

Physical factors affecting the relative abundance of native and invasive amphipods in the St. Lawrence River

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Abstract: The Ponto-Caspian amphipod *Echinogammarus ischnus* (Stebbing, 1899) is reportedly replacing the North American amphipod *Gammarus fasciatus* Say, 1818, in the lower Great Lakes, but the two species appear to coexist in the upper St. Lawrence River several years after invasion by *E. ischnus*. A multi-site survey in the river between Lake Ontario and Montreal (Quebec) found that *E. ischnus* and *G. fasciatus* respond differently to substrate characteristics, water chemistry variables, and current velocity. Both species increase in abundance in the presence of dreissenid mussels. However, *E. ischnus* density is positively correlated with current velocity and an increasing proportion of gravel-sized sediment, while *G. fasciatus* density is positively correlated with benthic filamentous algal (*Cladophora* spp.) biomass, macrophyte biomass, and pH. Habitat heterogeneity within the river may be promoting the coexistence of native and exotic amphipods by allowing them to segregate along physicochemical gradients.

Résumé : L'amphipode ponto-caspien *Echinogammarus ischnus* (Stebbing, 1899) est, rapporte-t-on, en train de remplacer l'amphipode nord-américain *Gammarus fasciatus* Say, 1818 dans les Grands Lacs inférieurs. Les deux espèces semblent cependant coexister dans le cours supérieur du Saint-Laurent plusieurs années après l'invasion de *E. ischnus*. Un inventaire dans de multiples sites du fleuve entre le lac Ontario et Montréal (Québec) indique que *E. ischnus* et *G. fasciatus* réagissent différemment aux caractéristiques du substrat, aux variables chimiques de l'eau et à la vitesse de courant. La densité des deux espèces croît en présence des bivalves dreissenidés. Cependant, la densité d'*E. ischnus* est en corrélation positive avec la vitesse du courant et une proportion accrue des gravillons dans les sédiments, alors que la densité de *G. fasciatus* est en corrélation positive avec la biomasse des algues filamenteuses benthiques (*Cladophora* spp.), la biomasse des macrophytes et le pH. L'hétérogénéité de l'habitat de la rivière peut sans doute favoriser la coexistence des amphipodes indigènes et exotiques en leur permettant de s'isoler le long de gradients physicochimiques.

[Traduit par la Rédaction]

Introduction

Freshwater communities worldwide are being rapidly altered by a variety of anthropogenic stressors, including exotic species introductions (Ricciardi et al. 1998; Sala et al. 2000; Ricciardi and Atkinson 2004). Although most species introductions cause little detectable change in freshwater communities, some produce substantial impacts including the loss of native species through competitive exclusion (Moyle and Light 1996; Ricciardi et al. 1998). Impacts vary spatially because exotic species may exclude native species at some sites while coexisting with them at others (Bulnheim 1980; MacNeil et al. 2001a, 2001b; Zanatta et al. 2002), suggesting that site-specific environmental factors mediate

the effects of species introductions (Ricciardi 2003). Biodiversity loss due to species introductions is most pronounced in insular habitats such as lakes and islands (D'Antonio and Dudley 1995; Simberloff 1995). Therefore, the coexistence of species might be more likely to occur in large heterogeneous environments, because of a greater availability of refugia and the presence of physicochemical gradients across which species' distributions may segregate (McLachlan 1993; Lombardo 1997; Vivian-Smith 1997).

A recent invader to North American freshwater ecosystems, the Ponto-Caspian amphipod *Echinogammarus ischnus* (Stebbing, 1899) is apparently replacing a similar confamilial species, the native amphipod *Gammarus fasciatus* Say, 1818 in Lake Erie and Lake Ontario (Dermott et al. 1998; Van Overdijk et al. 2003). This replacement could have food-web ramifications because *G. fasciatus* is an important prey item for forage fishes (Vanderploeg et al. 2002). However, data from benthic samples collected in June 2002 suggest that the two species are coexisting in the upper St. Lawrence River between the outflow of Lake Ontario and Montreal (Quebec) (M. Palmer, unpublished data) several years after the initial discovery of *E. ischnus* near Montreal in 1998 (A. Ricciardi, unpublished data).

The St. Lawrence River is one of the largest river systems in the world, spanning over 1200 km from Lake Ontario to

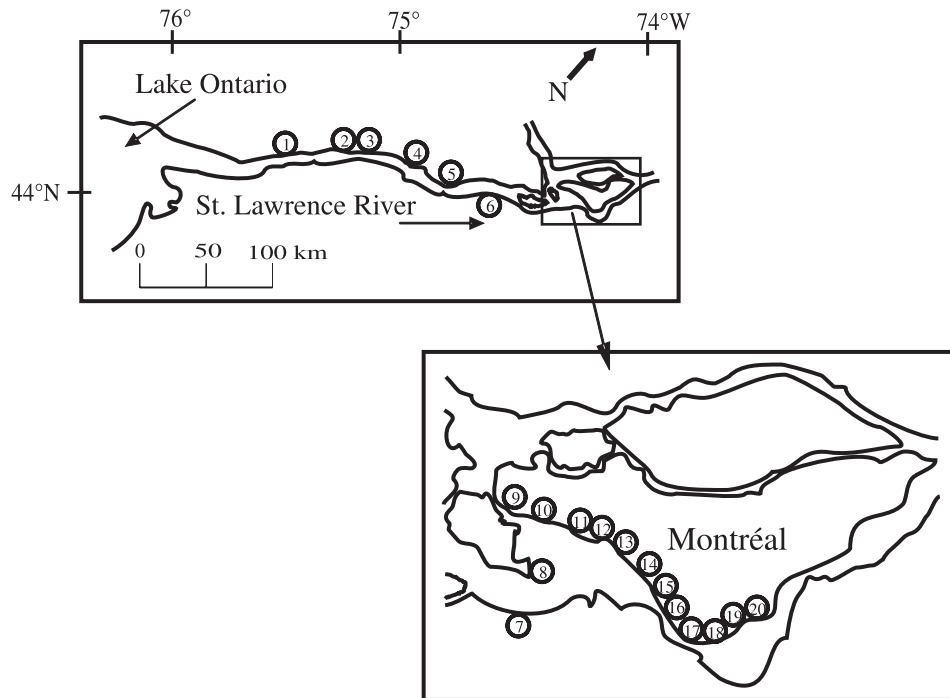
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Fig. 1. Map of St. Lawrence River sampling sites (○).

the Gulf of St. Lawrence in the north Atlantic Ocean. Along its course, the river undergoes multiple changes in width, depth, current velocity, climatic condition, and shoreline topography. It encompasses fluvial lakes and islands and is joined by several smaller rivers, with the largest being the Ottawa River near Montreal. These features render the St. Lawrence River a physically heterogeneous system at multiple spatial scales. *Echinogammarus ischnus* and *G. fasciatus* might be segregating along this heterogeneity, thereby minimizing competition.

In this study, we use a multi-site survey to determine the distributions and abundances of *E. ischnus* and *G. fasciatus* in relation to habitat variables in the upper St. Lawrence River. We first address the hypothesis that *E. ischnus* density is a function of distance from upstream (potential source) populations near the outflow of Lake Ontario, which is thought to be the original point of *E. ischnus* introduction in the river (Dermott et al. 1998). If *E. ischnus* dominates at upstream sites and *G. fasciatus* becomes proportionally more abundant at sites lower in the system, then this suggests that *E. ischnus* is replacing *G. fasciatus* as it spreads downstream. Alternatively, *E. ischnus* might spread via jump dispersal and subsequent radial population growth from multiple-isolated populations (MacIsaac et al. 2001), and the expansion of these local foci could progressively exclude *G. fasciatus*. We test the latter possibility by comparing amphipod densities at multiple sites in 2002 to those at the same sites in 2003.

Conversely, if *E. ischnus* and *G. fasciatus* are coexisting in the St. Lawrence River, we predict that the two species respond optimally to different abiotic environmental conditions. To test this prediction, we relate the densities of *E. ischnus* and *G. fasciatus* to a suite of physicochemical variables; we focus primarily on water quality variables and benthic substrate characteristics, which are considered im-

portant determinants of amphipod distribution and abundance (Ress 1972; Olyslager and Williams 1993; Lancaster and Mole 1999), as well as amphipod species replacement and coexistence (Dick and Platvoet 1996; MacNeil et al. 2001a, 2001b). Finally, we relate the relative abundances of these species to local densities of dreissenid mussels, *Dreissena polymorpha* (Pallas, 1771) and *Dreissena bugensis* Andrusov, 1897, which are known to enhance associated populations of gammarid amphipods through the provision of nourishment (biodeposits) and microhabitat (Ricciardi et al. 1997; Stewart et al. 1998).

Methods

Sampling protocol

Twenty St. Lawrence River sites were sampled (Fig. 1). During September–October 2002, 12 sites on the Island of Montreal were sampled; however, in 2003, sampling was expanded to include a total of 20 sites from Prescott (Ontario) to Montreal (Quebec), all of which were sampled in July–August and again in September–October. Sites were defined by their flow regime (determined by visual inspection during sampling) and shoreline habitat (Table 1), covered an area about 100 m², and were at least 2 km apart.

At each site, 5–10 quadrats of 0.25 m² were sampled (10 quadrats produce a statistical power of 83%; Eckblad 1991), with quadrat placement determined haphazardly by throwing the quadrat frame. Site characteristics that were measured include mean depth, ranked current velocity, water quality (temperature, pH, turbidity, and calcium), substrate quality (mean substrate size, rock surface area, and percent sediment composition of cobble and gravel), and biotic variables (biomass of *Cladophora* Kützting, 1843, macrophyte biomass, *Dreissena* density, and amphipod densities).

Table 1. St. Lawrence River site descriptions (Fig. 1) and total number of 0.25-m² quadrats sampled (*N*).

Site	Shoreline description	Flow values 1–4 (1, low; 4, rapids)	<i>N</i>
1	Prescott	Large rock slabs below a steep mud bank, roadside	3
2	Iroquois	Boulder and grass shore, public park/golf course	2
3	Morrisburg	Cobble beach, public park	2
4	Moulinette	Cobble beach, public park	2
5	Cornwall	Grass shore, public park	2
6	St. Anicet	Large cove, grass shore, residential area	1
7	Chateauguay	Sand and driftwood beach	3
8	Île Pérrot	Sand beach, public park	2
9	Parc Bertold	Grass shore, public park	1
10	St. Louis	Boat launch, residential	1
11	Bord de l'eau	Cobble beach, public wharf	2
12	Valois Bay	Weed and cobble shore, near roadside	1
13	Summerlea	Cobble shore, public beach	2
14	Lachine	Small cove, cobble shore, public park	1
15	Lytette	Grass shore, public park	1
16	78°	Grass shore, public park	2
17	40°	Grass shore, public park	4
18	Senecal	Weed bed	4
19	Allard	Grass shore, public park	2
20	Parc Richard	Weed and mud slope, developmental area	3

Mean depth was determined by measuring the vertical distance from the substrate to the water surface at three evenly spaced central points in the quadrat. Temperature was read from a thermometer held ~5 cm above the bottom sediments. Mean substrate size was calculated as follows: (i) percent cover was determined visually for each substrate type in the quadrat with the aid of equally spaced markings on the quadrat frame; (ii) percent-cover values were multiplied by each substrate's corresponding phi ($-\log_2$) value (i.e., bed-rock = -9.967, boulder = -8, cobble = -5.8, gravel = -3.5, sand = 2, silt = 6.5, and clay/mud = 9); (iii) results for each substrate type were added to produce the mean substrate size, following Mellina and Rasmussen (1994). Total rock surface area was determined by removing and measuring all cobbles and boulders weighing less than ~11 kg. The surface area for each rock was estimated from three orthogonal measurements using Dall's (1979) equation for ellipsoidal shapes:

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

Once all overlying rocks were collected, the percent composition of underlying sediment composed of cobble and gravel (sediment types in which amphipods were found to burrow) was visually determined. Cobble and gravel sediment to a depth of 2 cm was then collected by hand. When overlying sediment was made up of boulders too large to remove, it was assumed that the immediately underlying sediment was the same. All *Cladophora* spp. and macrophytes rooted within the quadrat were removed and their blotted wet mass was measured using a Denver Instrument APX-602 balance. *Dreissena* density was determined by removing (with a knife) and counting all mussels >2 mm length within the quadrat.

Amphipods were collected by shaking and scouring all rocks, cobble, and gravel sediment, *Cladophora* spp., macro-

phytes, and *Dreissena* spp. in a filled water bucket for several minutes. The water was then poured through a 500- μm sieve, and amphipods were extracted with forceps and placed in 70% ethanol. Amphipods retained by the sieve included juveniles ~2 mm long. All amphipods were sorted using a HundWetzlar SM33 stereoscope and identified to species using standard morphological characteristics (Witt et al. 1997).

A 1-L water sample was collected at each site to measure water quality variables. The pH was measured using a Fisher Scientific Accumet AP63 meter. Turbidity and calcium concentration (Ca^{2+} in milligrams per litre) were determined using LaMotte Turbidity Model TTM and Hardness Model PHT-CM-DR-LT kits, respectively.

Statistical analysis

All analyses were done using SAS/STAT[®] statistical software release 8th ed (SAS Institute Inc. 1999). The mean (m) – variance (s^2) relationship for total amphipod density indicated that a $\log_{10}(x + 1)$ transformation was required for normalizing *E. ischnus* and *G. fasciatus* variances (Downing 1979). This relationship was determined for quadrats ($s^2 = 0.52m^{3.02}$, $r^2 = 0.99$, $p = 0.0780$) and seasonal site means ($s^2 = 0.40m^{1.88}$, $r^2 = 0.90$, $p = 0.0001$).

Paired sample *t* tests were used to determine whether mean *E. ischnus* and *G. fasciatus* densities at the 12 Montreal sites during September–October differed between 2002 and 2003. Site-level differences in *E. ischnus* and *G. fasciatus* densities over the three sampling periods were detected using Tukey–Kramer multiple comparison tests.

Predictive models

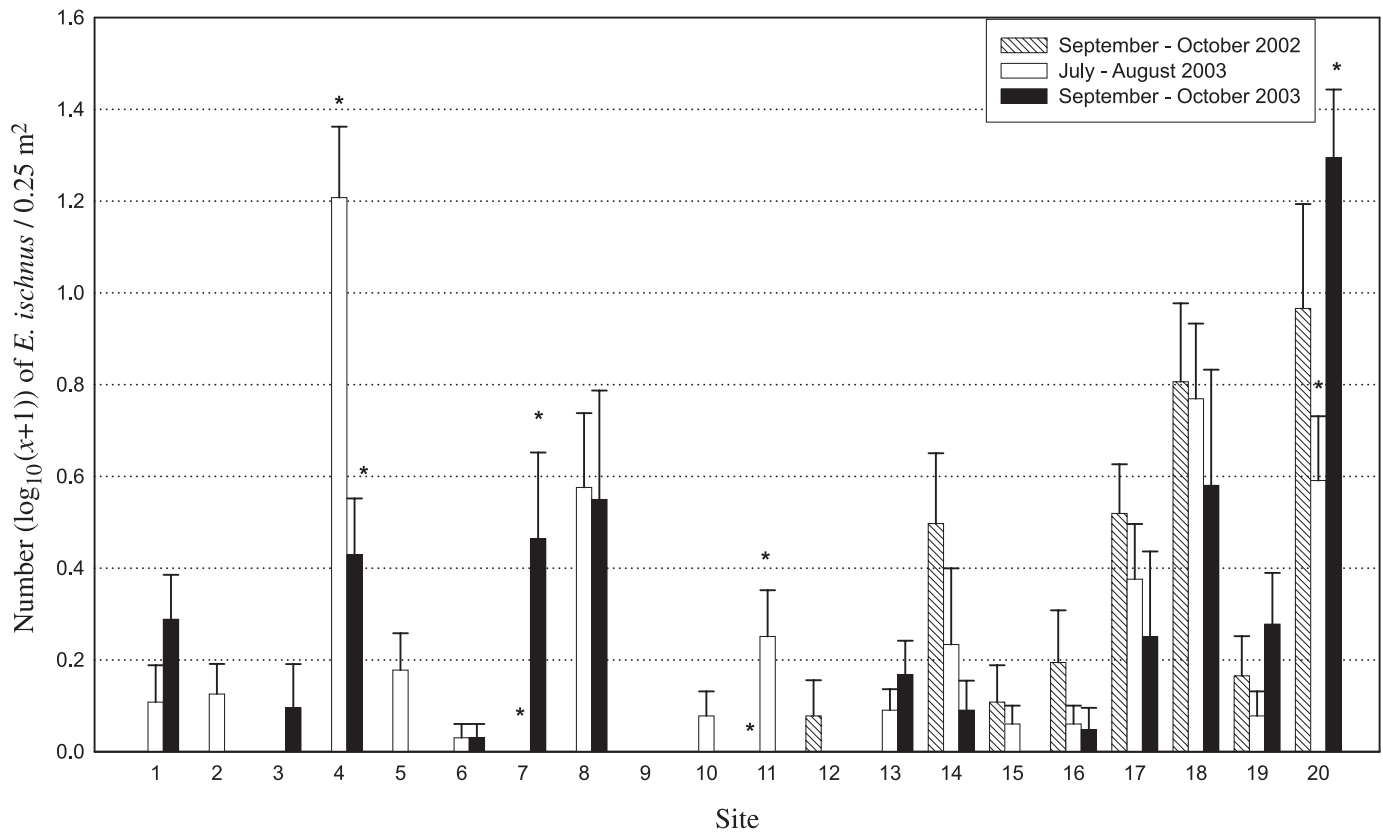
Predictor variables were examined for normality, linearity, and irregularities such as clusters of outliers. Mean depth, turbidity, and calcium showed irregularities that could not be corrected by transformation and therefore were removed

Table 2. Mean amphipod densities and percent species abundance of *Echinogammarus ischnus* and *Gammarus fasciatus* for 20 St. Lawrence River sites (Fig. 1) over three sampling periods.

Site	September–October 2002				July–August 2003				September–October 2003			
	Amphipod density (no./0.25 m ²)		Percentage of		Amphipod density (no./0.25 m ²)		Percentage of		Amphipod density (no./0.25 m ²)		Percentage of	
	<i>E. ischnus</i>	<i>G. fasciatus</i>	<i>E. ischnus</i>	<i>G. fasciatus</i>	<i>E. ischnus</i>	<i>G. fasciatus</i>	<i>E. ischnus</i>	<i>G. fasciatus</i>	<i>E. ischnus</i>	<i>G. fasciatus</i>	<i>E. ischnus</i>	<i>G. fasciatus</i>
1 Prescott	—	—	—	—	95.2	3	97	9.8	21	79		
2 Iroquois	—	—	—	—	4.1	7	93	0	0	0		
3 Morrisburg	—	—	—	—	10.4	0	100	62.2*	0	100		
4 Moulinette	—	—	—	—	53.1	39	61	7.7	24	76		
5 Cornwall	—	—	—	—	152	1	99	33.6*	0	100		
6 St. Anicet	—	—	—	—	36.5	3	97	2.5	2	98		
7 Chateauguay	—	—	—	—	248.2*	0	100	11*	32	68		
8 île Pérot	—	—	—	—	93.6	30	70	69	25	75		
9 Parc Bertold	0.6	0	100	—	398.4	0	100	31.1	0	100		
10 St. Louis	0.9	0	100	—	13.9	1	99	2.3	0	100		
11 Bord de l'eau	0.4	0	100	—	6.2	11	89	4.6	0	100		
12 Valois Bay	0.9	6	94	—	79.4	0	100	6.6	0	100		
13 Summerlea	10.8*	0	100	—	28.9	1	99	40.6	2	98		
14 Lachine	40.3	22	78	—	39.9	4	96	58.8	2	98		
15 Lyette	9.5	5	95	—	16.2	1	99	8.5	0	100		
16 78 ^e	2.1	23	77	—	4.4	3	97	3.4	2	98		
17 40 ^e	3.3	79	21	—	2.9	70	30	3.4	33	67		
18 Senecal	11.8	83	17	—	9.2	73	27	27*	44	56		
19 Allard	13	6	94	—	19	10	90	8.3	13	87		
20 Parc Richard	26.7	90	10	—	15.8	46	54	37.3	73	27		

Note: Values represent the mean of 10 quadrats except for those marked with an asterisk, which are based on 5 quadrats. A dash represents a site that was not sampled during the sampling period.

Fig. 2. Mean (+SE) density of *Echinogammarus ischnus* for 20 St. Lawrence River sites (Fig. 1). Significant seasonal site differences are indicated by asterisks.



from the analysis. Percent sediment cobble and gravel were arcsine transformed and rock surface area was square-root transformed to achieve normality. *Cladophora* and macrophyte biomasses were $\log_{10}(x + 0.01)$ transformed. *Dreissena* density was $\log_{10}(x + 1)$ transformed.

The following analysis was done at both the quadrat and site (sampling season means) scale for each amphipod species independently. Univariate plots were generated to relate amphipod density to the remaining variables (current velocity, temperature, pH, mean substrate size, rock surface area, percent sediment cobble, percent sediment gravel, *Cladophora* biomass, macrophyte biomass, and *Dreissena* density). Increased type II error from the use of multiple univariate tests was controlled by sequential Bonferroni correction (Rice 1989). Variables found to be significant at $p \leq 0.05$ in univariate analysis (prior to Bonferroni correction) were used in a stepwise regression to construct a predictive model for amphipod density. Those variables that explained at least 5% of the variation (at $p \leq 0.05$) in amphipod density were retained in the stepwise model.

Results

Gammarus fasciatus was found during every sampling period at all 20 sites except for 1 site in September–October 2003, where no amphipods of either species were collected. *Echinogammarus ischnus* was present at 19 sites but dominant at only 3 sites. One of the four Montreal sites without *E. ischnus* in September–October 2002 had the species present a year later (at very low density); two of the four sites

had low *E. ischnus* density in July–August 2003 (Table 2). Neither *E. ischnus* occurrence nor its abundance was a function of site distance from Prescott near the outflow of Lake Ontario (Fig. 2).

Echinogammarus ischnus and *G. fasciatus* densities were highly variable and did not show a consistent seasonal pattern (Figs. 2, 3). However, amphipod density was greatest in July–August at 14 sites, all of which were dominated by *G. fasciatus*. Mean *E. ischnus* and *G. fasciatus* densities at the 12 Montreal sites did not differ between September–October 2002 and September–October 2003 (paired t values = 0.2592 and 0.0028, $df = 11$, respectively).

Echinogammarus ischnus density was related to 9 of 10 variables at the quadrat scale (Table 3). Current velocity and *Dreissena* density explained 27% of the variation in *E. ischnus* density at the quadrat scale (stepwise regression, $p < 0.0001$). At the site level, *E. ischnus* density was related to current velocity, mean substrate size, percent sediment gravel, and *Dreissena* density; the site-level predictive model explained 42% of variation in *E. ischnus* density ($p = 0.0059$; Table 4).

Gammarus fasciatus density was related to every variable except percent sediment gravel at the quadrat scale (Table 3). *Cladophora* biomass, macrophyte biomass, and *Dreissena* density were kept in the stepwise regression model and explained 40% of the variation in *G. fasciatus* density ($p < 0.0001$). At the site level, percent sediment gravel, *Cladophora* biomass, and pH were related to *G. fasciatus* density; *Cladophora* biomass and pH explained 37% of *G. fasciatus* variation ($p = 0.0033$; Table 4).

Fig. 3. Mean (+SE) density of *Gammarus fasciatus* for 20 St. Lawrence River sites (Fig. 1). Significant seasonal site differences are indicated by asterisks.

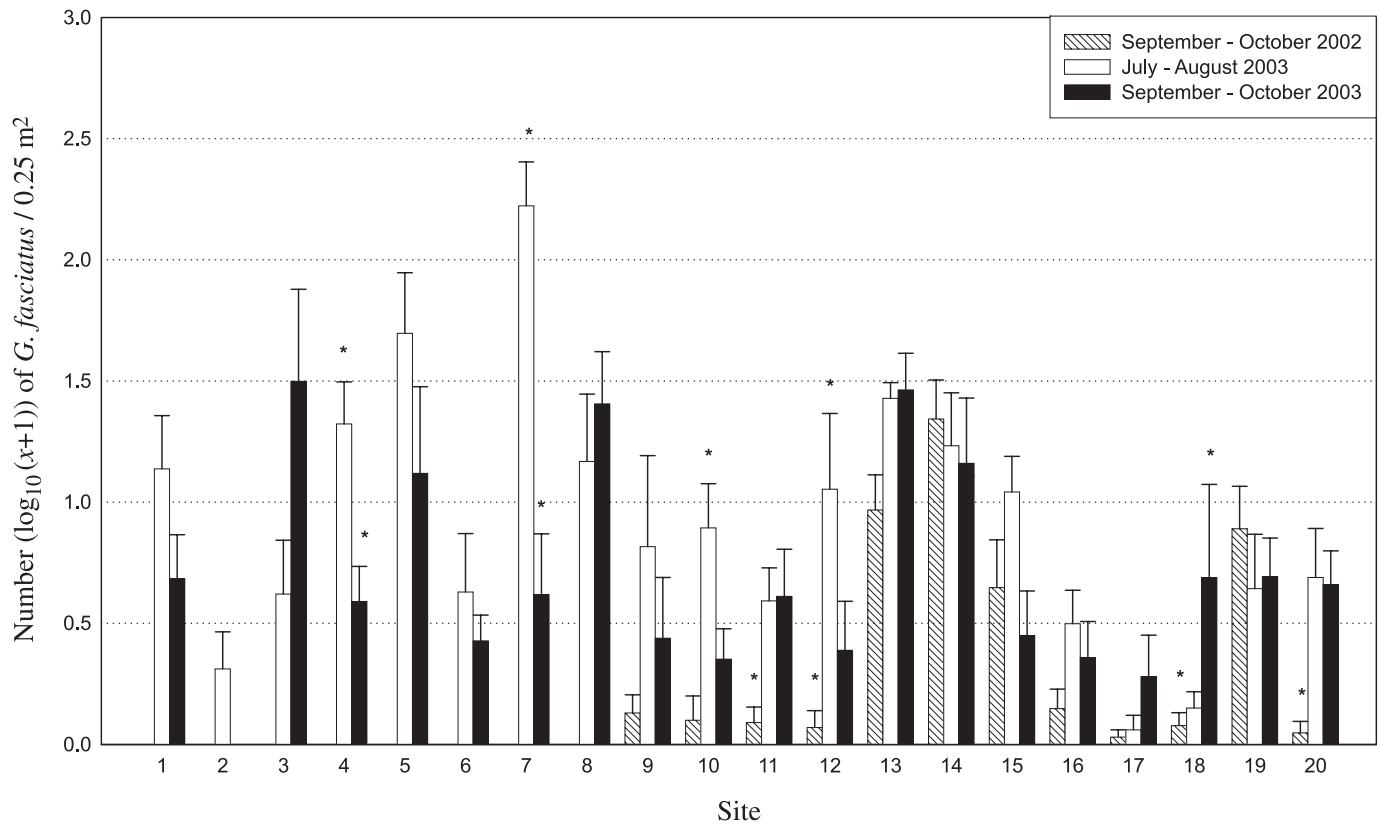


Table 3. Univariate relationships for amphipod densities ($\log_{10}(x + 1)$) and measured variables at the quadrat and site scales.

Variable	Quadrat				Site			
	<i>E. ischnus</i>		<i>G. fasciatus</i>		<i>E. ischnus</i>		<i>G. fasciatus</i>	
	R^2	p	R^2	p	R^2	p	R^2	p
Current velocity	0.17	<0.0001*	-0.02	0.0046*	0.26	0.0001*	-0.07	0.0552
Temperature (°C)	0.00	0.6888	0.01	0.0469	0.00	0.8918	0.06	0.0802
pH	-0.01	0.0173	0.08	<0.0001*	-0.01	0.4608	0.24	0.0002*
Mean substrate size (phi)	-0.06	<0.0001*	-0.01	0.0217	-0.11	0.0142	-0.00	0.7879
Rock surface area (mm)	0.05	<0.0001*	0.14	<0.0001*	0.03	0.2616	0.06	0.0753
Percent sediment: cobble	0.02	0.0073*	0.03	0.0002*	0.01	0.5912	0.02	0.3685
Percent sediment: gravel	0.12	<0.0001*	-0.01	0.0728	0.17	0.0026*	-0.12	0.0127
<i>Cladophora</i> biomass (g)	-0.00	0.7123	0.25	<0.0001*	-0.03	0.2184	0.25	0.0002*
Macrophyte biomass (g)	0.01	0.0162	0.14	<0.0001*	0.02	0.3271	0.07	0.0607
<i>Dreissena</i> density (no./0.25 m ²)	0.17	<0.0001*	0.10	<0.0001*	0.09	0.0359	0.07	0.0559

Note: Asterisks indicate relationships that are significant after sequential Bonferroni correction.

Discussion

At many sites in the lower Great Lakes, *E. ischnus* has replaced *G. fasciatus* as the dominant amphipod, and in some cases *G. fasciatus* was locally extirpated, often within a year of the first detection of *E. ischnus* (Dermott et al. 1998). By contrast, we found that *G. fasciatus* has remained the dominant amphipod throughout most of the upper St. Lawrence River 6 years after the discovery of *E. ischnus* in the river at Prescott in 1997 (Dermott et al. 1998). Although *E. ischnus* was present throughout the river (occasionally at high local densities) during the survey, it outnumbered *G. fasciatus*

only at a few sites. The relative abundance of the two species was not a function of distance from the upstream *E. ischnus* source populations in Lake Ontario; *E. ischnus* was not more abundant at western sites than at eastern sites. Thus, its abundance cannot be explained by simple linear diffusion. Furthermore, there is no evidence that *E. ischnus* is progressively replacing *G. fasciatus*, even at a slower rate than that seen in the Great Lakes, because neither species' density differed significantly between September–October 2002 and September–October 2003 at the 12 Montreal sites. These results suggest that *E. ischnus* and *G. fasciatus* are co-existing in the St. Lawrence River.

Table 4. Stepwise regression models at the quadrat and site scale for amphipods in the St. Lawrence River.

Species	Scale	N	Model	R ²	p
<i>E. ischnus</i>	Quadrat	490	Log ₁₀ density = flow rate + log ₁₀ (<i>Dreissena</i> density)	0.27	<0.0001
	Site	52	Log ₁₀ density = flow rate + log ₁₀ (<i>Dreissena</i> density) + arcsine percent sediment gravel	0.41	0.0059
<i>G. fasciatus</i>	Quadrat	490	Log ₁₀ density = log ₁₀ (<i>Cladophora</i> biomass) + log ₁₀ (macrophyte biomass) + log ₁₀ (<i>Dreissena</i> density)	0.40	<0.0001
	Site	52	Log ₁₀ density = log ₁₀ (<i>Cladophora</i> biomass) + pH	0.37	0.0033

Note: Variables included in the model explain ≥5% of the variation in amphipod density and are significant at $p \leq 0.05$ in univariate analysis before sequential Bonferroni correction.

This coexistence is not likely a result of temporal segregation, as amphipod densities did not vary consistently over seasons. Instead, coexistence appears to be due, at least in part, to differential microhabitat use. Current velocity and substrate type were significant predictors of species' densities. Whereas both species showed a similar positive response to *Dreissena* spp. as substrate, *E. ischnus* was more abundant in areas of strong current and, at the site level, the availability of gravel sediment; by contrast, *G. fasciatus* was dependent upon algal substrate (as measured by *Cladophora* biomass and macrophyte biomass) and water pH levels.

Both species responded positively to *Dreissena* density, likely because of increased habitat complexity provided by the mussel shells and, to a lesser degree, increased nourishment from mussel fecal deposits (Ricciardi et al. 1997). *Dreissena* beds are composed of clumped mussels with abundant interstitial spaces that amphipods can use as microhabitat and refugia from predators (González and Downing 1999). *Echinogammarus ischnus* is found in close association with *Dreissena* spp. in its native range (Köhn and Waterstraat 1990), and so was expected to have a higher affinity than *G. fasciatus* for *Dreissena*-covered substrate. After *Dreissena* spp. became established in North America, the substrate generalist *G. fasciatus* (Dermott et al. 1998) quickly adapted to their presence and showed great increases in abundance as a result of the added interstitial habitat (Ricciardi et al. 1997; Stewart et al. 1998; Ricciardi 2003).

Current velocity was the most important predictor of *E. ischnus* density in the St. Lawrence River. This was expected, given that *E. ischnus* is a lotic species native to large rivers in its home range. After being introduced to North America, *E. ischnus* quickly replaced *G. fasciatus* at high flow and wave-exposed sites in the Great Lakes and connecting channels, particularly in the St. Clair, Detroit, and Niagara rivers, while it reached relatively low densities in calm lentic waters in the same region (Dermott et al. 1998). *Gammarus fasciatus*, although often abundant in areas of moderate flow, is generally found in lakes and slow-moving rivers (Bousfield 1958).

Echinogammarus ischnus is a rocky-substrate specialist that uses its uropods and antennae to move across hard surfaces (Dermott et al. 1998). Unstable fine sediment (clay/mud, silt, and sand) is apparently unsuitable for *E. ischnus* activity. Rocky substrate also provides amphipods with microhabitats in the form of pits and interstitial spaces that can serve as refugia from predators; in fact, Ward and Porter (1993) proposed that the number of interstices provided is more important than the size of the substrate. Fine substrates are densely packed and thus offer few habitable interstitial

spaces. *Echinogammarus ischnus* was typically found on the underside of cobbles, which perhaps explains why its density was related to the amount of underlying sediment composed of gravel. Gravel sediments contain abundant interstitial pores that not only serve as microhabitats but also permit a constant flow of oxygenated water and food particles.

Gammarus fasciatus density was greatest on algal substrates, as predicted by Dermott et al. (1998). *Gammarus fasciatus* has a strong affinity for the filamentous alga *Cladophora* spp. (Stewart and Haynes 1994; Dermott et al. 1998; Van Overdijk et al. 2003). *Gammarus fasciatus* is able to cling to algal filaments (M. Palmer, personal observations) and appears to effectively use spaces between filaments as shelter.

Freshwater amphipod coexistence through niche differentiation has been studied elsewhere (Dick and Platvoet 1996; MacNeil et al. 1999; MacNeil et al. 2001a, 2001b), and patterns of coexistence have been related to substrate type (MacNeil et al. 2001a) and water quality (MacNeil et al. 2001b). These variables are also important determinants of relative amphipod abundances in our study. However, Palmer and Ricciardi (2005) found that predation by fish and crayfish also contributed to the coexistence of *E. ischnus* and *G. fasciatus* on substrates consisting of *Dreissena* spp. in the St. Lawrence River. This suggests that biotic factors such as direct competition, intraguild predation, and predation, and their interaction with abiotic factors must also be examined to better understand the mechanisms that allow species to coexist in some areas, while being mutually exclusive in others.

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