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Predicting zebra mussel fouling on native mussels from physicochemical variables

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SUMMARY

1. Predictive models of impact are needed for the risk assessment of invasive species. One such species is the Eurasian zebra mussel (*Dreissena polymorpha*), a fouling bivalve that overgrows and kills native mussels (Unionidae) in many North American lakes and rivers. The level of mortality in a native mussel population increases with the fouling intensity – i.e. the mean number of zebra mussels attached to each native mussel.

2. We conducted a multi-site survey within the St Lawrence and Richelieu rivers (Quebec, Canada) to determine whether zebra mussel fouling intensity can be predicted from environmental variables. We found fouling intensity to be positively correlated with calcium concentration [Ca^{2+}] and negatively correlated with sediment size, but not affected by local macrophyte cover.

3. A multiple regression model that includes calcium concentration and sediment size explains 86% of variation in fouling intensity across all sites.

4. Analysis of data from invaded sites in North America and Europe revealed a nonlinear relationship in which fouling intensity increases with calcium concentration up to an asymptotic threshold of 24 mg L^{-1} Ca^{2+}.

5. Our results suggest that the community-level impacts of zebra mussels are mediated by abiotic environmental variables and gradients in these variables may provide local habitat refugia for native mussels.

Keywords: biodiversity, *Dreissena*, empirical models, invasive species, Unionidae

Introduction

Biological invasions are a leading cause of extinctions (Clavero & García-Berthou, 2005). However, their impacts on native species vary along environmental gradients, such that an invader may displace a native species in part of the invaded range while coexisting with it elsewhere (e.g. D'Antonio, Tunison & Loh, 2000; MacNeil *et al*., 2001). There is a need to develop predictive models of impact that can be used in risk assessment of invasive species, but the context-dependent nature of impact poses a formidable challenge to prediction (Parker *et al*., 1999; Byers *et al*., 2002). One promising but underused approach is to link impact or a proxy of impact to a suite of environmental variables known to have strong effects on the invader's abundance (Ricciardi, 2003).

A recent invader that has caused substantial ecological impacts in North American lakes and rivers is the Eurasian zebra mussel (*Dreissena polymorpha* Pallas) – a byssally-attached bivalve that rapidly colonizes and overgrows hard surfaces, including the shells of other molluscs. It thus causes intense fouling of native freshwater mussels (Order Unionoida, 'unionids'), burrowing bivalves that live partially buried in mixed sediments with a portion of their shell exposed to the water column to carry out their filtration activity. Their exposed shell provides a colonizable surface for zebra mussel larvae, which may remain in the water column for a few weeks prior

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to settlement (Stanczykowska, 1977; McMahon & Bogan, 2001). Unionid mussels are North America's most imperiled faunal group (Ricciardi & Rasmussen, 1999), with 70% of the *c.* 300 described species considered endangered, threatened or already extinct (Williams *et al.*, 1993). Previously, habitat degradation was the primary cause of their decline, but the recent invasion of the zebra mussel has added another major threat to unionid diversity. Having evolved in the absence of dominant fouling organisms, North American unionid mussels have no adaptive mechanism to resist the effects of zebra mussel fouling (but see Nichols & Wilcox, 1997), which can impair the unionid's locomotion, feeding, respiration and excretion in such a way as to deplete its energy reserves (Haag *et al.*, 1993; Baker & Hornbach, 1997, 2000). Hence, there is a strong link between fouling intensity (the mean number of zebra mussels attached to a unionid) and the level of mortality within a unionid population (Ricciardi, Whoriskey & Rasmussen, 1995). Consequently, rapid declines of unionid populations have followed zebra mussel invasion in North America (Schloesser & Nalepa, 1994; Ricciardi, Whoriskey & Rasmussen, 1996; Martel *et al.*, 2001; Nalepa *et al.*, 2001). In lakes and rivers where zebra mussel fouling intensities have reached high levels, unionid populations have suffered near total extirpation within 4–8 years of invasion (Ricciardi, Neves & Rasmussen, 1998). European unionid populations, on the other hand, do not appear to be as sensitive to zebra mussel fouling, possibly because they have developed tolerance or adaptations from a shared evolutionary history in Europe prior to the last glaciation (Ricciardi *et al.*, 1998), or there has been a long-term equilibrium following strong initial impacts that went unrecorded in the past (Strayer & Malcom, 2007).

Fouling intensity on unionids increases with local zebra mussel density (Ricciardi, 2003), which varies with environmental factors such as the calcium ion concentration [Ca^{2+}] of the water. Field and laboratory studies suggest that the minimum calcium threshold for zebra mussel settlement and growth is 8–12 mg L^{-1} (Sprung, 1987; Vinogradov *et al.*, 1993; Hincks & Mackie, 1997; Jones & Ricciardi, 2005); however, zebra mussel population densities appear to peak only at concentrations $\geq$20 mg L^{-1} (Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). By contrast, healthy unionid populations can be sustained at concentrations as low as 3 mg L^{-1} (McMahon & Bogan, 2001), suggesting that a low calcium concentration can provide a refuge for unionids, while intermediate concentrations may permit their coexistence with zebra mussels.

Other factors that may influence fouling intensity on unionids are ambient substrate quality and the abundance of submerged macrophytes. The availability of suitable substrate is crucial to the survival of settling zebra mussel larvae (Stanczykowska, 1977; Lewandowski, 1982), and local zebra mussel abundance increases with substrate particle size (Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). Unionid mussels are most abundant in mixed sediments (Sietman, Furman & Pursell, 1999; McMahon & Bogan, 2001), including sandy or silty areas where their shells may be the only substrate available for zebra mussel colonization. However, neighbouring coarse substrates such as rocks or submerged macrophytes might intercept zebra mussel larvae (Lewandowski, 1982; Diggins *et al.*, 2004). If this is the case, then local mean sediment size and macrophyte cover could influence the vulnerability of unionid populations to fouling and contribute to variation in zebra mussel impacts across sites.

Our study aimed to determine whether the fouling intensity of zebra mussels on unionids can be predicted by a combination of these environmental variables. We tested the hypothesis that fouling intensity on unionids will increase across sites with increasing calcium concentration, finer sediment particle size and reduced macrophyte cover.

Methods

Study area

We conducted a survey of 15 sites in the Richelieu and St Lawrence Rivers (Fig. 1), which were colonized by zebra mussels in 1990 and 1996, respectively (Mellina & Rasmussen, 1994; Ricciardi *et al.*, 1996; de Lafontaine & Cusson, 1997). Unionids were sampled and calcium concentrations were measured during late August and early September 2002–2005, whereas sediment particle size and percent macrophyte cover were measured in 2004 and 2005. We chose to sample in late summer to allow for the completion of major zebra mussel settlement events. Although veligers can be sampled throughout the autumn, peak densities

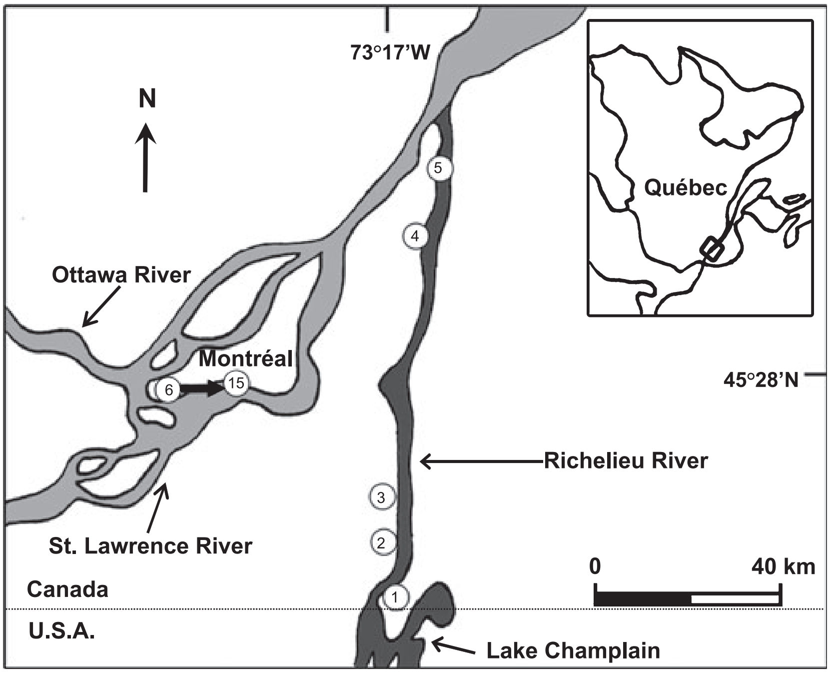

Fig. 1 Map of study sites along the Richelieu River and the St Lawrence River.

generally occur in mid-July (de Lafontaine & Cusson, 1997; Costan & de Lafontaine, 2000). Sampling sites were selected based on their accessibility and the presence of unionid populations; in addition to these criteria, sites in the St Lawrence River were selected to represent a broad range of calcium concentrations. 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 & Rasmussen, 1994). In the Richelieu River, calcium concentration is relatively homogeneous and remains stable between 15 and 18 mg L^{-1} (de Lafontaine & Cusson, 1997; A. Ricciardi, unpubl. data).

Sampling procedures

All sites were accessed from shore and sampled manually by SCUBA divers. This procedure minimized the manipulation of fouled unionids and thus limited the loss of attached zebra mussels. We collected unionids from a 1-m^2 polyvinyl chloride quadrat, cast haphazardly on the substrate. We decided *a priori* to collect five replicate quadrats at each site from 2002 and 2004, as this was expected to yield a precision of ±20% when sampling unionid densities of 10–30 mussels m^{-2} (Downing & 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 10 at all sites to improve our measures of sediment particle size and macrophyte cover.

We collected all visible unionids from each quadrat and probed the upper 10 cm of sediment by hand to locate individuals buried immediately beneath the surface. Each unionid, along with its attached zebra mussels, was sealed in a collection bag while underwater. Samples were stored in a cooler and transported to the laboratory within 3 h of collection. In the laboratory, each live unionid was cleaned by hand and all attached zebra mussels were removed and counted. Although zebra mussel-unionid mass ratios are preferred measures of infestation because they better represent encumbrance on unionids (Ricciardi, 2003), in this study we are concerned with patterns of fouling and how fouling varies with site-specific factors. Mass ratios are influenced by the mean size of unionids, which also varies across sites, and thus would potentially introduce confounding effects in our model. Therefore, we measured zebra mussel fouling intensity by the mean number of live zebra mussels (>2 mm in length) attached to living unionids. Occasionally, quagga mussels (*Dreissena bugensis* Andrusov), another invader, were also found attached to unionids, but they comprised <0.05% of all attached dreissenids. In order to minimize the impact of our sampling on the unionid populations in 2005, live unionids that were not fouled by zebra mussels were processed in the field and then returned to their original location.

Calcium concentration ($[Ca^{2+}]$ mg L^{-1}) at each site was determined by taking replicate water samples (in 1-L plastic bottles) that were measured in the laboratory using the LaMotte Hardness Test (Model PHT-CM-DR-LT; LaMotte Company, Chestertown, MD, U.S.A). Point source data for 2004 and 2005 were aggregated to obtain an overall site mean for use in statistical analysis. For 10 of the 15 sites, we were able to supplement our point source data with measurements taken in 2002 and 2003.

Mean sediment particle size was determined *in situ* by visual estimates of the per cent aerial cover of each sediment type within each quadrat. For this purpose, we used a 1-m^2 quadrat subdivided by thin wire into a grid of 16 cells. Each sediment type was assigned a diameter range that was converted to the phi scale, i.e. $-\log_2$ diameter in mm (Hakanson & Jansson, 1983), according to the categories in Table 1. The phi value for each sediment type was multiplied by its percent cover and then summed to obtain a mean weighted particle size for each quadrat (cf. Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). All measurements of substrate composition were performed by the same diver to minimize bias. Quadrat data for 2004 and 2005 were combined to obtain overall site means for use in statistical analysis.

Submerged macrophytes within each quadrat were visually inspected *in situ* to estimate their percent cover. Given that macrophyte cover was expected to vary annually, an overall site mean was calculated independently for each sampling year and means were arcsin$^{0.5}$-transformed to normalize the variable for statistical analyses (Zar, 1999).

Table 1 Sediment size classes and associated phi values, modified from the Wentworth scale (Hakanson & 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

Statistical analyses

Univariate least-squares regression analysis was used to relate mean fouling intensity ($\log_{10}$-transformed) to environmental variables for the 15 survey sites. Mean fouling intensity was $\log_{10}$-transformed because data spanned two or more orders of magnitude and this transformation normalized the data for statistical analyses (Zar, 1999). Calcium concentration and sediment particle size were measured as overall site means using data from multiple years. Because fouling intensities varied with time since invasion, our chosen response variable for calcium and sediment size was the maximum mean fouling intensity recorded at each site (Table 2). Macrophyte cover was measured as an annual site mean; 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. Stepwise multiple regression analysis was used to determine the amount of variation explained by a combination of significant environmental variables.

In addition, published data from sites in North America and Europe (Table 3) were assembled to test for a global relationship between fouling intensity and calcium concentration. The maximum mean fouling intensity was derived from multi-year data (where available) from each site. Inspection of the transformed data suggested an asymptotic function; therefore, nonlinear regression analysis was applied. A range of potential transition points for the asymptote were visually estimated from the plotted data and their significance was tested using piecewise regression (Toms & Lesperance, 2003). All statistical analyses were performed using SAS Systems for Windows Version 8 (SAS Institute Inc., Cary, NC, U.S.A.).

Results

Mean fouling intensities ranged from 0 to 37 zebra mussels per unionid across our survey sites (Table 2), and only one site (site 6, located nearest to the inflow of the Ottawa River) remained free of zebra mussels throughout the sampling period. Stepwise multiple regression yielded a highly significant model ($P < 0.0001$) in which calcium concentration and

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)

Site	Fouling intensity (no. zm/unionid)	Macrophytes (% cover)	Maximum mean fouling intensity (no. zm/unionid)	Calcium concentration (Ca^{2+} mg L^{-1})	Substrate size (phi value)
Site 1					
2002	5.8 (0.6)		5.8	15.7 (0.4)	−2.14 (1.20)
2003	1.1 (0.3)				
2004	2.6 (0.3)	18.0 (6.4)			
Site 2					
2002	24.2 (2.5)		36.6	16.5 (0.5)	7.54 (0.43)
2003	19.0 (3.6)				
2004	36.6 (5.6)	26.0 (11.8)			
2005	*	52.5 (9.6)			
Site 3					
2002	6.2 (0.8)		12.4	15.2 (1.0)	4.20 (0.73)
2003	4.8 (1.1)				
2004	12.4 (3.0)	47.0 (11.8)			
2005	4.1 (1.1)	11.3 (2.7)			
Site 4					
2002	0.7 (0.2)		1.1	17.1 (1.1)	−2.11 (1.30)
2004	1.1 (0.2)	12.0 (5.1)			
2005	0.6 (0.2)	0.00 (0)			
Site 5					
2002	0.4 (0.3)		1.0	14.9 (1.7)	3.22 (1.86)
2004	1.0 (0)	6.0 (2.6)			
Site 6					
2002	0 (0)		0.0	9.2 (0.7)	−2.83 (0.94)
2004	0 (0)	16.0 (4.7)			
2005	0 (0)	37.0 (9.2)			
Site 7					
2002	0.1 (0.02)		0.1	9.1 (0.5)	4.68 (0.63)
2003	0 (0)				
2004	0.1 (0.1)	46.0 (14.6)			
2005	0.02 (0.01)	46.0 (10.0)			
Site 8					
2004	0.2 (0.03)	56.0 (16.3)	0.2	9.4 (0.2)	4.00 (0.43)
2005	0.1 (0.02)	21.3 (8.2)			
Site 9					
2004	0.02 (0.02)	29.0 (5.6)	0.02	11.2 (0.6)	−5.11 (0.55)
2005	0.01 (0.01)	62.5 (4.0)			
Site 10					
2002	0.01 (0.01)		0.02	11.8 (1.0)	−5.70 (0.17)
2004	0.01 (0.01)	77.0 (4.1)			
2005	0.02 (0.01)	39.8 (6.5)			
Site 11					
2004	1.3 (0.8)	19.0 (7.1)	3.0	16.0 (1.2)	1.26 (0.57)
2005	3.0 (–)	10.7 (5.3)			
Site 12					
2004	*	55.0 (5.3)	0.5	15.0 (0.6)	−3.99 (0.59)
2005	0.5 (0.5)	39.0 (8.9)			
Site 13					
2002	1.2 (0.4)		4.5	18.2 (1.0)	2.60 (0.34)
2004	2.4 (0.7)	78.5 (2.4)			
2005	4.5 (1.3)	87.5 (2.3)			
Site 14					
2002	5.3 (0.9)		6.0	18.2 (1.0)	2.33 (0.72)

Table 2 (*Continued*)

Site	Fouling intensity (no. zm/unionid)	Macrophytes (% cover)	Maximum mean fouling intensity (no. zm/unionid)	Calcium concentration (Ca^{2+} mg L^{-1})	Substrate size (phi value)
2003	*				
2004	6.0 (4.3)	79.5 (5.1)			
2005	*	79.0 (3.3)			
Site 15					
2004	1.3 (0.2)	77.0 (5.4)	1.4	19.4 (1.8)	−1.40 (0.62)
2005	1.4 (0.2)	75.0 (6.3)			

Values reported are the site means with standard errors in parentheses.
*Instances in which no fouling intensity could be calculated due to the absence of live unionids.

Table 3 Additional site information used for global calcium analysis

Site	Maximum mean fouling intensity (no. zm/unionid)	Calcium concentration (Ca^{2+}mg L^{-1})	Reference
European systems			
Lake Mikolajskie, Poland	52	45	Lewandowski, 1976; Stanczykowska, 1977
Lake Naroch, Belarus	135	33	Burlakova *et al*., 2000, 2006
Lake Myastro, Belarus	10	33	Burlakova *et al*., 2000, 2006
Lough Erne, Ireland	59	60	Maguire *et al*., 2003; Rosell *et al*., 1999; C.M. Maguire, pers. comm.
N. American systems			
Lake Erie – western basin	216	34	Haag *et al*., 1993
Lake St Clair	642	33	Gillis & Mackie, 1994
Lake Oneida	742	40	Harman, 1994; CNYRPDB, 2003
Lower Ohio River	445	40	Sickel & Leek, 1994; P. Morrison, USFWS, pers. comm.
Hudson River	17	27	Strayer & Malcom, 2007
Upper Illinois River	254	66	Whitney *et al*., 1995; Allen & Ramcharan, 2001
Lake Pepin, Mississippi River	500	60	Hart *et al*., 2001
Richelieu River			
Campbell	1.8	16	Ricciardi, unpubl. data
St Lawrence River			
Lake St Louis	7.7	23	Ricciardi *et al*., 1996
Prescott	62	29	Ricciardi *et al*., 1996; Jones & Ricciardi, 2005
Soulanges Canal – East	23.3	24	Ricciardi *et al*., 1996
Soulanges Canal – West	44	30	Ricciardi *et al*., 1995; Jones & Ricciardi, 2005
Lac St Pierre	47	31	Ricciardi *et al*., 1995; Ricciardi, unpubl. data

sediment size (phi) collectively explain 86% of the variation in maximum mean fouling intensity (Fig. 2). Calcium concentration and sediment size are not correlated with each other ($P = 0.21$).

Maximum mean fouling intensity increases with calcium concentration and declines with increasing sediment size (Table 4; Fig. 2); the variance explained by each of these variables is 61% and 36% respectively. For the sediment size relationship, five sites have calcium concentrations of <12 mg L^{-1}, which are near or below the minimum threshold for zebra mussel occurrence (Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). When these low-calcium sites are excluded, sediment size explains 58% of the variation in maximum mean fouling intensity (Table 4). Contrary to one of our predictions, fouling intensity is not correlated with local macrophyte cover in 2004 or 2005, regardless of whether low-calcium sites are excluded from the analysis.

Data from sites across North America and Europe suggest a global relationship in which fouling intensity increases asymptotically over a broad range of calcium concentrations (Fig. 3). Maximum mean fouling intensity increases with calcium to a threshold

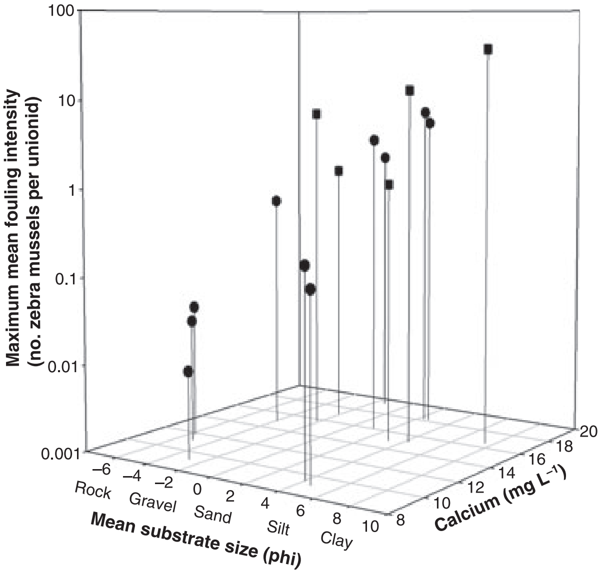

Fig. 2 Maximum mean fouling intensity as a function of calcium concentration and mean sediment size (measured on the phi scale). Circles are sites from the St Lawrence River and squares are sites from the Richelieu River. Stepwise multiple regression yielded a highly significant model ($r^2 = 0.86$, $P < 0.0001$): $\log_{10}(y + 0.01) = 0.22\,[\mathrm{Ca}^{2+}] + 0.13\,\mathrm{phi} - 3.29$.

concentration of 24 mg L^{-1} (Chow test, $P < 0.005$) in a nonlinear model that explains 82% ($P < 0.0001$) of the variation: $\log_{10}(y + 0.01) = -6.19 + 8.63\,(1 - e^{-0.09x})$.

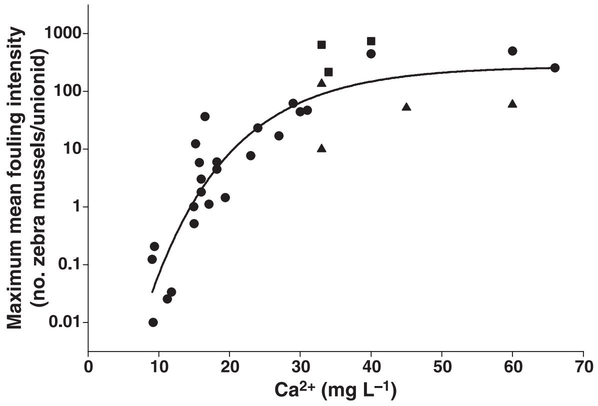

Fig. 3 Maximum mean fouling intensity as a function of calcium concentration: $\log_{10}(y + 0.01) = -6.19 + 8.63[1 - e^{-0.09x}]$; $r^2 = 0.82$, $P < 0.0001$. Circles are North American river sites, squares are North American lake sites and triangles are European lake sites.

Discussion

Effect of calcium concentration

Zebra mussel distribution is limited by the dissolved calcium (Ca^{2+}) content of the water (Ramcharan, Padilla & Dodson, 1992; Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005) and the minimum concentration required for occurrence may be near 8–12 mg L^{-1} (Vinogradov *et al.*, 1993; Hincks & Mackie, 1997; Jones & Ricciardi, 2005). Field studies demonstrate that adult zebra mussel densities peak at calcium concentrations ≥20 mg L^{-1} (Ramcharan *et al.*, 1992; Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). All 15 sites in our survey had calcium concentrations lower than 20 mg L^{-1} (range = 9.1–19.4 mg L^{-1}, median = 15.2 mg L^{-1}), but fouling intensity was strongly correlated with calcium concentration across these sites. In our survey, sites with calcium concentrations between 16 and 18 mg L^{-1} were capable of supporting mean fouling intensities of 10–37 zebra mussels per unionid. Although extirpation of unionid populations tends to occur at mean fouling intensities of >100 per unionid, which are commonly attained in calcium-rich habitats (Nalepa, 1994; Schloesser & Nalepa, 1994; Ricciardi *et al.*, 1995, 1996; Martel *et al.*, 2001), significant reductions of unionid populations have been observed at mean intensities as low as 10 zebra mussels per unionid (Ricciardi *et al.*, 1996).

A synthesis of data from disparate sites in North America and Europe (Fig. 3) suggests a nonlinear relationship between maximum mean fouling intensity and calcium concentration. The relationship becomes asymptotic at concentrations of >24 mg L^{-1},

Table 4 Univariate linear regressions of two physicochemical variables

Variable	*n*	*b* (SE)	Intercept (SE)	r^2	*P*-value
Calcium [Ca^{2+}], mg L^{-1}	15	0.24 (0.05)	−3.51 (0.78)	0.61	0.0006
Mean substrate size, phi units	15	0.16 (0.06)	NS	0.36	0.018
Mean substrate size, phi units (sites with [Ca^{2+}] > 12 mg L^{-1})	10	0.12 (0.04)	0.39 (0.13)	0.58	0.01

The response variable is maximum mean fouling intensity [log(y + 0.01)-transformed] of unionids by zebra mussels.
NS, not significant.

which is above those recorded at our survey sites. The presence of a threshold is consistent with observed nonlinear effects of calcium concentration on zebra mussel biomass and survival (Jones & Ricciardi, 2005), as well as on juvenile growth rates (Hincks & Mackie, 1997). Further support for the model is provided by independent data from Lake Wawasee in Indiana and Lake Balaton in Hungary. Lake Wawasee is a marl lake; estimates of calcium are not available for the lake itself, but the mean calcium concentration in the surrounding river basin is 177 mg L^{-1} (Horvath *et al.*, 1996). A maximum mean fouling intensity of 130 zebra mussels per unionid was recorded in the lake (D.W. Garton, pers. comm.), which is within the range predicted by our model if we assume a mean calcium concentration in the lake equivalent to the river basin. Lake Balaton has a calcium concentration of 33 mg L^{-1} (Biró, 1997) and has lost at least one-third of its unionid population in the decades following invasion by zebra mussels (Sebestyen, 1937; Ponyi, 1992). Wagner (1936) described a maximum infestation exceeding 1000 zebra mussels on individual unionids in the lake. Mean fouling intensities were not recorded but can be deduced through back-transformation, using the model by Ricciardi (2003): given a mean field density of 25000 zebra mussels per m^2 (Wagner, 1936), the expected mean fouling intensity is *c.* 200 zebra mussels per unionid – which is again within the range predicted by our model, even though it may be lower than the maximum mean infestation.

The presence of a threshold highlights the importance of examining variation across a broad gradient of habitat types and geographical regions. Results from our own survey sites alone would suggest only a simple linear relationship between fouling intensity and calcium concentration, whereas an examination of published data from predominantly calcium-rich North American and European lakes would have shown no relationship.

Influence of larval supply and its relationship with calcium concentration

A potential confounding factor in our study is zebra mussel larval supply from upstream sources. Dreissenid mussels are among the few freshwater bivalves that have a truly planktonic larval stage, and their larvae can remain in the water column for a few weeks (Stanczykowska, 1977; McMahon & Bogan, 2001). As a result, recruitment of riverine dreissenid populations is thought to be driven largely by upstream sources of larvae (Stoeckel *et al.*, 1997; Thorp, Alexander & Cobbs, 2002). Both our study systems are influenced by larval supply from populations in upstream lakes. Lake Champlain is the primary source of zebra mussel larvae for the Richelieu River (de Lafontaine & Cusson, 1997) and may account for the gradient in adult zebra mussel abundance (de Lafontaine *et al.*, 2002), particularly downstream of the Chambly basin, a fluvial lake that probably traps mussel larvae. Similarly, fouling intensities at sites located downstream of the Chambly basin are lower than those at upstream sites, despite a relatively constant calcium concentration.

The relationship between fouling and larval dynamics at our St Lawrence River sites is more difficult to interpret. Analysis of data from a previous study (sites 1–9 in Jones & Ricciardi, 2005) shows no significant relationship between zebra mussel abundance (biomass) and ranked distance along the St Lawrence River between Cornwall, Ontario and its confluence with the Ottawa River at Montreal (Spearman's correlation, $P = 0.16$). Nevertheless, the observed pattern of fouling intensity in our study may be partially driven by a gradient in larval supply to sites along the southwestern shore of the island of Montreal, where water from the Ottawa River (which has no zebra mussel populations) mixes with water from the St Lawrence River (Mellina & Rasmussen, 1994). Given the complex hydrodynamics of our study area, it is difficult to assess the extent to which zebra mussel populations at sites closest to the Ottawa River outflow are limited by larval supply rather than by low calcium concentrations. The occurrence of zebra mussels at these sites suggests that larvae can arrive by dispersal, albeit probably in fewer numbers because of dilution. If larval dilution was the dominant factor influencing zebra mussel distribution, we would expect a gradual decline in zebra mussel fouling intensity across these sites. Instead, we observe a precipitous decline (by at least one order of magnitude) in fouling intensity when calcium concentration falls below 12 mg L^{-1}, near the minimum calcium threshold for the normal development and long-term survival of zebra mussels (Sprung, 1987; Vinogradov *et al.*, 1993; Hincks & Mackie, 1997). This pattern was also observed for zebra mussel biomass measured along the same shoreline (Jones & Ricciardi, 2005). Similarly, in the global relationship (Fig. 3), fouling intensity declines rapidly with calcium concentration below 24 mg L^{-1}, although all the data points comprising the steep portion of the curve are from the St Lawrence and Richelieu rivers, recorded in this study and in previous surveys. There is a lack of published data from other calcium-poor sites that could validate the model.

Effect of sediment size

Sediment size is also a predictor of local zebra mussel occurrence and density (Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). It is heterogenous across our study sites (Table 2) and thus its influence on fouling intensity is not confounded by a geographic gradient in larval supply. Zebra mussel fouling intensity on unionids varies inversely with sediment size (Fig. 2), which contrasts with the observed pattern of zebra mussel population density increasing with sediment size (Mellina & Rasmussen, 1994; Jones & Ricciardi, 2005). In models demonstrating the latter pattern, mean sediment size was derived from all types of benthic substrates available for zebra mussel settlement, including the shells of unionids, whereas our model (Fig. 2) considers ambient sediment size – i.e. the quality of alternative substrate surrounding the unionids. Because zebra mussel field density and fouling intensity are strongly correlated (Ricciardi, 2003), one might expect fouling intensities to be greater in rocky habitats. However, we find the opposite pattern, which suggests that zebra mussel larvae might be selecting or passively focusing on unionid shells when suitable alternative substrates are scarce; in such areas, unionids themselves are the functional equivalent of coarse sediments in terms of size. Unionid mussels may be preferred substrate for settling zebra mussels (Ricciardi *et al.*, 1996) or, alternatively, they may provide the only colonizable surfaces in habitats dominated by fine or unstable mixed sediments (Toczylowski, Hunter & Armes, 1999).

The context dependence of impacts

Our results suggest that at least some impacts of zebra mussel colonization vary predictably along environmental gradients, which complements recent studies that have demonstrated the influence of key environmental variables on interactions between exotic and native aquatic organisms (e.g. MacNeil *et al.*, 2001; Alcaraz, Bisazza & García-Berthou, 2007). Low calcium concentrations may prevent local zebra mussel populations from reproducing or attaining high densities, but lethal fouling intensities may still occur if an upstream source of larvae is available and if unionids are the principal source of colonizable substrate in the area. In our study, the two sites with the highest fouling intensities (sites 2 & 3, see Table 2) do not correspond to those sites with the highest calcium concentrations. However, both sites are characterized by fine sediment, potentially causing larvae to focus on unionid shells; for example, site 2 has the highest recorded fouling intensity (*c.* 37 zebra mussels/unionid) and the smallest ambient sediment size (phi = 7.54). On the other hand, unionid populations occurring in calcium-poor habitats may be able to escape high fouling intensities, despite the presence of fine sediments; two sites (sites 7 & 8) with silty sediments and calcium concentrations <9.5 mg L^{-1} have fouling intensities of only <1 zebra mussel/unionid, well below the minimum intensities associated with significant reductions in unionid populations (Ricciardi *et al.*, 1996).

Thus, spatial heterogeneity within a system appears to be important in the creation of refugia for native species from the impacts of exotic species (e.g. Hasegawa & Maekawa, 2006), especially where the physiological tolerances of native and exotic species differ along an environmental gradient (Laha & Mattingly, 2006). Indeed, in some habitats unionid populations appear to persist in the presence of zebra mussels. Tucker & Atwood (1995) reported a diverse unionid assemblage co-occurring with a small zebra mussel population in a backwater lake of the Illinois River, whereas in the main river channel unionids were heavily fouled and exhibited elevated mortality (Whitney, Blodgett & Sparks, 1995). In Lake Erie, following their extirpation from offshore sites, live unionids continue to be found in littoral areas (Schloesser *et al.*, 1997; Nichols & Amberg, 1999; Bowers & de Szalay, 2004). Diverse unionid assemblages were found in some deltas and bays of Lake St Clair, several years after most unionid populations were eliminated by zebra mussels (Zanatta *et al.*, 2002). Each of these apparent refugia is a shallow, lake-connected habitat subject to large water-level and temperature fluctuations. Such fluctuations may be tolerable to unionids (McMahon & Bogan, 2001), while subjecting zebra mussels to unfavorable warm temperatures and periods of aerial exposure that limit their survivorship on unionid shells. Furthermore, when these fluctuations occur in areas dominated by fine sediments, the burrowing behaviour of unionids can remove attached zebra mussels (Nichols & Wilcox, 1997). Fouling intensity is further limited by the presence of predators that can specialize on zebra mussels (Bowers *et al.*, 2005). These cases demonstrate that combinations of abiotic and biotic variables mediate interactions between exotic and native species, resulting in context-dependent impacts. Although context dependence poses a challenge to prediction, syntheses of multi-site data across environmental gradients can identify important explanatory variables and reveal general patterns of impact.

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