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

by

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Abstract

Freshwater ecosystems worldwide are being altered by multiple stressors. One of the most important stressors is biological invasion – the introduction of exotic species, which can contribute to the loss of native species. The effects of an introduced species are correlated with its abundance and typically vary across ecosystems, suggesting that its impact on native species is mediated by its environment, i.e. the physical habitat and the recipient community. However, there are few studies that explore the effects of environment on the interactions between exotic and native species. My thesis examines the influence of physical habitat variables and community interactions on the relative abundance of exotic and native freshwater crustaceans in the St. Lawrence River.

The Eurasian amphipod *Echinogammarus ischnus* invaded the Great Lakes-St. Lawrence River system in the mid-1990s and has replaced the native North American *Gammarus fasciatus* as the dominant amphipod in littoral areas throughout Lake Erie and Lake Ontario. *Echinogammarus* has been found to be particularly dominant on rocky substrates covered with zebra mussels (*Dreissena polymorpha*), suggesting that the exotic mussels are promoting this species replacement. However, data from a preliminary survey in 2002 suggest *Gammarus* remains dominant in the upper St. Lawrence River, and the two species may be coexisting at many sites where *Dreissena* is abundant (M. Palmer, unpublished data). The primary objectives of my research were to (1) determine whether *Echinogammarus* and *Gammarus* are coexisting in the St. Lawrence River and (2) ascertain and quantify environmental variables mediating the relative abundance of these amphipods.

A multi-site survey revealed that *Echinogammarus* and *Gammarus* are sympatric in the St. Lawrence River. This coexistence is due, in part, to differential habitat use facilitated by the heterogeneity of the river. *Echinogammarus* dominates amphipod abundance in areas with high current velocity and rocky substrates while *Gammarus* dominates in areas with high algal biomass and was found to respond positively to increased pH levels. Both amphipod species were also found to thrive in dreissenid beds. To more closely examine the relationship between *Dreissena* and the amphipods, I used an *in-situ* predator-exclusion experiment with *Dreissena*-covered and uncovered substrates. Surprisingly, I found that the native and exotic amphipods showed similar increases in abundance on dreissenid substrates and *Echinogammarus* was more susceptible to large predators on such substrates even though it was hypothesized that *Echinogammarus*, which has evolutionary experience with the mussels, would be better able than *Gammarus* to use *Dreissena* as habitat and refugia from predators. These findings suggest that resident species are also promoting the coexistence of the two amphipods by providing habitat and preferentially reducing the abundance of *Echinogammarus* as compared to *Gammarus*. Overall, my research demonstrates that both abiotic (river heterogeneity) and biotic (resident community composition) variables are mediating the coexistence and local abundance of *Echinogammarus* and *Gammarus* in the St. Lawrence River.

Résumé

Partout dans le monde, les écosystèmes d'eau douce sont affectés par plusieurs facteurs de stress. L'introduction d'espèces exotiques, ou invasion biologique, peut contribuer à l'élimination d'espèces indigènes et représente un des facteurs de stress les plus important pour les écosystèmes. L'impact de l'invasion d'une espèce sur l'écosystème qui l'accueille est corrélé avec l'abondance de l'espèce invasive et varie généralement d'un écosystème à l'autre. Ceci laisse croire que l'environnement (c'est à dire l'habitat physique et la communauté d'accueil) est médiateur de l'impact de l'invasion biologique sur les espèces indigènes. Malgré ces constatations, très peu d'études ont concentré leur attention sur les effets de l'environnement sur les interactions entre espèces exotiques et indigènes. La présente recherche vise à examiner l'influence des variables de l'habitat physique et des interactions de la communauté biologique sur l'abondance relative des crustacés exotiques et indigènes d'eau douce du fleuve Saint-Laurent.

L'amphipode eurasien *Echinogammarus ischnus* a envahi le système des Grands Lacs et du fleuve Saint-Laurent au milieu des années 1990 et a depuis remplacé *Gammarus fasciatus,* un amphipode indigène de l'Amérique du Nord, comme amphipode dominant des ères littorales des lacs Érie et Ontario. *Echinogammarus* est particulièrement dominant sur les surfaces rocheuses couvertes de moules zébrées (*Dreissena polymorpha*), ce qui suggère que ces moules exotiques promeuvent le remplacement de *Gammarus* par *Echinogammarus.* Par contre, *Gammarus* demeure l'espèce dominante en amont du fleuve Saint-Laurent et les deux espèces peut coexister dans plusieurs sites où *Dreissena* est retrouvée en abondance (M. Palmer, les données

non publiées). Les objectifs primaires de ma recherche étaient à (1) détermine si *Echinogammarus* et *Gammarus* coexistent dans la Rue. La Rivière de Lawrence et (2) vérifie et quantifie des variables écologiques agit en le médiateur l'abondance relative de ces amphipods.

Une étude de multi-site a révélé que *Echinogammarus* et *Gammarus* sont sympatric dans la Rue. Lawrence Rivière. Cette coexistence est dûe, partiellement, à l'usage d'habitat différentiel facilité par l'hétérogénéité de la rivière. *Echinogammarus* domine l'abondance de amphipod dans les secteurs avec l'haute vélocité actuelle et les substrats rocheuxs pendant que *Gammarus* domine dans les secteurs avec l'haute biomasse des algues et a été trouvé pour répondre absolument aux niveaux de pH augmentés. Les deux espèce de amphipod a été aussi trouvée pour prospérer dans les lits de dreissenid. Plus de près examiner la relation entre *Dreissena* et le amphipods, j'ai utilisé une expérience de prédateur-exclusion de dans-situ avec les substrats *Dreissena*-Couverts et découverts. Etonnamment, j'ai trouvé que le amphipods natal et exotique a montré des augmentations similaires dans l'abondance sur les substrats de dreissenid et *Echinogammarus* étaient plus susceptibles aux grands prédateurs sur tels substrats bien qu'il a été posé une hypothêse que *Echinogammarus*, qui a l'expérience évolutionniste avec les moules, serait meilleur capable que *Gammarus* pour utiliser *Dreissena* comme l'habitat et refugia des prédateurs. Ces constatations suggèrent que la présence de *Dreissena* promeut la co-existence des deux amphipodes en fournissant un habitat et en réduisant préférentiellement l'abondance d'*Echinogammarus* par rapport à celle de *Gammarus*. En tout et partout, le présent projet de recherche a démontré que des variables propres à l'environnement physique telles que l'hétérogénéité du fleuve, ainsi que des variables biologiques telles que la composition de la communauté d'accueil, sont médiateurs de la co-existence et de l'abondance locale de *Echinogammarus* et de *Gammarus* dans le fleuve Saint-Laurent.

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Preface

The Faculty of Graduate Studies and Research of McGill University requires that the following statements be made in order to inform the reader of Faculty regulations:

Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis. If this option is chosen, connecting texts that provide logical bridges between different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: a Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

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This thesis carries a credit weight of 39 credits, from a total of 45 credits required for the Master's degree. Graduate credits are a measure of the time assigned to a given task in the graduate program. They are based on the consideration that a term of full-time graduate work is equivalent to 12 to 16 credits, depending on the intensity of the program.

This thesis consists of two chapters prepared as manuscripts for publication in peer-reviewed scientific journals. Chapter 1 has been submitted to Canadian Journal of Zoology and Chapter 2 has been submitted to Canadian Journal of Fisheries and Aquatic Sciences. I designed and executed the sampling protocol and experimental setup for the research presented herein, under the supervision of Dr. Anthony Ricciardi (Redpath Museum and McGill School of Environment). Dr. Ricciardi contributed significantly to the development of this research by providing theoretical discussions and technical advice, as well as editorial criticisms, and thus is a co-author on both manuscripts.

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General Introduction

North American freshwater communities are undergoing rapid alterations due to increasing rates of invasion and extinction (Moyle et al. 1986; Ricciardi and Rasmussen 1999; Rahel 2002). Introduced species may directly contribute to the extirpations of native species through various impacts, but generalizations predicting the outcome of nonindigenous and native species interactions are rare (Moyle and Light 1996; Parker et al. 1999). What governs the competitive displacement or coexistence of species is a fundamental issue in community ecology (Morin 1999).

Invasive species may exclude natives at some sites while coexisting with them at others (Nichols and Wilcox 1997), suggesting that site-specific environmental factors mediate species interactions (Ricciardi 2003). The gradient hypothesis (Fox and Fox 1986) proposes that physical environmental gradients determine an invader's abundance and, therefore, its impact on native species. An alternative view is that the composition of the recipient community determines the outcome of an invasion and an invader's impact (Ricciardi & Atkinson 2004). The biotic resistance hypothesis (Levine and D'Antonio 1999) suggests that interactions with resident species can repel an introduced species or reduce its abundance locally (Robinson and Wellborn 1988). Conversely, resident invaders may facilitate subsequent invaders and enhance their impacts through synergistic interactions – a concept termed "invasional meltdown" (Simberloff and Von Holle 1999). However, few studies have tested these hypotheses for aquatic communities. In this thesis, I explore the effects of abiotic and biotic environmental variables on the interactions between invasive and native crustaceans.

The Eurasian amphipod crustacean *Echinogammarus ischnus* was first discovered in North America in the Detroit River in 1995 (Witt et al. 1997). By 2002 it had spread to all of the Great Lakes and as far downstream in the St. Lawrence River as Montreal (Quebec) (Dermott et al. 1998; Nalepa et al. 2001; Vanderploeg et al. 2002; A. Ricciardi, unpublished data). As *Echinogammarus* spread throughout Lake Huron and Lake Ontario, it replaced the native North American species *Gammarus fasciatus* as the dominant amphipod at many sites (Dermott et al. 1998; Van Overdijk et al. 2003). However, this replacement has not yet been observed in the St. Lawrence River. Thus, the river offers an opportunity to examine what factors are controlling the relative densities of the two species. This thesis is the first study to examine these factors in a system where *Echinogammarus* and *Gammarus* apparently coexist (based on a preliminary survey of 24 sites in June, 2002; M. Palmer, unpublished data).

The St. Lawrence River is a heterogeneous environment that offers both physical and chemical gradients across which species may be able to segregate. If *Echinogammarus* and *Gammarus* have differential responses to physico-chemical variables, the abiotic environment may mediate their interactions and allow them to coexist. The biotic environment (i.e. resident species) may also influence the relative densities of the two amphipods. Two Eurasian mussels (*Dreissena polymorpha* and *D. bugensis*) invaded the system in the early 1990's (Mellina and Rasmussen 1994; Ricciardi et al. 1996), and the structural complexity of the beds formed by their colonies stimulate increases in amphipod abundance as they provide amphipods with interstitial habitat and potential refugia from large predators (Ricciardi et al. 1997; González and Downing 1999). However, *Echinogammarus* may be expected to achieve a greater increase on dreissenid beds than does *Gammarus*, because *Echinogammarus* is found in close association with the mussel in their native Eurasia (Köhn and Waterstraat 1990) and may be well adapted to using *Dreissena* as habitat and a refuge from predators. Therefore, *Dreissena* and resident predators may influence the relative densities (and thus the coexistence) of *Echinogammarus* and *Gammarus*.

The first objective of my research was to determine whether *Echinogammarus* is replacing *Gammarus* in the St. Lawrence River (similar to the pattern seen in the Great Lakes) or if the two species are coexisting, as suggested by my preliminary survey. My second objective was to identify environmental factors influencing the relative densities of the two amphipod species. My specific hypotheses are as follows:

H_1: *Echinogammarus* density in the St. Lawrence River is a function of distance from upstream source populations in Lake Ontario (Chapter 1).

H_2: *Echinogammarus* density is increasing while *Gammarus* density is decreasing throughout the upper St. Lawrence River (Chapter 1).

H_3: *Echinogammarus* and *Gammarus* densities are related to, and respond in a similar manner to, the same physico-chemical parameters in the St. Lawrence River (Chapter 1).

H_4: *Echinogammarus* shows a greater increase in density in the presence of *Dreissena* than does *Gammarus* (Chapter 2).

H_5: *Echinogammarus* is less susceptible than *Gammarus* to predators in the presence of *Dreissena* (Chapter 2).

In Chapter 1, I use a two year, multi-site survey to examine patterns of abundance of *Echinogammarus* and *Gammarus* in the St. Lawrence River. I statistically relate amphipod densities to water quality variables and substrate characteristics to determine whether *Echinogammarus* and *Gammarus* respond to different abiotic environmental factors. Differential responses might permit the two species to segregate spatially and coexist in the river. In Chapter 2, *Echinogammarus* and *Gammarus* responses to *Dreissena* and predation are compared using an in-situ predator-exclusion experiment with *Dreissena*-covered and uncovered substrates. This is the first experimental study relating the relative abundances of invasive and native species to the effects of facilitation (by mussels) and predation (by fish and crayfish).

The replacement or coexistence of *Echinogammarus* and *Gammarus* has ecological implications because *Gammarus* is an important prey item for St. Lawrence River forage fishes such as yellow perch (Ringler and Johnson 1982), and it is not yet known whether *Echinogammarus* will be a dietary equivalent. Additionally, gammarid amphipods feed upon dreissenid biodeposits that accumulate contaminants; if *Echinogammarus* contaminant transfer rates differ from those of *Gammarus*, bioaccumulation in higher trophic levels may be altered (c.f. Bruner et al. 1994).

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Chapter 1

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

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

Introduction

Freshwater communities worldwide are being rapidly altered by a variety of anthropogenic stressors, including exotic species introductions (Ricciardi and Rasmussen 1999; Sala et al. 2000). Although many species introductions result in little detectable change in freshwater communities (Moyle and Light 1996), some cause substantial impacts including the loss of native species through competitive exclusion (Ricciardi et al. 1998). Impacts vary spatially as exotic species may exclude native species at some sites while coexisting with them at others (Bulnheim 1980; Nichols and Wilcox 1997; MacNeil et al. 2001a,b), 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, owing to a greater availability of refugia and the presence of physico-chemical 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* (Witt et al. 1997) is apparently replacing the native amphipod *Gammarus fasciatus* in Lake Erie and Lake Ontario (Dermott et al. 1998; Van Overdijk et al. 2003). This replacement may have food web ramifications because *Gammarus* 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 may be coexisting throughout 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 *Echinogammarus* near Montreal in 1998 (A. Ricciardi, unpublished data).

The St. Lawrence River is one of the largest river systems in the world; it spans over 1200km flowing northeast from Lake Ontario to the Gulf of St. Lawrence and emptying into the North Atlantic Ocean. Along its course, the St. Lawrence River undergoes multiple changes in size (i.e. river width and depth), current velocity, climatic condition and shoreline topography, it encompasses fluvial lakes and islands and is joined by several smaller rivers, the largest being the Ottawa River which empties just south of Montreal. These features make the St. Lawrence River an extremely heterogeneous system at multiple spatial scales. Benthic habitat, in particular, is highly variable throughout the St. Lawrence River. This heterogeneity may be allowing *Echinogammarus* and *Gammarus* to segregate, thereby avoiding competitive exclusion and promoting the coexistence of the species.

In this study, I use a multi-site survey to determine whether the amphipod species *Echinogammarus* and *Gammarus* are coexisting in the St. Lawrence River and the factors mediating their interactions. I first address the hypothesis that *Echinogammarus* density is a function of distance from upstream source populations. Prescott (Ontario) near the outflow of Lake Ontario is thought to be the original point of *Echinogammarus* introduction in the river (Dermott et al. 1998) and if *Echinogammarus* dominates at upstream sites while *Gammarus* becomes proportionally more abundant at sites lower in the system, it will suggest that *Echinogammarus* is extirpating *Gammarus* as it spreads downstream. Alternatively, *Echinogammarus* may be excluding *Gammarus* from the river via jump dispersal followed by radial population growth (MacIsaac et al. 2001).

This method of extirpation is controlled by patch dynamics (Levin et al. 1993) and occurs when an invader is transported throughout a system (in this case by water currents and human-mediated vectors) and establishes multiple isolated populations. These local foci may then expand until the entire system is invaded. If this is the case in the St. Lawrence River, *Echinogammarus* density should increase as *Gammarus* density decreases over time; I will test this form of extirpation by comparing amphipod densities in 2002 to those in 2003.

If *Echinogammarus* and *Gammarus* are indeed coexisting in the St. Lawrence River, I predict that the two species respond to different optimal abiotic environmental parameters, thus allowing them to segregate and avoid competitive exclusion. To test whether the two amphipod species are segregating along abiotic gradients, I relate the densities of *Echinogammarus* and *Gammarus* to a suite of physico-chemical variables, focusing primarily on water quality variables and benthic substrate characteristics. These factors are considered important determinants of amphipod distribution and abundance (Ress 1972; Olyslager and Williams, 1993; Attrill et al. 1999; Lancaster and Mole 1999) as well as amphipod species replacement and coexistence (Dick and Platvoet 1996; MacNeil et al. 2001a,b). My specific hypotheses are detailed in Appendix 1.

Methods

Sampling Protocol

Twenty St. Lawrence River sites were sampled (Figure 1). During September-October 2002, 12 sites on the Island of Montreal were sampled; however, in 2003, sampling was expanded to encompass 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 m^2 and were at least 2 km apart.

At each site, 5-10 quadrats of 0.25 m^2 area were sampled (ten replicates to 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, conductivity, turbidity and calcium), substrate quality (mean substrate size, rock surface area, and percent sediment composition of cobble and gravel) and biotic variables (*Cladophora* biomass, macrophyte biomass, *Dreissena* density and amphipod densities).

Mean depth was determined by measuring the 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 substrate. Mean substrate size was calculated as follows: first, percent cover was determined visually for each substrate type in the quadrat with the aid of equally spaced markings on the quadrat frame. Then, percent cover values were multiplied by each substrate's corresponding phi ($-\log_2$) value (bedrock = -9.967, boulder = -8, cobble = -5.8, gravel = -3.5, sand = 2, silt = 6.5 and clay/mud = 9). Finally, 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 using Dall's (1979) equation for ellipsoidal shapes:

Surface area = (π/3) * (length × width + length × breadth + width × breadth).

Once all overlying rocks were collected, the percent composition of underlying sediment made up 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 substrate was made up of boulders too large to remove, it was assumed that the immediately underlying sediment was the same. All *Cladophora* present and macrophytes rooted within the quadrat were removed and blotted wet weight was measured using a Denver Instrument APX-602 balance. *Dreissena* density was determined by collecting and counting all mussels > 5 mm length within the quadrat.

Amphipods were collected by shaking and scouring all rocks, cobble and gravel sediment, *Cladophora*, macrophytes and *Dreissena* 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 were sorted using a HundWetzlar SM33 stereoscope, and identified to species using standard morphological characteristics described by Witt et al. (1997).

A 1-L water sample was collected at each site to measure water quality variables. A Fisher Scientific Accumet AP63 meter was used to measure pH and conductivity. Turbidity and calcium concentration (Ca^{2+} in mg/L) were determined using LaMotte Turbidity Model TTM and Hardness Model PHT-CM-DR-LT kits.

Statistical analysis

All analyses were done using SAS statistical software (Version 8) (SAS Institute 1999). The mean (m)-variance (s^2) relationship for total amphipod density indicated that a $\log_{10}(x + 1)$ transformation was required for normalizing *Echinogammarus* and *Gammarus* 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 *Echinogammarus* and *Gammarus* densities at the 12 Montreal sites during September-October differed between 2002 and 2003. Site level differences in *Echinogammarus* and *Gammarus* 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 dealt with by transformation and were thus removed 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. Because pH and conductivity were strongly correlated (Pearson $R = -0.98$, $p < 0.0001$), conductivity was removed from the analysis.

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 rate due to the use of multiple univariate tests was controlled by sequential Bonferroni correction (Rice 1989). A predictive model relating amphipod density to the variables found to be significant at $p \leq 0.05$ in univariate analysis (before sequential Bonferroni correction) was then created using stepwise regression. Variables that explained at least 5% of the variation (at $p \leq 0.05$) in amphipod density were retained in the model.

Results

Gammarus was found during every sampling period at all 20 sites except one site in September-October 2003 where no amphipods of either species were collected. *Echinogammarus* was present at 19 sites but dominant at only three. One of the four Montreal sites without *Echinogammarus* in September-October 2002 had the species present a year later (at very low density); two of the four sites had low *Echinogammarus* density in July-August 2003 (Table 2). Neither *Echinogammarus* occurrence nor its abundance was a function of site distance from Prescott (Figure 2).

Echinogammarus and *Gammarus* densities were highly variable and did not show a consistent seasonal pattern (Figures 2-3). However, amphipod density was greatest in July-August at 14 sites, all of which were dominated by *Gammarus*. Mean *Echinogammarus* and *Gammarus* densities at the 12 Montreal sites did not differ between September-October 2002 and 2003 (paired t-value = 0.2592 and 0.0028, d.f. = 11, respectively).

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

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

Discussion

At many sites in the lower Great Lakes, *Echinogammarus* has replaced *Gammarus* as the dominant amphipod, and in some cases *Gammarus* was locally extirpated; this replacement often occurred within a year of the detection of *Echinogammarus* (Dermott et al. 1998). By contrast, I found that *Gammarus* has remained the dominant amphipod in the St. Lawrence River six years after the initial discovery of *Echinogammarus* in the river at Prescott in 1997 (Dermott et al. 1998). Although *Echinogammarus* was present throughout the river (occasionally at high local densities) during the survey, it only outnumbered *Gammarus* at a few sites. The relative density of the two species was not a factor of distance from the upstream *Echinogammarus* source populations in Lake Ontario; *Echinogammarus* was not more abundant at western sites compared to eastern sites. This suggests that a simple diffusion model (Hengeveld 1989) cannot be applied to *Echinogammarus* spread. Additionally, it does not appear that *Echinogammarus* is progressively replacing *Gammarus*, even at a slower rate than that seen in the Great Lakes, as neither species' density differed significantly between September-October 2002 and 2003 at the 12 Montreal sites. These results suggest that *Echinogammarus* and *Gammarus* are coexisiting in the St. Lawrence River.

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, in part, to differential microhabitat use. In particular, current velocity and substrate type were significant predictors of species' densities. Whereas both species showed a similar positive response to *Dreissena* substrate, *Echinogammarus* was more abundant in areas of strong current and, at the site level, the availability of gravel sediment; by contrast, *Gammarus* was dependent upon algal substrate (as measured by *Cladophora* and macrophyte biomass) and water pH levels.

Both amphipod 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). Dreissenid beds are composed of tightly packed mussels that create interstitial spaces that amphipods can use as microhabitat and refugia from predators (González and Downing 1999). *Echinogammarus* is found in close association with *Dreissena* in its native range (Köhn and Waterstraat 1990). After *Dreissena* became established in North America, the substrate generalist *Gammarus* (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).

Current velocity was found to be the most important predictor of *Echinogammarus* density in the St. Lawrence River. This was expected as *Echinogammarus* is a riverine species native to large rivers in its home range. After being introduced to North America, *Echinogammarus* quickly replaced *Gammarus* at high flow and wave-exposed sites in and around the Great Lakes, particularly in the St. Clair, Detroit and Niagara Rivers, while it reached relatively low densities in quiet waters in the same area (Dermott et al. 1998). Conversely, *Gammarus*, although often abundant in areas of moderate flow, is generally found in lakes and slow-moving rivers (Bousfield 1958). It is not surprising that the same pattern is being seen in the St. Lawrence River.

Echinogammarus is a rocky substrate specialist able to use 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 *Echinogammarus* activity. Rocky substrate also provides amphipods with microhabitats in the form of pits and interstitial spaces that can be used as refugia from predators; indeed, Ward and Porter (1993) proposed that the number of interstices provided is more important than the size of the substrate. Fine substrates are closely packed resulting in few habitable interstitial spaces.

Echinogammarus was usually found on the underside of appropriate substrate such as cobbles, which perhaps explains why its density was related to the amount of underlying sediment composed of gravel. These sediments have multiple interstitial spaces suitable for small invertebrates. Furthermore, the porous nature of gravel sediment permits a constant flow of oxygenated water and food particles.

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

Freshwater amphipod coexistence through niche differentiation has been studied elsewhere (Dick and Platvoet 1996; MacNeil et al.1999; MacNeil et al. 2001a,b), 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 my study. However, 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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Table 1. St. Lawrence River site descriptions (Figure 1) and total number of 0.25 m^2 quadrats sampled.

	Site	Shoreline	Flow: 1 to 4 (1=low, 4=rapids)	N
1	Prescott	large rock slabs below a steep mud bank, roadside	3	20
2	Iroqouis	boulder and grass shore, public park/golf course	2	20
3	Morrisburg	cobble beach, public park	2	15
4	Moulinette	cobble beach, public park	2	20
5	Cornwall	grass shore, public park	2	15
6	St. Anicet	large cove, grass shore, residential area	1	20
7	Chateauguay	sand and driftwood beach	3	10
8	Île Pérrot	sand beach, public park	2	20
9	Parc Bertold	grass shore, public park	1	30
10	St. Louis	boat launch, residential	1	30
11	Bord de l'eau	cobble beach, public warf	2	30
12	Valois Bay	weed and cobble shore, near roadside	1	30
13	Summerlea	cobble shore, public beach	2	25
14	Lachine	small cove, cobble shore, public park	1	30
15	Lyette	grass shore, public park	1	30
16	78^e	grass shore, public park	2	30
17	40^e	grass shore, public park	4	30
18	Senecal	weed bank	4	25
19	Allard	grass shore, public park	2	30
20	Parc Richard	weed and mud slope, developmental area	3	30

Table 2. Amphipod densities (per 0.25 m^2) and percent species abundance for 20 St. Lawrence River sites over three sampling periods. Sites are numbered west to east with sites 9-20 located on the island of Montreal. Values represent the mean of n = 10 quadrats (0.25 m^2) except for those marked with an * where values are based on n = 5. Sites not sampled during a sampling period are shown by a dash.

		September-October 2002			July-August 2003			September-October 2003		
	Site	Amphipod Density (0.25 m^2)	% *E. ischnus*	% *G. fasciatus*	Amphipod Density (0.25 m^2)	% *E. ischnus*	% *G. fasciatus*	Amphipod Density (0.25 m^2)	% *E. ischnus*	% *G. fasciatus*
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 Pérrot	-	-	-	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

Table 3. Univariate relationships for amphipod $\log_{10}(x + 1)$ densities and measured variables at the quadrat and site scale. Relationships significant after sequential Bonferroni correction indicated by an asterisk.

	Quadrat				Site			
	Echinogammarus		*Gammarus*		*Echinogammarus*		*Gammarus*	
Variable	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value
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**
Cladophora 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
Dreissena density (per 0.25 m^2)	0.17	**< 0.0001***	0.10	**< 0.0001***	0.09	**0.0359**	0.07	0.0559

Table 4. Stepwise regression models at the quadrat and site scale for amphipods in the St. Lawrence River. Variables included in the model explain ≥ 5% of variation in amphipod density and were significant at $p \leq 0.05$ in univariate analysis before sequential Bonferroni correction.

Species	**Scale**	**N**	**Model**	**R^2**	**p-value**
Echinogammarus	Quadrat	490	log density = flow rate + log *Dreissena* density	0.27	<0.0001
	Site	52	log density = flow rate + log *Dreissena* density + arcsin percent sediment gravel	0.41	0.0059
Gammarus	Quadrat	490	log density = log *Cladophora* weight + log macrophyte weight + log *Dreissena* density	0.40	<0.0001
	Site	52	log density = log *Cladophora* weight + pH	0.37	0.0033

Figure 1. Map of St. Lawrence River sampling sites (indicated by circled numbers).

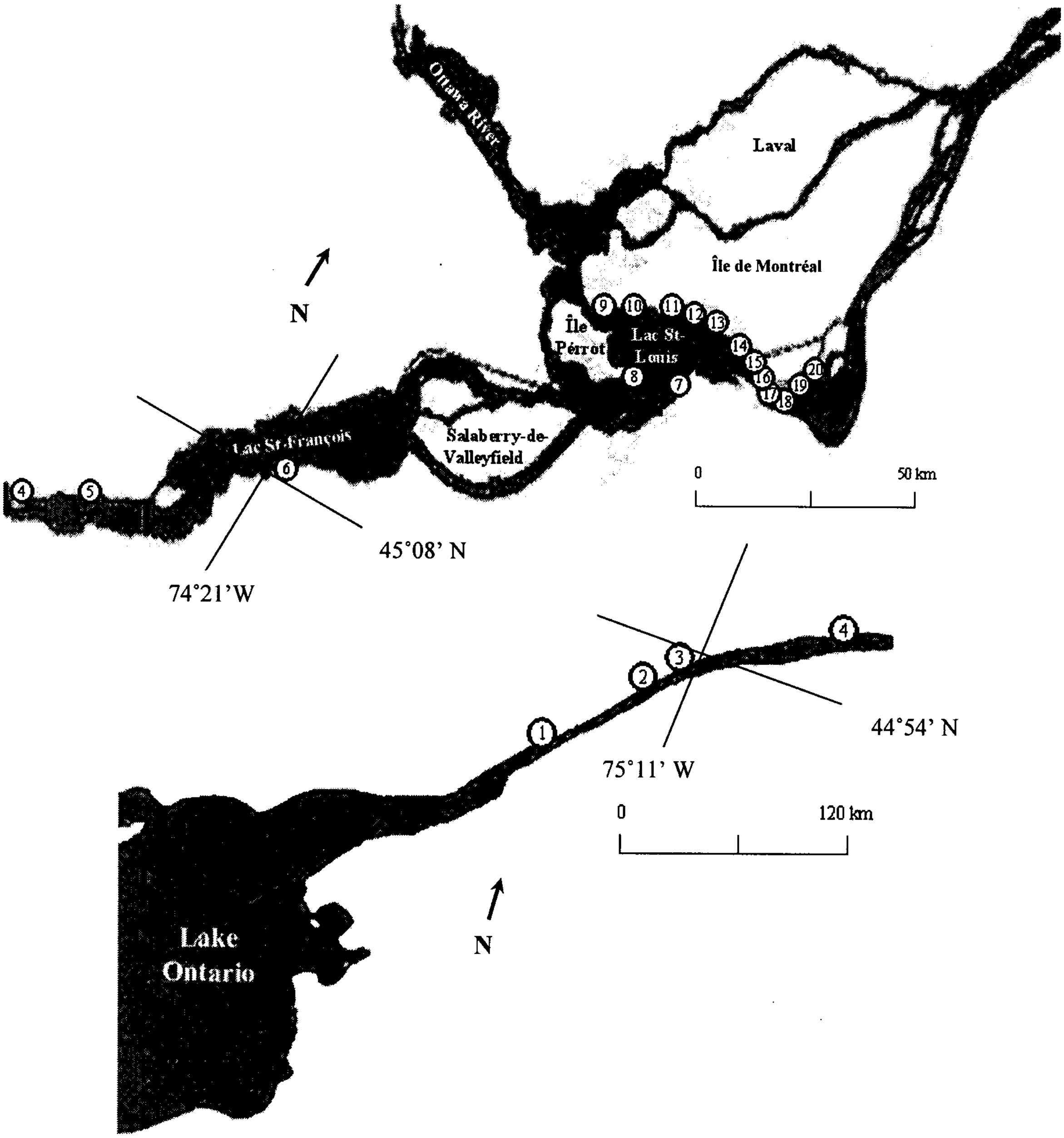

Ottawa River
Laval
Île de Montréal
N
Île Pérrot
Lac St-Louis
9
10
11
12
13
14
15
16
17
18
19
20
8
7
Lac St-François
Salaberry-de-Valleyfield
4
5
6
0
50 km
45°08' N
74°21'W
1
2
3
4
44°54' N
75°11' W
0
120 km
Lake Ontario
N

Figure 2. Mean *Echinogammarus* density ($\log_{10}$ x + 1) per 0.25 m^2 for 20 St. Lawrence River sites. Refer to Figure 1 for site locations corresponding to x-axis values. Significant seasonal site differences are indicated by an asterisk.

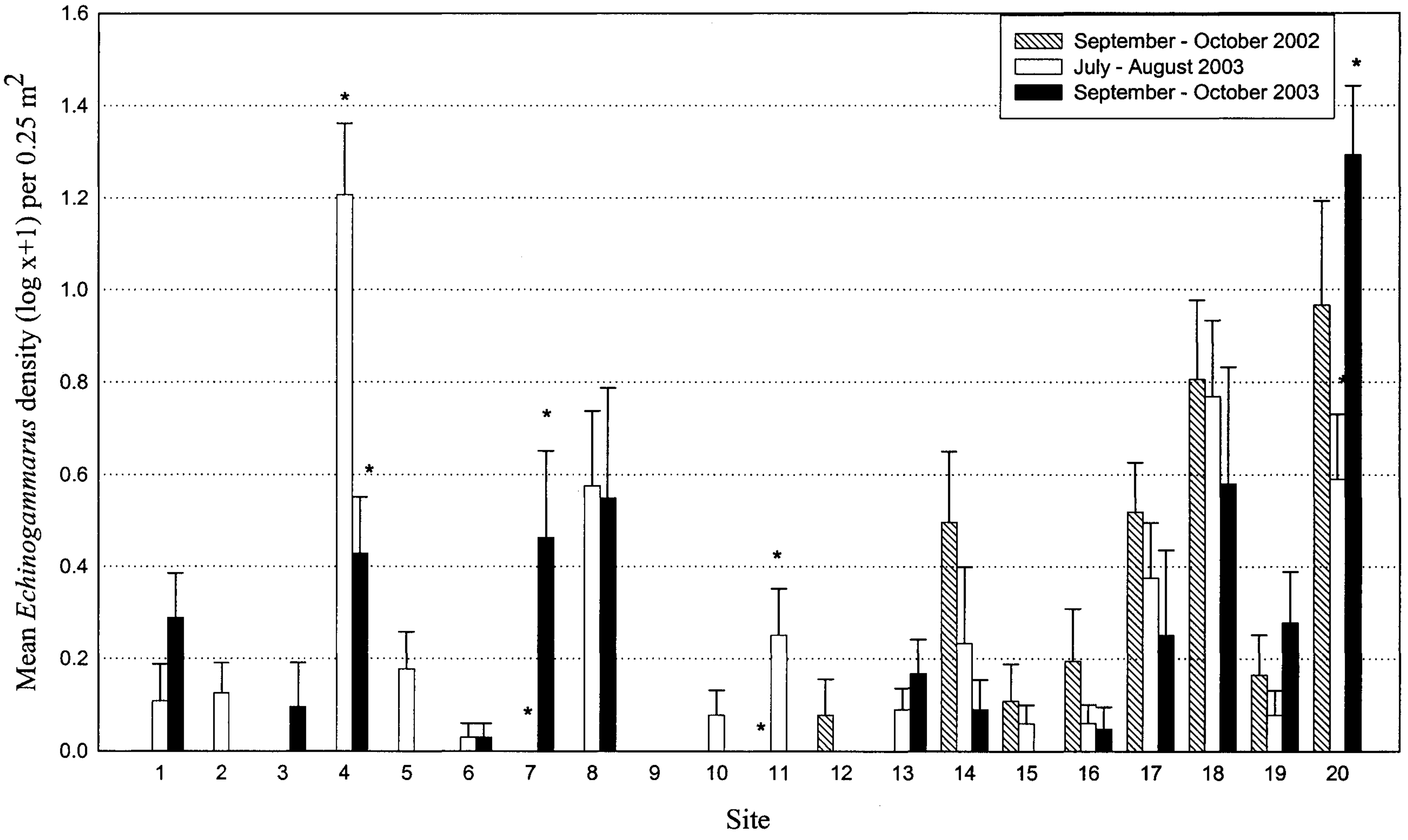
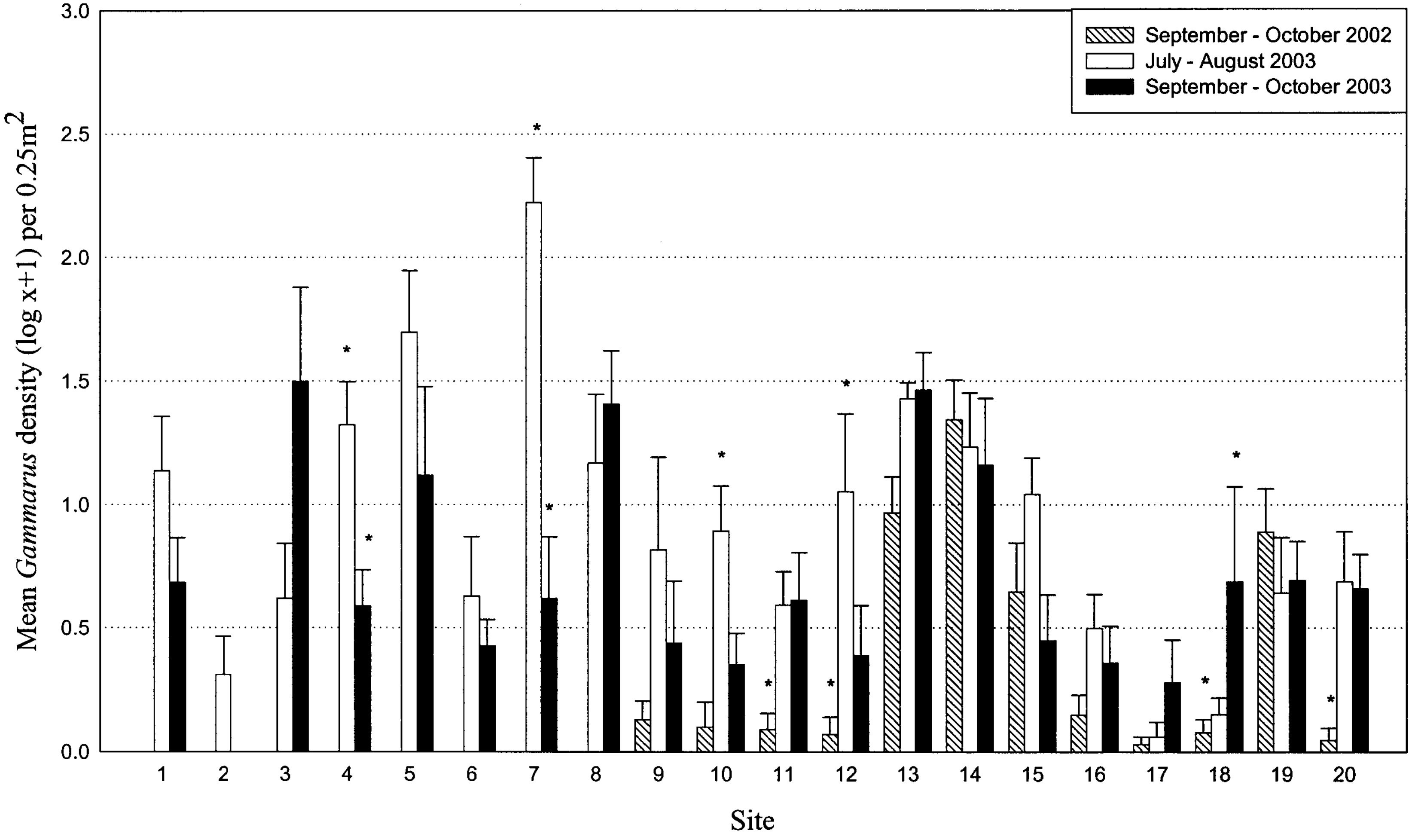

September - October 2002
July - August 2003
September - October 2003
Mean *Echinogammarus* density (log x+1) per 0.25 m^2
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Site
*

Figure 3. Mean *Gammarus* density ($\log_{10}$ x + 1) per 0.25 m^2 for 20 St. Lawrence River sites. Refer to Figure 1 for site locations corresponding to x-axis values. Significant seasonal site differences are indicated by an asterisk.


September - October 2002
July - August 2003
September - October 2003
Mean *Gammarus* density (log x+1) per 0.25m^2
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Site
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
*

Connecting Statement

In Chapter 1 it was shown that the invasive amphipod *Echinogammarus ischnus* and the native amphipod *Gammarus fasciatus* respond differentially to many abiotic environmental factors. However, it was found that both species showed a positive response to the presence of dreissenid mussels. Chapter 2 examines the interaction strength between the two amphipod species and *Dreissena* and how these relationships are affected by predation.

Chapter 2

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

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 *D. bugensis*), dominate rocky substrata throughout the system and might be promoting the rapid expansion of *Echinogammarus* by providing habitat and refugia from predation. Using an *in-situ* predator exclusion experiment, we tested the hypothesis that *Echinogammarus* is better able than *Gammarus* to use colonies as refugia, and thus is less susceptible to resident predators in the St. Lawrence River. Co-occurring *Echinogammarus* and *Gammarus* showed similar increases in density in the presence of *Dreissena* in spite of *Echinogammarus* having evolutionary experience with *Dreissena*. Predators reduced the density of both species but *Echinogammarus* was more susceptible to predation on dreissenid substrates, suggesting that predation mediates the coexistence of *Gammarus* and *Echinogammarus* in the river.

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 2004). 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 *Dreissena polymorpha* and the quagga mussel *D. bugensis* (Ricciardi 2001). 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 including 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 (Jaździewski 1980). *Echinogammarus* 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; Palmer and Ricciardi, unpublished data). Throughout much of this invaded range, *Echinogammarus* appears to be replacing taxonomically and morphologically similar species, such as the native North American amphipod *Gammarus fasciatus* (Dermott et al. 1998; Stewart et al. 1999; Nalepa et al. 2001). This replacement seems particularly prevalent on *Dreissena*-covered substrates (Dermott et al. 1998).

Formed by clumped mussels attached to stable 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 an increased abundance as a result of this enhanced microhabitat complexity (Ricciardi et al. 1997; Gonzalez 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 use *Gammarus* as a common prey item (Harnois et al. 1992; Pothoven et al. 2000). *Echinogammarus* occurs naturally in dreissenid colonies in its native range and may be adapted to living in mussel beds (Köhn and Waterstraat 1990). Therefore, *Echinogammarus* may be better able than *Gammarus* (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 lesser ability to use interstitial spaces may render *Gammarus* more exposed to predation, and thus disadvantaged in competition with *Echinogammarus*.

In this study, we use a predator-exclusion experiment to investigate whether *Dreissena* is facilitating the replacement of native amphipods by *Echinogammarus*. Specifically, we test the hypotheses that (1) *Echinogammarus* shows a stronger positive response to *Dreissena* than does *Gammarus*, and (2) *Echinogammarus* and *Gammarus* 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 (Québec), which is located within a fluvial lake (Lac St-Louis) on the St. Lawrence River (73°51'01"; 45°22'0.5"). Pointe-du-Moulin is a public park where human activities near the shore are prohibited. It is a shallow water (< 3 m) site with a substrate of bedrock and a few scattered boulders. The 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 dolomieui*, eels *Anguilla rostrata* and crayfish *Orconectes* spp (M. Palmer, personal observations). The experiment was carried out over two years: September to October 2002, July to August 2003 and September to October 2003.

Experimental treatments consisted of a combination of predator-exclusion cages and artificial substrates (cement bricks 19 cm x 9 cm x 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* bricks in 2003. Ten replicates of each treatment combination (uncaged, open caged and caged zero (ZD), low (LD) and high (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 seven 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 three days for both bricks and shells, bricks designated as LD and HD were covered with a layer of empty shells. Non-toxic aquarium silicone was used to attach the shells to the upper surface of the bricks (~ 9.5 cm x 4.5 cm for LD bricks and 19 cm x 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 x 20 cm x 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 had one open side (20 cm x 19 cm). Bricks were placed centrally in the cages. Bricks were placed at depths of 1.5-2 m; placement and orientation were random except that all bricks were separated by at least 2 m. After five weeks, all bricks were collected and placed into 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 lab within 2-4 hours. Amphipods were collected by filtering the water contained in each bag through a 500 μm mesh-sieve and by removing all invertebrates from the brick with forceps, as well as by rinsing each brick with water passed through another 500 μm 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 mean (m)-variance (s^2) relationship 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 differed among treatments in 2002 and 2003. Analysis of variance (ANOVA) tests were then used to identify treatment differences for individual species. *Echinogammarus* and *Gammarus* densities in 2002 were examined using 2-fixed factor (*Dreissena* and cage type) ANOVAs. The 2003 densities were evaluated using 3-fixed factor (season, *Dreissena* and cage type) ANOVAs. Individual density differences for *Echinogammarus* in 2002 and 2003 were detected using Tukey-Kramer multiple comparison procedure for factors with significant interactions. The same procedure was used for *Gammarus* in 2003, while 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).

ANCOVA was also used to compare the relationship between *Echinogammarus* and *Gammarus* 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 *Echinogammarus* and *Gammarus*. 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 1999).

Results

All bricks were recollected in 2002. However, a single ZD brick found outside of 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 each time 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* was the dominant amphipod over all treatment combinations (Figure 1) and 79% of its variance was explained by *Dreissena*, cage type and their interaction (Table 2). *Echinogammarus* density was 2.2 times greater on HD bricks than on ZD bricks and was reduced on ZD bricks in open cages compared to uncaged bricks (adjusted $p = 0.027$). *Gammarus* density was five times higher on HD bricks compared to LD bricks and was not affected by predation (Table 2; Figure 1b). 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 *Echinogammarus* density (Table 2). *Echinogammarus* density was

2.1 times higher in September-October than July-August and increased by a factor of 2.7 and 4 on LD and HD bricks, respectively, compared to ZD bricks. Predation reduced *Echinogammarus* density on LD and HD bricks in July-August ($p = 0.007$ and 0.023, respectively). Cage treatments had a negative effect on *Echinogammarus* density on ZD bricks. This trend was significant in September-October ($p = 0.027$) but nonsignificant in July-August ($p = 0.084$; Figure 2a).

Gammarus was the dominant amphipod in 2003 (Figure 2). Season, *Dreissena*, cage type, and their interactions explained 80% of the variation in *Gammarus* density (Table 2). *Gammarus* was 1.1 times more abundant in July-August than September-October. Densities on LD and HD bricks were, respectively, 2.9 and 3.8 times higher than on ZD bricks. *Gammarus* was negatively affected by predation but differences on *Dreissena*-covered bricks were not significant ($p > 0.05$; Figure 2b). Predation weakened the relationship between *Echinogammarus* and *Dreissena* (ANCOVA $p = 0.0004$; Figure 3a), but had no effect on the relationship between *Gammarus* and *Dreissena* ($p = 0.569$; Figure 3b).

The relationship between *Echinogammarus* and *Gammarus* differed between 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 (Figure 4) $r^2 = 0.59$, $p < 0.0001$; July-August 2003 (Figure 5a) $r^2 = 0.25$, $p < 0.0001$; September-October 2003 (Figure 5b) $r^2 = 0.76$, $p < 0.0001$). These relationships remained significant when zero values were removed.

Discussion

Although both the invasive amphipod *Echinogammarus* and the native *Gammarus* were present on experimental substrates in 2002, *Echinogammarus* was numerically dominant. In the following year, *Gammarus* outnumbered *Echinogammarus*. These findings contrast those in the Great Lakes where *Echinogammarus* 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 *Echinogammarus* has been present in the St. Lawrence River near Montreal since at least 1998 (A. Ricciardi, unpubl. data) and specimens collected in 2002 contained reproductive individuals (indicated by the presence of eggs) and three size-classes (M. Palmer, unpublished data), the species has likely been established at Pointe-du-Moulin for at least a year prior to this experiment; *Echinogammarus* 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 *Gammarus* densities at the site are not known and so density comparisons pre- and post-invasion cannot be made.

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. (1998c) 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, suggesting 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. 1998a; Van Overdijk et al. 2003). Surprisingly, *Gammarus* showed a similar (in 2003) or more rapid increase (in 2002) in density than did *Echinogammarus* on *Dreissena*-covered bricks. These results do not support the hypothesis of greater (coevolved) interaction strength between *Echinogammarus* and *Dreissena* (Ricciardi and MacIsaac 2000).

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

The greater enhancement of *Gammarus* in the presence of *Dreissena* may be a result of differing colonization abilities of the two amphipod species. *Gammarus* has a higher fecundity and shorter generation time than *Echinogammarus* (Dermott et al. 1998). During our experiments, *Gammarus* was also more abundant on surrounding natural substrates (Palmer and Ricciardi, unpublished data), perhaps giving it first access to the added experimental substrate. However, the proportion of total amphipod density made up by *Echinogammarus* was higher on experimental substrates than on natural *Dreissena* and *Vallisneria* substrates in 2003 (30% versus 15%, respectively; Palmer and Ricciardi, unpublished data), which indicates that *Echinogammarus* 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. 1998c), may have affected amphipod colonization if *Echinogammarus* and *Gammarus* differ in their foraging ability and resource use. Nevertheless, even when *Echinogammarus* was more prevalent on experimental substrates (in 2002), *Gammarus* still produced a greater increase in density when *Dreissena* was present.

Amphipod densities may have been too low for space competition to occur within the experimental *Dreissena* colonies. High *Dreissena* abundance might reduce amphipod competition by adding an abundant resource over which the two species can segregate. Positive responses by both species to the same extrinsic factors might account for the positive relationship between *Echinogammarus* and *Gammarus* (Figures 4-5). Van Overdijk et al. (2003) also found that the two species were positively correlated on experimental scales. Perhaps *Echinogammarus* 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 the invader dominates (Dermott et al. 1998).

Effect of Predation

Predator-access cages

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

Our findings do not support the hypothesis that predation is mediating the replacement of *Gammarus* by *Echinogammarus* 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 *Echinogammarus*, preventing it from becoming competitively dominant. Additional support for this conclusion is given by Stewart et al. (1998b, 1999) who found that when the species occurred separately the presence of large predators did not affect *Gammarus* biomass but coincided with a decline in *Echinogammarus* biomass.

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

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

	Wilks' λ	F	Numerator / denominator df	p value
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

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

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

Figure 1. Mean (± standard error) (a) *Echinogammarus* and (b) *Gammarus* density on ZD (zero) and HD (high) *Dreissena*-cover bricks in September-October 2002. White bars represent uncaged reference bricks (n = 10), striped bars represent open cage bricks (n = 9) and black bars represent caged bricks (n = 10). Bars with different letters are statistically different (α = 0.05).

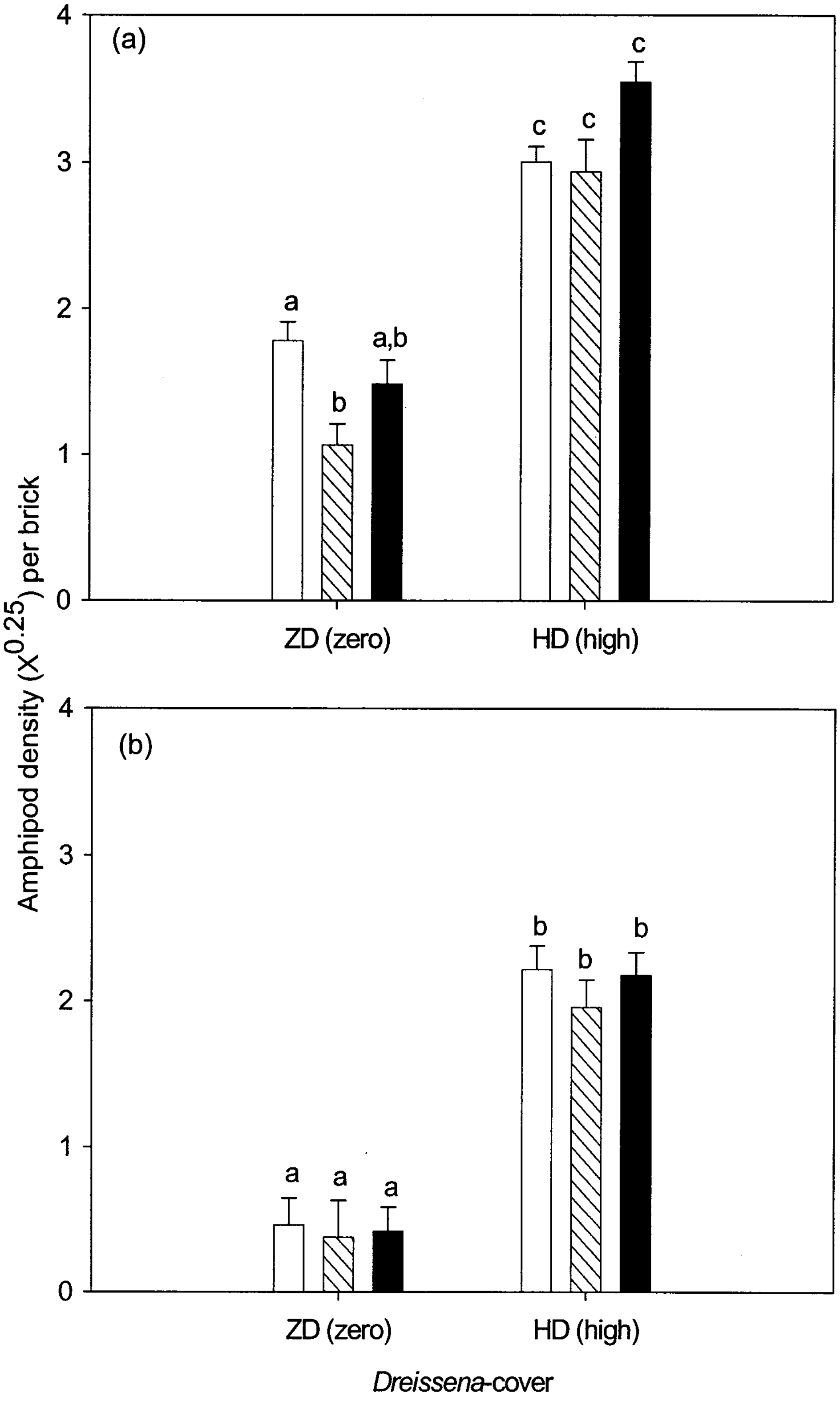

(a)
(b)
Amphipod density ($X^{0.25}$) per brick
0
1
2
3
4
a
b
a,b
c
c
c
a
a
a
b
b
b
ZD (zero)
HD (high)
Dreissena-cover

Figure 2. Mean (± standard error) (a) *Echinogammarus* and (b) *Gammarus* density per brick for two seasons in 2003. Significant differences between uncaged and caged bricks within *Dreissena*-covers (ZD = zero, LD = low and HD = high) and seasons are indicated by an asterisk ($p \leq 0.05$).

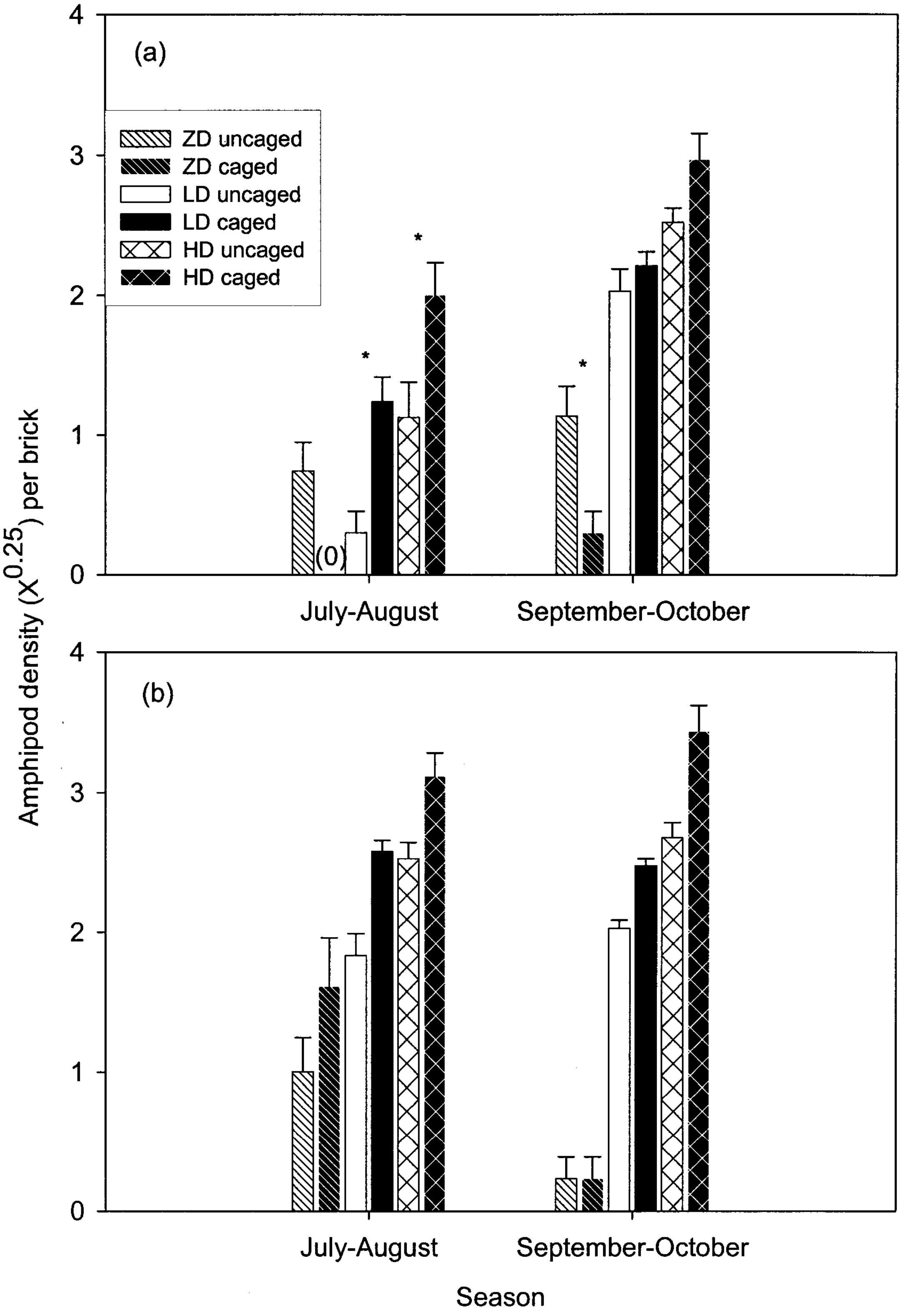

(a)
(b)
ZD uncaged
ZD caged
LD uncaged
LD caged
HD uncaged
HD caged
Amphipod density ($X^{0.25}$) per brick
0
1
2
3
4
(0)
*
*
*
July-August
September-October
Season

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

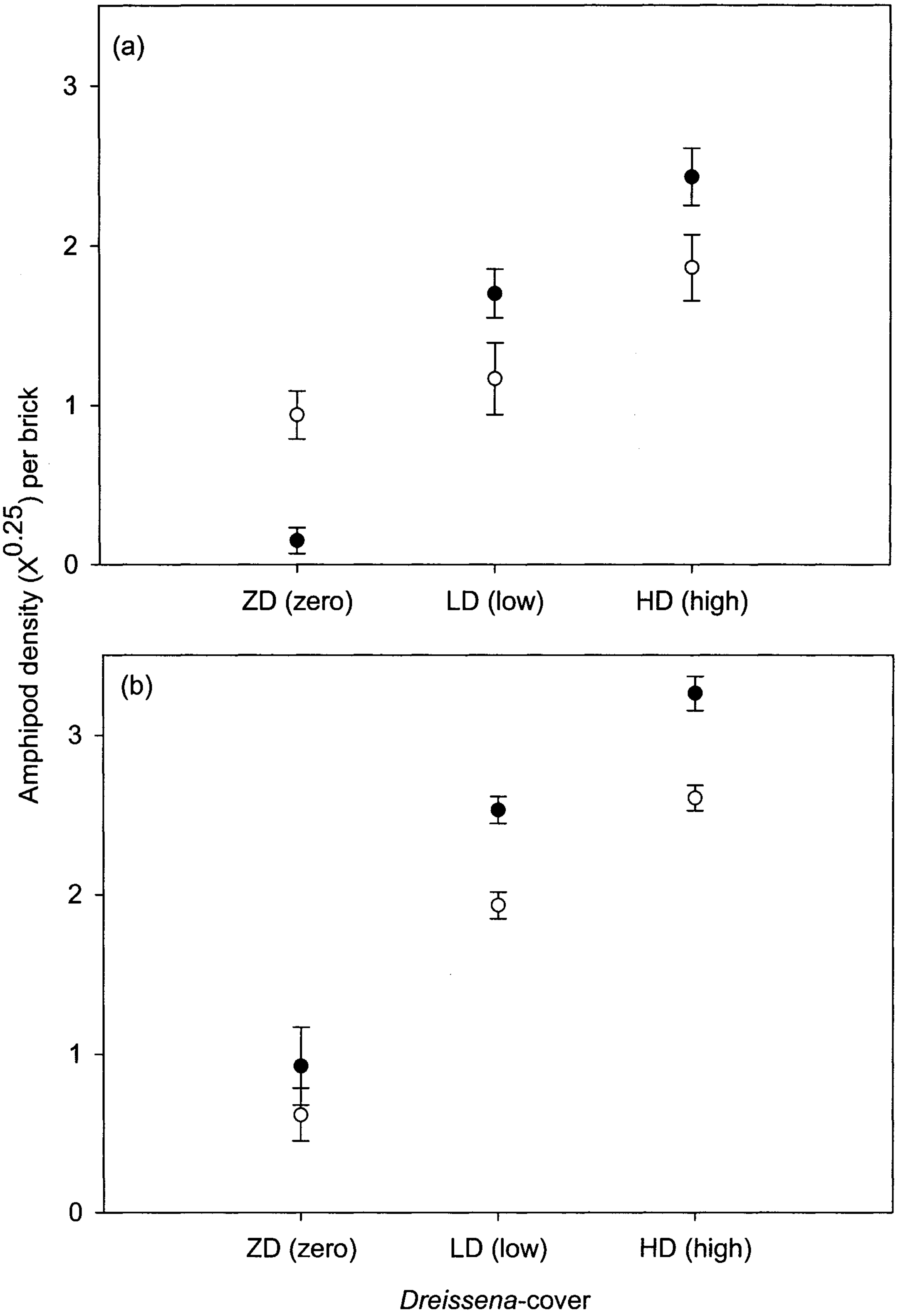
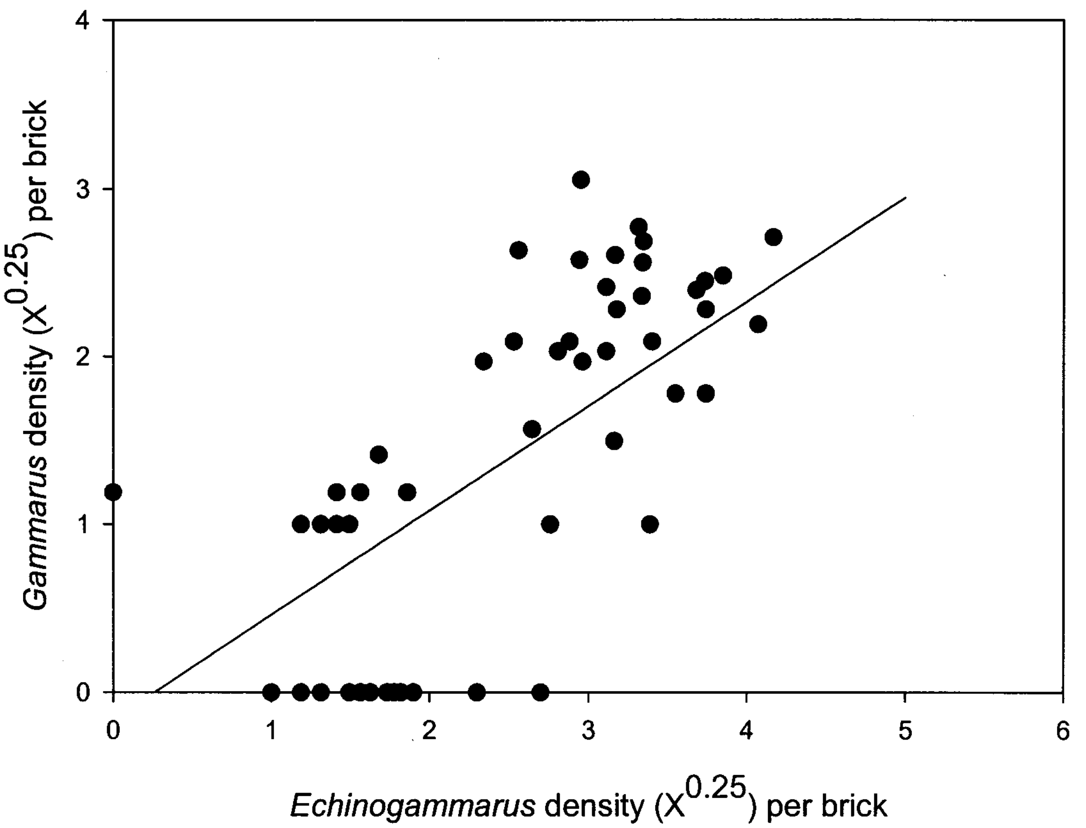
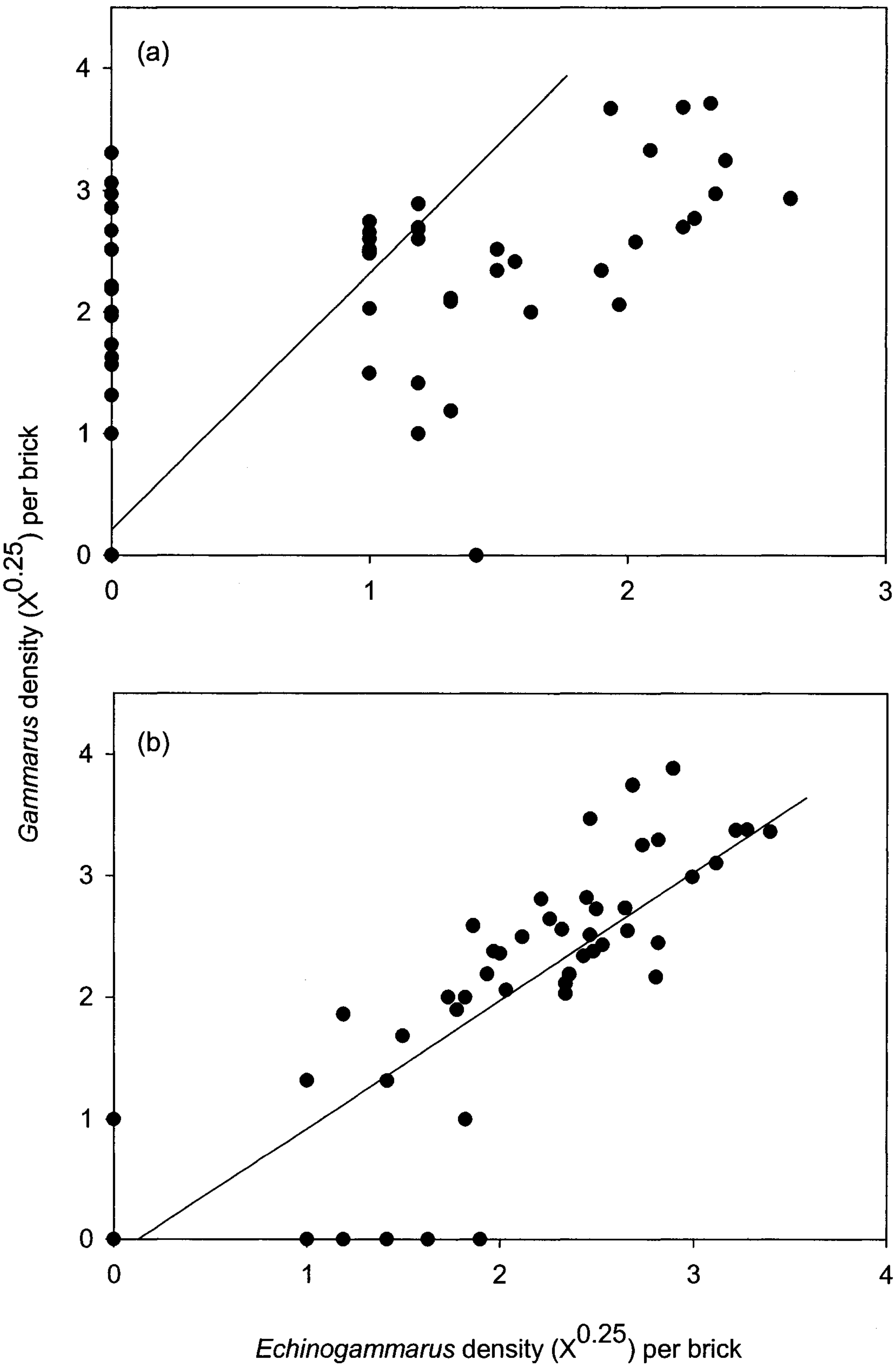

(a)
(b)
0
1
2
3
Amphipod density ($X^{0.25}$) per brick
ZD (zero)
LD (low)
HD (high)
Dreissena-cover

Figure 4. Relationship between *Echinogammarus* and *Gammarus* 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 $y = 0.6832x + 0.0083$, $r^2 = 0.52$, $p < 0.0001$, $n = 39$.



Gammarus density (X^0.25) per brick
Echinogammarus density (X^0.25) per brick
0
1
2
3
4
0
1
2
3
4
5
6

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


(a)
(b)
0
1
2
3
4
0
1
2
3
4
Gammarus density ($X^{0.25}$) per brick
Echinogammarus density ($X^{0.25}$) per brick

General Conclusions

This research demonstrates that the invasive amphipod *Echinogammarus ischnus* is well-established in the upper St. Lawrence River and is sympatric with the native amphipod *Gammarus fasciatus*. My results indicate that both abiotic and biotic environmental factors are mediating the relative abundance of, and interactions between, *Echinogammarus* and *Gammarus*. A field survey (Chapter 1) found that *Echinogammarus* is the dominant amphipod in high current velocity, rocky habitats while *Gammarus* dominates in areas with high algal biomass. It also found that the relative abundance and distribution of *Echinogammarus* is not explained by proximity to its original site of invasion in the lower Great Lakes. An experimental study (Chapter 2) found that both amphipod species increase their abundance in response to the presence of *Dreissena*; however, *Echinogammarus* is more susceptible than *Gammarus* to large predators on dreissenid-covered substrates. I reason that the differential responses of the two amphipods to environmental factors are contributing to their coexistence in the St. Lawrence River. Future work needs to examine more precisely the antagonistic interactions between the native and invasive amphipods, such as intraguild predation, and their effect on local amphipod abundance in the river.

Appendix 1

Table 1. Specific hypotheses for all variables examined in Chapter 1.

Variable	Hypothesis	Justification	Reference
Current velocity	H_0: The relationship between current velocity and amphipod abundance does not differ by species. H_A: *Echinogammarus* is more abundant than *Gammarus* at high current velocity sites.	*Echinogammarus* is native to large rivers and is particularly abundant on wave-washed shores and high current areas at invaded sites in the Great Lakes while *Gammarus* is native to lakes and slow moving rivers.	Dermott et al. 1998
Depth	H_0: The relationship between water depth and amphipod abundance does not differ by species. H_A: *Echinogammarus* is more abundant than *Gammarus* at deeper depths.	A field survey in Lake Erie found that *Echinogammarus* density increased with increasing depth while *Gammarus* decreased in abundance with depth.	VanOverdijk et al. 2003
Temperature	H_0: The relationship between water temperature and amphipod abundance does not differ by species. H_A: *Echinogammarus* is more abundant than *Gammarus* at high temperatures.	In Lake Erie, *Echinogammarus* was found to increase in abundance in August as compared to July while *Gammarus* abundance decreased over the summer (i.e. as temperatures increased).	VanOverdijk et al. 2003
pH	H_0: The relationship between water pH and amphipod abundance does not differ by species. H_A: *Echinogammarus* and *Gammarus* differ in their relationship with pH.	pH has been found to be an important determinant of amphipod species abundance in other systems.	MacNeil et al. 2000
Conductivity	H_0: The relationship between water conductivity and amphipod abundance does not differ by species. H_A: *Echinogammarus* shows a weaker relationship with conductivity than *Gammarus* does.	*Echinogammarus* is a euryhaline species and should be able to tolerate a wider range of conductivities than *Gammarus*, a freshwater species.	-
Turbidity	H_0: The relationship between turbidity and amphipod abundance does not differ by species. H_A: *Echinogammarus* is less abundant than *Gammarus* at high turbidity sites.	*Echinogammarus* was not found in turbid areas such as the Canard River in a Great Lakes survey conducted in 1996 and 1997.	Dermott et al. 1998

Table 1. cont'd

Variable	**Hypothesis**	**Justification**	**Reference**
Calcium	H_0: The relationship between water calcium and amphipod abundance does not differ by species. H_A: *Echinogammarus* is less abundant than *Gammarus* at low calcium sites.	*Echinogammarus* is native to the Ponto-Caspian, an area high in calcium and other Ponto-Caspian invaders such as *Dreissena* spp. have been found to be limited to high calcium areas.	c.f. Mellina and Rasmussen 1994
Substrate size	H_0: The relationship between substrate size and amphipod abundance does not differ by species. H_A: *Echinogammarus* is more abundant than *Gammarus* on large substrates.	*Echinogammarus* is a rocky substrate specialist and should be adapted to using large, stable substrate.	Dermott et al. 1998
Rock surface area	H_0: The relationship between rock surface area and amphipod abundance does not differ by species. H_A: *Echinogammarus* and *Gammarus* differ in their relationship with rock surface area.	Amphipods of both species are often found clinging to rocks but one species may be more dependant upon the availability of such substrate.	M. Palmer, personal observations
Cobble and gravel sediment	H_0: The relationship between cobble and gravel sediment abundance and amphipod abundance does not differ by species. H_A: *Echinogammarus* and *Gammarus* differ in their relationship with cobble and gravel sediment abundance.	Amphipods of both species were found to burrow into cobble and gravel-sized sediment but one species may be more dependent upon the availability of these sediments.	M. Palmer, personal observations
Cladophora abundance	H_0: The relationship between *Cladophora* abundance and amphipod abundance does not differ by species. H_A: *Echinogammarus* is less abundant than *Gammarus* at high *Cladophora* abundance.	*Gammarus* has been shown to be more abundant than *Echinogammarus* on *Cladophora* substrate in Lake Erie.	VanOverdijk et al. 2003
Macrophyte abundance	H_0: The relationship between macrophyte abundance and amphipod abundance does not differ by species. H_A: *Echinogammarus* is less abundant than *Gammarus* at high macrophyte abundance.	High macrophyte abundance areas in Lakes St. Clair and Erie were found to be dominated by *Gammarus*.	Dermott et al. 1998
Dreissena abundance	H_0: The relationship between *Dreissena* abundance and amphipod abundance does not differ by species. H_A: *Echinogammarus* is more abundant than *Gammarus* at high *Dreissena* abundance.	*Echinogammarus* is found in close association with *Dreissena* in their native range.	Köhn and Waterstraat 1990

Appendix 2

Table 1. Data (untransformed) used in field survey predictor models (September-October 2002 water and substrate quality variables).

Site	n	Temperature (°C)	Temperature SD	pH	Mean Substrate Size (Phi)	Mean Substrate Size SD	Rock Surface Area (mm)	Rock Surface Area SD	Cobble Sediment (%)	Cobble Sediment SD	Gravel Sediment (%)	Gravel sediment SD
9	10	17.4	0.4	7.05	0.4	4.7	17432	10670	0.0	0.0	31.7	34.4
10	10	17.9	0.2	8.04	-1.3	5.5	9820	10409	5.0	15.8	35.0	36.6
11	10	17.2	0.3	7.87	-1.8	3.9	15452	12573	0.0	0.0	42.5	20.2
12	10	17.0	0.0	9.01	2.2	5.7	4979	8158	0.0	0.0	5.0	15.8
13	5	16.2	0.3	7.71	2.9	1.0	10257	5675	0.0	0.0	38.7	12.6
14	10	16.9	0.2	8.07	-4.6	0.8	19388	17128	50.5	43.6	36.2	37.5
15	10	18.1	0.2	8.66	-3.7	1.2	10981	8977	5.3	11.7	71.8	25.8
16	10	19.0	0.0	8.32	5.4	2.5	2810	4555	0.0	0.0	39.3	35.3
17	10	20.0	0.0	7.65	-3.4	0.8	16530	8224	10.0	31.6	80.0	33.7
18	10	20.8	0.3	7.89	-6.5	0.8	25361	8266	32.7	33.2	59.0	32.7
19	10	20.3	0.5	8.45	3.1	4.0	8104	9008	28.8	28.7	34.7	12.0
20	10	20.0	0.0	7.99	0.8	3.1	13130	8208	9.0	16.6	72.7	28.0

Table 2. Data (untransformed) used in field survey predictor models (September-October 2002 biological variables).

Site	**Echino** *Density.*	***Echino* SD**	**Gammarus** *Density*	***Gammarus* SD**	***Cladophora* Biomass (g)**	***Cladophora* SD**	**Macrophyte Biomass (g)**	**Macrophyte SD**	**Dreissena** *Density*	**Dreissena SD**
9	0.0	0.0	0.6	1.3	0.0	0.1	0.2	0.5	0.2	0.6
10	0.0	0.0	0.9	2.8	0.0	0.0	0.0	0.0	0.0	0.0
11	0.0	0.0	0.4	1.0	0.5	1.1	2.5	5.1	0.7	1.1
12	0.5	1.6	0.4	1.3	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	10.8	10.0	0.0	0.0	47.9	61.1	0.4	0.5
14	4.9	8.1	35.4	32.0	0.3	0.4	0.0	0.0	2.6	3.2
15	0.6	1.6	8.9	11.7	5.5	7.2	0.2	0.5	0.0	0.0
16	1.4	3.2	0.7	1.3	0.2	0.3	15.6	19.6	0.0	0.0
17	3.2	2.8	0.1	2.8	0.2	0.4	2.6	8.1	0.0	0.0
18	11.5	15.5	0.3	0.7	0.0	0.1	0.0	0.0	0.2	0.4
19	0.8	1.4	12.2	11.0	0.0	0.1	161.5	120.7	0.2	0.4
20	26.5	40.3	0.2	0.6	0.2	0.3	40.9	47.3	0.0	0.0

Table 3. Data (untransformed) used in field survey predictor models (July-August 2003 water and substrate quality variables).

Site	**n**	**Temperature (°C)**	**Temperature SD**	**pH**	**Mean Substrate Size (Phi)**	**Mean Substrate Size SD**	**Rock Surface Area (mm)**	**Rock Surface Area SD**	**Cobble Sediment (%)**	**Cobble Sediment SD**	**Gravel Sediment (%)**	**Gravel sediment SD**
1	10	24.2	0.4	8.66	-3.6	3.4	14068	7590	17.0	23.0	18.5	23.1
2	10	24.0	0.0	8.43	-7.9	0.2	1854	5863	0.0	0.0	0.0	0.0
3	10	23.5	0.0	8.46	-7.5	0.6	5747	6180	28.8	21.9	6.8	12.3
4	10	24.0	0.0	8.36	-4.7	1.7	12685	8198	0.0	0.0	63.0	32.2
5	10	23.7	2.1	8.89	-5.6	2.0	130245	134876	14.8	31.9	23.8	21.0
6	10	27.3	0.5	8.56	5.0	2.9	2765	2916	0.0	0.0	5.0	15.8
7	5	25.0	0.0	8.83	-4.6	2.6	20369	4316	10.0	22.4	13.0	21.7
8	10	25.7	0.5	9.16	-5.6	6.4	7268	7766	0.0	0.0	0.0	0.0
9	10	23.8	0.9	8.89	2.7	5.7	7276	6256	0.0	0.0	13.7	16.5
10	10	24.0	0.0	8.85	-0.2	3.4	13494	5604	0.0	0.0	25.0	32.6
11	10	21.1	0.0	8.67	-3.5	3.2	21773	12463	18.5	30.4	25.8	26.2
12	10	27.8	0.3	9.35	7.8	2.5	2519	5918	0.0	0.0	0.0	0.0
13	10	19.0	0.0	9.29	-2.8	2.2	21768	11014	10.3	18.1	23.5	19.2
14	10	17.0	0.0	8.26	-6.3	1.2	26628	13288	39.8	38.4	18.3	20.0
15	10	21.8	0.3	8.42	-1.0	3.5	8769	6557	0.0	0.0	47.3	24.6
16	10	21.2	1.0	8.70	2.8	2.7	8473	8593	0.0	0.0	0.0	0.0
17	10	21.0	0.0	8.40	-2.3	2.0	8377	5778	0.0	0.0	37.5	28.4
18	10	20.6	0.5	8.47	-7.2	1.8	17700	12419	20.0	19.4	55.8	36.3
19	10	21.0	0.0	8.93	-1.6	3.4	6394	5780	1.0	3.2	58.0	25.3
20	10	21.1	0.2	8.48	-4.6	1.0	10645	4858	2.0	6.3	75.0	17.2

Table 4. Data (untransformed) used in field survey predictor models (July-August 2003 biological variables).

Site	**Echino** *Density.*	***Echino* SD**	**Gammarus** *Density*	***Gammarus* SD**	***Cladophora* Biomass (g)**	***Cladophora* SD**	**Macrophyte Biomass (g)**	**Macrophyte SD**	**Dreissena** *Density*	**Dreissena SD**
1	0.6	1.6	94.6	269.7	1.9	5.3	0.9	1.5	0.8	1.2
2	0.5	0.8	3.6	8.7	0.1	0.2	9.0	28.5	3.5	7.5
3	0.0	0.0	10.4	13.8	5.3	9.2	0.0	0.0	0.0	0.0
4	21.9	14.9	31.2	22.3	0.0	0.0	4.9	9.6	148.0	182.8
5	0.8	1.3	129.4	157.4	17.4	22.6	7.1	9.0	5.6	11.3
6	0.1	0.3	36.4	106.1	0.0	0.0	44.2	106.0	0.3	0.5
7	0.0	0.0	248.2	281.3	11.4	6.4	0.3	0.7	0.0	0.0
8	7.0	13.3	86.6	199.5	2.5	7.0	18.1	20.3	25.7	0.5
9	0.0	0.0	398.4	1210.9	49.6	154.8	7.2	22.7	0.0	0.0
10	0.3	0.7	13.6	14.9	0.0	0.0	0.0	0.1	0.0	0.0
11	1.4	2.5	4.8	5.0	0.2	0.2	0.7	1.3	0.0	0.0
12	0.0	0.0	79.4	144.4	2.0	3.0	4.6	8.0	0.3	0.7
13	0.3	0.5	28.6	14.1	1.4	1.8	65.0	37.4	0.1	0.3
14	4.0	11.0	35.9	34.2	5.3	5.1	0.1	0.3	0.0	0.0
15	0.2	0.4	16.0	14.4	2.0	3.3	24.1	76.2	0.0	0.0
16	0.2	0.4	4.2	6.2	1.2	2.8	2.5	5.1	0.0	0.0
17	2.6	4.3	0.3	0.9	0.8	1.1	0.0	0.0	0.0	0.0
18	8.6	7.9	0.6	1.0	1.2	1.9	1.6	4.6	20.6	0.5
19	0.3	0.7	18.7	45.2	5.7	9.3	17.7	42.7	0.1	0.3
20	5.3	7.3	10.5	14.1	3.2	3.6	56.9	76.8	0.0	0.0

Table 5. Data (untransformed) used in field survey predictor models (September-October 2003 water and substrate quality variables).

Site	n	Temperature (°C)	Temperature SD	pH	Mean Substrate Size (Phi)	Mean Substrate Size SD	Rock Surface Area (mm)	Rock Surface Area SD	Cobble Sediment (%)	Cobble Sediment SD	Gravel Sediment (%)	Gravel sediment SD
1	10	15.0	0.0	7.89	-5.0	1.7	14836	8060	7.0	10.6	32.0	23.8
2	10	12.0	0.0	8.00	-8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	5	7.0	0.0	8.35	-7.7	0.2	9093	5601	53.0	46.6	0.0	0.0
4	10	8.0	0.0	8.08	-5.1	2.4	9586	9330	3.3	10.5	35.3	25.9
5	5	8.0	0.0	8.42	0.4	3.6	4957	4904	0.0	0.0	16.7	23.6
6	10	18.0	0.0	8.23	4.9	1.9	4189	5278	10.0	25.4	5.5	10.7
7	5	20.3	0.3	8.52	-3.3	1.0	20414	7390	29.3	11.4	28.3	16.8
8	10	20.0	0.0	9.07	-6.5	4.6	8529	8096	0.0	0.0	0.0	0.0
9	10	22.0	0.0	9.12	2.2	3.4	5361	6174	0.0	0.0	0.0	0.0
10	10	21.3	0.3	9.11	-4.0	2.1	7014	5415	0.0	0.0	19.7	20.7
11	10	6.0	0.0	7.83	-6.0	1.5	13699	9468	65.0	48.7	15.0	33.5
12	10	21.5	0.0	9.31	3.7	4.6	5672	9876	1.0	3.2	4.0	8.4
13	10	21.9	0.9	9.30	-4.8	2.4	17365	12921	13.1	19.2	10.3	16.0
14	10	13.8	2.9	8.25	-6.5	1.3	16746	10400	24.3	34.5	23.3	29.9
15	10	18.0	0.0	7.94	-4.9	1.2	6322	4781	10.7	15.2	52.2	27.5
16	10	18.9	0.7	8.50	-0.5	3.2	3149	4068	0.0	0.0	18.7	24.3
17	10	6.2	0.4	7.74	-2.6	0.5	4071	4113	0.0	0.0	57.0	25.9
18	5	7.5	0.0	7.78	-3.9	2.9	9366	5562	6.7	14.9	33.7	30.3
19	10	7.0	0.0	7.81	-2.7	2.7	6241	7107	3.3	10.5	30.3	23.1
20	10	18.8	0.3	8.42	-4.2	0.6	5972	4464	0.0	0.0	95.0	15.8

Table 6. Data (untransformed) used in field survey predictor models (September-October 2003 biological variables).

Site	**Echino** *Density.*	***Echino* SD**	**Gammarus** *Density*	***Gammarus* SD**	***Cladophora* Biomass (g)**	***Cladophora* SD**	**Macrophyte Biomass (g)**	**Macrophyte SD**	**Dreissena** *Density*	**Dreissena** **SD**
1	1.5	2.2	8.3	9.7	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	0.4	0.9	61.8	40.7	11.0	6.8	0.0	0.0	0.0	0.0
4	2.7	2.8	5.0	5.6	0.6	1.2	0.0	0.1	7.6	20.9
5	0.0	0.0	33.6	39.7	0.1	0.3	8.5	12.8	3.0	4.6
6	0.1	0.3	2.4	2.2	0.0	0.0	1.9	2.7	0.0	0.0
7	3.4	4.9	7.6	12.6	0.0	0.0	1.8	3.5	1.4	1.7
8	17.4	40.3	51.6	60.5	0.0	0.0	28.7	49.8	2.6	4.1
9	0.0	0.0	31.3	94.5	2.2	6.6	0.0	0.0	0.0	0.0
10	0.0	0.0	2.3	3.2	0.2	0.2	2.8	8.8	0.0	0.0
11	0.0	0.0	4.6	3.8	1.0	1.7	0.0	0.1	0.0	0.0
12	0.0	0.0	6.6	13.0	0.4	4.6	26.1	61.1	0.0	0.0
13	0.7	1.1	39.9	26.7	0.8	1.5	151.3	193.0	0.8	1.1
14	0.4	1.0	58.4	97.4	6.2	11.6	6.3	13.1	16.0	34.3
15	0.0	0.0	8.5	22.0	0.1	0.2	2.4	7.7	0.4	0.7
16	0.2	0.6	3.2	5.4	0.0	0.0	4.0	7.2	0.0	0.0
17	1.8	3.5	1.6	2.2	0.1	0.2	0.0	0.0	0.0	0.0
18	5.8	7.4	21.2	39.5	0.1	0.1	14.0	13.2	7.5	0.0
19	1.7	2.9	6.6	5.3	0.3	0.5	4.1	12.4	0.0	0.0
20	31.6	33.0	5.7	5.3	0.1	0.2	18.2	26.0	0.0	0.0

Appendix 3

Table 1. Data used in predator-exclusion experiment with *Dreissena*-covered and uncovered substrates (ZD = zero, LD = low and HD = high *Dreissena*-cover).

Season	***Dreissena* -cover**	**Cage type**	**n**	***Echinogammarus* mean density/brick**	***Echinogammarus* SD**	***Gammarus* mean density/brick**	***Gammarus* SD**
2002							
September-October	ZD	no	10	13.6	15.5	0.8	1.3
	ZD	open	10	2.1	1.6	0.6	0.9
	ZD	full	10	9.3	17.3	0.5	0.7
	HD	no	10	86.5	35.1	31.1	25.9
	HD	open	9	95.8	70.8	25.0	19.3
	HD	full	10	170.4	77.7	27.6	15.7
2003							
July-August	ZD	no	10	1.5	1.5	4.7	7.1
	ZD	full	10	0	0	25.0	38.0
	LD	no	10	0.3	0.5	15.7	13.8
	LD	full	10	4.7	5.7	46.4	17.5
	HD	no	9	5.7	9.5	44.8	21.5
	HD	full	10	23.1	12.7	108.2	60.8
September-October	ZD	no	10	4.3	4.6	0.4	1.0
	ZD	full	10	0.3	0.5	0.4	1.0
	LD	no	10	22.5	18.6	17.7	6.3
	LD	full	9	26.2	14.0	38.3	9.3
	HD	no	10	44.0	22.7	56.1	28.5
	HD	full	8	82.1	33.3	144.6	46.7