Influence of physicochemical factors on the distribution and biomass of invasive mussels (*Dreissena polymorpha* and *Dreissena bugensis*) in the St. Lawrence River

Lisa A. Jones and Anthony Ricciardi

Abstract: Twenty sites along the St. Lawrence River were sampled to determine if the distribution and abundance of invasive mussels (zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*)) are explained by physicochemical variables. Calcium concentration, substrate size, and depth independently explained significant proportions of variation in biomass for both species. Zebra mussel populations occurred at calcium levels as low as 8 mg $Ca \cdot L^{-1}$, but quagga mussels were absent below 12 mg $Ca \cdot L^{-1}$, suggesting that they have higher calcium requirements. Both species increased in biomass with increasing substrate size but displayed contrasting patterns with depth. Using combinations of these environmental variables, we developed stepwise multiple regression models to predict zebra mussel biomass and quagga mussel biomass. The zebra mussel model included calcium concentration, substrate size, and depth ($r^2 = 0.36$, $P < 0.0001$), while the quagga mussel model included only substrate size and depth ($r^2 = 0.32$, $P < 0.0001$). These results suggest that dreissenid mussel abundance (and correlated impacts) will vary predictably across environmental gradients, but the same predictive model will not be accurate for both species.

Résumé : Nous avons échantillonné 20 sites le long du Saint-Laurent pour voir s'il est possible d'expliquer la répartition et l'abondance des moules envahissantes (la moule zébrée (*Dreissena polymorpha*) et la moule quagga (*Dreissena bugensis*)) d'après les variables physico-chimiques. Les concentrations de calcium, la taille du substrat et la profondeur expliquent de façon indépendante des portions importantes de la variation en biomasse des deux espèces. Les populations de moules zébrées se retrouvent à des concentrations de calcium aussi faibles que 8 mg $Ca \cdot L^{-1}$, mais les moules quagga sont absentes aux concentrations inférieures à 12 mg $Ca \cdot L^{-1}$, ce qui indique que ces dernières ont des besoins plus élevés en calcium. Les biomasses des deux espèces augmentent en fonction de la taille du substrat, mais elles suivent des patrons différents en fonction de la profondeur. En combinant ces variables du milieu, nous avons mis au point des modèles de régression multiple pas à pas pour prédire les biomasses des moules zébrées et des moules quagga. Le modèle des moules zébrées comprend les concentrations de calcium, la taille du substrat et la profondeur ($r^2 = 0{,}36$, $P < 0{,}0001$) et celui de la moule quagga contient seulement la taille du substrat et la profondeur ($r^2 = 0{,}32$, $P < 0{,}0001$). Ces résultats indiquent que l'abondance des bivalves dreissénidés et les impacts reliés varient de façon prédictive le long de gradients de l'environnement, mais qu'un même modèle prédictif ne peut être précis pour les deux espèces.

[Traduit par la Rédaction]

Introduction

A central goal of ecology is to explain patterns of species distribution and abundance. A predictive understanding of such patterns for invasive species, in particular, has both fundamental and applied importance because effective management of the damage caused by invasive species requires advanced knowledge of where the impact will be greatest (Parker et al. 1999). The impact of an invader is strongly correlated with its abundance (Parker et al. 1999; Ricciardi 2003); therefore, by relating an invader's abundance to environmental variables, predictive models can be developed that would help managers anticipate which habitats will be most affected by invasion. A valuable approach toward developing such models is the statistical synthesis of multisite data from invaded regions (Ramcharan et al. 1992; Mellina and Rasmussen 1994; MacIsaac et al. 2000).

Predictive models are rare for aquatic invasive species, including the zebra (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*), whose introduction into the Great Lakes in the late 1980s resulted in significant ecological and economic impacts (O'Neill 1997; Vanderploeg et al. 2002). Both species are native to rivers in the Black Sea region (Rosenberg and Ludyanskiy 1994) and were likely introduced via ballast water discharge from transoceanic vessels. The zebra mussel was first detected in Lake St. Clair in 1988 (Hebert et al. 1989) and has since spread rapidly into most river systems and hundreds of inland lakes in eastern North

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America (Ram and McMahon 1996). Quagga mussels were recorded only a year later in Lake Erie but have had a much more limited range expansion, thus far restricted mainly to the lower Great Lakes and the upper St. Lawrence River (Mills et al. 1993, 1996). By 1992, both species were present throughout the St. Lawrence River between Lake Ontario and Montreal, Quebec (Ricciardi et al. 1996). Initial colonization of the St. Lawrence River by dreissenid mussels is assumed to be the result of an eastward expansion through the lower Great Lakes and passive downstream dispersal from Lake Ontario (Griffiths et al. 1991; Mills et al. 1993). Today, the St. Lawrence River is still the only large North American river invaded by both species.

Although zebra mussels have an invasion history spanning nearly two decades in North America and extensive studies have been conducted on their life history and ecology, there exist few models to predict their distribution and abundance. Current models for zebra mussel populations in lakes and rivers are derived from their physiological and ecological requirements and include environmental factors such as calcium concentration (Ramcharan et al. 1992; Mellina and Rasmussen 1994), substrate size (Mellina and Rasmussen 1994), pH (Ramcharan et al. 1992), and total phosphorus (Wilson and Sarnelle 2002). In the St. Lawrence River, calcium concentration and substrate size have been found to have the strongest influence on zebra mussel occurrence and population density, respectively (Mellina and Rasmussen 1994). Zebra mussels require calcium for shell growth and osmoregulation (Vinogradov et al. 1993; McMahon 1996) and their populations are not viable below a threshold concentration estimated to be approximately 15 mg $Ca \cdot L^{-1}$ (Mellina and Rasmussen 1994). In addition, hard substrate is required for the settlement and survival of postveliger zebra mussels, at least during the early stages of invasion (Stanczykowska 1977; Lewandowski 1982). Indeed, zebra mussel density was correlated with substrate size in the St. Lawrence River in the early 1990s (Mellina and Rasmussen 1994). Zebra mussels preferentially settle and reach peak densities on hard substrates such as bedrock and boulders (Dermott and Munawar 1993). Over time, however, zebra mussels also colonize soft sediments, in some cases reaching densities comparable with those found on hard substrates (Berkman et al. 1998, 2000; Haltuch et al. 2000). Therefore, as time progresses, the strength of the relationship between zebra mussel density and substrate size could weaken. After more than a decade since the colonization of the St. Lawrence River, it is of interest to know whether the relationships observed by Mellina and Rasmussen (1994) still hold for zebra mussels and whether similar relationships exist for quagga mussels.

To date, no predictive models of abundance exist for quagga mussels and little is known about their environmental tolerances (McMahon 1996). Although the two species are closely related, they appear to have different patterns of distribution and abundance in relation to environmental factors. For example, zebra mussels preferentially colonize and dominate hard substrates in shallow waters (Dermott and Munawar 1993; Karatayev et al. 1998), whereas quagga mussels colonize a broader range of depths and substrates, often dominating colder, deeper waters and fine sediments (Dermott and Munawar 1993; Claxton et al. 1998; Mills et al. 1999). Therefore, different models may be required to predict the abundance of each species.

The objective of this study was to determine whether variation in dreissenid biomass in the upper St. Lawrence River (from the outflow of Lake Ontario to the Island of Montreal) is explained by calcium concentration, substrate size, and depth. We hypothesized that (*i*) calcium concentration would predict the occurrence but not the abundance of zebra and quagga mussels, (*ii*) substrate size would have no significant influence on zebra and quagga mussel biomass, and (*iii*) zebra mussel biomass would be greatest in shallow waters, while quagga mussel biomass would be greatest in deeper waters.

Methods

Study area

From mid-July to early September 2003, we sampled 20 sites located along the St. Lawrence River system between Prescott, Ontario, and Lac St. Louis at Lachine, Quebec (Fig. 1). Each site was sampled once over an approximate area of 100 m^2. This portion of the river was chosen because of the large variability in substrate quality and calcium concentration. A distinct calcium gradient occurs along the southwest shore of the island of Montréal, where the humic water of the Ottawa River mixes with the alkaline water of the main stem of the St. Lawrence River (Mellina and Rasmussen 1994). Ten of our study sites were established within this gradient to capture the variability in calcium (Fig. 1). Sampling depth across all sites ranged from 0.6 to 8.8 m (Table 1).

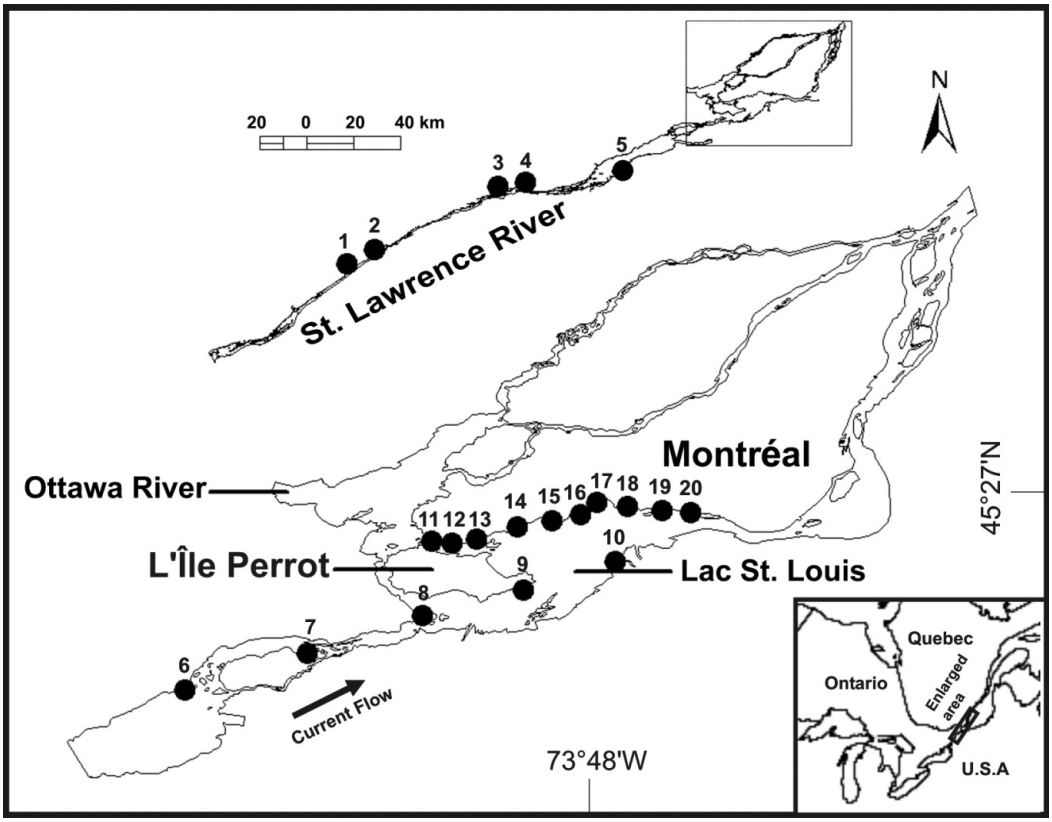
Sampling techniques

All sites were accessed from shore using self-contained underwater breathing apparatus (SCUBA), which allowed for accurate observation of bottom substrate. At each site, 10 replicate quadrats (enclosed by a 0.25-m^2 polyvinylchloride frame) were randomly placed on the bottom substrate (or on the canal walls at site 8; Table 1), with approximately 5–6 m between replicates. Owing to logistical constraints, fewer quadrats (five to nine) were sampled at three sites, and to capture local variability in depth and substrate, 11–16 quadrats were sampled at three other sites (Table 1). Water depth was measured at each quadrat location.

Substrate size

Substrate composition was determined in situ by visually estimating the percent areal coverage of each substrate type within the quadrat (listed in Table 2). The frame of the quadrat was premarked at specified intervals to ensure accurate estimations. If substrate composition was visibly homogenous, then mussels were collected from a smaller quadrat (0.0625 m^2) that was randomly placed within the 0.25-m^2 frame. Substrate size was classified a priori using a modification of the Wentworth classification (Hakanson and Jansson 1983). The average diameter (d) in millimetres for each substrate type was converted to the phi scale by transforming them to their negative log base 2 ($-\log_2 d$) values (Table 2). The phi value for each substrate type was multiplied by its percent areal cover and then summed to give the mean weighted particle size for each quadrat (following

Fig. 1. Map of study sites along the St. Lawrence River. All sites are located between the outflow of Lake Ontario to the eastern tip of the island of Montréal (shown expanded).



Mellina and Rasmussen 1994). The ability to correctly classify substrate types in situ was verified by comparing visual estimations with measured diameters for 10 quadrats. Differences between these two methods did not exceed 5%. All measurements were performed by the same diver to minimize bias in assessing substrate characteristics.

Biomass

To estimate dreissenid biomass, we removed all visible mussels within the quadrat by hand and placed in marked, plastic collection bags. Quadrats were reexamined by two divers to ensure that no mussels were missed. Collection bags were stored in a cooler and transported back to the laboratory within 3 h of collection. Once in the laboratory, mussels were cleaned by hand, rinsed through a 1.0-mm-mesh sieve, and blotted dry to remove excess water. To minimize variation in wet mass during processing, we stored samples with water refrigerated at 4 °C until they were measured. This method successfully reduced the problem of shell gaping. We measured fresh mass (wet weight including shells) for zebra and quagga mussels to the nearest 0.1 g using an electronic balance. Biomass, rather than density, was the chosen measure of abundance because it is a better predictor of an invader's impact (Young et al. 1996; Wilson and Sarnelle 2002) and is less sensitive to errors caused by the incomplete removal of small, newly settled mussels from quadrats. We identified all mussels to species using a combination of morphological characters (Pathy and Mackie 1993; Claxton et al. 1997). The shell morphology of many quagga mussels collected at site 9 (Table 1) had external shell features that made identification difficult. The ventral surface was flattened with a ventrolateral ridge, as is occasionally observed in zebra mussels. Therefore, genetic analysis (mtDNA cytochrome *b* gene with polymerase chain reaction and autosequencing; Stepien et al. 2003) was used to confirm the species identity of these mussels (C.A. Stepien, Lake Erie Center, University of Toledo, 6200 Bayshore Road, Oregon, OH 43618, USA, personal communication).

Calcium concentration

On each sampling occasion, we took two water samples in 1.0-L plastic bottles. From these samples, calcium concentration (milligrams Ca^{2+} per litre, converted from milligrams $CaCO_3$ per litre) was measured with a LaMotte hardness model PHT-CM-DR-LT kit (LaMotte Company, Chestertown, Maryland) and the mean of the two sample measurements was used in our statistical analysis. For half of the sites, we were able to compare our values with measurements taken during the summer of 2002 and 2003, and they were found to be similar (±2 mg $Ca \cdot L^{-1}$).

Statistical analyses

All statistical analyses were performed using the SAS System for Windows V8 (SAS Institute Inc., Cary, North Carolina). To avoid violating assumptions underlying regression analysis and to directly test for the effect of local environmental variables on variation in biomass, we removed all quadrats with zero mussel biomass from the analysis. To test the putative calcium threshold of 15 mg $Ca \cdot L^{-1}$ (Mellina and Rasmussen 1994), we used χ^2 analysis to examine whether

Table 1. Dreissenid biomass and physicochemical variables for 20 sites sampled along the St. Lawrence River (refer to Fig. 1 for site locations).

Site	No. of quadrats	Species	Biomass ($g \cdot m^{-2}$)	Substrate size (phi scale)	Depth (m)	Ca^{2+} ($mg \cdot L^{-1}$)
1	11	Z	86.1 (30.5)	–0.04 (2.0)	5.8 (0.8)	28.8 (0.2)
		Q*	622.8 (167.3)			
2	10	Z*	600.6 (143.4)	–0.84 (0.5)	2.7 (0.1)	28.4 (0.1)
		Q	177.6 (68.8)			
3	10	Z	78.6 (31.0)	–5.46 (1.4)	2.2 (0.4)	25.6 (0.1)
		Q	90.4 (36.0)			
4	10	Z*	370.5 (91.1)	–2.77 (1.4)	1.4 (0.1)	28.8 (0.3)
		Q	32.5 (7.3)			
5	10	Z	260.6 (73.6)	0.91(1.5)	3.0 (0.1)	26.0 (0.2)
		Q	33.8 (15.6)			
6	10	Z	1969.0 (423.7)	–7.92 (0.4)	2.1 (0.2)	30.0 (0.7)
		Q	1384.9 (431.0)			
7	10	Z	1588.1 (293.1)	–8.71 (0.2)	1.9 (0.4)	22.4 (0.1)
		Q	896.2 (243.8)			
8	16	Z	479.9 (118.2)	–4.04 (2.1)	3.5 (0.3)	26.0 (2.2)
		Q*	1722.6 (309.6)			
9	10	Z	690.7 (155.1)	–9.13 (0.1)	2.0 (0.2)	26.4 (1.2)
		Q	788.4 (198.6)			
10	10	Z*	1435.8 (200.5)	–6.56 (0.7)	1.5 (0.2)	24.8 (0.6)
		Q	153.4 (55.7)			
11[a]	10	Z	0.0	–6.09 (0.8)	1.5 (0.2)	7.6 (0.5)
		Q	0.0			
12	10	Z	5.4 (4.0)	8.81 (0.2)	1.3 (0.1)	10.0 (0.5)
		Q	0.0			
13	15	Z*	12.6 (4.2)	7.62 (0.3)	1.3 (0.1)	9.6 (0.1)
		Q	0.0			
14	9	Z	3.4 (2.0)	–6.52 (0.2)	1.3 (0.1)	8.0 (0.4)
		Q	0.0			
15	10	Z*	266.8 (91.2)	3.18 (1.4)	1.5 (0.2)	12.4 (0.2)
		Q	5.6 (3.0)			
16	5	Z	487.5 (118.8)	4.10 (2.4)	1.7 (0.1)	14.4 (0.4)
		Q	12.5 (10.9)			
17	10	Z*	457.0 (82.6)	7.52 (0.5)	1.4 (0.1)	23.8 (0.1)
		Q	21.4 (13.7)			
18	8	Z*	758.1 (412.3)	–3.08 (1.9)	1.5 (0.1)	13.2 (0.1)
		Q	44.2 (27.4)			
19	10	Z*	168.4 (51.3)	–7.72 (0.5)	1.3 (0.1)	18.4 (0.4)
		Q	7.1 (5.6)			
20	10	Z*	2183.4 (536.1)	–8.55 (0.4)	1.7 (0.1)	23.6 (0.6)
		Q	28.9 (12.2)			

Note: Values reported are the site means with standard error in parentheses. An asterisk indicates species with significantly higher average biomass per one square metre ($P < 0.05$) following sequential Bonferroni correction at $\alpha = 0.05$. Z, zebra mussels (*Dreissena polymorpha*); Q, quagga mussels (*Dreissena bugensis*).

[a]No statistical test done; biomass = 0 for both zebra mussels and quagga mussels.

the frequency of zero biomass values for both zebra and quagga mussels was independent of being above or below this threshold. In all regression analyses, zebra and quagga mussel biomass values were log transformed to reduce the influence of any extreme values and to stabilize variance (Downing 1979). Separate sequential Bonferroni corrections ($\alpha = 0.05$) were used to control the overall error rate of multiple tests (Rice 1989).

Univariate models were used to determine the variation in biomass across all quadrats that could be accounted for by individual predictor variables. Both linear and curvilinear regressions were tested. All significant regression slopes (both zebra and quagga mussels) were tested for homogeneity (Zar 1999). Finally, stepwise multiple regression models were developed to determine the combinations of environmental variables that explained the most variation in zebra mussel and quagga mussel biomass across quadrats.

Results

Mean zebra mussel and quagga mussel biomass varied broadly across sites (from 0 to 2183.4 ± 536.1 $g \cdot m^{-2}$ and

Table 2. Substrate size classification and calculated phi values (modified from the Wentworth scale and Hakanson and Jansson (1983)).

Substrate type	Average diameter (mm)	Phi value
Clay–mud	<0.002	9.000
Silt	0.010	6.500
Sand	0.250	2.000
Gravel	13.250	–3.728
Cobble	73.000	–6.190
Rock	210.500	–7.718
Boulder	400.000	–8.644
Bedrock or artificial substrate	>700.000	–9.451

from 0 to 1722.6 ± 309.6 $g \cdot m^{-2}$, respectively) (Table 1). Zebra mussels were found at 19 of the 20 sites and had a significantly higher biomass than quagga mussels at nine of these sites (t tests, $P < 0.005$, significant after sequential Bonferroni correction) (Table 1). Quagga mussels were present at 16 of the 20 sites but had a significantly higher biomass than zebra mussels at only two sites: site 8 (Soulanges Canal) and site 1 (Prescott, Ontario) (t tests, $P < 0.006$, significant after sequential Bonferroni correction) (Table 1). Only one site, located at the outflow of the Ottawa River (site 11), was devoid of both zebra and quagga mussels (Table 1; Fig. 1).

Calcium concentration, substrate size, and depth independently explained significant proportions of variation in biomass for both species (Table 3). Calcium concentration alone explained 21% and 10% of the variability in zebra mussel and quagga mussel biomass, respectively. Zebra mussel biomass increased with calcium concentrations up to 25 $mg \cdot L^{-1}$ but was reduced at sites with calcium concentrations above 25 mg $Ca \cdot L^{-1}$ (Fig. 2*a*). We found a strong log-linear relationship for zebra mussel biomass versus calcium below the putative threshold of 15 mg $Ca \cdot L^{-1}$ ($r^2 = 0.51$, $P < 0.0001$), but no relationship was found above 15 mg $Ca \cdot L^{-1}$ ($P = 0.21$).

Quagga mussel biomass was related to calcium concentration by a simple linear model ($r^2 = 0.10$, $P = 0.0005$) (Fig. 2*b*). For both zebra mussels and quagga mussels, χ^2 analysis revealed a higher than expected frequency of zero biomass values located below 15 mg $Ca \cdot L^{-1}$ than above ($\chi^2 = 48.39$, df = 1, $P = 0.001$, and $\chi^2 = 91.51$, df = 1, $P = 0.001$, respectively). Quagga mussels did not occur at sites below 12 mg $Ca \cdot L^{-1}$, and zebra mussels did not occur at sites below 8 mg $Ca \cdot L^{-1}$.

Both zebra and quagga mussel biomass declined with decreasing substrate size (i.e., increasing phi value), which explained 20% and 11% of the variation in their respective biomasses (Fig. 3). Nonetheless, high levels of biomass for both species were still observed in quadrats dominated by silt–mud (Fig. 3). The relationship between biomass and substrate size was not significantly different between species ($b_{D.\ polymorpha} = –0.05$, $b_{D.\ bugensis} = –0.05$; t test, $P > 0.50$ and $\text{intercept}_{D.\ polymorpha} = 2.27$, $\text{intercept}_{D.\ bugensis} = 1.96$; t test, $P > 0.50$).

Regression slopes for biomass against depth were significantly different for the two species ($b_{D.\ polymorpha} = –0.12$ and $b_{D.\ bugensis} = 0.16$; t test, $P < 0.05$). Quagga mussel biomass increased with depth (Fig. 4*a*), whereas zebra mussel biomass decreased with depth (Fig. 4*b*). Depth explained only a small proportion (≤10%) of the variation in biomass for either species.

Stepwise multiple regression showed that substrate size, calcium concentration, and depth collectively explained 36% of the variation in zebra mussel biomass ($P < 0.0001$) (Table 4). Only substrate size and depth significantly explained variation in quagga mussel biomass ($r^2 = 0.32$, $P < 0.0001$) (Table 4). Results for both models were robust to the order in which variables were entered.

Discussion

Few studies have attempted to develop empirical models of zebra mussel occurrence or abundance in river systems. No such attempt has been made for quagga mussels. To date, models of zebra mussel occurrence have been constructed from limnological variables (e.g., water hardness), while abundance models have included some measure of substrate availability. Here, we use an approach that combines these variables. Our analysis shows that about one third of the variation in dreissenid biomass in the upper St. Lawrence River is explained by calcium concentration, substrate size, and depth.

Calcium concentration as a predictor

Zebra mussels require calcium for shell production, growth, and survival. Previous studies have shown that calcium concentration limits the occurrence of zebra mussels but has proven to be a poor predictor of their numerical density (Stanczykowska 1964; Ramcharan et al. 1992; Mellina and Rasmussen 1994). In regards to occurrence, laboratory studies have found the minimum calcium threshold for normal development and long-term survival of zebra mussels to range from 8.5 to 12 mg $Ca \cdot L^{-1}$ (Sprung 1987; Vinogradov et al. 1993; Hincks and Mackie 1997). Meanwhile, field studies in North America to date have found no zebra mussels below 15 mg $Ca \cdot L^{-1}$ (Mellina and Rasmussen 1994; Strayer et al. 1996; Allen and Ramcharan 2001). Our study lends equivocal support for this threshold. More empty (zero biomass) quadrats occurred at sites with calcium levels below the 15 mg $Ca \cdot L^{-1}$ threshold than expected by chance. However, even at calcium levels below this threshold, quadrats were found containing zebra mussels, including some with high biomass (up to 3225.6 $g \cdot m^{-2}$ at 13 mg $Ca \cdot L^{-1}$, site 18). It was not until concentrations below 10 mg $Ca \cdot L^{-1}$ that zebra mussel biomass declined precipitously and until 7.6 mg $Ca \cdot L^{-1}$ that mussels were absent. This suggests that the threshold for occurrence may be between 8 and 10 mg $Ca \cdot L^{-1}$, which is consistent with the findings of Hincks and Mackie (1997), who reported negative growth of juvenile zebra mussels at calcium levels below 8.5 mg $Ca \cdot L^{-1}$. Whether zebra mussels are able to reproduce in such low calcium concentrations remains to be tested, but it indicates that at least settlement and growth are possible. This apparent lower calcium threshold for zebra mussels may be a reflection of their adaptive ability. Zebra mussels are a phenotypically plastic and fecund species with a high potential for rapid adaptation to new environments (Mills et al.

Table 3. Univariate linear regressions of three physicochemical variables with log-transformed biomass for zebra mussels (*Dreissena polymorpha*) (n = 162) and quagga mussels (*Dreissena bugensis*) (n = 123).

	Zebra mussels					Quagga mussels			
Variable	b (SE)	b_1 (SE)	Intercept (SE)	r^2	P	b (SE)	Intercept (SE)	r^2	P
$[Ca^{2+}]$ (mg·L^{-1})	0.29 (0.06)	–0.01 (0.002)	–0.64 (0.56)	0.21	<0.0001	0.06 (0.02)	0.60 (0.44)	0.10	0.0005
Substrate size (mm)	–0.05 (0.01)	—	2.27 (0.06)	0.20	<0.0001	–0.05 (0.01)	1.96 (0.09)	0.11	<0.0001
Depth (m)	–0.12 (0.04)	—	2.69 (0.10)	0.05	0.0030	0.16 (0.04)	1.79 (0.13)	0.10	0.0005

Note: Quadrats with zero zebra or quagga mussel biomass were excluded from their respective analyses. Regressions shown are significant after sequential Bonferroni correction (α = 0.05). b is slope and b_1 is slope for the second-degree term (calcium^2) for the quadratic linear regression model.

Fig. 2. Relationship between (*a*) zebra mussel (*Dreissena polymorpha*) and (*b*) quagga mussel (*Dreissena bugensis*) biomass (log transformed) and calcium concentration across quadrats. Quadrats with zero biomass for zebra mussels or quagga mussels were excluded from their respective analyses. The regression equations for zebra and quagga mussel biomass, respectively, are log biomass = –0.64 + 0.29·calcium – 0.01·calcium^2 (r^2 = 0.21, P < 0.0001, n = 162) and log biomass = 0.60 + 0.06·calcium (r^2 = 0.10, P = 0.0005, n = 123). The dotted line (*i*) represents the threshold calcium concentration of 15 mg·L^{-1} below which no zebra mussels were found in a previous study in the St. Lawrence River (Mellina and Rasmussen 1994).

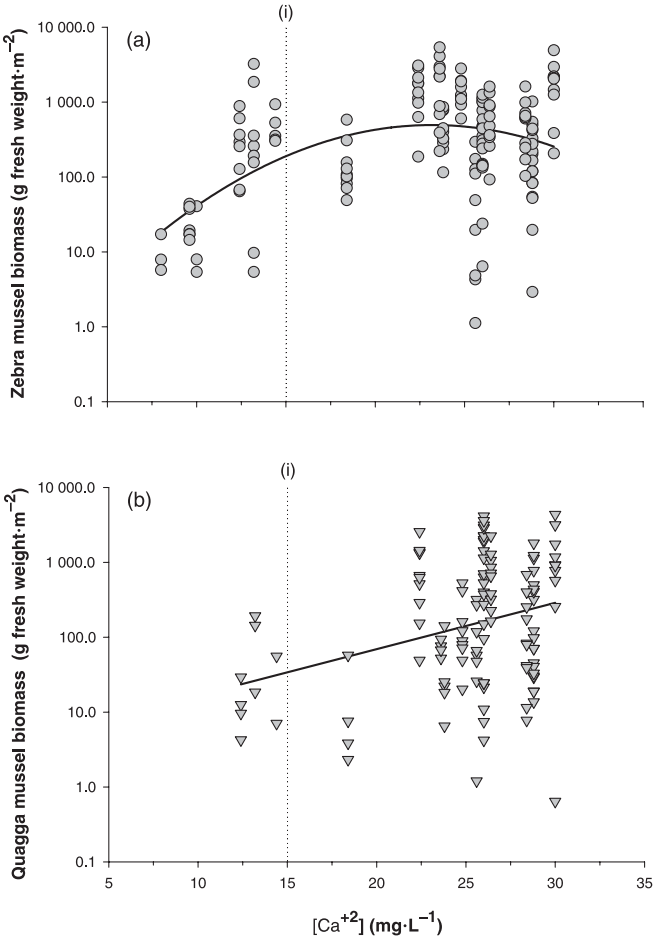
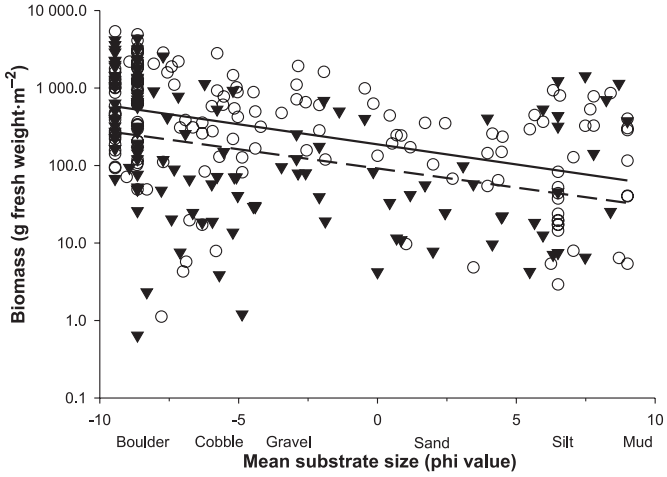


Fig. 3. Relationship between zebra mussel (*Dreissena polymorpha*) (circles, solid line) and quagga mussel (*Dreissena bugensis*) (triangles, broken line) biomass (log transformed) and substrate size expressed as mean weighted phi value (–log$_2$, mm) per quadrat. Quadrats with zero biomass for zebra mussels or quagga mussels were excluded from their respective analyses. The regression equations for zebra and quagga mussel biomass, respectively, are log biomass = 2.27 – 0.05·substrate size (r^2 = 0.20, P < 0.0001, n = 162) and log biomass = 1.96 – 0.05·substrate size (r^2 = 0.11, P = 0.0001, n = 123).



1996). Therefore, while the presence of a dense zebra mussel population below 12 mg Ca·L^{-1} is highly unlikely, predictions that use this critical value to map the potential spread of zebra mussels (e.g., Neary and Leach 1992) may ultimately underestimate zebra mussel distribution. In summary, zebra mussel biomass in the St. Lawrence River increased linearly with increasing calcium concentrations below 15 mg Ca·L^{-1}, peaked between 23 and 25 mg Ca·L^{-1}, and decreased thereafter, suggesting a unimodal response to calcium concentration. A negative effect of high calcium levels was also observed by Hincks and Mackie (1997), who found that adult mortality increased above 25 mg Ca·L^{-1} and maximum juvenile growth rates decreased above 32 mg Ca·L^{-1}.

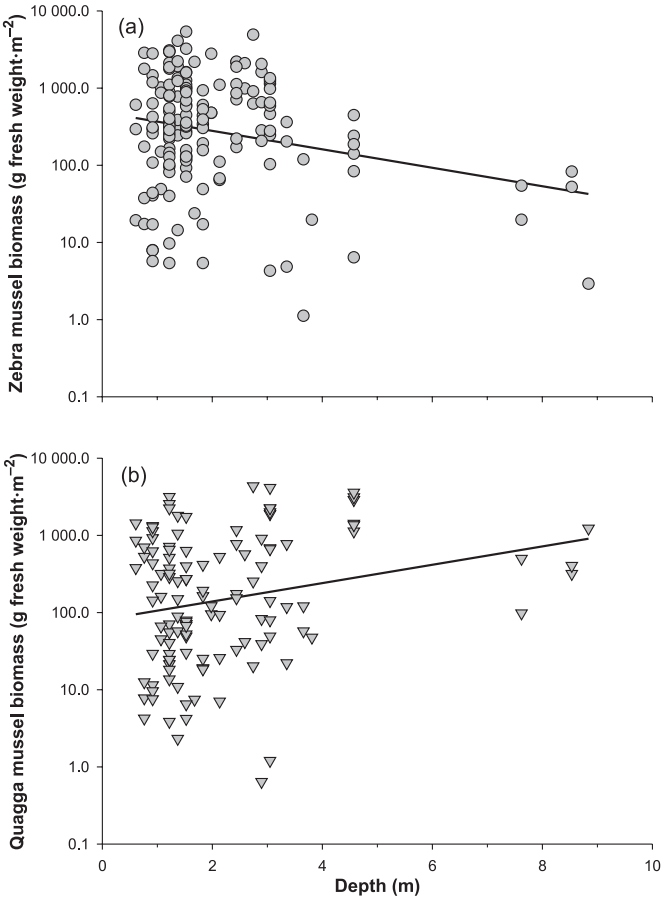
In contrast with the detailed studies on the effect of calcium on zebra mussels, very little is known of the calcium requirements and tolerance limits of quagga mussels (McMahon 1996). We compared the frequency of empty (zero biomass) quagga mussel quadrats at sites above and below the reported zebra mussel threshold of 15 mg Ca·L^{-1}. The observed frequency of zero biomass values at concentrations below 15 mg Ca·L^{-1} was significantly higher than expected by chance. Quagga mussels were not found below 12 mg Ca·L^{-1}, suggesting that they have higher calcium requirements than zebra mussels. Furthermore, unlike zebra

Table 4. Stepwise multiple regression models developed to predict log-transformed biomass for zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) across quadrats from three independent physicochemical predictor variables.

	Equation	r^2	P	n
Zebra mussels	log biomass = 1.62 – 0.03·substrate size (0.01)** + 0.05·calcium (0.01)** – 0.19·depth (0.04)**	0.36	<0.0001	162
Quagga mussels	log biomass = 1.25 – 0.08·substrate size (0.01)** + 0.26·depth (0.04)**	0.32	<0.0001	123

Note: Numbers in parentheses are standard error of estimated coefficients and n is sample size. Quadrats with zero zebra or quagga mussel biomass were excluded from their respective analyses. Variables were retained in the model if significant at $P = 0.05$. **, $P < 0.0001$.

Fig. 4. Relationship between (*a*) zebra mussel (*Dreissena polymorpha*) and (*b*) quagga mussel (*Dreissena bugensis*) biomass (log transformed) and depth across quadrats. Quadrats with zero biomass for zebra mussels or quagga mussels were excluded from their respective analyses. The regression equations for zebra and quagga mussel biomass, respectively, are log biomass = 2.69 – 0.12·depth ($r^2 = 0.05$, $P = 0.003$, $n = 162$) and log biomass = 1.79 + 0.16·depth ($r^2 = 0.10$, $P = 0.0005$, $n = 123$).



mussels, quagga mussel biomass did not decline at high calcium concentrations. These results agree with a recent study of dreissenid mussels in Russian rivers, which concluded that quagga mussels tolerate higher calcium levels than zebra mussels (Zhulidov et al. 2004).

One potential criticism is that our measurements of calcium concentration are point measurements that do not incorporate seasonal and annual fluctuations. However, seasonal fluctuations in calcium concentrations tend to be limited in hardwater systems like the St. Lawrence River (Wetzel 1983). Moreover, our calcium concentrations are similar to those previously found in the St. Lawrence River (Mellina and Rasmussen 1994) as well as to measurements taken from the previous 2 years at 10 of our sites (A. Ricciardi, unpublished data).

Substrate size as a predictor

Substrate size is an ecological determinant of zebra mussel density (Mellina and Rasmussen 1994). The shell morphology of adult zebra mussels allows them to attach firmly to solid surfaces (Morton 1993), and adults preferentially colonize hard substrata in rivers and lakes (Dermott and Munawar 1993; Mellina and Rasmussen 1994; Karatayev et al. 1998). Following their initial introduction into the Great Lakes, zebra mussel populations grew explosively, reaching densities of 300 000 individuals·m^{-2} on rocky substrates (Griffiths et al. 1991; Leach 1993). Similarly, in the early stages of invasion of the St. Lawrence River, the highest zebra mussel densities occurred on hard substrates and substrate size explained 38% of the variation in mussel density (Mellina and Rasmussen 1994). However, the importance of primary hard substrate may diminish over time as zebra mussels begin to form byssally attached mats that expand from hard-substrate nuclei onto adjacent soft substrates such as sand, mud, and gravel (Hunter and Bailey 1992; Berkman et al. 2000). Zebra mussel occurrence and abundance on soft substrates within the Great Lakes has progressively increased, even without the assistance of hard nuclei in some areas (Berkman et al. 2000; Haltuch et al. 2000). This being the case, we expected that substrate size would not remain an important predictor of zebra mussel abundance in the St. Lawrence River 10 years after invasion. Yet, in our study, substrate size accounted for 20% of the variation in zebra mussel biomass (which is highly correlated with mussel density; $r^2 = 0.91$, $P < 0.0001$). However, we observed frequent use of soft substrates by zebra mussels and biomasses as high as 900 g·m^{-2} on sand and silt sediments.

Unlike zebra mussels, quagga mussels are thought to prefer soft substrata (Dermott and Munawar 1993; Dermott and Kerec 1997), but the relationship between substrate size and quagga mussel biomass has not been previously tested. In the Dneiper River drainage basin of the Ukraine, quagga mussels displaced zebra mussels from the rocky littoral zone within 4–12 years and similar trends are emerging in the Great Lakes (Mitchell et al. 1996; Mills et al. 1999) and St. Lawrence River (Ricciardi and Whoriskey 2004). This species shift suggests that, given enough time, the quagga mussel can eventually dominate a broad range of substrates (Mills et al. 1999; Stoeckmann 2003). Considering this pat-

tern of invasion and that quagga mussels have been present in the St. Lawrence River system since at least 1992, it was surprising to find a relationship between substrate size and quagga mussel biomass. Moreover, despite suggested differences in substrate affinity, zebra and quagga mussels responded similarly to variation in substrate size.

Native unionids and macrophytes are also common substrates for dreissenid colonization (Lewandowski 1976; Ricciardi et al. 1996; Diggins et al. 2004). The presence of unionid mussels was a significant predictor of zebra mussel density in the multiple regression models of Mellina and Rasmussen (1994). However, unionids in the St. Lawrence River have declined substantially because of zebra mussel fouling (Ricciardi et al. 1996) and are now scarce in most areas of the river. While neither macrophytes nor unionid shells were abundant at any of our study sites, they represent potentially important substrates that could be incorporated in future models for other river systems.

Depth as a predictor

Zebra mussels generally reach their highest densities in shallow water, whereas quagga mussels tend to dominate deeper waters (Dermott and Munawar 1993; Mills et al. 1993). In Lake Erie, zebra and quagga mussels coexist at depths from 8 to 110 m, but only quagga mussels are present at depths greater than 110 m (Mills et al. 1999). However, it was not known whether a similar pattern would occur in the upper St. Lawrence River, where depth outside the shipping channel rarely exceeds 10 m. In our study, we found that zebra mussel biomass decreased with depth, while quagga mussel biomass increased, even over a narrow depth range (<9 m). Depth zonation of the two dreissenids has been suggested to be related to differences in temperature and silt tolerances as well as substrate preferences (Domm et al. 1993; Mitchell et al. 1996). However, temperature did not differ over the depth range of our study, and the two species have overlapping substrate preferences (and there is no simple relationship between substrate size and depth at littoral sites in the St. Lawrence River). This pattern may reflect differences in tolerance to natural disturbance and periodic aerial exposure (Mitchell et al. 1996; Ricciardi and Whoriskey 2004). Quagga mussels have a lower desiccation tolerance (Ricciardi et al. 1995) and their rounded shells might not be able to adhere as tightly to hard substrates (Pathy and Mackie 1993; Mills et al. 1996) and could thus be dislodged by wave action or ice scour.

Other factors affecting abundance and distribution

Some of the residual variation in dreissenid biomass might be explained by turbidity, which varies spatially and temporally in large heterogeneous river systems. Increased turbidity can dilute seston quality by increasing the fraction of suspended inorganic material (e.g., silt, clay). Seston quality affects bivalve respiration rate (Stoeckmann 2003), which is correlated with growth rate (Madon et al. 1998; Stoeckmann and Garton 2001). When seston quality is poor, quagga mussels have a lower respiration rate (Summers et al. 1996) and are more efficient than zebra mussels at acquiring food (Stoeckmann 2003). Zebra mussels have difficulty processing high levels of suspended inorganic particles (Madon et al. 1998). Therefore, under turbid conditions, quagga mussels should be less energetically stressed and attain higher biomasses than zebra mussels.

Another factor is larval supply. Riverine populations of dreissenids are considered to be dependent on larval recruitment from upstream lentic populations (Thorp et al. 2002). The dominant water source along the north shore of Montreal is from the Ottawa River, which has scarce zebra mussel populations and no known quagga mussel populations. Although mixing of water from both rivers occurs along the north shore (thus creating the calcium gradient), and complex current flows may allow for limited upstream dispersal (Thorp et al. 2002), a quantitative measure of larval supply could help tease apart the abiotic (calcium) and biotic (larval supply) effects on dreissenid occurrence.

Stepwise regression models

Despite that zebra and quagga mussels are closely related and functionally similar, the range of habitats that they may invade are significantly different. The multiple regression models that we developed for these two species differed in three important ways. First, while all three factors were retained in the zebra mussel model, only depth and substrate size were kept in the quagga mussel model. Second, the most important predictor of zebra mussel biomass (substrate size) differed from the most important predictor of quagga mussel biomass (depth). Third, while zebra mussel biomass decreased with increasing water depth, quagga mussel biomass increased. These findings suggest that one general model is not sufficient for predicting both zebra and quagga mussel biomass.

In summary, we have identified some important environmental factors that explain the distribution and biomass of zebra and quagga mussels. We found that calcium concentration sets a minimum threshold level for presence of both species but that quagga mussels appear to have a higher calcium requirement. The occurrence of zebra mussels at calcium concentrations as low as 8 mg $Ca \cdot L^{-1}$ indicates that they are able to colonize a broader range of habitats than previously expected. More than a decade after colonization, both zebra and quagga mussel biomass peaked on hard substrates, indicating that the two species have overlapping substrate preferences, contrary to conventional descriptions. However, substrate size is not as important in explaining zebra mussel abundance as it was during the early stages of invasion in the St. Lawrence River, which suggests that the accuracy of predictive models may change over time. In spite of the narrow depth range of this study, contrasting patterns of biomass for both species occurred with depth, with a trend toward quagga mussel domination in deeper waters. Finally, we derived a predictive model of biomass for each species from different combinations of local environmental variables, which demonstrated that models for one species are not appropriate for the other species. These variables provide a useful basis for predicting future zebra mussel and quagga mussel distribution and biomass in other invaded river systems.

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