Factors affecting the impact of invasive mussels on native freshwater mussels.

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Abstract

Biological invasions are among the leading causes of species diversity loss; however, the impacts of invasion are context-dependent and can vary with the local environment. The mechanisms governing variation in impact and their relationship to specific abiotic and biotic factors remain largely unexplored. Recent local declines in native unionid mussels have been attributed to the invasion of North American lakes and rivers by the Eurasian zebra mussel (*Dreissena polymorpha*), as a result of intense fouling of unionid shells by zebra mussels. My research investigated the role of abiotic and biotic factors in mediating the impact of zebra mussels on native mussels. I examined the impact of zebra mussels on unionids in a habitat thought to be suboptimal for zebra mussels and compared this to the impact observed in other invaded habitats. A predictive model relating fouling intensity to local environmental variables (calcium concentration, sediment particle size) was developed, and a predator-exclusion experiment was conducted to investigate the role of predation in mediating fouling intensity. Overall, I found that two abiotic factors of the local environment were significant predictors of fouling intensity and that relationships used to predict the impact of zebra mussels could be extended to a broader range of habitats.

Résumé

Les invasions biologiques sont parmis les causes principales de la perte de biodiversité. Par contre, les impacts reliés aux invasions biologiques varient selon le milieu environmental. Les mécanismes responsables de cette variation, ainsi que le rôle des facteurs abiotiques et biotiques méritent d'être mieux étudiés. Les déclins récents des moules indigènes dans les eaux douces d'Amérique du Nord ont été reliés à l'invasion de la Moule zébrée (*Dreissena polymorpha*) en raison des effets néfastes causés par l'infestation des coquilles des moules indigènes par les moules zébrées. Ma recherche a examiné le rôle des facteurs abiotiques et biotiques dans la médiation de l'impact des moules zébrées sur les moules indigènes. J'ai examiné l'impact des moules zébrées sur les moules unionidés dans un milieu sous-optimal pour les moules zébrées. J'ai ensuite comparé ceci à l'impact observé dans d'autres systèmes envahis par les moules zébrées. Un modèle prédictif reliant l'intensité d'infestation à des facteurs environmentaux locaux (concentration de calcium, taille du substrat) a été développé. Aussi, j'ai entrepris une expérience d'exclusion de prédateurs pour examiner l'effet potentiel de la prédation sur l'infestation des moules unionidés par les moules zébrées. En résumé, j'ai trouvé que certain facteurs abiotiques pouvaient prédire de façon significative l'intensité d'infestation et que les modèles prédictifs de l'impact des moules zébrées pouvaient être utilisés à travers une variété de milieux environnementaux.

Contribution of Authors

Preface

This thesis was prepared in accordance with the Faculty of Graduate and Postdoctoral Studies Office's "Thesis Submission Guidelines"

"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 (not the reprints) of one or more published papers. These texts must conform to the "Guidelines for Thesis Preparation" with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. (Reprints of published papers can be included in the appendices at the end of the thesis.)

The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next...As manuscripts for publication are frequently very concise documents, where appropriate, additional material must be provided (e.g., in appendices) in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.

In general, when co-authored papers are included in a thesis the candidate must have made a substantial contribution to all papers included in the thesis. In addition, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. This statement should appear in a single section entitled "Contributions of Authors" as a preface to the thesis."

My thesis was completed under the supervision of Dr. Anthony Ricciardi at McGill University. Funding was provided by a Natural Science and Engineering Research Council PGS-M to A. Jokela and the Fellowship in Environment awarded to A. Jokela by the J.W. McConnell Foundation. I conducted all field work and laboratory measurements in 2004 and 2005, which included unionid sampling, the predator-exclusion experiment, and measurements of all environmental variables (calcium, substrate, macrophyte cover). I also wrote all original manuscripts. Data for the 1st and 3rd manuscripts were supplemented with long-term unionid data from Dr. A. Ricciardi. Dr. A. Ricciardi assisted with the design, as well as with the analysis and editing of the final manuscripts.

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Last but not least, I would like to thank my parents who have been incredibly supportive throughout my masters by sending positive vibes of encouragement and often driving up for a visit when I needed an extra boost. Your financial support was also incredibly appreciated. It is in large part thanks to you that I was able to accomplish this educational goal. Thank you so much.

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General Introduction

Biological invasion – the introduction and establishment of species beyond their native range – is a leading cause of species extinction (Clavero and García-Berthou, 2005). Most assessments of invasion as a cause of extinction focus on global species loss (Gurevitch and Padilla, 2004; Ricciardi, 2004). However, a species can lose many distinct populations without becoming globally extinct, and the loss of such populations can have local effects on ecosystem function (Hughes et al., 1997; Luck et al., 2003). The impacts of an introduced species are context dependent because they vary with local abiotic and biotic conditions (Parker et al., 1999; Ricciardi, 2003; Ricciardi and Atkinson, 2004). The combined effects of abiotic and biotic factors can mediate the outcome of interspecific interactions (Dunson and Travis, 1991), and environmental gradients can create conditions under which exotic and native species can coexist (Laha and Mattingly, 2006). As such, identifying habitats where populations of native species can persist in the presence of exotic species is of fundamental and applied importance to conservation biology. One particular example in which numerous populations have been extirpated due to the effects of an exotic species is that of North American mussels following the invasion of the Eurasian zebra mussel, *Dreissena polymorpha.*

North America contains the world's richest diversity of freshwater mussels (Unionidae, "unionids") with 297 recognized taxa (Williams et al., 1993). Unionids are a key component of freshwater ecosystems because of their role in particle dynamics (Strayer et al., 1994), nutrient cycling (Nalepa et al., 1991) and sediment mixing (McCall et al., 1979). In the United States and Canada, unionids have been declining for many decades, making them North America's most imperiled faunal group (Ricciardi and Rasmussen, 1999). Of the 297 described taxa, 213 are considered endangered, threatened, or of special concern (Williams et al., 1993). Their decline has been attributed to multiple stressors, most of which are related to habitat degradation. The development of dams and channels, combined with the effects of dredging, agricultural practices, and riparian deforestation have resulted in severe habitat degradation (Bogan, 1993; Williams et al., 1993). Not only are unionids directly affected by these actions, but they also suffer indirectly as populations of many of their host fishes (which are essential for unionid reproduction) are also declining (Bogan, 1993).

While habitat degradation has been a leading cause of unionid population declines, the introduction of the Eurasian zebra mussel (*Dreissena polymorpha*) to North America is a relatively recent additional threat to their survival. Unionids are infaunal bivalves that live at the sediment-water interface and are oriented such that half of their shells are often exposed for siphoning. In contrast, zebra mussels are epifaunal bivalves that live byssally attached to hard substrates (Mackie, 1991), including the exposed shells of unionids. Studies have suggested that zebra mussels preferentially settle on the shells of live unionids (Lewandowski, 1976; Ricciardi et al., 1996). Fouling by zebra mussels is thought to impair unionids by smothering their siphons, preventing valve opening and closing, and interfering with normal feeding and burrowing behaviour (reviewed by Mackie, 1991). The stress of high fouling intensities can deplete energy (e.g., glycogen) reserves required for surviving winter (Haag et al., 1993; Ricciardi et al., 1996; Baker and Hornbach, 1997, 2000). These impacts are amplified by the lack of evolutionary experience that North American unionids have had with dominant biofouling organisms. Being the only bysally-attached mollusc in North American freshwaters, zebra mussels are ecologically unique. Consequently, unionids have no specific adaptations to avoid or reduce fouling (but see Nichols and Wilcox, 1997), and their populations have suffered dramatic declines in areas where they co-occur with dense zebra mussel populations (reviewed by Ricciardi et al., 1995, 1998).

Since its discovery in 1988 in Lake St. Clair (Hebert et al., 1989), the zebra mussel has rapidly invaded all of the Great Lakes and several large river systems (Ludyanskiy et al., 1993). Throughout their entire invaded range, zebra mussels have been found attached to unionids (Nalepa, 1994; Schloesser and Nalepa, 1994; Tucker et al. 1993; Ricciardi et al., 1995; Cusson and de Lafontaine 1998). In systems where the fouling of unionids by zebra mussels has reached high levels, rapid extirpation of unionid populations has occurred within 8 years (Ricciardi et al., 1998). Mortality of unionids is generally correlated with fouling intensity (Ricciardi et al., 1995; Ricciardi 2003), and fouling intensity has been shown to be strongly correlated with local zebra mussel field density (Ricciardi, 2003). Zebra mussel density varies widely across habitats with different physicochemical characteristics (Ramcharan et al., 1992; Mellina and Rasmussen, 1994; Karatayev et al., 1998; Jones and Ricciardi, 2005). Interestingly, recent evidence suggests that unionids can coexist with zebra mussels in some rare habitats where fouling is either minimal or not persistent (Nichols and Amberg, 1999; Zanatta et al., 2002; Bowers and de Szalay, 2004). The mechanisms governing variation in impact and their relationship to specific environmental factors remain largely unexplored. The objective of my thesis is to examine the context-dependency of impacts by testing abiotic and biotic factors that are hypothesized to mediate the effects of zebra mussel fouling on native mussels.

In Chapter 1, I examine unionid fouling by zebra mussels and associated impacts in a low calcium environment – the Richelieu River. Calcium is important for zebra mussel shell growth and osmoregulation (Vinogradov et al., 1993; McMahon, 1996) and research has demonstrated the relationship between calcium concentration and zebra mussel distribution and abundance (Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). Meanwhile, previous work linking fouling intensity and unionid population mortality has focused on calcium-rich systems (Ricciardi et al., 1996; Ricciardi, 2003). In this chapter, I tested the prediction that fouling intensities and associated mortality of unionid populations would be lower in a calcium-poor river.

In Chapter 2, I examine the potential role of predators in mediating the interaction between native and exotic mussels. Zebra mussel fouling of unionids is a form of interference competition. Because predators can reduce the effects of competition at lower trophic levels (Paine, 1966; Leibold, 1996; Celik et al. 2002), they could conceivably allow unionids to persist locally in the presence of zebra mussels. Many organisms have been found to consume zebra mussels, although a relatively small number of native species do so in substantial quantities (Morrison et al., 1997; Magoulick and Lewis, 2002; MacIsaac, 1994; Mitchell and Bailey, 2000). Among these known predators, freshwater drum (*Aplodinotus grunniens*) are abundant in the Richelieu River. In this chapter, I use a predator-exclusion experiment to test the hypothesis that exposure to molluscivores, such as freshwater drum, can reduce fouling intensities of unionids by zebra mussels.

Finally, in Chapter 3, I examine whether fouling intensity of unionids could be predicted by a combination of environmental variables known to affect zebra mussel abundance. Two abiotic factors that can influence local zebra mussel occurrence and density are calcium concentration and sediment particle size (Ramcharan et al., 1992; Mellina and Rasmussen, 1994; Karatayev et al., 1998; Jones and Ricciardi, 2005). In addition, submerged macrophytes can act as substrate for zebra mussel attachment, especially for juvenile mussels (Karateyev et al., 1998; Diggins et al., 2004); therefore, dense macrophyte beds may possibly limit the amount of fouling on unionids by intercepting settling mussel larvae. Spatial heterogeneity in freshwater systems may create gradients in these environmental variables that provide local areas of habitat where native unionid mussel populations can escape lethal fouling. In this chapter, I use linear regression models to test the following hypotheses: fouling intensity will increase in habitats with increasing calcium concentration, finer sediment particle size, and reduced macrophyte cover.

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Zebra mussel fouling of native mussels (Unionidae) in a low calcium river

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Abstract

Recent local declines in native unionid mussels have been attributed to the invasion of North American lakes and rivers by fouling bivalves, Eurasian zebra mussels (*Dreissena polymorpha*). In systems in which zebra mussels are abundant, intense fouling has caused mass die-offs to occur within only a few years of invasion – often leading to the near total extirpation of the unionid population in < 8 years of invasion. These systems are characterized by high calcium concentrations ($[Ca^{2+}] > 25 mg \cdot L^{-1}$), in which zebra mussels thrive. We examined zebra mussel fouling of unionids in the Richelieu River, a low-calcium tributary of the St. Lawrence River, where some unionid populations have persisted nearly a decade after zebra mussel invasion. Fouling varied spatially along the river with some sites maintaining chronically-low fouling intensities. The mortality of unionid populations (estimated as the proportion of recent dead individuals) was correlated with fouling intensity across sites in which unionids were carrying, on average, a mass of zebra mussels equal to at least 10% of their own mass. Unionid densities declined across all sites over time and, at the site that had the highest fouling intensity, a population was extirpated within nine years. However, high mortality was also measured at a few locations where zebra mussel fouling remained virtually insignificant, indicating the presence of other stressors. This study extends the range of abiotic conditions in which zebra mussels are known to exert significant ecological impacts.

Keywords: exotic species, aquatic invasions, biodiversity, Unionidae, biofouling, ecological impacts

Introduction

The ecological impacts of an introduced species are context dependent, varying with local abiotic and biotic conditions (Parker et al., 1999; Ricciardi, 2003; Ricciardi and Atkinson, 2004). A predictive understanding of the conditions in which an invader's impacts threaten native populations is critical for effective conservation of native biodiversity. Impacts on biodiversity are most severe when the introduced organism represents an ecologically distinct species in the invaded community (Ricciardi and Atkinson, 2004). The introduction of the Eurasian zebra mussel (*Dreissena polymorpha*) to North America added a biofouling mollusc to freshwater communities that have no evolutionary history with such organisms (Hebert et al., 1989; Ricciardi et al., 1998). Zebra mussels attach to virtually any solid surface, particularly the shells of other bivalves, which can be rapidly overgrown and smothered (Ricciardi et al., 1995). Having evolved without exposure to dominant fouling organisms, North American unionid mussels have no adaptive mechanism to resist the effects of zebra mussel attachment (but see Nichols and Wilcox, 1997). This fouling by zebra mussels impairs unionid locomotion, feeding and respiration, thus depleting its energy reserves (Haag et al., 1993; Schloesser et al., 1996; Baker and Hornbach, 1997, 2000). Consequently, rapid declines of unionid populations have typically followed zebra mussel invasion of North American lakes and rivers (Schloesser and Nalepa, 1994; Ricciardi et al., 1996; Nalepa et al., 2001; Martel et al., 2001; Schloesser et al., 2006).

Unionid mussels are already North America's most imperiled faunal group (Ricciardi and Rasmussen, 1999) with 70% of the ~300 described taxa considered endangered, threatened, or of special concern, primarily as a result of habitat degradation (Williams et al., 1993). However, zebra mussel invasion has accelerated the rate of extirpation of unionid populations by ten-fold (Ricciardi et al., 1998). Unionid populations tend to suffer near total extirpation within 4 to 8 years in lakes and rivers that support high densities ($> 3000\text{m}^{-2}$) of zebra mussels (Ricciardi et al., 1998). Mortality of unionid populations is correlated with zebra mussel fouling intensity, and the level of fouling varies widely across habitats with different limnological characteristics (Ricciardi et al., 1995; Ricciardi, 2003). Recent evidence suggests that unionids can coexist with zebra mussels in rare habitats in which fouling is minimal or not persistent (Nichols and

Amberg, 1999; Zanatta et al., 2002; Bowers and de Szalay, 2004). Habitats that have viable unionid populations are particularly important for conservation, as they could serve as target areas for translocation initiatives (Cope and Waller, 1995; Hallac and Marsden, 2001).

The Richelieu River is a tributary of the St. Lawrence River that drains Lake Champlain and flows northwards over a distance of 124km (Groison, 2000). In 1993, zebra mussels were discovered in the southern part of Lake Champlain (Stickney, 1996) and subsequently spread northward in the lake (de Lafontaine and Cusson, 1997). Zebra mussel veligers were found in the Richelieu River in the summer of 1996 (de Lafontaine and Cusson, 1997) and fouled unionids were observed by 1997 (Cusson and de Lafontaine, 1998). However, the size of zebra mussels found in the river in 1997 represented two separate cohorts, with one cohort being at least one year of age (Cusson and de Lafontaine, 1998), suggesting that colonization of the river substrate began as early as 1996. Although there exist few quantitative studies on the density of zebra mussels in the Richelieu River, some information about their distribution and abundance is known. In particular, a steep gradient in zebra mussel abundance occurs in the river with very low abundances downstream of the Chambly basin, a lentic area near the mid-section of the river (de Lafontaine et al., 2002). The only quantitative study of an upstream site was performed in 1998 and found a mean density of 88 (± 41.7) zebra mussels$\cdot$m^{-2} (de Lafontaine and Comiré, 2004). Despite the presence of zebra mussels in the Richelieu River for at least nine years, our surveys have found unionid populations remaining at multiple sites, suggesting that unionids may be able to survive in this invaded system.

One of the most important abiotic factors affecting zebra mussel distribution and abundance is calcium concentration. Zebra mussels can colonize waters with a calcium concentration of 15mg$\cdot$L^{-1} (Mellina and Rasmussen, 1994) and adult mussels can survive in habitats with concentrations as low as 12mg$\cdot$L^{-1} (Vinogradov et al., 1993; Jones and Ricciardi, 2005). Although the effect of calcium concentration on zebra mussel colonization appears to act as a threshold effect, evidence suggests that the effect of calcium on adult abundance may act in a different way. Studies of zebra mussel abundances along a calcium concentration gradient found that densities begin to peak only at concentrations ≥ $20\text{mg}\cdot\text{L}^{-1}$ (Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). The Richelieu River has a stable calcium concentration of $16\text{-}18\text{mg}\cdot\text{L}^{-1}$ (de Lafontaine and Cusson, 1997; Ricciardi, unpublished data), and therefore may be a suboptimal habitat for zebra mussels.

The goal of this study was to investigate how zebra mussels affect unionids in a calcium-poor riverine system. We conducted a multi-site survey to examine the relationship between unionid mortality and zebra mussel fouling intensity in the Richelieu River and compared it to other systems. Specifically, we tested the prediction that fouling intensities and associated mortality of unionid populations are lower in the Richelieu River than in calcium-rich systems.

Methods

Unionid mussels were collected from 10 sites along the Richelieu River on various dates from 1998 to 2005 (Figure 1; Table 1). Most of the Richelieu River is bordered by private property; therefore, sites were chosen based on both accessibility and on the presence of unionid populations. Each year, sampling was done between June and early October. All sites were accessed from shore (with the exception of Site 5, which required the use of a boat) and were sampled by SCUBA divers. This method minimized the manipulation of fouled unionids, thereby limiting the loss of attached zebra mussels. Unionids were collected from a 1m^2 polyvinyl chloride quadrat, cast randomly on the substrate. It was decided *a priori* to collect five replicate quadrats at each site, which was expected to yield a precision of ± 20% when sampling unionid densities of 10-30 $\text{mussels}\cdot\text{m}^{-2}$ (Downing and Downing, 1992). When few (<10) or no unionids were collected within the first five quadrats, an additional five quadrats were sampled. All visible unionids, including empty shells, were collected from each quadrat, and the upper 10cm of sediment was probed by hand to collect individuals buried immediately beneath the surface. Each unionid, along with its attached zebra mussels, was removed by hand and sealed in a collection bag. Samples were stored in a cooler and transported to the laboratory within three hours of collection. In addition, calcium concentration in the river was measured by taking two replicate water samples at each site in 1L plastic bottles.

Calcium concentrations ([Ca^{2+}]$mg \cdot L^{-1}$) were measured using the LaMotte Hardness Test Kit (Model PHT-CM-DR-LT).

In the laboratory, each unionid was identified to species following Clarke (1981). Shell lengths (± 0.01mm) were measured using electronic digital calipers. Each live unionid was cleaned by hand and all attached zebra mussels were removed. The unionid and attached zebra mussels were then washed through a 1mm sieve, blotted dry, and weighed separately on an electronic balance to measure their respective fresh weights (± 0.01g). All mussels collected from one site were combined and two measurements of zebra mussel fouling intensity were measured: (1) the mean number of live zebra mussels attached to living unionids, and (2) the zebra mussel-unionid mass ratio, i.e., the fresh weight of attached zebra mussels divided by the fresh weight of the living unionid host. The mass ratio explains more variance in unionid mortality than does the number of attached zebra mussels, as individuals of both taxa vary substantially in size (Ricciardi et al., 1996). Unionid mortality within a population was estimated from the number of recent dead unionids (i.e., dead within the last year), which were distinguished from older shells by their intact hinge ligament and uneroded nacre, as proposed by Ricciardi et al. (1995). Least-squares regression analysis was used to relate zebra mussel-unionid mass ratio ($\log_{10}$ transformed) to the proportion of recent dead unionids ($\arcsin^{0.5}$ transformed) in the population at each site. The resulting model was compared to that of Ricciardi et al. (1996) by analysis of covariance (ANCOVA).

Results

Fouling intensities and unionid density in the Richelieu River

In the summer of 2002, 8 of the 10 field sites were sampled. Mean unionid densities ranged from 1.2 to $39m^{-2}$, and mean fouling intensities ranged from 0.17 to 24 zebra mussels per unionid (Table 1). Some of these mean fouling intensities are similar to those reported in the St. Lawrence River prior to mass die-offs of unionid populations (Ricciardi et al., 1996). However, in contrast to these St. Lawrence River sites, fouling intensities in the Richelieu River sites have not increased steadily over time across all sites (Figure 2). Although Site 4 shows a large increase in the mean number of attached zebra mussels from 2003 to 2004 (Figure 2A), it did not result in an increased mass ratio

(Figure 2B), because the mean size of attached zebra mussels decreased at this site in 2004. Furthermore, regression analysis of fouling intensity over time for the entire river shows no significant trend (Figure 3; r^2=0.095, p=0.095).

Changes in live unionid density over time were also recorded at a number of sites in the Richelieu River for which more than three years of data exist. In contrast to what has been observed in many other systems invaded by zebra mussels, some unionid populations did not decline significantly over time (Figure 4). Although the unionid population at Site 4 became extirpated by 2005, populations at Site 1 and Site 6 did not significantly decline over the same sampling period. However, the absence of a significant decline for populations at Site 1 and Site 6 does not necessarily imply the sustainability of these populations, especially given the high annual mortality (40 to 78% recent dead) recorded at these sites in some years (Table 1).

Mass ratios and unionid mortality in the Richelieu River

The relationship between recent unionid mortality (proportion of unionids that are recent dead) and the mean mass ratio of attached zebra mussels and their unionid hosts was compared with the model derived by Ricciardi et al. (1996) for calcium-rich systems (i.e., systems with calcium concentrations ≥ 25 mg·L^{-1}; r^2=0.75). The majority of the Richelieu River data lie outside the 95% confidence intervals of the Ricciardi et al. (1996) model (Figure 5) and regression analysis for all Richelieu River sites found no significant relationship between fouling intensity and recent unionid mortality (r^2=0.089, p=0.165). However, we also found that a few unionid populations (primarily located downstream of Chambly basin) with extremely low fouling intensities (generally 0 to 1 zebra mussel per unionid) suffered high recent mortality, indicating the effect of other stressors. In order to examine the impact primarily associated with zebra mussel fouling, data from populations with mass ratios lower than 0.01 (i.e., unionids carrying less than 10% of their weight in zebra mussels) were excluded from further analysis. Regression analysis of the remaining data reveals that the mass ratio explains over 24% (p=0.0317) of the variation in recent unionid mortality (Figure 6). Although there is a greater amount of unexplained variance for the Richelieu River, this relationship is not significantly different from the earlier model described by Ricciardi et al. (1996) (Figure 6; ANCOVA, p>0.25).

Unionid species richness

A total of 11 unionid species have been collected from the Richelieu River, with assemblages downstream of the Chambly basin being more diverse than upstream assemblages (Table 2). Quantitative sampling of unionid populations in this study recorded 8 different species, with only 2 species (*Elliptio complanata* and *Lampsilis radiata*) represented in the upstream portion of the river (Table 3). *Elliptio complanata* dominated unionid abundances at all sites, while *Lampsilis radiata* was also present at all sites, but at lower densities. The occurrence of the other six species was relatively rare and sporadic through time.

Previous studies have found that *L. radiata* is more sensitive to zebra mussel fouling than *E. complanata* (Ricciardi et al., 1996; Hallac and Marsden, 2000; Martel et al., 2001). Densities of these two species at sites for which at least three years of data were collected show similar trends (Figure 7). In 2002, *E. complanata* was the dominant species at each of these sites. At Site 4, the extirpation of *L. radiata* preceded that of *E. complanata* (Figure 7a); no *L. radiata* was found in 2004 and all unionids disappeared by 2005. At Site 6, *E. complanata* remained at a density of ~7m^{-2}, while *L. radiata* densities were very low in 2004 and 2005 (Figure 7b). Finally, at Site 1, *E. complanta* densities remained relatively high, while *L. radiata* steadily declined (Figure 7c).

Discussion

Fouling intensities in the Richelieu River

Fouling intensities in the Richelieu River are modest compared to those reported from the Great Lakes region. Mean fouling intensities in the Great Lakes were on the order of 300-400 zebra mussels per unionid prior to extirpation of unionid populations (Nalepa, 1994; Schloesser and Nalepa, 1994). They are also modest when compared to those reported from the Rideau River, where mean fouling intensities were greater than 600 zebra mussels per unionid prior to extirpation (Martel et al., 2001). Fouling intensities in the Richelieu River were one order of magnitude lower than in the Great Lakes and the Rideau River, but are similar to those reported 1 to 3 years prior to mass die-offs of unionid populations in the St. Lawrence River (Ricciardi et al., 1996).

However, in contrast with the St. Lawrence River, fouling intensities and the mass ratios in the Richelieu have not increased steadily over time. For two of the sites sampled over multiple years (Figure 2), the mean number of attached zebra mussels per unionids remained < 10, and the mean mass ratio did not exceed 0.4, which is well below the threshold mean mass ratio of 1.0 that is associated with severe (> 90%) mortality of unionid populations (Ricciardi et al., 1996). Fouling intensities in the Richelieu River are also similar to those reported prior to large declines (> 50%) in the Hudson River (Strayer and Smith, 1996). In the Hudson River, fouling intensities did not steadily increase over time, but remained ≤ 10 zebra mussels per unionid with a small peak near 20 zebra mussels per unionid in the mid 1990s (Strayer and Malcom, in revision). In this particular system, unionid population declines were primarily attributed to a sudden reduction in phytoplankton biomass, a result of heavy filtration by a high density of zebra mussels (Caraco et al., 1997).

It is not clear why fouling intensities in the Richelieu River have remained generally low in the river despite the presence of zebra mussels in the river for at least nine years. Unfortunately, we do not have or know of any quantitative estimates of zebra mussel density in the upper Richelieu River for the past 7 years so perhaps low fouling intensities are a reflection of chronically low zebra mussel densities in the river. We can identify a number of factors which suggest that zebra mussels have not been steadily increasing over time in the river. First, it has been found that fouling intensity of unionids is well correlated with local zebra mussel density (Ricciardi et al., 1995). Therefore, a general lack of increase in fouling intensity in the river likely reflects a similar lack of increase in zebra mussel density, modified by selective mortality of highly fouled individuals. Secondly, veliger sampling during the first years of colonization of the Richelieu River demonstrated that Lake Champlain was the source of zebra mussels in the river, based on the density gradient of veligers and the timing of larval appearance in both the lake and river (de Lafontaine and Cusson, 1997). Years later, the maintenance of a sharp zebra mussel abundance gradient between the lower and upper sections of the Richelieu River (de Lafontaine and Comiré, 2004) suggests that Lake Champlain is still the dominant source of zebra mussels in the river. Measurements of seasonal mean veliger densities in the portion of Lake Champlain that flows into the Richelieu River have varied annually with a relative lull in production between 2001 and 2004 (based on long-term data from the Vermont Department of Environmental Conservation, available at http://www.anr.state.vt.us/dec/waterq/lakes /htm/lp_lczebramon.htm). If Lake Champlain is indeed the major source of larvae for the Richelieu River, we would expect changes in zebra mussel density in the river to reflect changes in the lake. Therefore, since larval supply has not been steadily increasing over time, there is no reason to expect that zebra mussel densities in the river have been increasing. Finally, the calcium concentration of the Richelieu River remains steady at 16-18mg·L^{-1} (de Lafontaine and Cusson, 1997; Ricciardi, unpublished data; this study). This is below 20mg·L^{-1}, the concentration at which adult densities tend to peak (Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). Therefore, it is possible that zebra mussel populations are not reaching densities as high as those observed in other systems. In fact, we observed many patches of hard substrate (i.e., rocks, concrete blocks) uncolonized or only partially colonized, which is not typical of systems that sustain high densities of zebra mussels. Nor is there any evidence that zebra mussels are forming colonies on the softer sediments of the river.

Unionid mortality in the Richelieu River

Previous research identified a strong correlation between unionid population mortality and the mean mass ratio of attached zebra mussels and their unionid hosts, at calcium-rich sites, i.e., where $[Ca^{2+}] \geq 25$mg·L^{-1} (Ricciardi et al., 1996; Ricciardi, 2003). The relationship found in the Richelieu River is not significantly different from that found for calcium-rich sites, but shows greater variation with some sites having much higher unionid population mortality than predicted by the previous model. High mortality at some Richelieu River sites with extremely low fouling intensities (i.e., those sites excluded from analysis) suggests the presence of additional environmental stressors in the river. As a result, environmental stressors are likely compounding the effect of zebra mussel fouling leading to high unionid mortality at some sites. Threats to North American unionid populations have included changes in flow velocity and sedimentation due to artificial impoundments and channelization, as well as industrial and urban pollution (reviewed by McMahon, 1991). In the Richelieu River, environmental stressors are mainly related to agriculture, as > 65% of the basin is exploited by agricultural practices; consequently, nutrient and sediment loading, as well as an accumulation of various types of pesticides impact the river (Groison, 2000). In addition, we cannot rule out the possibility that intense filtering by upstream zebra mussel populations has further stressed unionids by limiting food resources, even at sites with low local zebra mussel densities. A study in the Hudson River demonstrated a sharp reduction in phytoplankton biomass following the invasion of zebra mussels (Caraco et al., 1997) and this event was deemed to be the cause of a concomitant decline in the river's unionid population, despite the absence of intense fouling by zebra mussels at the time (Strayer and Smith, 1996).

Although some sites in the Richelieu River demonstrated higher than predicted unionid mortality, we also found a number of sites where mortality was relatively low despite the long-term presence of zebra mussels. Furthermore, mortality of unionid populations in the Richelieu River has been generally slower than that reported for other North American rivers invaded by zebra mussels (Table 4). Not surprisingly, sites that suffered no significant declines in unionid populations had chronically low zebra mussel densities. Estimated mean peak zebra mussel densities were $170m^{-2}$ for Site 1 and $460m^{-2}$ for Site 4, which are 8 to 20 times lower than densities normally associated with steep unionid declines (Table 5). These zebra mussel field densities were inferred from mean unionid fouling intensity using Ricciardi et al.'s (1995) model, and likely overestimate the density of zebra mussels because unionids provide virtually all of the colonizable hard substrate at these particular sites. It is important to note that the absence of a significant decline in unionid populations at some sites does not necessarily mean that unionid populations are viable. Although not statistically significant, the unionid population at Site 1 declined by 38% between 2002 and 2003, and the population at Site 6 declined by 25% between those years. Such declines are likely to have a severe impact on populations of long-lived animals such as unionids. It is also not clear from the data whether remaining unionid populations will continue to suffer declines over time or whether they may persist, albeit at lower densities. This was observed in the Hudson River, where a long-term study of unionid populations found that unionid populations stabilized after suffering initial declines following zebra mussel invasion of the river (Strayer and Malcom, in revision).

Species diversity in the Richelieu River

At least 11 species of unionids have been found in the Richelieu River in the late 1990s while zebra mussels were colonizing the river. We found eight species of unionids at Site 9 in the Richelieu River, which is about half of the historic species richness of freshwater mussels in the St. Lawrence River (Clarke, 1981). However, Site 9 is one of the sites at which fouling intensity of zebra mussels was negligible, but where high mortality of unionid species was observed. This suggests that species richness at this site is threatened by other environmental stressors. Although some unionid populations persist at multiple sites in the river where zebra mussel abundance is high, a few species are rare and others that were common (e.g. *Lampsilis* spp.) appear to be particularly sensitive to fouling. Differential sensitivity to fouling has been attributed to variations in life history traits (e.g. brooding time) and shell morphology (Haag et al., 1993; Gillis and Mackie, 1994). *Lampsilis radiata* has been shown to be more sensitive than *Elliptio complanata* in a variety of invaded systems (Ricciardi et al., 1996; Hallac and Marsden, 2000; Martel et al., 2001), and this is consistent with our observations in the Richelieu River, suggesting that the long-term impacts of zebra mussel infestation in the river may involve reduced unionid species richness.

Conclusions

This case study demonstrates that at least some impacts of zebra mussel invasion are predictable across a broad range of abiotic conditions. The Ricciardi et al. (1996) regression model derived for calcium-rich sites predicted the trend in mortality of unionid populations from zebra mussel fouling intensity in the Richelieu River, a low-calcium system. High unionid population mortality (>80% recent dead) was observed at a few sites where zebra mussel fouling was high, demonstrating that zebra mussels can exert strong local impacts even in suboptimal (low-calcium) habitats. However, the broad spatial and temporal variation in mortality demonstrates the presence of other stressors, and limits site-specific predictions about unionid population trends. The absence of significant population declines at some sites nine years after zebra mussel invasion raises the possibility that some species of unionids will persist in the Richelieu River despite chronic fouling by zebra mussels.

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Figure Captions

Fig. 1 - Map of study sites along the Richelieu River.

Fig. 2 - Zebra mussel fouling intensity on unionids at Richelieu River sites for which at least 3 years of data were collected: (a) Mean number of zebra mussels (± SE) per unionid; (b) Mean mass ratio (± SE).

Fig. 3 –Mean zebra mussel fouling intensity on unionids over time throughout the Richelieu River

Fig. 4 – Mean live unionid density (± SE) at Richelieu River sites for which at least 3 years of data were collected.

Fig. 5 - Unionid mortality (proportion of recent dead individuals) as a function of the mean zebra mussel-unionid mass ratio. Solid circles represent data adapted from Ricciardi et al. (1996) by the addition of data from Hallac and Marsden (2000) and from A. Ricciardi and L.E. Johnson (unpublished data). Solid line represents the regression model from the modified Ricciardi et al. (1996) data along with the 95% confidence intervals (dashed lines): $\sin^{-1}(y^{0.5}) = 0.48 \log_{10}x + 1.012$ ($r^2 = 0.766$, $p < 0.0001$). Open circles represent all the Richelieu River data from this study.

Fig. 6 - Unionid mortality (proportion of recent dead individuals) as a function of the mean zebra mussel-unionid mass ratio. Solid circles and solid line represent the regression model from the modified Ricciardi et al. (1996) data. Open circles and dashed line represent the regression model for Richelieu River sites that have mean mass ratios exceeding 0.01: $\sin^{-1}(y^{0.5}) = 0.43 \log_{10}x + 1.045$ ($r^2 = 0.244$, $p = 0.0317$). No significant difference was found between these two models (ANCOVA, $p > 0.25$).

Fig. 7 - Mean (±SE) density of *Elliptio complanata* and *Lampsilis radiata* at three sites: (a) Site 4; (b) Site 6; (c) Site 1.

Table 1 - Fouling intensity, unionid density, and unionid mortality for the 10 sites sampled along the Richelieu River (refer to Fig. 1 for site locations). Values reported are the site means with standard errors in parantheses. An asterik represents instances in which no fouling intensity could be calculated due to the absence of live unionids.

Site	Fouling Intensity		Unionid Density	Unionid Mortality
	#ZM/unionid	Mass ratio	(m^{-2})	(% recent dead)
Site 1				
2004	2.60 (0.33)	0.16 (0.03)	8 (1.5)	11.1
2003	1.12 (0.31)	0.07 (0.02)	6.8 (2.2)	43.3
2002	5.85 (0.61)	0.35 (0.04)	11 (1.8)	15.4
Site 2				
2002	1.79 (0.17)	0.09 (0.01)	39 (25.8)	14.8
Site 3				
1999	19.22 (1.21)	0.07 (0.01)	17 (3.7)	43.0
1998	5.57 (0.56)	0.12 (0.01)	23.3 (6.5)	12.3
Site 4				
2005	**	**	0.0 (0)	100
2004	36.63 (5.64)	0.23 (0.10)	1.6 (1.2)	78.4
2003	19.00 (3.61)	0.37 (0.12)	2.4 (0.7)	88.2
2002	24.23 (2.52)	0.47 (0.05)	6.2 (1.7)	57.5
Site 5				
1999	15.59 (1.84)	0.25 (0.04)	9.0 (2.3)	50.0
1998	36.91 (3.30)	0.86 (0.07)	11.3 (1.7)	56.3
Site 6				
2005	4.08 (1.14)	0.06 (0.02)	6.3 (2.0)	40.0

2004	12.40 (2.97)	0.14 (0.02)	6 (1.8)	78.4
2003	4.79 (1.14)	0.16 (0.04)	7.6 (1.8)	13.6
2002	6.19 (0.81)	0.15 (0.02)	10.2 (4.1)	13.6
Site 7				
2003	2.80 (1.62)	0.19 (0.06)	2.9 (2.3)	93.3
2002	5.30 (0.71)	0.16 (0.03)	5.4 (0.8)	35.7
Site 8				
2002	0.17 (0.17)	0.001 (0.001)	1.2 (0.2)	45.5
Site 9				
2005	0.56 (0.24)	0.01 (0.005)	3.2 (0.7)	57.9
2004	1.10 (0.20)	0.02 (0.004)	10.2 (2.0)	33.8
2002	0.71 (0.19)	0.01 (0.002)	8.2 (0.8)	54.9
Site 10				
2004	1 (0)	0.02 (0.01)	0.2 (0.1)	0
2002	0.42 (0.26)	0.004 (0.002)	2.4 (0.9)	0

Table 2 - List of species found in the Richelieu River relative to the Chamby Basin

River Section	Species	Reference
Upstream of Chambly Basin	*Elliptio complanata*	This study; de Lafontaine and Comiré, 2004
	Lampsilis radiata	This study; de Lafontaine and Comiré, 2004
	Lampsilis cardium	de Lafontaine and Comiré, 2004
	Ligumia recta	de Lafontaine and Comiré, 2004
	Pyganodon cataracta	de Lafontaine and Comiré, 2004
Downstream of Chambly Basin	*Alasmidonta undulata*	de Lafontaine and Comiré, 2004
	Anodontoides ferussacianus	This study
	Elliptio complanata	This study; de Lafontaine and Comiré, 2004
	Elliptio dilatata	This study; de Lafontaine and Comiré, 2004
	Lampsilis cardium	This study; de Lafontaine and Comiré, 2004
	Lampsilis radiata	This study; de Lafontaine and Comiré, 2004
	Lasmigona costata	de Lafontaine and Comiré, 2004
	Leptodea fragilis	This study; de Lafontaine and Comiré, 2004
	Ligumia recta	This study; de Lafontaine and Comiré, 2004
	Pyganodon cataracta	This study; de Lafontaine and Comiré, 2004
	Pyganodon grandis	de Lafontaine and Comiré, 2004

Table 3 - Mean density and total numbers of each unionid species collected in the Richelieu River from 1998 to 2004. For each year, first line represents the mean unionid density with the standard error of the mean in parantheses. The second line (in bold characters) represents the total number collected with the number of $1m^2$ quadrats sampled in parantheses. An asterisk denotes years in which a $0.25m^2$ quadrat was used.

	Species							
Site	*Elliptio complanata*	*Lampsilis radiata*	*Elliptio dilatata*	*Ligumia recta*	*Lampsilis cardium*	*Pyganodon cataracta*	*Leptodea fragilis*	*Anodontoides ferussacianus*
Site 1								
2004	7.8 (1.46)	0.2 (0.20)	0	0	0	0	0	0
	39(5)	**1 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
2003	1.6 (0.56)	0.1 (0.10)	0	0	0	0	0	0
	16 (10)*	**1 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***
2002	9.4 (1.63)	1.6 (0.40)	0	0	0	0	0	0
	47 (5)	**8 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
Site 2								
2002	37.6 (25.93)	1.4 (0.4)	0	0	0	0	0	0
	188 (5)	7 (5)	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
Site 3								
1999	17 (3.67)	0	0	0	0	0	0	0
	85 (5)	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
1998	18.75 (6.25)	11 (1.41)	0	0	0	0	0	0
	75 (4)	**18 (4)**	**0 (4)**	**0 (4)**	**0 (4)**	**0 (4)**	**0 (4)**	**0 (4)**
Site 4								
2005	0	0	0	0	0	0	0	0
	0 (10)	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**
2004	1.6 (1.17)	0	0	0	0	0	0	0
	8 (5)	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
2003	0.3 (0.15)	0.3 (0.15)	0	0	0	0	0	0
	3 (10)*	**3 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***
2002	5.4 (1.29)	0.8 (0.49)	0	0	0	0	0	0
	27 (5)	4 (5)	**0(5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**

Site 5								
1999	8.67 (2.33)	0.33 (0.33)	0	0	0	0	0	0
	26 (3)	**1 (3)**	**0 (3)**	**0 (3)**	**0 (3)**	**0 (3)**	**0 (3)**	**0 (3)**
1998	11 (1.41)	0.25 (0.25)	0	0	0	0	0	0
	44 (4)	**1 (4)**	**0 (4)**	**0 (4)**	**0 (4)**	**0 (4)**	**0 (4)**	**0 (4)**
Site 6								
2005	6.2 (2.03)	0.1 (0.1)	0	0	0	0	0	0
	62 (10)	**1 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**
2004	5.8 (1.67)	0.2 (0.2)	0	0	0	0	0	0
	29 (5)	**1 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
2003	1.4 (0.34)	0.5 (0.22)	0	0	0	0	0	0
	14 (10)*	**5 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***	**0 (10)***
2002	10 (4.22)	0.2 (0.2)	0	0	0	0	0	0
	50 (5)	**1 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
Site 7								
2003	0.57 (0.43)	0.14 (0.14)	0	0	0	0	0	0
	4 (7)*	**1 (7)***	**0 (7)***	**0 (7)***	**0 (7)***	**0 (7)***	**0 (7)***	**0 (7)***
2002	5.4 (0.81)	0	0	0	0	0	0	0
	27 (5)	**0 (5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**
Site 8								
2002	1 (0.32)	0.2 (0.2)	0	0	0	0	0	0
	5 (5)	**1 (5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**	**0(5)**
Site 9								
2005	2 (0.63)	0.8 (0.37)	0.2 (0.20)	0.2 (0.20)	0	0	0	0
	10 (5)	**4 (5)**	**1 (5)**	**1 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**
2004	8.2 (1.36)	12 (0.37)	0	0	0.2 (0.20)	0.2 (0.20)	0	0.2 (0.20)
	41 (5)	**6 (5)**	**0 (5)**	**0 (5)**	**1 (5)**	**1 (5)**	**0 (5)**	**1 (5)**
2002	6.4 (1.03)	0.8 (0.49)	0	0	0	0	0.4 (0.40)	0
	32 (5)	**4 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**2 (5)**	**0 (5)**
Site 10								
2004	0	0.2 (0.13)	0	0	0	0	0	0
	0 (10)	**2 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**	**0 (10)**
2002	1.8 (0.58)	0.4 (0.25)	0	0	0	0	0.2 (0.20)	0
	9 (5)	**2 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**0 (5)**	**1 (5)**	**0 (5)**

Table 4 - Comparison of zebra musel impacts on native unionid mussels in various North American rivers. NR is used for cases in which no record was available.

River	**Max. mean fouling recorded** (no. zm/unionid)	**Max. mean mass ratio recorded** (g zm/g unionid)	**No. of years before first major die-off** (>40% mortality)	**Calcium concentration** (Ca^{2+}mg/L)	**Reference**
Richelieu	37	0.9	6-7	16-18	This study
Detroit	NR	>1	6	27-38	Schloesser et al., 1998
Hudson	~17	NR	3	22-24	Strayer, D.L., Smith, L.C., 1996; Strayer, D.L., Malcom, H.M., in press
Illinois	225	NR	3	63-[66]-67	Whitney et al., 1995
Upper Mississippi	106	NR	4	39-[49]-62	Tucker, J., Theiling, C., 1999; Hart et al., 2001
Ohio River	253	NR	5	33-[35]-37	Morrison, P., pers.comm.
Upper St. Lawrence	52	0.9	4	18-36	Ricciardi et al., 1996
Rideau	1366	1.2	3-4	19-[30]-44	Martel et al., 2001

Table 5 - Time to near total extirpation (>90% decline) of unionid populations in calcium-rich (>25mgCa^{2+}·L^{-1}) habitats invaded by *Dreissena* (modified from Ricciardi et al. 1998)

Location	Approximate no. of years before > 90% decline[1]	Peak *Dreissena* density (m^{-2})	Reference
Lake St Clair	< 8	3200	Nalepa et al. (1996)
Lake Erie			
Western basin	4	342 000	Schloesser and Nalepa (1994)
Presque Isle Bay	4		Schloesser and Masteller (1999)
Detroit River	< 8	> 2500	Schloesser et al. (1998); Yankovich and Haffner (1993)
Lake Oneida, New York	4	30 000	Ricciardi et al. (1998)
Lake Wawasee, Indiana	4	11 350	Ricciardi et al. (1998)
Loon Lake, Indiana	< 5	48 400	Ricciardi et al. (1998)
Upper St Lawrence River			
Various sites	< 5	4000-20 000	Ricciardi et al. (1996)
Rideau River	10	> 100 000	Martel et al. (2001)

[1] Number of years after first recorded sighting of adult *Dreissena*.

Fig. 1

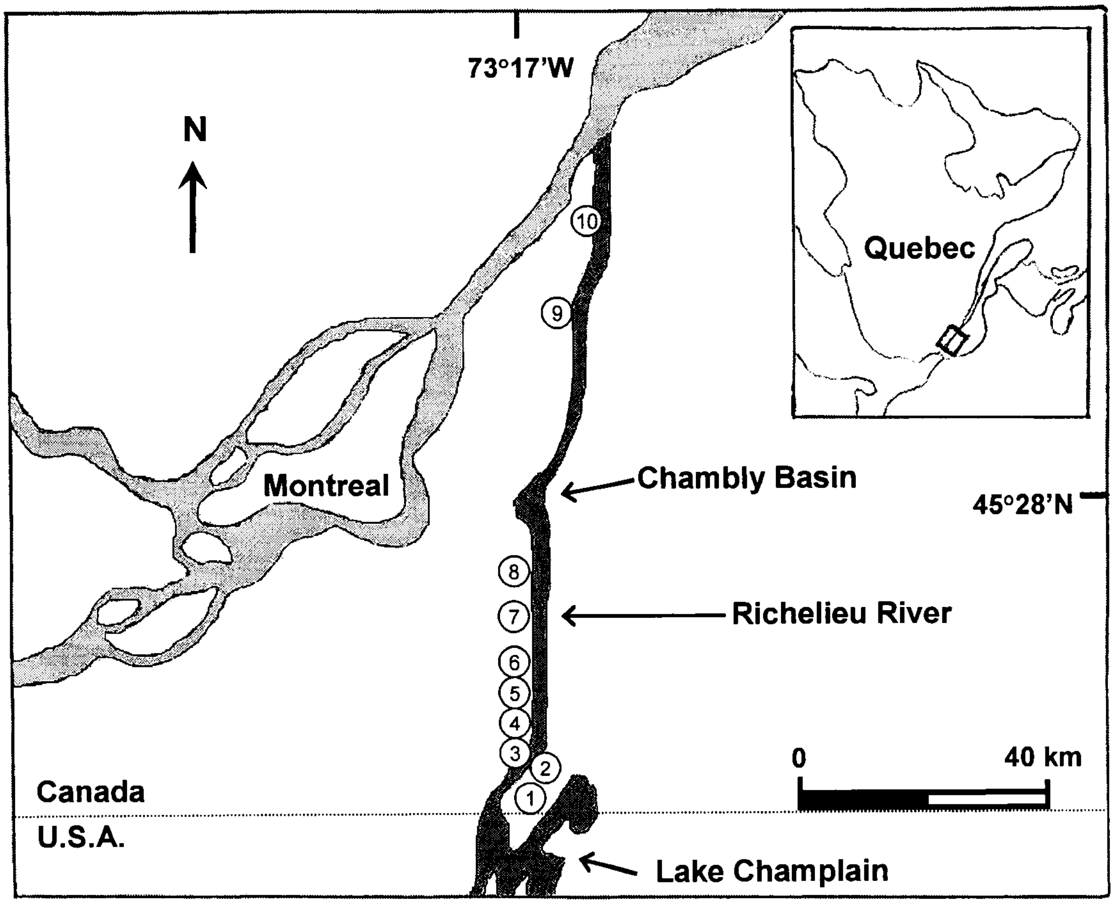
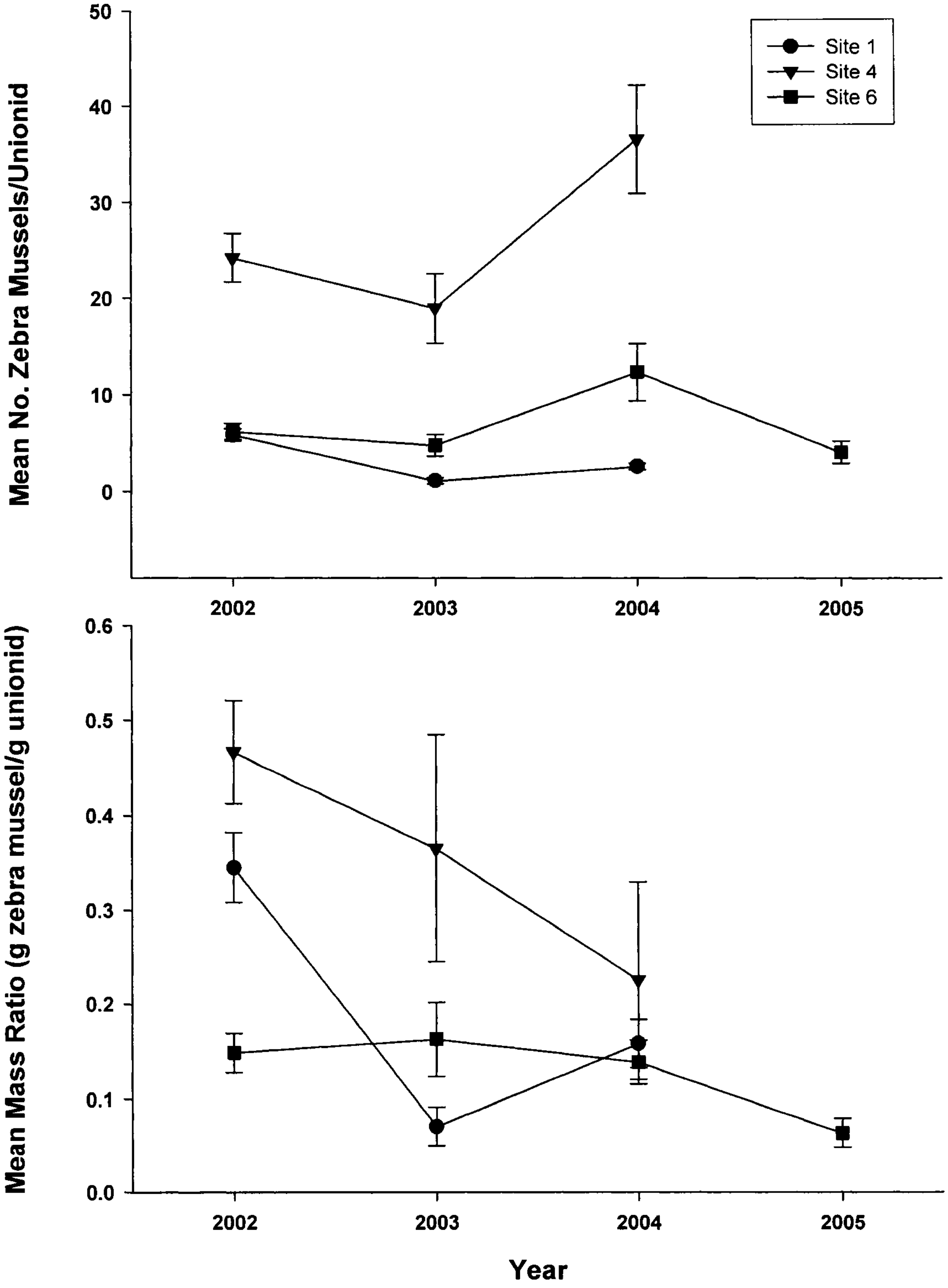

73°17'W
N
Quebec
Montreal
Chambly Basin
45°28'N
Richelieu River
10
9
8
7
6
5
4
3
2
1
0
40 km
Canada
U.S.A.
Lake Champlain

Fig. 2



Site 1
Site 4
Site 6
Mean No. Zebra Mussels/Unionid
50
40
30
20
10
0
2002
2003
2004
2005
Mean Mass Ratio (g zebra mussel/g unionid)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
2002
2003
2004
2005
Year

Fig. 3

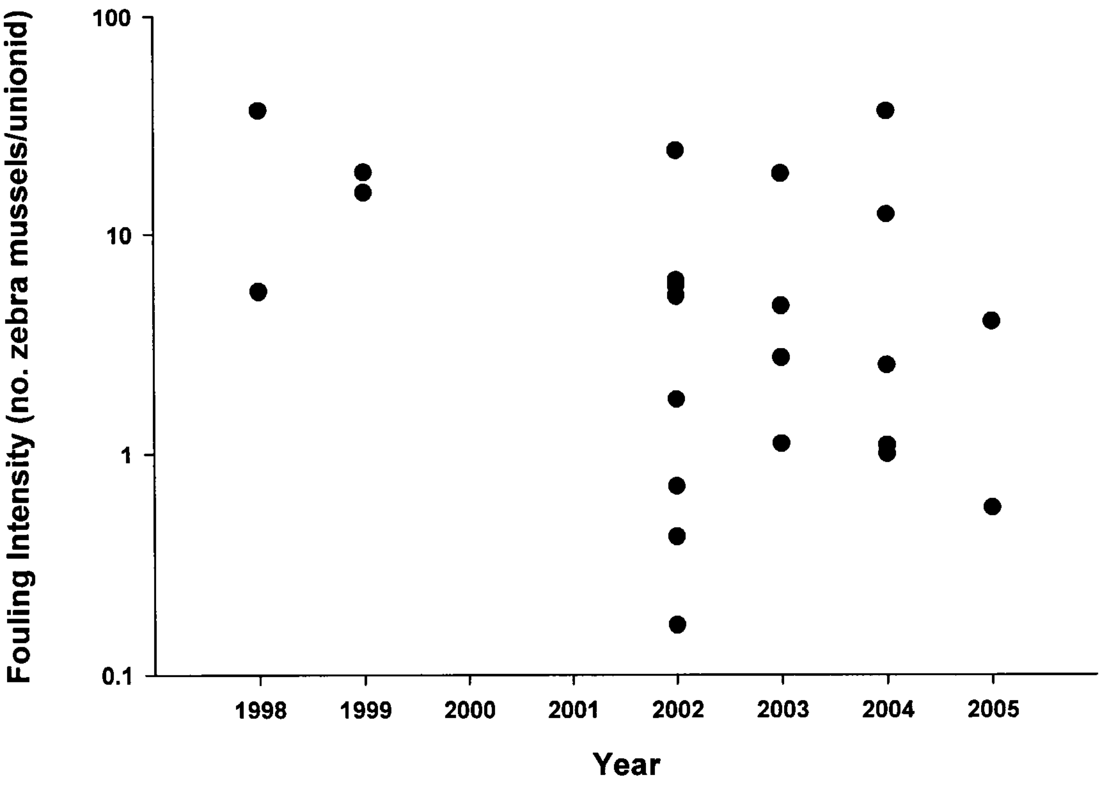
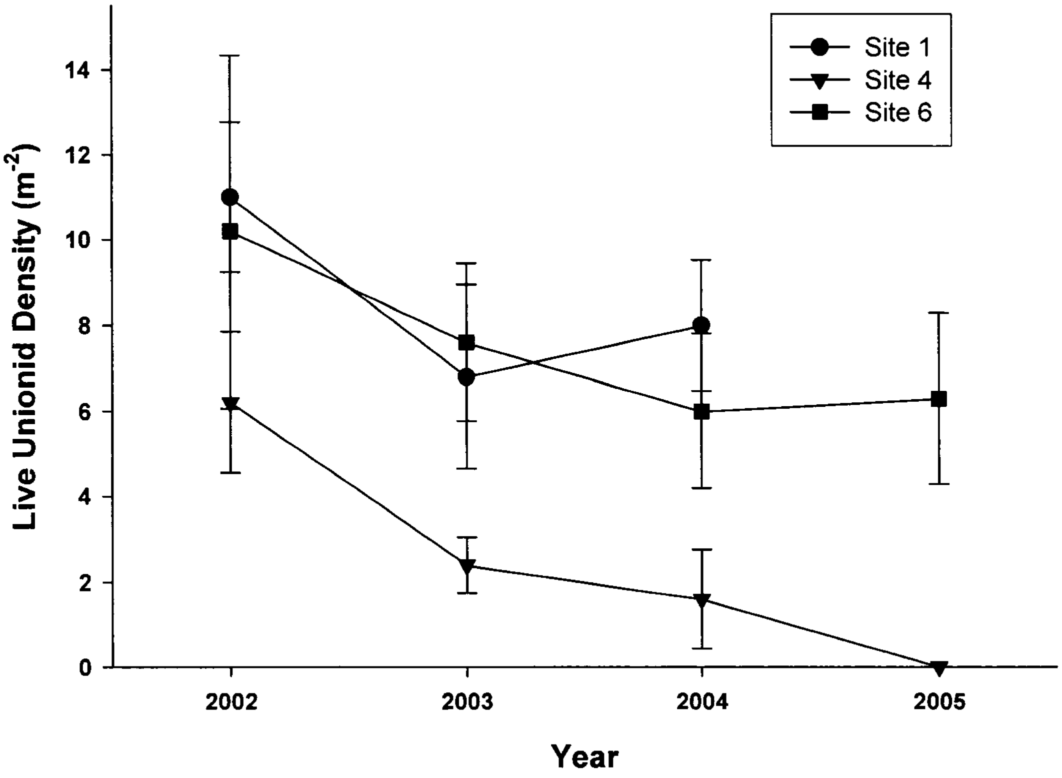

Fouling Intensity (no. zebra mussels/unionid)
100
10
1
0.1
1998
1999
2000
2001
2002
2003
2004
2005
Year

Fig. 4



Site 1
Site 4
Site 6
Live Unionid Density (m^{-2})
0
2
4
6
8
10
12
14
2002
2003
2004
2005
Year

Fig. 5

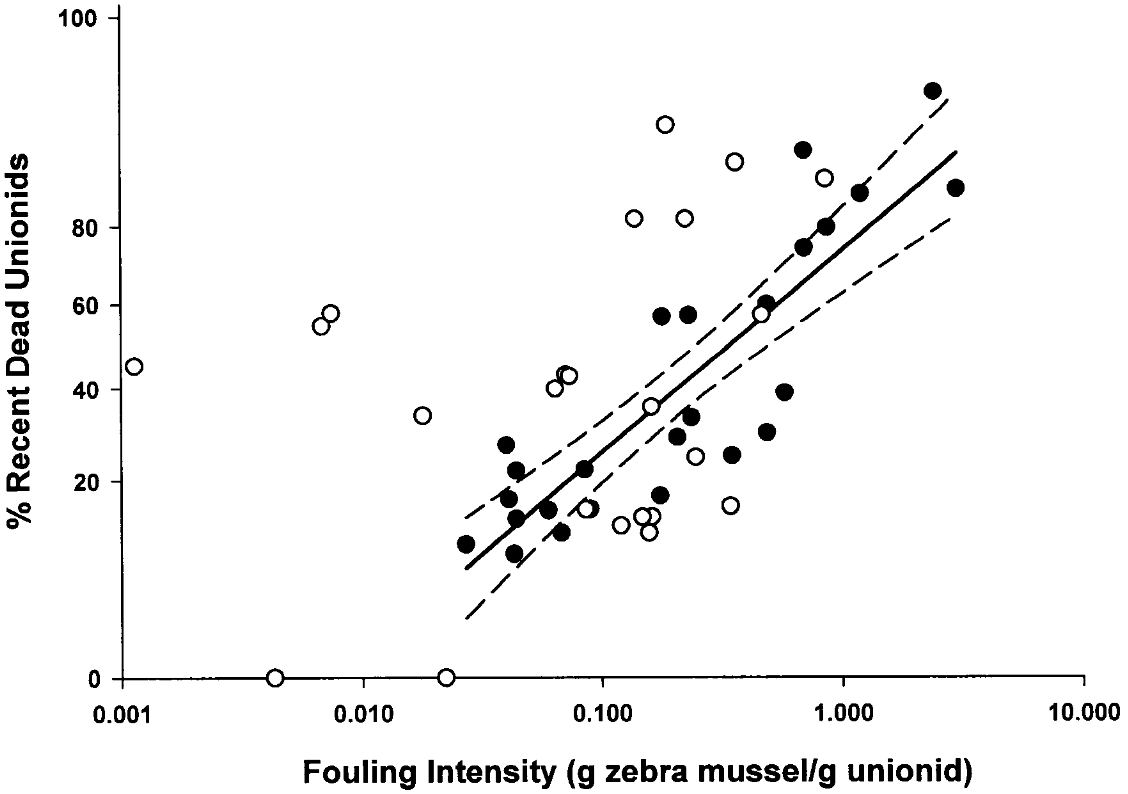

% Recent Dead Unionids
100
80
60
40
20
0
0.001
0.010
0.100
1.000
10.000
Fouling Intensity (g zebra mussel/g unionid)

Fig. 6

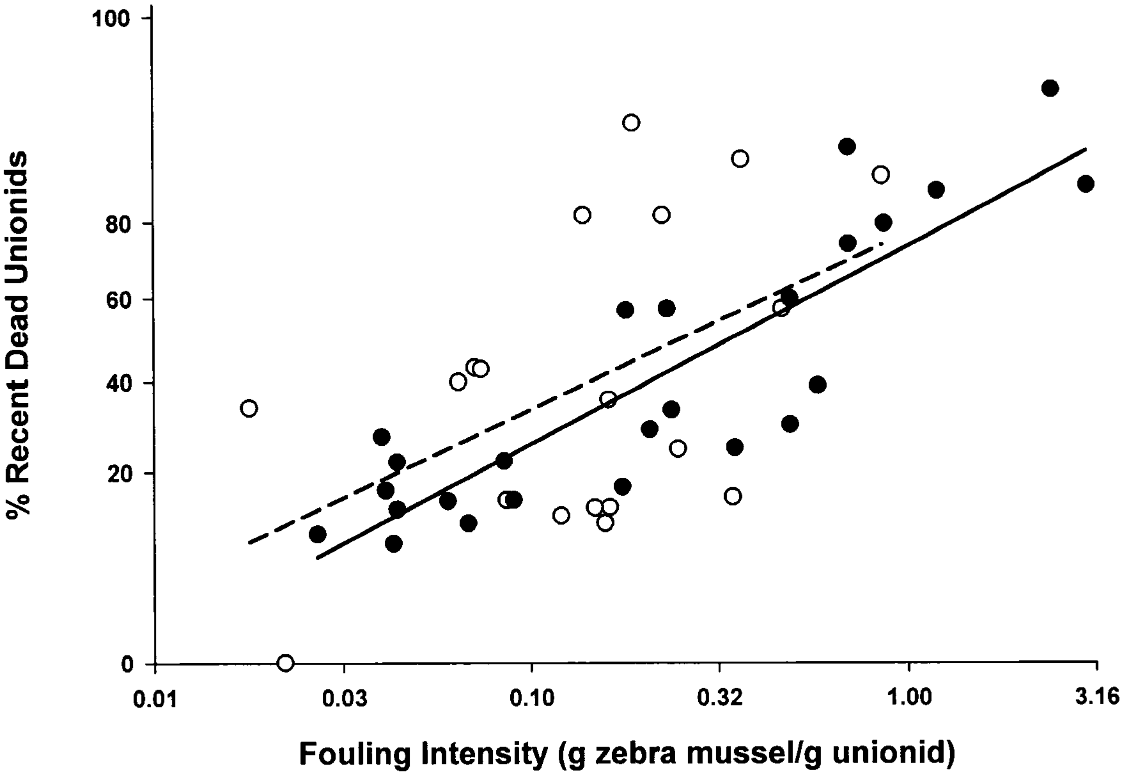
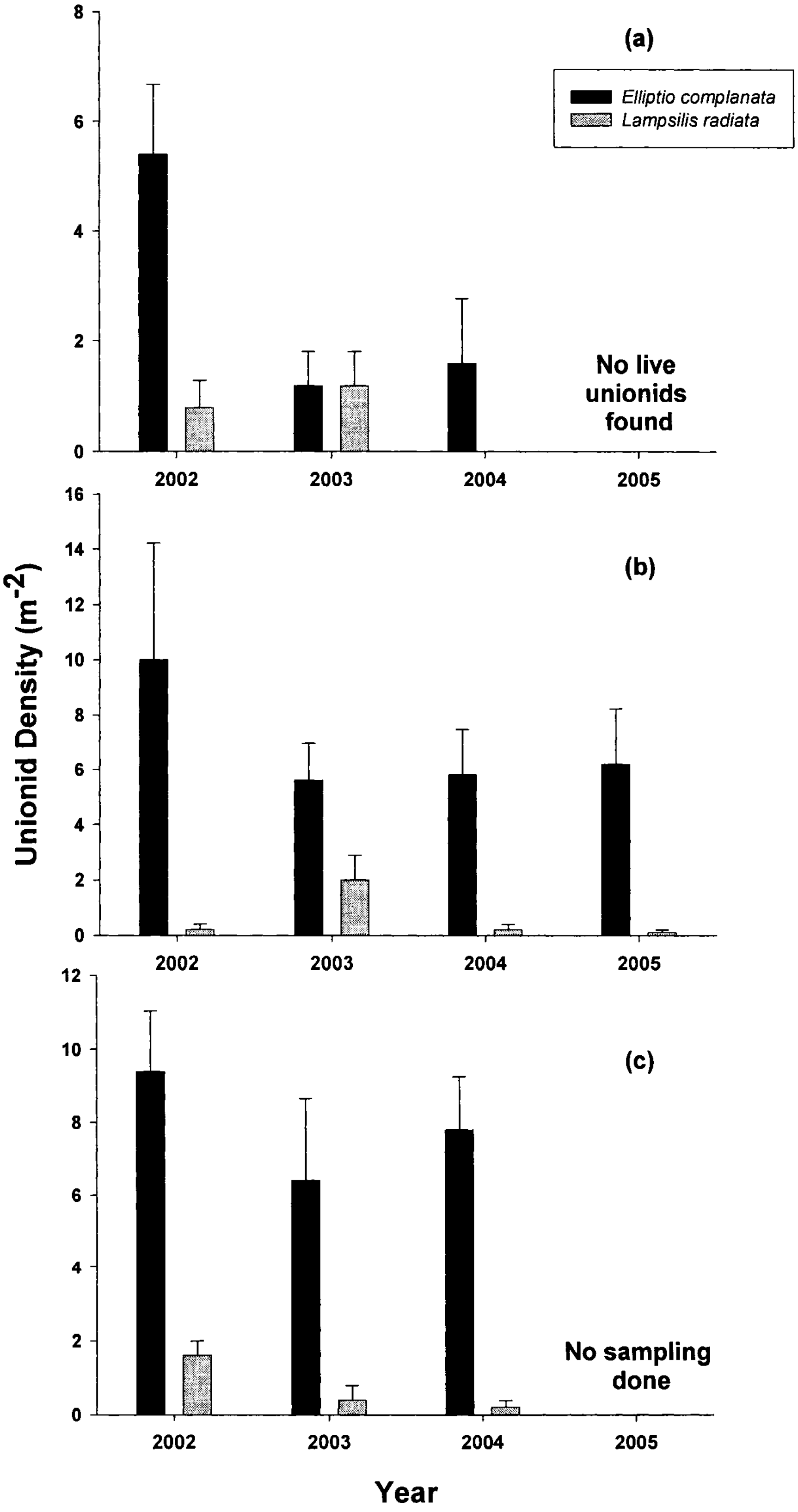

% Recent Dead Unionids
100
80
60
40
20
0
0.01
0.03
0.10
0.32
1.00
3.16
Fouling Intensity (g zebra mussel/g unionid)

Fig. 7



8
6
4
2
0
(a)
■ Elliptio complanata
▨ Lampsilis radiata
No live unionids found
2002
2003
2004
2005
16
14
12
10
8
6
4
2
0
(b)
2002
2003
2004
2005
12
10
8
6
4
2
0
(c)
No sampling done
2002
2003
2004
2005
Unionid Density (m^{-2})
Year

Connecting Statement

Unlike many other North American lakes and rivers that have been invaded by zebra mussels, fouling intensities of unionids throughout much of the Richelieu River have remained relatively low over time, and some sites have unionid populations that are persisting longer than would be expected in the presence of zebra mussels. I suspect that the low calcium concentration of the river may be playing a role in this by preventing the development of dense zebra mussel populations. However, other factors influencing fouling intensities in this system deserve to be investigated.

One potential factor is predation. A few native North American organisms have been found to substantially consume zebra mussels, including the molluscivorous fish *Aplodinotus grunniens* (freshwater drum). Freshwater drum are abundant in the Richelieu River and it is conceivable that they are consuming zebra mussels that are attached to unionids. In the next chapter, I investigate the potential role of molluscivores in mediating the interaction between zebra mussels and unionids.

Effect of molluscivores on the intensity of fouling of unionids by zebra mussels

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Abstract

One of the most conspicuous impacts of the zebra mussel (*Dreissena polymorpha*) invasion of North American lakes and rivers has been the fouling of native unionid mussels. Fouling of unionid shells by zebra mussels is a form of interference competition, by which clusters of zebra mussels on unionid shells interfere and impair normal unionid behaviour. A number of species are known to feed on zebra mussels, including freshwater drum (*Aplodinotus grunniens*). The Richelieu River is a system in which both fouled unionids and freshwater drum are found. A predator-exclusion experiment was performed in both 2004 and 2005 at a site in the Richelieu River to determine whether exposure to molluscivores could reduce fouling intensities. The experiment in 2004 examined the effect of exposure to molluscivores on naturally occurring unionid patches. The 2005 experiment varied levels of fouling intensities in order to determine if predators demonstrated preferences for larger clusters of zebra mussels. Overall, results from both experiments found no effect of exposure to molluscivores on the fouling intensity of unionids by zebra mussels. Although the experimental design does not allow us to rule out the possibility that predators are not feeding on zebra mussels attached to unionids, it can be concluded that they are not helping to control fouling intensities.

Keywords: exotic species, aquatic invasions, interference competition, Unionidae, exclusion experiment

Introduction

Competition and predation are two ecological mechanisms that are important in structuring communities. Predators can often reduce competition at lower trophic levels, thereby mediating the coexistence of two or more species (Paine, 1966; Lubchenco, 1978). Examples of predators influencing the outcome of competition at lower trophic levels have been documented for marine intertidal assemblages, terrestrial folivores, seed-eating assemblages, and freshwater lake ecosystems (reviewed in Leibold, 1996). One potential impact of biological invasion is the competitive displacement of native species by exotic species (Mack et al., 2000). Cases in which native predators reduce the impact of exotic species are of both fundamental and applied importance to conservation biology. An example of this phenomenon has recently been observed in a freshwater reservoir, where a native predatory insect mediated the coexistence of a native and exotic crustacean (Celik et al., 2002).

Since its discovery in 1988 in Lake St. Clair (Hebert et al., 1989), the zebra mussel rapidly expanded its range to include all of the Great Lakes and several large river systems (Ludyanskiy et al., 1993). Zebra mussels attach to almost all solid surfaces, including the shells of freshwater mussels (Ricciardi et al., 1995). Zebra mussel fouling of native unionid mussels is a form of interference competition. The presence of attached zebra mussels can lead to depleted energy reserves by interfering with and impairing unionid locomotion, feeding, and respiration (Haag et al., 1993; Schloesser et al., 1996; Baker and Hornbach, 1997, 2000). Fouling of unionids by zebra mussels has caused massive unionid mortality, and in systems where fouling intensities have reached high levels, rapid extirpation of unionids has occurred within 8 years (Ricciardi et al., 1998). As such, the presence of a molluscivore that could consume large numbers of zebra mussels may be able to reduce their impact on unionids. Two cases of exotic mussel densities being reduced by the presence of native molluscivores have been documented. One involves the 29-fold reduction of the invasive clam *Corbicula fluminea* by an assemblage of molluscivorous fish in a freshwater reservoir (Robinson and Wellborn, 1988). The other involves the 65% reduction of the introduced mussel *Musculista senhousia* by a native snail (Reusch, 1998), Organisms that have been found to consume zebra mussels include fish (Morrison et al., 1997; Thorp et al., 1998; Magoulick and Lewis, 2002; Bartsch et al., 2005), crayfish (MacIsaac, 1994; Perry et al., 1997), and waterfowl (Mitchell and Bailey, 2000). Among the studies reporting fish predation of zebra mussels, one common predator is the freshwater drum, *Aplodinotus grunniens*. Freshwater drum are well adapted to feeding on molluscs owing to their specialized upper and lower pharyngeal teeth (Scott and Crossman, 1973; French, 1993). In Lake Erie, zebra mussels were recorded in the guts of three different size classes of freshwater drum, and the importance of zebra mussels in the diets of freshwater drum increased with total fish length (French and Bur, 1992).

The Richelieu River is a river system in which at least 11 species of unionids have been documented (de Lafontaine and Comiré, 2004). The Richelieu River was invaded by zebra mussels in 1996 (de Lafontaine and Cusson, 1997), and fouled unionids were first documented in 1997 (Cusson and de Lafontaine, 1998). Despite the presence of zebra mussels in this river for at least nine years, our surveys have found unionid populations still remaining at some sites in the river (see Manuscript 1). Interestingly, freshwater drum are known to be abundant in the Richelieu River and molluscs tend to be more important in the diet of river dwelling-drum than that of lake-dwelling drum (Scott and Crossman, 1973). We examined one large drum collected in the river and found its gastrointestinal tract to be full of zebra mussel shells (unpublished data). The goal of this study was to investigate the potential role of native molluscivores in mediating the interaction between unionids and zebra mussels. Specifically, a predator-exclusion experiment was conducted at a site in the Richelieu River in order to test the hypothesis that exposure to molluscivores would reduce fouling intensities of unionids by zebra mussels.

Methods

Study Area

The predator-exclusion experiment was conducted at a site on the Richelieu River (Site 1, see Manuscript 1) where freshwater drum have been historically present and where fishermen report good catches (Mongeau et al., 1974). Another potential predator of zebra mussels, large pumpkinseed *Lepomis gibbosus* (French, 1993), are also ubiquitous at this site. This site was also chosen because of the presence of a fouled unionid population. In 2004, the average unionid density was 8 ± $1.5m^{-2}$ and the number of attached zebra mussels per unionid ranged from 0 to 7 (mean=2.6). Our survey of the site in 2005 revealed similar unionid densities as well as a larger range of fouling intensities.

2004 Experiment

In 2004, a preliminary predator-exclusion experiment was performed. Ten $1m^2$ cages were deployed in the shallow area (1-1.25m) of the site where the unionid population naturally occurs. Cages were made of $1.25cm^2$ stainless steel mesh (cage dimensions: 100cm × 100cm × 20cm) and the sides were connected using plastic cable ties. Cages were assembled on shore and then placed over experimental plots by divers. The bottom of each cage was left open to allow for placement over experimental plots. Each cage was marked with flagging tape and anchored to the substrate by attaching horizontal mesh panels weighted down by bricks. Cages were selectively placed by divers in order to cover at least 5 unionids in an area where a similar amount of unionids could be found outside the cages. This was necessary so that "Cage" and "No Cage" treatments could be compared at the end of the experiment.

The cages were deployed on July 11, 2004 and the experiment was retrieved on October 8, 2004. At the time of retrieval, a $1m^2$ polyvinyl chloride quadrat was placed immediately next to each cage treatment. All visible unionids were collected from within the quadrat and the upper 10cm of sediment was probed by hand to collect individuals buried immediately beneath the sediment. Each unionid with its attached zebra mussels was removed by hand and placed in a sealed, marked collection bag while underwater. Next, the tops of the cages were removed and unionids were collected from inside the cages using the same methodology. All collection bags were stored in a cooler and returned to the laboratory within three hours of collection.

In the laboratory, all attached zebra mussels were removed from each live unionid and counted. Zebra mussel fouling intensity was measured by the mean number of live zebra mussels attached to living unionids. Shell length (± 0.01mm) of each attached zebra mussel was measured using electronic digital calipers.

A two-sample *t*-test was used to compare the number of attached zebra mussels per unionid in "Cage" versus "No Cage" treatments. In order to conform to the assumptions of the test, values were $(x + 0.5)^{0.5}$ transformed (Zar 1999). The mean shell length of attached zebra mussels was also compared using a two-sample *t*-test for both treatments.

2005 Experiment

The predator-exclusion experiment was repeated in the summer of 2005, but the experimental design was modified in order to address limitations of the 2004 experiment. The 2005 experiment was replicated at two depths: 1.25m (Shallow) and 2.75m (Deep). Unionids were collected from the Shallow area for use in all experimental plots at both depths. Although no live unionids were found at the Deep site, the presence of many shells in the sediment suggests that a unionid population had been present at the site in the recent past. The Shallow site was accessed from shore by SCUBA divers while the Deep site required the use of a small boat to transport cages and unionids.

The experiment consisted of two treatments: (1) "No Cage" ($1m^2$ plot with marked corners) and (2) "Cage" ($1m^2$ plot covered by a predator-exclusion cage). Cage design and construction were the same as in the previous year. At the beginning of the experiment, we cleared each $1m^2$ plot of all live unionids, dead unionid shells and macrophytes. Fouled unionids were then collected, brought to the surface, and assigned to one of three levels of fouling: (1) Low (1-3 zebra mussels/unionid), (2) Medium (5-7 zebra mussels/unionid), and (3) High (8-10 zebra mussels/unionid). Some attached zebra mussels were removed to obtain an equal number of unionids for each level of fouling. In order to reflect the local population density and to meet logistical constraints, seven unionids from each fouling level were randomly selected and placed within each marked plot. Treatment-fouling combinations were replicated three times.

The experiments ran for a period of three months. The Shallow site experiment was deployed on July 1 and retrieved on September 25, while the Deep site experiment was deployed on July 6 and retrieved September 24. At the time of retrieval, the "No Cage" and "Cage" treatments were collected and processed using the same methodology as in the previous year.

Analysis of variance (ANOVA) was used to identify treatment differences at each experimental depth. Two-factor fixed effects ANOVAs (treatment and level) were conducted, followed by Tukey multiple comparison procedures. Prior to analysis, a significant effect of the cage on zebra mussel recruitment was detected. Cages appeared to inhibit settlement of new zebra mussels since recruitment was higher in the uncaged treatments than in the caged treatments; therefore, all zebra mussels less than 15mm in shell length were excluded from the analysis. This threshold was chosen because only zebra mussels ≥ 10mm were used at the start of the experiment and zebra mussels in North America can grow up to 15-20mm in one year (Mackie and Schloesser, 1996). All statistical analyses were performed using SAS Systems for Windows V8 (SAS Institute Inc., Cary, North Carolina).

Results

2004 Experiment

No significant difference was found between the number of zebra mussels attached to unionids inside and outside of cages ($p = 0.88$). Unionids inside cages carried a mean of 2.50 ± 0.12 zebra mussels, while unionids outside cages carried a mean of 2.48 ± 0.16 zebra mussels (Figure 1a). Power analysis post-retrieval indicated that a reduction of 30% in fouling intensity in the "No Cage" treatment would have been required in order to detect a significant difference. Shell lengths of attached zebra mussels were also compared in order to determine if there was an effect of prey size. No significant difference was found between the shell lengths of zebra mussels attached to unionids inside and outside of cages ($p = 0.91$). The mean shell length of attached zebra mussels was 21.32 ± 0.14mm inside of cages and 21.25 ± 0.18mm outside of cages (Figure 1b).

2005 Experiment

Unionids from all experimental plots were retrieved at the end of the experiment. Some individuals disappeared during the course of the experiment, but there were never fewer than six unionids retrieved and there was no significant difference between the numbers retrieved from both treatments. For both the Shallow and Deep sites, the final number of attached zebra mussels across all levels of fouling was never lower in the "No

Cage" treatment than in the "Cage" treatment, suggesting that excluded predators had no effect on fouling intensities (Figure 2).

At both the "Medium" and "High" levels of fouling, the final number of attached zebra mussels was lower than the initial number (Figure 2), indicating that some form of zebra mussel mortality occurred during the experiment. In the Shallow site, at the "High" level of fouling, the number of attached zebra mussels in the caged treatment experienced greater reduction than that of the uncaged treatment (Figure 2a); thus the effect of treatment at the shallow site was marginally significant in the ANOVA (Table 1). The effect of fouling level was significantly different (Table 1), but this is because the relative fouling intensities for all three levels (Low, Medium, and High) remained unchanged at the end of the experiment.

Discussion

Results from both predator-exclusion experiments found that fouling intensity in the "No Cage" treatment was not significantly lower than in "Cage" treatment, suggesting that exposure to molluscivores had no effect on the naturally occurring fouling intensity of unionids by zebra mussels. During the 2004 experiment, two main issues arose concerning the experimental design. First, it is possible that the experiment was performed at a depth too shallow for large fish such as freshwater drum to feed. Secondly, mean fouling intensity in both treatments was ~2 zebra mussels per unionid. Such small values may have made it difficult to detect significant differences. More importantly, it is also possible that molluscivorous fish prefer focusing their foraging efforts on larger clumps of zebra mussels, thereby having less of an impact on these small fouling intensities. For these reasons, a modified field experiment was repeated the following year. The experiment in 2005 was conducted at two depths in order to address the possibility that molluscivores would preferentially feed further offshore. A second factor, fouling intensity, was also added to determine whether molluscivores preferentially feed on larger clumps of attached zebra mussels.

The results of the 2005 experiment also suggested that exposure to predation had no effect on fouling intensity of unionids by zebra mussels. These results contrast previous findings by Bowers et al. (2005) in an experimental study at Crane Creek Marsh, a marsh connected to Lake Erie but protected from offshore waves by a dike. The present study took place at a site in the Richelieu River that was not isolated from the larger fluvial environment. For large molluscivores such as freshwater drum, feeding on zebra mussels attached to inshore unionids may not be an efficient means of foraging. Dense populations of zebra mussels are found in the river on nearby structures, such as concrete bridge pilings (pers. obs.), and molluscivorous fish might be focusing their foraging efforts on these areas. Although a settlement experiment on artificial substrate in Crane Creek Marsh found high levels of colonization (Bowers and de Szalay, 2004), the absence of dense zebra mussel patches in the marsh itself may have favored concentrated foraging on zebra mussels attached to unionids there.

It is also possible that effects of predation may have escaped detection if molluscivores are preferentially feeding on juvenile zebra mussels. Evidence of size-selective mussel predation has been documented for freshwater drum; French and Love (1996) found an upper limit of 21.4mm shell length, while Morrison et al. (1997) found an upper limit of 13mm shell length. Meanwhile, using the strong allometric relationship between zebra mussel septum length and total length (Hamilton, 1992), We were able to estimate that the size range of mussels found in the gut contents of a drum collected from the Richelieu River by our lab was 6.23-[11.90]-20.07mm (unpublished data). In the 2005 experiment, any effect of predation on the lower size classes of zebra mussels would have been obscured by the exclusion of recruits (<15mm) from our analysis. However, numbers of recruits were higher outside the cages indicating that macropredators had relatively no effect on these smaller zebra mussels. Furthermore, results from the 2004 experiment, in which no differential settlement was detected, found no significant difference in zebra mussel shell lengths between treatments. If predation on smaller individuals was indeed taking place, this would have been reflected in a greater average shell length in the "No Cage" treatment.

During the course of the 2005 experiment, zebra mussels were lost from both the "Cage" and "No Cage" treatments at "High" and "Medium" fouling intensities, most likely as a result of baseline mortality of adult zebra mussels unrelated to predation. Alternatively, predation inside the cages by smaller animals such as crayfish may have equaled that which occurred outside the cages. Crayfish may have been able to burrow underneath the cages and gain access to the attached zebra mussels, but no crayfish were observed within any of the cages at the time of retrieval. Another possibility is that mortality related to cage effects equaled that of predation outside the cages. Negative cage effects on zebra mussel survival could include restricted water flow due to cage fouling, which may limit the availability of food to mussels within the cages and may also contribute to increased sedimentation (Virnstein, 1978; Peterson, 1979). However, retrieved cages were free of any significant fouling. Finally, it is also possible that zebra mussels were lost due to translocation from unionids onto other substrates (Ackerman et al., 1994). This is not a likely possibility seeing that unionids in all experimental plots represented virtually all of the hard colonizable substrate.

A significant difference between predation treatments involved only the "High" fouling intensity treatment at the Shallow site, but in the opposite direction than predicted. Fouling intensity in the caged treatment was significantly lower than in the uncaged treatment. Again, this might reflect a negative effect of cages on zebra mussel survival, but the mechanism is unknown.

In conclusion, although it is impossible to rule out some limited predation of zebra mussels by molluscivores, our results demonstrate that predation is not occurring at a magnitude sufficient to control fouling intensities. Therefore, it is unlikely that coexistence of unionids and zebra mussels at this site is being mediated by molluscivores.

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Figure Captions

Fig. 1 – Comparison of (a) fouling intensity of unionids by zebra mussels and (b) shell length of attached zebra mussels between the “No Cage” and “Cage” treatment for the 2004 experiment. Bars represent treatment means (± SE).

Fig. 2 - Results from the 2005 predator-exclusion experiment for both the (a) Shallow and (b) Deep sites. Points represent the mean (± SE) final infestation intensity. An asterisk represents a significant difference between treatments ($p<0.05$).

Table 1: Analysis of variance (ANOVA) for fouling intensities from the 2005 predator-exclusion experiment at the Shallow and Deep sites.

	MS	*F*	df	*p*
Shallow				
Model	10.14	28.21	5	< 0.0001
Treatment	1.89	5.25	1	0.0408
Level	23.03	64.04	2	< 0.0001
Treatment x Level	1.39	3.86	2	0.0507
Error	0.36		17	
Deep				
Model	9.87	20.72	5	< 0.0001
Treatment	0.013	0.03	1	0.87
Level	24.43	51.27	2	< 0.0001
Treatment x Level	0.244	0.51	2	0.6116
Error	0.476		17	

Fig. 1

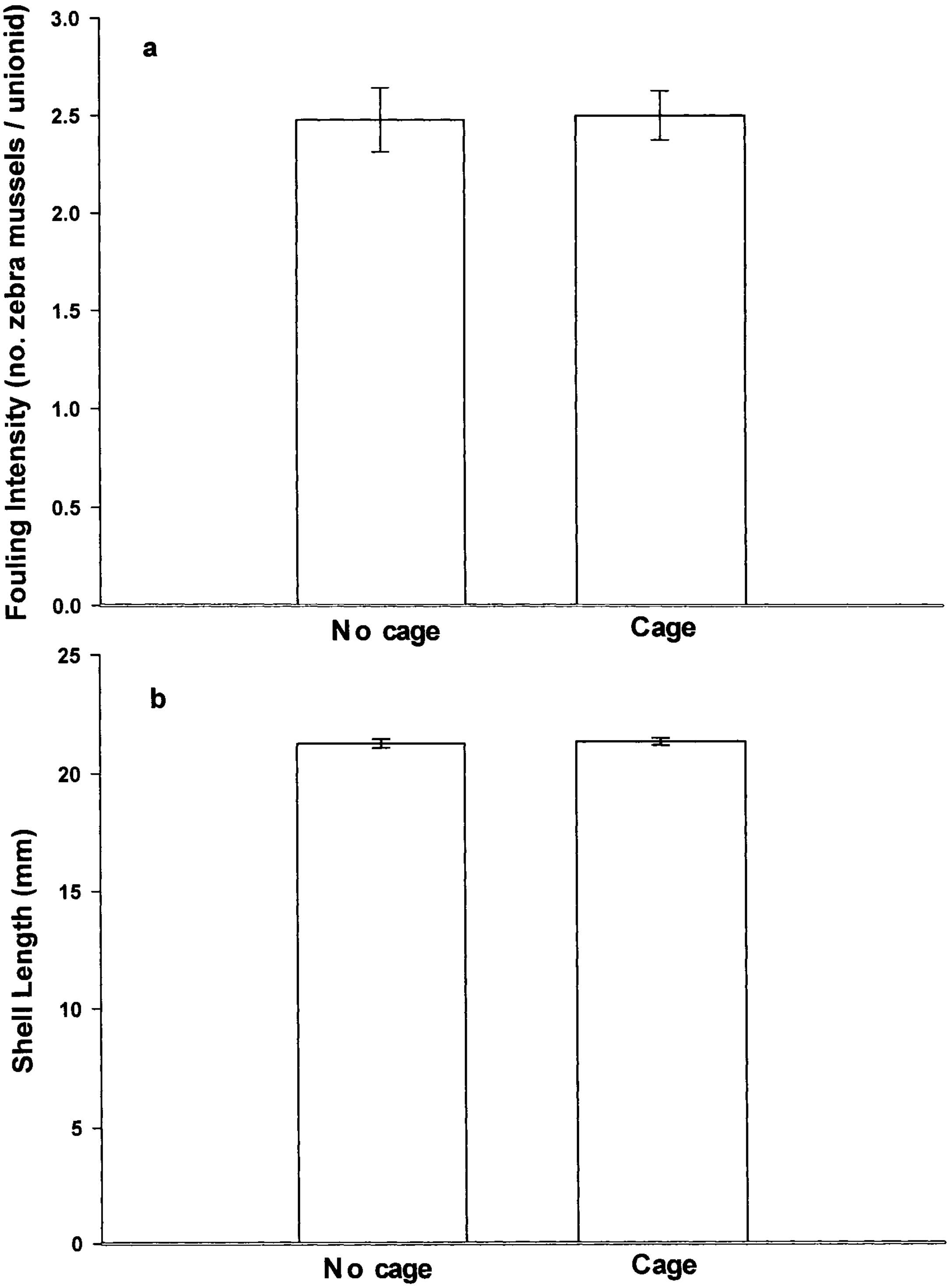
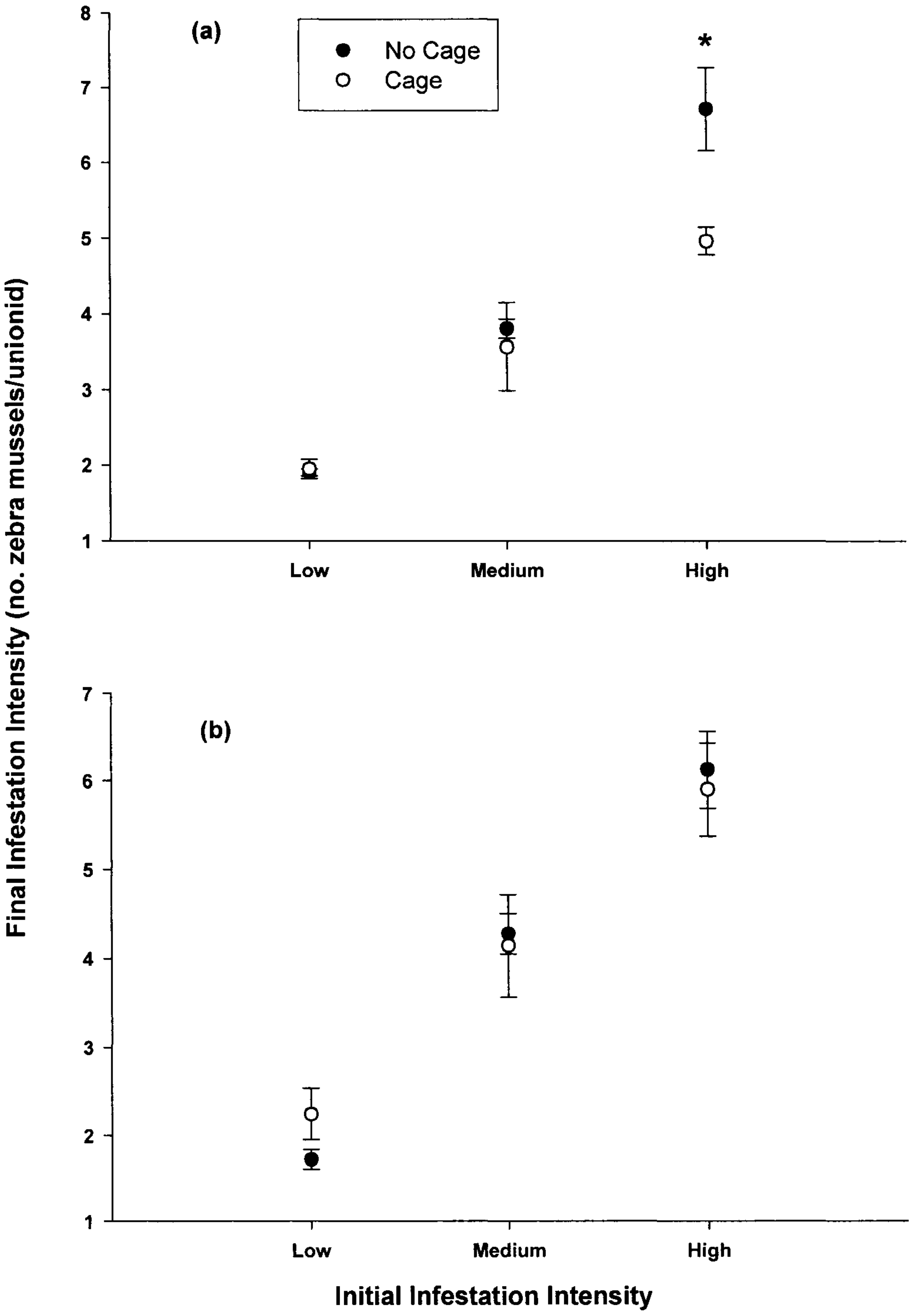

a
Fouling Intensity (no. zebra mussels / unionid)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
No cage
Cage
b
Shell Length (mm)
25
20
15
10
5
0
No cage
Cage

Fig. 2


(a)
● No Cage
○ Cage
*
8
7
6
5
4
3
2
1
Low
Medium
High
(b)
7
6
5
4
3
2
1
Low
Medium
High
Final Infestation Intensity (no. zebra mussels/unionid)
Initial Infestation Intensity

Connecting Statement

Results from the predator-exclusion experiment suggested that predation is not an important factor in mediating fouling intensity of unionids by zebra mussels in the Richelieu River. At this point, empirical evidence linking abiotic factors to fouling intensity is lacking, and consequently it is not clear to what extent environmental factors influence the interaction between the invasive and native mussels. In the final chapter, I examine whether fouling intensity of unionids can be predicted by a combination of environmental variables known to affect zebra mussel abundance.

Effect of environmental variables on fouling intensity of unionids by zebra mussels

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Abstract

Biological invasions are among the leading causes of species diversity loss; however, impacts of invasion are context-dependent and can vary with the local environment. The introduction of the Eurasian zebra mussel (*Dreissena polymorpha*) to North American lakes and rivers has led to the widespread fouling of native unionid mussels resulting in massive mortality of unionid populations in systems that support high densities of zebra mussels. A multi-site survey across two river systems (St. Lawrence River and Richelieu River) was conducted to determine whether fouling intensity of unionids by zebra mussels varied with environmental variables. We found that fouling intensity increased with increasing calcium concentration and decreasing sediment size, while macrophyte cover had no effect on fouling intensity. A stepwise regression model, which included both calcium concentration ($Ca^{2+} mg \cdot L^{-1}$) and sediment size (measured on the Φ scale), was developed to predict fouling intensity ($r^2 = 0.86$; $p < 0.0005$). This study suggests that habitat heterogeneity may help mediate the impact of exotic species by creating pockets of refugia for native species.

Keywords: aquatic invasions, predictive model, biofouling, Unionidae, context-dependence

Introduction

In ecological research many hypotheses have been put forward in order to explain the generation and maintenance of species diversity (reviewed by Whittaker et al., 2001). One of these is that of habitat heterogeneity, where increased heterogeneity provides more niches and thus allows for greater diversity in resource use, leading to an increase in species diversity (Bazzaz, 1975; Tews et al., 2004). Biological invasions are among the leading causes of biodiversity loss (Clavero and García-Berthou, 2005); however, the impact of exotic species is context-dependent and varies with environmental conditions (Parker et al., 1999; Ricciardi, 2003; Ricciardi and Atkinson, 2004). Habitat heterogeneity may thus provide pockets of refugia for native species from the impacts of exotic species. This may be especially important along environmental gradients where the response of native and exotic species differs along the gradient (Laha and Mattingly, 2006).

One of the most conspicuous impacts of the introduction of the Eurasian zebra mussel (*Dreissena polymorpha*) to North American lakes and rivers has been the fouling of native unionid mussels (Strayer, 1999). Fouling of native mussels by zebra mussels can deplete unionid energy reserves by interfering with and impairing their locomotion, feeding, and respiration (Haag et al., 1993; Schloesser et al., 1996; Baker and Hornbach, 1997, 2000). As a result, fouling of unionids by zebra mussels has caused massive unionid mortality, and in systems where fouling intensities have reached high levels, rapid extirpation of unionid populations has occurred within 8 years (Ricciardi et al., 1998). Mortality of unionids is correlated with fouling intensity (Ricciardi et al., 1995; Ricciardi 2003), and fouling intensity has been shown to be strongly correlated with local zebra mussel field density (Ricciardi 2003). It follows that factors affecting zebra mussel density are likely to also affect their fouling intensity on unionid mussels.

One important abiotic factor shown to influence local zebra mussel occurrence and density is calcium concentration (Ramcharan et al., 1992; Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). Calcium is required for zebra mussel shell growth and osmoregulation (Vinogradov et al., 1993; McMahon, 1996). Colonization by zebra mussels can occur in waters with concentrations of $15\text{mg}\cdot\text{L}^{-1}$, although the threshold for adult survival can be as low as $12\text{mg}\cdot\text{L}^{-1}$ (Vinogradov et al., 1993; Jones and Ricciardi, 2005). In general however, studies of zebra mussel abundances along a calcium concentration gradient found that adult densities tend to peak at concentrations ≥ 20mg·L^{-1}(Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). In contrast, unionid mussels are much more tolerant of low calcium waters and healthy populations are sustained in waters with concentrations < 3mg·L^{-1} (reviewed by McMahon, 1991). As a result, environments with low calcium concentrations may limit zebra mussel fouling of unionids and allow for their coexistence and provide refugia for unionids.

Another important physical factor for zebra mussel abundance is substrate quality (Mellina and Rasmussen, 1994; Karatayev et al., 1998; Jones and Ricciardi, 2005). The availability of hard substrate is necessary for the survival of postveliger zebra mussels (Stanczykowska, 1977; Lewandowski, 1982) and local zebra mussel density has been found to increase with an increase in substrate particle size (Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). The shells of unionid mussels also serve as hard substrate and it has been suggested that zebra mussels preferentially colonize the shells of living unionids (Lewandowski, 1976; Ricciardi et al. 1996). Unionid mussels can occupy a variety of substrate types (Strayer, 1981; reviewed by McMahon, 1991) but are most abundant in mixed sediments (but see Sietman et al., 1999). In habitats where soft substrates (i.e., mud, silt) predominate, unionid shells are generally the only hard colonizable substrate for zebra mussels (Toczylowski et al., 1999).

Finally, one potentially important biotic factor in regulating fouling intensity of unionids may be the presence of submerged macrophytes, which can act as substrate for zebra mussel attachment, especially for juveniles (Karateyev et al., 1998; Diggins et al., 2004). Unionid populations that occur amid dense macrophyte beds may be less vulnerable to fouling if macrophytes intercept settling zebra mussels and provide alternative substrate for attachment.

The goal of this study was to explore the importance of context-dependency in making predictions about the impact of exotic species. This was done by determining if fouling intensity of unionid mussels by zebra mussels can be predicted by a combination of local environmental variables. Specifically, the following hypotheses were tested: fouling intensity will increase in habitats with increasing calcium concentration, finer sediment particle size, and reduced macrophyte cover.

Methods

Study Area

A multi-site survey was conducted at 15 sites located in both the Richelieu and St. Lawrence Rivers (Figure 1). Unionids were sampled and calcium concentrations were measured on various dates in late August-early September from 2002 to 2005, whereas substrate composition and percent macrophyte cover were measured at all sites in 2004 and 2005. Sampling sites were selected based on both accessibility and the presence of unionid populations. Sites along the St. Lawrence River were also chosen in order to reflect the natural variability in calcium concentration. A natural calcium gradient exists along the southwest shore of the island of Montreal, as a result of the mixing of calcium-rich water from the St. Lawrence River with calcium-poor water from the Ottawa River (Mellina and Rasmussen, 1994). In contrast, calcium in the Richelieu River remains relatively stable between 16-18mg$\cdot$L^{-1} (de Lafontaine and Cusson, 1997; Ricciardi, unpublished data).

Sampling Procedures

All sites were accessed from shore and were sampled by SCUBA divers. This method minimized the manipulation of fouled unionids, thereby limiting the loss of attached zebra mussels. We collected unionids from a 1m^2 polyvinyl chloride quadrat, cast randomly on the substrate. From 2002 to 2004, it was decided *a priori* to collect five replicate quadrats at each site, which was expected to yield a precision of ± 20% when sampling unionid densities of 10-30 mussels$\cdot$m^{-2} (Downing and Downing, 1992). When few (<10) or no unionids were collected within the first five quadrats, an additional five quadrats were sampled. In 2005, the number of replicates was increased to ten at all sites in order to improve sampling of substrate types and macrophyte cover.

We collected all visible unionids manually from each quadrat and probed the upper 10cm of sediment by hand to collect individuals buried immediately beneath the surface. Each unionid, along with its attached zebra mussels, was sealed in a collection bag underwater. Samples were stored in a cooler and transported to the laboratory within three hours of collection. In the laboratory, we cleaned each live unionid by hand and removed and counted all attached zebra mussels. Zebra mussel fouling intensity was measured by the mean number of live zebra mussels attached to living unionids. In order to minimize impact on the unionid populations in 2005, we processed live unionids that were not fouled by zebra mussels in the field and returned them to their original location.

Mean sediment particle size of each quadrat was determined *in situ* by visually estimating the percent aerial cover of each sediment type. We used thin metal wire to subdivide the $1 m^2$ quadrat into a grid of 16, to aid in accurate estimates of percent cover. Each sediment type was assigned a diameter range modified from the Wentworth scale. The different sediment types were then converted to the phi (Φ) scale by transforming the mean diameter (mm) of the different sediment classes to their $-\log_2$ values (Table 1; Hakanson and Jansson, 1983). The phi value for each sediment type was multiplied by its percent aerial contribution and then summed in order to obtain a mean weighted particle size for each quadrat (Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). The same diver performed all measurements of substrate composition in order to minimize bias. Quadrat data for 2004 and 2005 were combined in order to obtain overall site means for use in statistical analysis.

Macrophyte cover of each quadrat was also determined in situ by visually estimating the percent aerial cover of submerged macrophytes. Since macrophyte cover is likely to show annual variation, an overall site mean was calculated independently for each sampling year and means were $\text{asin}^{-0.5}$ transformed for statistical analyses (Zar, 1999).

Calcium concentration ($[Ca^{2+}] mg \cdot L^{-1}$) at each site was measured by taking replicate water samples (in 1L plastic bottles) that were measured in the laboratory using the LaMotte Hardness Test Kit (Model PHT-CM-DR-LT). Point source data for 2004 and 2005 were combined in order to obtain an overall site mean for use in statistical analysis. For 10 of the 15 sites, we were able to supplement point source data with measurements taken in 2002 and 2003. Also, we added three data points for which calcium concentration and fouling intensity existed to the analysis: one from the Richelieu River (Site 2, see Manuscript 1) and two from the St. Lawrence River (Soulanges Canal East and Lake St. Louis Site 1 from Ricciardi et al., 1996).

Statistical Analyses

Univariate least-squares regression analysis was used to relate the three different environmental variables to fouling intensity. Fouling intensity was measured each sampling year by the mean number of zebra mussels per unionid at each site. Calcium concentration and sediment particle size were measured as overall site means using data from multiple years. Therefore, the response variable for calcium and sediment size was the maximum mean fouling intensity recorded at each site (Table 2). Time since invasion differed in these two systems, but the use of maximum mean was validated by the fact that the maximum mean did not always correspond to the last available year of data. In contrast, macrophyte cover was measured as yearly site means; therefore, the response variable used was the mean fouling intensity of the corresponding sampling year and a separate regression analysis was performed for 2004 and 2005 data. Finally, stepwise multiple regression analysis was used to determine the amount of variation explained by a combination of significant environmental variables. All statistical analyses were performed using SAS Systems for Windows V8 (SAS Institute Inc., Cary, North Carolina).

Results

Over the sampling period, mean fouling intensities ranged from 0 to 36.6 zebra mussels per unionid (Table 2). Only one site (Site 6) has remained free of zebra mussels throughout the sampling period; this St. Lawrence River site corresponds to the one located nearest to the inflow of the Ottawa River.

Calcium concentration and substrate size were each found to explain a significant portion of the variation in fouling intensity of unionids by zebra mussels. Mean fouling intensity increased with calcium concentration (Figure 1), which explained 62% of its variation ($p<0.0001$). Mean fouling intensity increased with decreasing sediment size (Figure 2a), which explained 36% percent of the variation ($p=0.018$). Since calcium concentration is known to have a strong threshold effect (Vinogradov et al., 1993; Jones and Ricciardi, 2005), the relationship was also examined after excluding sites with concentrations < $12 \text{mg}\cdot\text{L}^{-1}$. The same trend was observed (Figure 2b), but in this case 58% of the variation in fouling intensity was explained by mean sediment size ($p=0.01$).

Calcium concentration and sediment size were not correlated with each other (*p*=0.21). Finally, macrophyte cover was not an important predictor of fouling intensity in 2004 or 2005, regardless of whether low calcium sites were excluded from the analysis. Stepwise multiple regression using calcium concentration and sediment size (phi) found that together, these two variables explained 86% of the variation in fouling intensity ($p<0.0001$) in a linear model: $\log(y+0.01) = 0.217 \bullet \text{calcium concentration} + 0.133 \bullet \text{phi} - 3.287$.

Discussion

Fouling by zebra mussels has caused massive mortality of unionid populations in many North American lakes and rivers. Mean fouling intensities in the Great Lakes were on the order of 300-400 zebra mussels per unionid prior to extirpation of unionid populations (Nalepa, 1994; Schloesser and Nalepa, 1994). Unionid extirpation also occurred in the Rideau River, where mean fouling intensities were greater than 600 zebra mussels per unionid (Martel et al., 2001). These fouling intensities were one order of magnitude higher than levels recorded prior to mass die-offs of unionid populations in the St. Lawrence River (Ricciardi et al., 1996). Overall, impacts of unionid fouling by zebra mussels have occurred across a variety of systems despite variation in fouling intensities. Few studies have explored empirical relationships between environmental variables and interspecific interactions between exotic and native organisms. Our results demonstrate that a large portion of the variation in fouling intensity of unionids by zebra mussels is explained by both calcium concentration and substrate size, thereby demonstrating the influence of environmental heterogeneity on the variation of impacts by an exotic species.

Calcium concentration

Freshwater bivalves require calcium for shell growth and maintenance, and calcium concentration has been shown to limit zebra mussel distribution (Ramcharan et al., 1992; Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). Jones and Ricciardi (2005) found that the threshold for zebra mussel occurrence is likely between 8-10mg·L^{-1}, whereas the positive growth of juveniles appears to require concentrations > 8.5mg·L^{-1} (Sprung, 1987) and larval survival requires concentrations > 12mg·L^{-1} (Hinks and

Mackie, 1997). Although not a strong predictor of zebra mussel density, field studies generally demonstrate that adult zebra mussel densities peak at calcium concentrations ≥ 20mg·L^{-1} (Mellina and Rasmussen, 1994; Jones and Ricciardi, 2005). The 18 field sites included in the present model for calcium concentration had values ranging from 9.1 to 24mg·L^{-1} and 16 of these sites had concentrations lower than 20mg·L^{-1}. Although the majority of sampling took place in habitats that are potentially suboptimal for zebra mussels, calcium concentration nonetheless explained 62% of the variation in fouling intensity. Sites with calcium concentrations between 16 and 18mg·L^{-1} were capable of supporting mean fouling intensities greater than 10 zebra mussels per unionid, up to a recorded mean of 36.6 zebra mussels per unionid, which is well within the range of infestations at which significant reductions of unionid populations have occurred (Ricciardi et al., 1996). Thus, we have extended the range of environmental calcium in which zebra mussels are known to exert strong ecological impacts.

One potential factor that may have influenced the results of this study is larval supply. It is conceivable that levels of fouling intensity are partly driven by a gradient in larval supply for sites along the southwest shore of the island of Montreal. Water along the southwest shore of the island results from a mixing of water from the Ottawa River which has no zebra mussels, and water from the St. Lawrence that flows from the densely populated Great Lakes (Mellina and Rasmussen, 1994). This may reduce the number of zebra mussels that are being delivered to sites closest to the Ottawa River outflow. However, calcium concentration at these sites is < 12mg·L^{-1}, which is below that required for larval survival (Hinks and Mackie, 1997). Furthermore, the model includes five sites from the Richelieu River. Lake Champlain has been established as the primary source of zebra mussel veligers to the Richelieu River (de Lafontaine and Cusson, 1997), where there is a steep gradient in zebra mussel abundance with very low abundances downstream of the Chambly basin, a lentic area near the mid-section of the river (de Lafontaine et al. 2002). Presumably, zebra mussel veligers are being trapped in the Chambly basin and limiting supply to the downstream portion of the river. Two of the Richelieu sites included in the model are downstream sites, but the calcium concentration at these sites is greater than 14mg·L^{-1}. In addition, in the Richelieu River, there is no correlation between distance from Lake Champlain and calcium concentration. Overall, the possibility that current-mediated larval supply is driving the calcium model is unlikely because sites from two systems with different larval dynamics are used in the model.

Sediment size

Sediment size has also been shown to be a predictor of zebra mussel occurrence and density (Mellina and Rasmussen, 1994; Karatayev et al., 1998; Jones and Ricciardi, 2005). Adult zebra mussel shell shape is preferentially adapted for attachment to hard substrates, while unionid mussels live at the sediment-water interface (reviewed by Mackie, 1991). Some studies have suggested that live unionids are preferred substrate for settling zebra mussels (Lewandowski, 1976; Ricciardi et al. 1996). This apparent preference has been suggested by Toczylowski et al. (1999) to be a result of the fact that in habitats with soft or unstable sediments, unionids represent the only colonizable hard substrate for zebra mussels since other substrates become silted over or are destabilized by current action. Zebra mussels are particularly sensitive to anoxic conditions in the sediment (Nichols and Wilcox, 1997; Karatayev et al., 1998). Attachment to unionids can help keep zebra mussel clusters out of these anoxic conditions as unionids maintain an upright position in the sediment (Toczylowski et al., 1999).

Our model for sediment size supports these previous findings, as fouling intensity of unionids by zebra mussels increased with decreasing sediment size (i.e., increasing phi). This contrasts the trend found from models that predict zebra mussel density from sediment size; these models show that increasing sediment size (i.e., decreasing phi) is linked to an increase in zebra mussel density (Mellina and Rasmussen, 1994; Karatayev et al., 1998; Jones and Ricciardi, 2005). Because zebra mussel field density and fouling intensity of unionids are strongly correlated (Ricciardi, 2003), one would expect fouling intensities to be greater in rocky habitats. However, results of our model demonstrate that this is not the case, possibly because zebra mussel larvae are selecting and focusing on unionid shells. Studies on post-settlement abundances of zebra mussels indicate that settlement preferences do exist (Marsden and Landsky, 2000; Kobak, 2004); however, active substrate selection was not documented. The observed differences in the abundance of newly settled zebra mussels were found to be related to post-settlement events, such as mortality, emigration and impaired attachment to some substrates (Kobak, 2004).

Context-dependence

These results strongly demonstrate that impacts of invasions are context-dependent, varying with local environment variables. For example, a habitat that is low in calcium may be suboptimal for the formation of dense zebra mussel populations; however, lethal fouling intensities may still occur if unionids in that habitat are the only colonizable substrate for zebra mussels. On the other hand, results also suggest that habitat heterogeneity may play an important role in creating pockets of refugia for native species from the impact of exotic species. For example, unionid populations occurring in rocky habitats with low calcium may be able to escape high fouling intensities and therefore persist in the presence of zebra mussels.

Indeed, unionid populations appear to persist in the presence of zebra mussels in some habitats. Tucker and Atwood (1995) found a diverse unionid assemblage co-occurring with a small zebra mussel population in a contiguous backwater lake of the Illinois River; the main channel of the river was densely colonized with zebra mussels and unionids experienced elevated mortality (Whitney et al., 1995). In Lake Erie, following their extirpation from the deeper waters, living unionids were discovered in nearshore waters of western Lake Erie as well as in wetlands connected to Lake Erie (Schloesser et al., 1997; Nichols and Amberg, 1999; Bowers and de Szalay, 2004). Zanatta et al. (2002) also found diverse unionid assemblages in some deltas and bays of Lake St. Clair. One common characteristic of these apparent refugia is that they are lake-connected habitats subject to large water-level and temperature fluctuations. Such fluctuations may expose zebra mussels to unfavorable environmental conditions and thus limit their survivorship on unionid shells. In addition, when these fluctuations occur in environments with soft sediments, the burrowing behaviour of unionids can help remove attached zebra mussels, which are intolerant of the anoxic conditions in the sediment (Nichols and Wilcox, 1997). Finally, predation has also recently been found to limit the fouling intensity of zebra mussels in one of these lake-connected habitats (Bowers et al., 2005). Together, these examples highlight the importance of considering multiple environmental variables acting together to mediate the interaction between native unionid mussels and exotic zebra mussels.

In summary, results from the multi-site survey have helped to identify two environmental variables that are important in explaining fouling intensity of unionids by zebra mussels. This model could be used to help predict habitats in which impacts of zebra mussels on unionids may be less severe when the two species occur in the same system, which could direct conservation efforts in invaded systems and potentially aid in the identification of possible translocation sites (Cope and Waller, 1995; Hallac and Marsden, 2001). Finally, this study has empirically demonstrated the role of the abiotic environment in contributing to variation in the impact of an exotic species on a native species.

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Figure Captions

Fig. 1 - Map of study sites along the Richelieu River and the St. Lawrence River.

Fig. 2 - Mean fouling intensity as a function of calcium concentration: $\log (y+0.01) = 0.19x - 2.89$ ($r^2 = 0.62$, $p < 0.0001$)

Fig. 3 - Mean fouling intensity as a function of mean sediment size (Φ) for (a) all 15 sampling sites: $\log (y+0.01) = 0.16x - 0.16$ ($r^2 = 0.36$, $p = 0.018$), and (b) excluding sites with calcium concentrations $< 12 \mathrm{mg \cdot L^{-1}}$ (excluded sites are shown as open symbols): $\log (y+0.01) = 0.12x + 0.39$ ($r^2 = 0.58$, $p < 0.01$).

Table 1 – Sediment size classes and associated phi values (modified from the Wentworth scale and Hakanson and Jansson, 1983).

Substrate Type	Mean Diameter (mm)	Phi Value
Clay/Mud	<0.0004	7.966
Silt	0.018	5.816
Sand	1.063	-0.087
Gravel	26	-4.700
Cobble	85	-6.409
Rock	210	-7.714
Boulder	650	-9.344
Bedrock	>1000	-9.966

Table 2- Fouling intensity, macrophyte cover, calcium concentration, and substrate size for the 15 sites sampled along the Richelieu and St. Lawrence rivers (refer to Fig. 1 for site locations). Values reported are the site means with standard errors in parentheses. An asterisk represents instances in which no fouling intensity could be calculated due to the absence of live unionids.

Site	Fouling Intensity (#ZM/unionid)	Macrophytes (% cover)	Maximum Mean Fouling Intensity (#ZM/unionid)	Calcium Concentration (Ca^{2+} mg/L)	Substrate Size (phi value)
Site 1			5.85	15.73 (0.42)	-2.14 (1.20)
2002	5.82 (0.61)				
2003	1.12 (0.31)				
2004	2.6 (0.33)	18.0 (6.4)			
Site 2			36.63	16.53 (0.53)	7.54 (0.43)
2002	24.23 (2.52)				
2003	19.00 (3.61)				
2004	36.63 (5.64)	26.0 (11.8)			
2005	**	52.5 (9.6)			
Site 3			12.40	15.20 (0.98)	4.20 (0.73)
2002	6.20 (0.81)				
2003	4.79 (1.14)				
2004	12.4 (2.97)	47.0 (11.8)			
2005	4.08 (1.14)	11.3 (2.7)			
Site 4			1.10	17.07 (1.07)	-2.11 (1.30)
2002	0.71 (0.19)				
2004	1.10 (0.20)	12.0 (5.1)			
2005	0.56 (0.24)	0.00 (0)			

Site 5			1.00	14.93 (1.75)	3.22 (1.86)
2002	0.42 (0.26)				
2004	1.00 (0)	6.0 (2.6)			
Site 6			0.00	9.20 (0.66)	-2.83 (0.94)
2002	0.00 (0)				
2004	0.00 (0)	16.0 (4.7)			
2005	0.00 (0)	37.0 (9.2)			
Site 7			0.20	9.40 (0.20)	4.00 (0.43)
2004	0.20 (0.03)	56.0 (16.3)			
2005	0.07 (0.02)	21.3 (8.2)			
Site 8			0.11	9.07 (0.48)	4.68 (0.63)
2002	0.06 (0.02)				
2003	0.00 (0)				
2004	0.11 (0.06)	46.0 (14.6)			
2005	0.02 (0.01)	46.0 (10.0)			
Site 9			0.02	11.20 (0.57)	-5.11 (0.55)
2004	0.02 (0.02)	29.0 (5.6)			
2005	0.01 (0.01)	62.5 (4.0)			
Site 10			0.02	11.80 (1.02)	-5.70 (0.17)
2002	0.01 (0.01)				
2004	0.01 (0.01)	77.0 (4.1)			
2005	0.02 (0.01)	39.8 (6.5)			

Site 11			3.00	16.00 (1.20)	1.26 (0.57)
2004	1.25 (0.75)	19.0 (7.1)			
2005	3.00 (-)	10.7 (5.3)			
Site 12			0.50	15.00 (0.60)	-3.99 (0.59)
2004	**	55.0 (5.3)			
2005	0.50 (0.50)	39.0 (8.9)			
Site 13			4.50	18.20 (1.00)	2.60 (0.34)
2002	1.16 (0.37)				
2004	2.38 (0.65)	78.5 (2.4)			
2005	4.50 (1.32)	87.5 (2.3)			
Site 14			6.00	18.20 (1.00)	2.33 (0.72)
2002	5.27 (0.90)				
2003	**				
2004	6.00 (4.34)	79.5 (5.1)			
2005	**	79.0 (3.3)			
Site 15			1.44	19.40 (1.80)	-1.40 (0.62)
2004	1.27 (0.21)	77.0 (5.4)			
2005	1.44 (0.19)	75.0 (6.3)			

Fig 1.

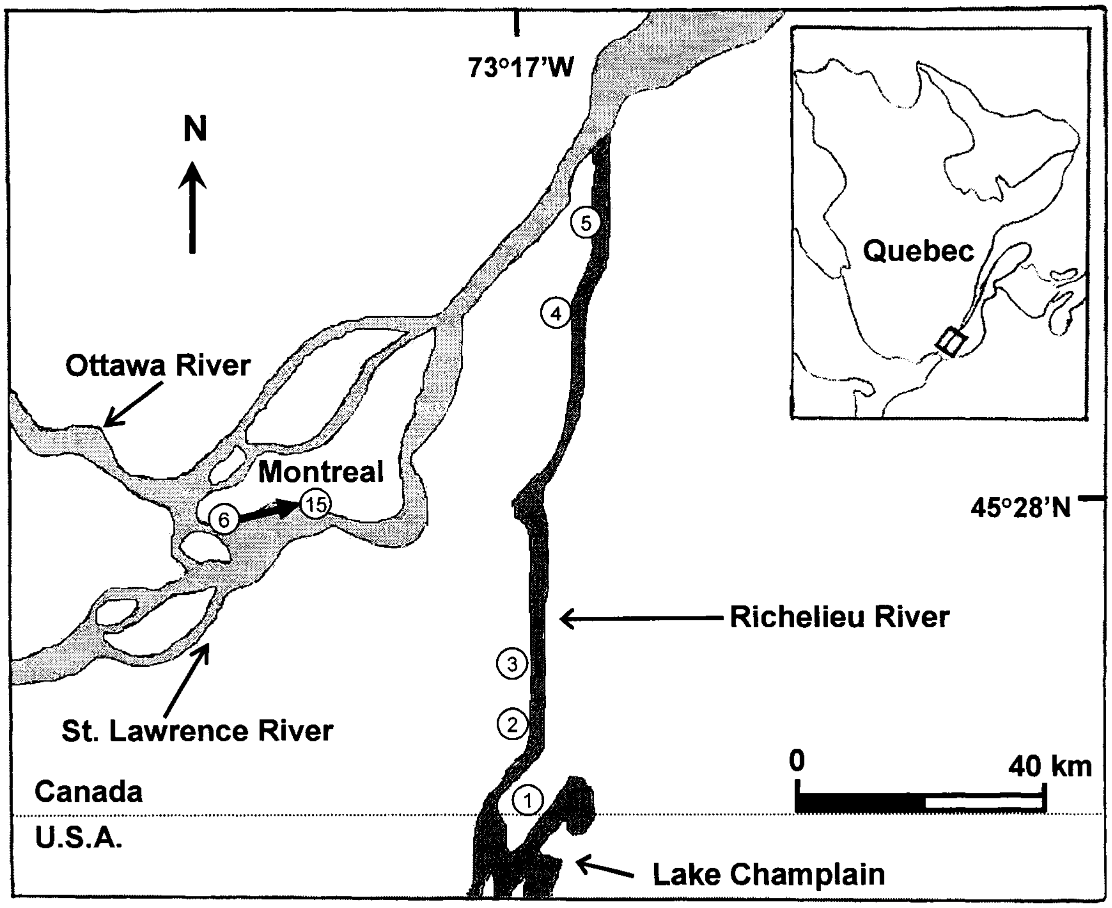
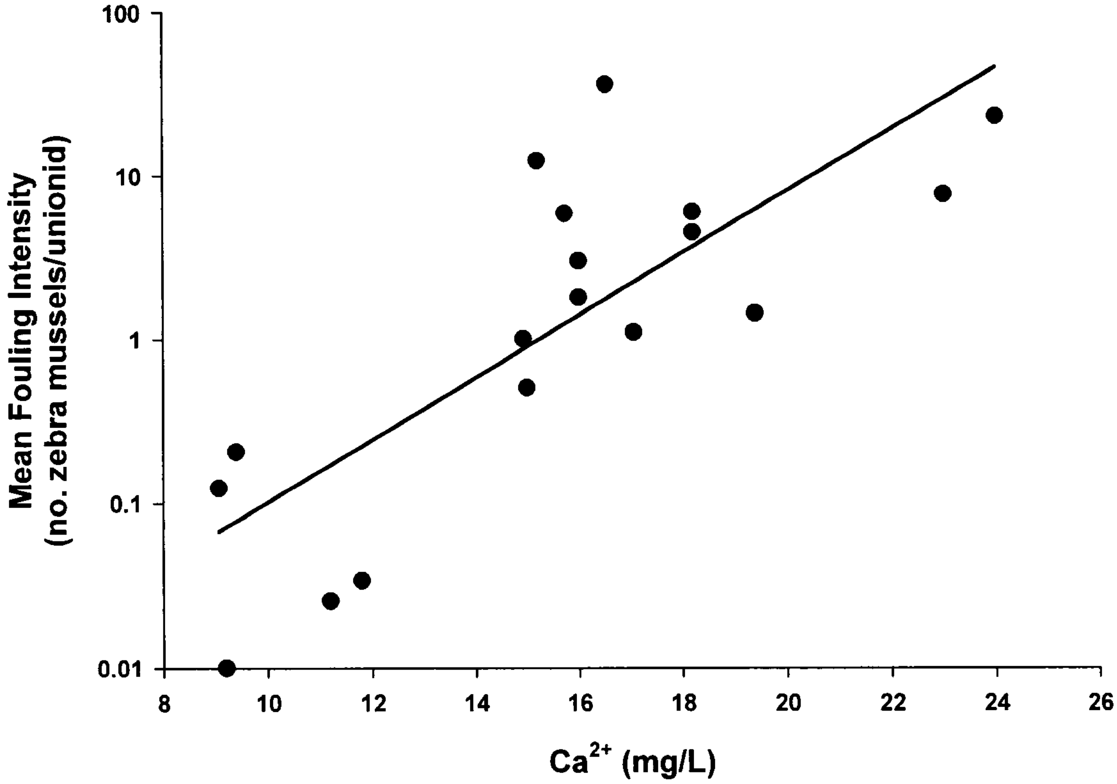
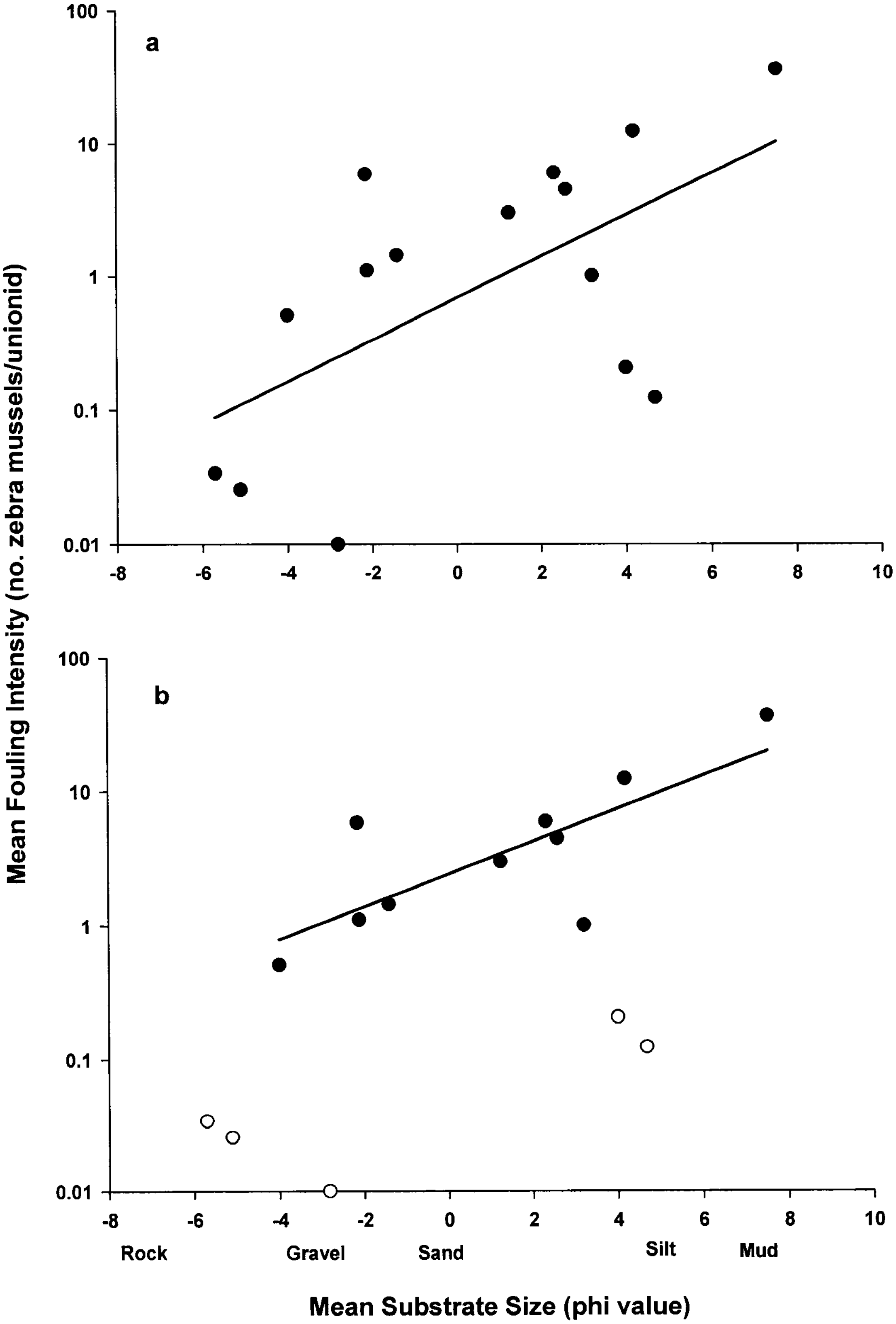

73°17'W
N
Quebec
Ottawa River
Montreal
6
15
5
4
45°28'N
Richelieu River
3
2
St. Lawrence River
0
40 km
Canada
1
U.S.A.
Lake Champlain

Fig. 2



Mean Fouling Intensity
(no. zebra mussels/unionid)
100
10
1
0.1
0.01
8
10
12
14
16
18
20
22
24
26
Ca^{2+} (mg/L)

Fig. 3


a
b
100
10
1
0.1
0.01
-8
-6
-4
-2
0
2
4
6
8
10
Rock
Gravel
Sand
Silt
Mud
Mean Fouling Intensity (no. zebra mussels/unionid)
Mean Substrate Size (phi value)

General Conclusion

The human-mediated introduction of species beyond their native range is a global environmental problem, which can only be expected to increase over time as global trade increases and associated vectors proliferate. A central goal of invasion ecology is to gain a predictive understanding of the impact of introduced species on their recipient communities (Parker et al., 1999). Being able to predict impacts of invaders is essential for risk assessment and prioritizing management responses to various invasion threats. However, predictive ability is complicated by abiotic and biotic factors that influence the interaction between the invader and its local environment.

One of the most conspicuous impacts of the zebra mussel (*Dreissena polymorpha*) invasion to North America has been the decimation of native unionid mussel populations. North American unionid assemblages are the most diverse on the planet (Williams et al., 1993). Therefore, a predictive understanding of the impact of zebra mussels on unionids over a broad range of environmental conditions is of interest to conservation biology, and could help identify habitats where unionids can escape lethal fouling by zebra mussels. The identification of such habitats would permit targeted conservation efforts (Cope and Waller, 1995).

In Chapter 1, I explored the fouling and associated mortality of unionid populations in a low-calcium river and compared these data to those from calcium-rich systems, which are thought to be more hospitable for zebra mussels. I found a similar relationship between fouling intensity by zebra mussels and the mortality of unionid populations in both these high and low calcium environments, suggesting that the overall impact of zebra mussels on unionids can be predicted over a broad range of habitats. However, I found greater variation in the low-calcium relationship, indicating the influence of other environmental stressors that may be important in contributing to unionid mortality in this particular system.

In Chapters 2 and 3, I explored specific factors of the biotic and abiotic environment on the fouling intensity of unionids. I found that exposure to predators at the experimental site did not significantly reduce fouling intensities, and was therefore not likely an important factor in mediating the interaction between the invasive and native mussels, at least in that area of the river. I also developed a predictive model of fouling intensity based on local calcium concentration and sediment particle size. This model demonstrates the context-dependency of the impact of zebra mussels, but also shows that a small number of environmental factors can explain a substantial fraction of the variation in impact.

Future Directions

The research that I have conducted in both the Richelieu and St. Lawrence Rivers has identified unionid populations that have persisted thus far despite the long-term presence of zebra mussels. Furthermore, based on the predictive model developed in the third chapter, some of these sites are expected to maintain very low fouling intensities over time. It would be of interest to continue long-term monitoring of these unionid populations to determine whether these sites can serve as permanent refugia. Such long-term monitoring should include assessments of reproductive success at these sites by including more detailed studies of unionid recruitment.

In addition, results from the Richelieu River have pointed to the possible influence of environmental stressors other than zebra mussels that are contributing to the mortality of unionid populations. At this point in time, very little quantitative information exists concerning the overall levels of urban, agricultural, and industrial pollution received by the river (Groison, 2000) and how they may be affecting unionid populations in the Richelieu River. If the Richelieu River is indeed providing some habitats where unionids can coexist with zebra mussels, an environmental assessment impact outlining other significant stressors and how they may be mitigated will be necessary for unionid conservation.

Finally, it would be of interest to test the large-scale applicability of the predictive model developed in the third chapter by testing its robustness in other invaded systems. Studies identifying possible unionid refugia were discussed in the third chapter and could serve as environments in which to test and, or refine the predictive model developed.

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