Press, Washington, D.C. In press.

Ricciardi, A., and Atkinson, S.K. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol. Lett. **7**: 781–784.

Ricciardi, A., and MacIsaac, H.J. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol. Evol. **15**: 62–65.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Can. J. Fish. Aquat. Sci. **54**: 2596–2608.

Robinson, J.V., and Wellborn, G.A. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea*: fish predation effects. Oecologia, **77**: 445–452.

Ryer, C.H. 1988. Pipefish foraging: effects of fish size, prey size, and altered habitat complexity. Mar. Ecol. Prog. Ser. **48**: 37–45.

SAS Institute Inc. 1999. SAS/STAT user’s guide, release 8 ed. SAS Institute Inc., Cary, N.C.

Simberloff, D., and Von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions, **1**: 21–32.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. W.H. Freeman and Co., New York.

Stewart, T.W., and Haynes, J.M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. J. Gt. Lakes Res. **20**: 479–493.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998*a*. An experimental analysis of crayfish (*Orconectes rusticus*) effects on a *Dreissena*-dominated benthic macroinvertebrate community in western Lake Erie. Can. J. Fish. Aquat. Sci. **55**: 1043–1050.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998*b*. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. J. Gt. Lakes Res. **24**: 868–879.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998*c*. Quantifying mechanisms for zebra mussel effects on benthic invertebrates: organic matter production and shell-generating habitat. J. N. Am. Benthol. Soc. **17**: 81–94.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1999. A field experiment to determine *Dreissena* and predator effects on zoobenthos in a nearshore, rocky habitat of western Lake Erie. J. N. Am. Benthol. Soc. **18**: 488–498.

Wisendon, P.A., and Bailey, R.C. 1995. Development of macroinvertebrate community structure associated with zebra mussel (*Dreissena polymorpha*) colonization of artificial substrates. Can. J. Zool. **73**: 1438–1443.

Witt, J.D.S., Hebert, P.D.N., and Morton, W.B. 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. Can. J. Fish. Aquat. Sci. **54**: 264–268.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **59**: 1209–1228.

Van Overdijk, C., Grigorovich, I.A., Mabee, T., Ray, W.J., Ciborowski, J.J.H., and MacIsaac, H.J. 2003. Microhabitat selection by the invasive amphipod *Echinogammarus ischnus* and native *Gammarus fasciatus* in laboratory experiments and in Lake Erie. Freshw. Biol. **48**: 567–578.