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Community-level effects of co-occurring native and exotic ecosystem engineers

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SUMMARY

1. Non-indigenous ecosystem engineers can substantially affect native biodiversity by transforming the physical structure of habitats. In the Great Lakes–St. Lawrence River system, introduced dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) and the native benthic macroalga *Cladophora* act as ecosystem engineers by increasing substratum complexity and providing interstitial habitat for benthic macroinvertebrates.

2. We manipulated the topography and perimeter-to-area ratio of patches of dreissenid mussels in a series of colonisation experiments conducted at two sites in the St. Lawrence River. Experimental substrata were variably colonised by *Cladophora*, prompting us to examine (i) how the topography of *Dreissena* patches affects benthic macroinvertebrate diversity and (ii) the extent to which the effects of *Dreissena* are altered by the presence of another habitat-modifying organism (*Cladophora*).

3. The results of our first experiment suggested that a patchy distribution of dreissenid mussels is an important driver of benthic diversity at small spatial scales. The results of our second and third experiments suggested that a native habitat engineer, *Cladophora*, modifies the impact of *Dreissena* on benthic macroinvertebrate communities.

4. While macroalgal blooms have been linked to the large-scale impacts of *Dreissena* on light and nutrient availability, *Dreissena* shells inhibited *Cladophora* growth at our experimental scale. These findings demonstrate that the interactions between habitat-modifying species can complicate efforts to predict the community-level effects of an invasion.

Keywords: benthic macroinvertebrates, *Cladophora*, *Dreissena*, ecological impact, non-indigenous species

Introduction

Since their introduction to North America in the 1980s, dreissenid mussels (*Dreissena polymorpha* (Pallas) and *Dreissena bugensis* Andrusov) have become a dominant component of benthic communities in many lakes and rivers. *Dreissena* spp. can act as ecosystem engineers (*sensu* Jones, Lawton & Shachak, 1997) by altering resource availability at lake-wide scales; filtration by *Dreissena* can substantially increase water clarity, thereby stimulating benthic algal growth, and redirects nutrients and energy from pelagic to littoral benthic communities (Lowe & Pillsbury, 1995; Strayer, Smith & Hunter, 1998; Mayer *et al*., 2002). *Dreissena* spp. also act as ecosystem engineers at local scales by creating structurally complex interstitial habitat between clumped mussels and by altering resource availability (e.g. deposited organic material) within mussel beds (Ricciardi, Whoriskey & Rasmussen, 1997; Stewart, Miner & Lowe, 1998; Mörtl & Rothhaupt, 2003). Clumped mussel shells alter benthic surface topography, hydrodynamic regime and passive sedimentation, and may serve as spatial refugia from predation and physical stresses for other

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invertebrates (Gutiérrez *et al.*, 2003). For these reasons, dense aggregations of *Dreissena* generally cause local increases in the total density and taxonomic richness of smaller-bodied benthic macroinvertebrates (Ward & Ricciardi, 2007). Experiments comparing the relative contribution of physical effects (empty shell treatments) and biological effects (filtration and biodeposition by living mussels) have attributed most of these impacts to the physical characteristics of mussel aggregations (Ricciardi *et al.*, 1997; Stewart *et al.*, 1998; Horvath, Martin & Lamberti, 1999; Mörtl & Rothhaupt, 2003).

Although *Dreissena* generally facilitates other benthic macroinvertebrates, negative impacts have also been reported. Of these, the most conspicuous are dramatic declines in unionid clams, which may be outcompeted for food or smothered by *Dreissena* fouling their shells (Ricciardi, Neves & Rasmussen, 1998; and references therein). *Dreissena* has also been associated with the decline of sphaeriid clams (Strayer *et al.*, 1998; Ward & Ricciardi, 2007) and crashes in populations of the burrowing amphipod *Diporeia* spp. in soft sediment habitats in the Great Lakes (Nalepa *et al.*, 1998, 2003; Lozano, Scharold & Nalepa, 2001). On rocky substrata, *Dreissena* may competitively exclude other primary space occupiers, such as net-spinning caddisflies and large snails (Wisenden & Bailey, 1995; Ricciardi *et al.*, 1997; Ward & Ricciardi, 2007). Furthermore, a reduction in evenness has also been associated with *Dreissena* invasion, indicating that some macroinvertebrate species benefit disproportionately from the modified habitat (Ward & Ricciardi, 2007).

The impact of *Dreissena* on benthic macroinvertebrate communities has typically been quantified by comparing communities in the presence and absence of dense mussel colonies, or by measuring changes in macroinvertebrate communities along a density gradient of *Dreissena*. However, mussels are often patchily distributed in space, and studies from marine systems have shown that the spatial distribution or patch topography of mussel beds can influence benthic macroinvertebrate abundance and diversity at local scales (Tsuchiya & Nishihira, 1985; Tanaka & Magalhães, 2002). For example, large patches of marine mussels support more species than small patches (Tsuchiya & Nishihira, 1985), and the abundance of some mobile grazers increases with the availability of patch edge habitat, which they may occupy preferentially as a defence against predators or physical stressors (Tanaka & Magalhães, 2002). Moreover, mussels and other ecosystem engineers are predicted to enhance species richness at large (e.g. landscape) spatial scales (that include both engineer-modified and unmodified habitat patches) owing to increased habitat heterogeneity (Jones *et al.*, 1997; Wright, Jones & Flecker, 2002; Badano *et al.*, 2006).

We conducted a series of field experiments to investigate the effect of *Dreissena* patch topography on freshwater benthic diversity. More specifically, we manipulated habitat heterogeneity, including (i) the number of *Dreissena*-modified and unmodified (bare substratum) habitat patches and (ii) the perimeter-to-area ratio of *Dreissena* patches, while holding spatial scale constant. We hypothesised that macroinvertebrate diversity would increase with both types of habitat heterogeneity.

Some of our experimental substrata were heavily colonised by native filamentous green algae, predominately *Cladophora*. The co-occurrence of *Dreissena* and *Cladophora* is becoming increasingly common, as recent and widespread macroalgal blooms throughout the Great Lakes are linked to the large-scale impacts of *Dreissena* (Haynes, Stewart & Cook, 1999; Higgins *et al.*, 2008; Malkin, Guildford & Hecky, 2008). In particular, *Cladophora* appears to be stimulated by increased water clarity and light availability and may also benefit from phosphorus inputs from mussel biodeposits (Higgins *et al.*, 2008; Malkin *et al.*, 2008). Like *Dreissena*, *Cladophora* can act as a physical ecosystem engineer by creating structurally complex habitat and spatial refugia, as well as reducing current velocity, enhancing sedimentation and shading the substratum (Feminella & Resh, 1991; Dodds & Gudder, 1992; Hart, 1992; Holomuzki, Pillsbury & Khandwala, 1999). Variable colonisation of our experimental substrata by *Cladophora* allowed an additional, unplanned comparison in our study and enabled us to determine whether this native species modifies the effect of the exotic ecosystem engineer, *Dreissena*, on benthic macroinvertebrate communities.

Methods

Study sites

Experiments were conducted in shallow water (<3 m depth) at two sites located in Lake St. Louis, a fluvial lake in the upper St. Lawrence River, Quebec, Canada. The first experiment was carried out at a site near Lachine, Quebec (73°41′11.5″W, 45°26′01″N) in a small bay. The benthic habitat at this site consists mainly of abundant cobbles and large boulders colonised by *Dreissena* and benthic algae (*Cladophora*) overlying a thick layer of silt. Zebra mussels (*D. polymorpha*) dominated the *Dreissena* assemblage, while quagga mussels (*D. bugensis*) constituted a minor component (<1%). The main fish species present were yellow perch [*Perca flavescens* (Mitchill)] and rock bass [*Ambloplites rupestris* (Rafinesque)]. Aquatic plant management (removal of macrophytes by dredging) occurred during the experiment and probably contributed to the high turbidity at this site.

The second and third experiments were conducted at Pointe-du-Moulin, Île Pérrot (73°51′15″W, 45°21′55″N), a historical site where human activities are restricted near the shore. This site has a faster flowing current and is less turbid than the Lachine site. Sediments mainly consist of limestone bedrock with scattered large boulders. Zebra and quagga mussels were patchily distributed and approximately equally abundant. The site had abundant macrophyte beds (predominantly *Vallisneria americana* Michx.). Common macroinvertebrate predators included yellow perch, rock bass, smallmouth bass (*Micropterus dolomieu* Lacepède) and crayfish (*Orconectes* spp.).

Experiment 1

Experimental substrata consisted of solid rectangular cement bricks (individually measuring 19 cm × 9 cm × 5.7 cm), which were subject to one of three *Dreissena* shell treatment levels ($n = 10$ replicates per treatment). These consisted of bricks with their upper surface (19 × 9 cm) entirely covered in a single layer of *Dreissena* shells (full shell treatment, mean 47 ± 15 mussels brick^{-1}), bricks with one half of their upper surface covered in *Dreissena* shells (half shell treatment, mean 25 ± 5 mussels brick^{-1}), and control bricks to which no *Dreissena* shells were attached. Dreissenid mussels were collected at the site from a depth of 1–3 m. Mussels were boiled, eviscerated and rinsed to remove all mussel tissue and attached invertebrates, and the shells were dried at ambient temperature for several days. Shell valves were then glued together and attached to experimental substrata at their base (anteroventral region) using non-toxic silicone aquarium glue.

The experimental substrata were deployed at Lachine from 1 September to 6 October 2003 (35 days). Bricks were collected by carefully placing them in plastic freezer bags while underwater, and transported to the laboratory where all macroinvertebrates retained on a 500-μm sieve were preserved in 70% ethanol and were later identified, usually to family, following Merritt & Cummins (1984), Pennak (1989), Thorp & Covich (1991) and Witt, Hebert & Morton (1997). One full shell brick was not recovered.

Experiment 2

Experimental substrata were subjected to one of four *Dreissena* shell treatment levels ($n = 20$ replicates per treatment), three of which were identical to those in Experiment 1 (full shell treatment, mean 46.9 ± 0.5 mussels brick^{-1}; half shell treatment, 23.3 ± 0.5; no shell treatment). An additional shell treatment was included to investigate the effects of mussel patch area-to-perimeter ratio on benthic biodiversity. As in the half shell treatment, this consisted of bricks with one half of their upper surface covered in *Dreissena* shells, but this time arranged in two patches of equal size (chequer, mean 23.5 ± 0.5 mussels brick^{-1}). In the chequer shell treatment, mean *Dreissena* density and total patch area were equal to that of the half shell treatment (85.5 cm^2), while total patch perimeter was equal to that of the full shell treatment (56 cm). These treatment densities were within the range of *Dreissena* densities found naturally at the study site. Experimental substrata were prepared following the same methodology as in Experiment 1.

Experimental substrata were deployed at Pointe-du-Moulin from 12 July to 20 September 2004 (70 days). Colonizing macroinvertebrates were collected and preserved following the methods of Experiment 1 and were identified to the lowest possible taxonomic level, usually to species or genus, following the references cited above, as well as Resh (1976) and Klemm (1985) to identify *Ceraclea* caddisflies and annelids, respectively, to at least the genus level. One control brick was not recovered. Experimental substrata were heavily colonised by attached filamentous macroalgae (predominantly *Cladophora* and hereafter referred to as such), which sometimes overgrew *Dreissena* patches. Because *Cladophora* was suspected to influence macroinvertebrate colonisation, it was removed from 40 bricks (n = 10 replicates from each *Dreissena* treatment) by scraping *Dreissena* shell and brick surfaces with forceps. *Cladophora* samples were dried at 70 °C for 24 h, and the dry weight was measured with a Denver Instrument (Denver, CO, U.S.A.) APX-602 electronic balance.

Experiment 3

Because of heavy fouling of Experiment 2 by *Cladophora*, the experiment was replicated in 2006. The study site, experimental design and methodology for Experiment 3 were identical to that for Experiment 2 except that substrata were exposed for 17 days less. Experimental substrata (n = 10 replicates per treatment; full, mean 56.1 ± 1.1 mussels brick^{-1}; half, 28.2 ± 0.9; chequer, 26.4 ± 1.3) were deployed from 20 July to 11 September 2006 (53 days). All bricks were recovered.

Statistical analysis

Univariate and multivariate analyses were used to test the general hypothesis that macroinvertebrate assemblages differed among *Dreissena* shell treatments and, for Experiments 2 and 3, to assess the extent to which *Cladophora* modified *Dreissena* effects. The duration and scheduling of the experiments did not allow extensive colonisation of our substrata by *Dreissena* (mean number of live mussels per brick ± SE = 0.67 ± 0.08); those few individuals found on the substrata were excluded from analysis because we were not concerned with testing the influence of *Dreissena* shells on *Dreissena* recruitment.

Univariate analyses were conducted on four community response variables: total macroinvertebrate density, taxonomic richness, Simpson's diversity index (D) and Simpson's evenness index (E_D). For Experiment 1, the effect of *Dreissena* shell treatment on each community response variable was analysed using an analysis of variance (ANOVA), followed by *a posteriori* Tukey's HSD tests when appropriate. For Experiments 2 and 3, the effects of experimental *Dreissena* shell treatment and unmanipulated *Cladophora* gradient on each community response variable were assessed using an analysis of covariance (ANCOVA) with *Cladophora* biomass as a covariate. These models were reduced to ANOVAS for *Dreissena* treatment effects by sequentially removing the interaction term and covariate when appropriate, as indicated by the significance of a general linear test. For Experiments 2 and 3, *Cladophora* biomass was compared among experimental *Dreissena* treatments using ANOVA. Univariate analyses were performed on square root transformed macroinvertebrate abundance and *Cladophora* biomass and were conducted using the R (v. 2.8.1) software package (R Development Core Team, Vienna, Austria).

The effects of *Dreissena* and *Cladophora* on non-dreissenid macroinvertebrate community composition were analysed using multivariate routines in the PRIMER (v. 6) software package (Clarke & Gorley, 2006). For each experiment, a matrix of Bray-Curtis dissimilarities between samples was produced using square root transformed, non-standardised abundances. We tested for differences among *Dreissena* treatment levels using analysis of similarity (ANOSIM; Experiment 1) and among *Dreissena* treatment levels and along *Cladophora* biomass gradient using permutational multivariate analysis of variance (PERMANOVA; Anderson, Gorley & Clarke, 2008; Experiments 2 and 3). The significance of each term was tested with 9999 random permutations of the relevant units. *Cladophora* biomass was square root transformed prior to these analyses. When ANOSIM or PERMANOVA detected a significant effect of *Dreissena* treatment, the similarity percentages (SIMPER) procedure was used to identify which taxa contributed most to the Bray-Curtis dissimilarity between *Dreissena* treatment levels. When PERMANOVA detected a significant effect of *Cladophora*, the relationship between *Cladophora* biomass and the abundance of individual macroinvertebrate taxa was examined using Spearman's rank correlation, and significance was assessed by t-tests. Non-metric multidimensional scaling (nMDS) ordination was performed on the Bray-Curtis dissimilarity matrix for each experiment to generate a graphical representation of the multivariate data.

Results

Experiment 1

A total of 20 non-dreissenid macroinvertebrate taxa were collected from experimental substrata. All 20 taxa were present on the half shell bricks, while a total of 13 and 14 taxa occurred on the control and full bricks, respectively (Table S1 in Supporting Information). The most abundant taxon was the amphipod *Gammarus fasciatus* Say, followed by chironomids, flatworms (Planariidae), Hydracarina and planorbid snails.

Total macroinvertebrate density increased significantly with successive increases in *Dreissena* shell cover (ANOVA, $F = 54.74$, $P < 0.0001$; Fig. 1a). Mean taxonomic richness was higher in both the half and full shell treatments than in the control treatment but did not differ significantly between half and full shell bricks (ANOVA, $F = 19.21$, $P < 0.0001$; Fig. 1b). Simpson's diversity index was significantly lower on full than on either control or half shell bricks, while the latter two did not differ (ANOVA, $F = 6.32$, $P = 0.006$; Fig. 1c). Simpson's evenness index was significantly higher in the control treatment than in either the half or full shell treatments (ANOVA, $F = 34.45$, $P < 0.0001$; Fig. 1d).

Multivariate analyses indicated that the macroinvertebrate assemblage structure differed across the *Dreissena* shell treatments (ANOSIM, Global $R = 0.42$, $P = 0.01$; Fig. 2a). Pair-wise comparisons indicated that there were significant differences in assemblage structure between the control and full shell bricks ($R = 0.59$, $P = 0.01$) and between the control and half shell bricks ($R = 0.49$, $P = 0.01$), but not between the half and full shell bricks ($R = 0.27$, $P = 0.1$). Assemblages on control bricks were also more dissimilar than those in either the half or full shell treatments; the average within-treatment Bray-Curtis similarity was 44.24 for control bricks, compared to 68.75 and 74.96 for half and full shell bricks, respectively. These patterns are reflected in the nMDS plot (Fig. 2a). The amphipod *Gammarus fasciatus* accounted for most of the Bray-Curtis dissimilarity between *Dreissena* treatment levels (SIMPER, Table S2 in Supporting Information). Other taxa that made an important contribution to dissimilarity between treatment levels include isopods (*Caecidotea*), caenid mayflies, flatworms (Planariidae), chironomids and planorbid snails.

Experiment 2

A total of 63 non-dreissenid macroinvertebrate taxa were identified from experimental substrata (Table S1), with 45, 43, 43 and 46 taxa collected from

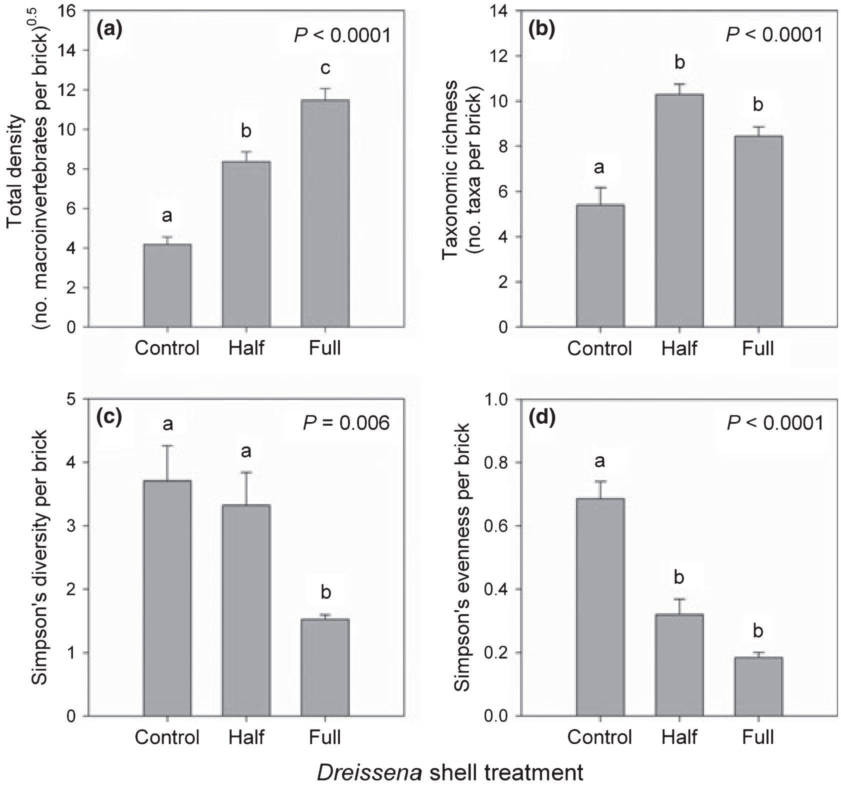

Fig. 1 (a) Total non-dreissenid macroinvertebrate abundance, (b) taxonomic richness, (c) Simpson's diversity index and (d) Simpson's evenness index on the three *Dreissena* shell treatments in Experiment 1. Data are expressed as mean (± SE) per brick. Letters denote significant differences between treatment levels (Tukey's tests, $P < 0.05$).

control, half, chequer and full bricks, respectively. The most abundant taxon was the native amphipod *Gammarus fasciatus*, followed by the non-indigenous Eurasian amphipod *Echinogammarus ischnus* (Stebbing), chironomids, the snail *Gyraulus deflectus* (Say) and the flatworm *Dugesia tigrina* Girard. Mean *Cladophora* biomass did not differ significantly among *Dreissena* treatment levels (Fig. 3a).

In univariate analyses, the *Dreissena* × *Cladophora* interaction term did not explain a significant amount of variation in any of the community response variables, nor did *Cladophora* biomass when it was included as a covariate (Table 1). *Dreissena* treatment did not explain a significant amount of variation in total macroinvertebrate density or Simpson's evenness index. When *Cladophora* was removed from the

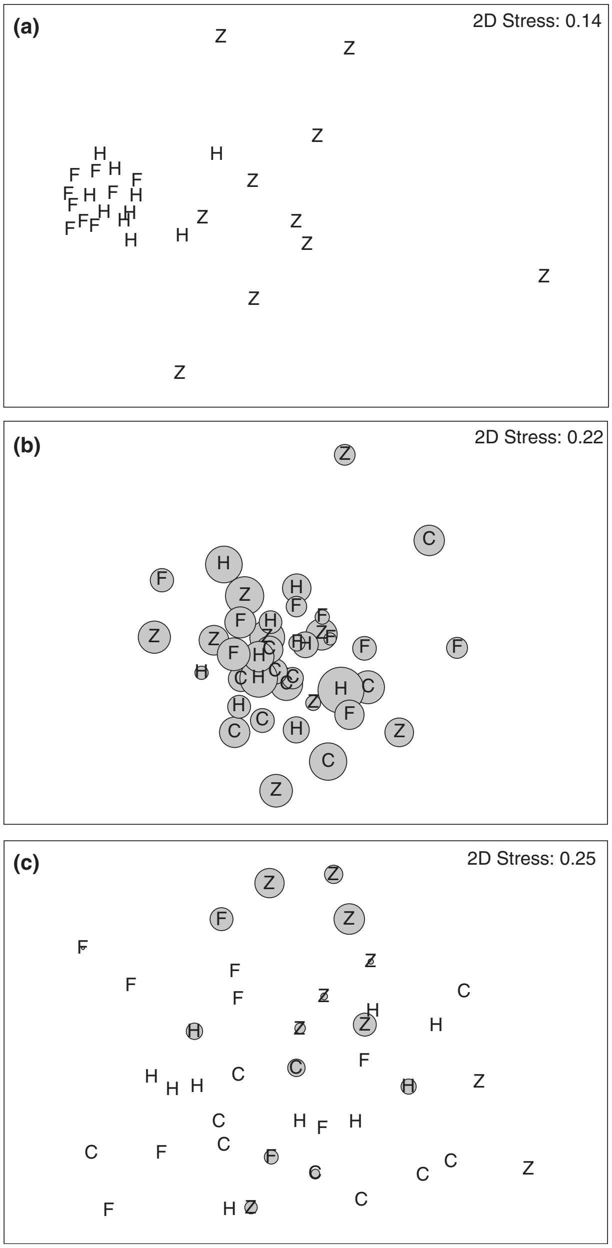

Fig. 2 Non-metric MDS ordination for (a) Experiment 1, (b) Experiment 2 and (c) Experiment 3, based on Bray-Curtis dissimilarity applied to square root transformed species abundances. Labels indicate control (Z), half (H), chequer (C) and full (F) *Dreissena* shell treatments. *Cladophora* biomass is indicated by the size of the 'bubbles' in (b) and (c).

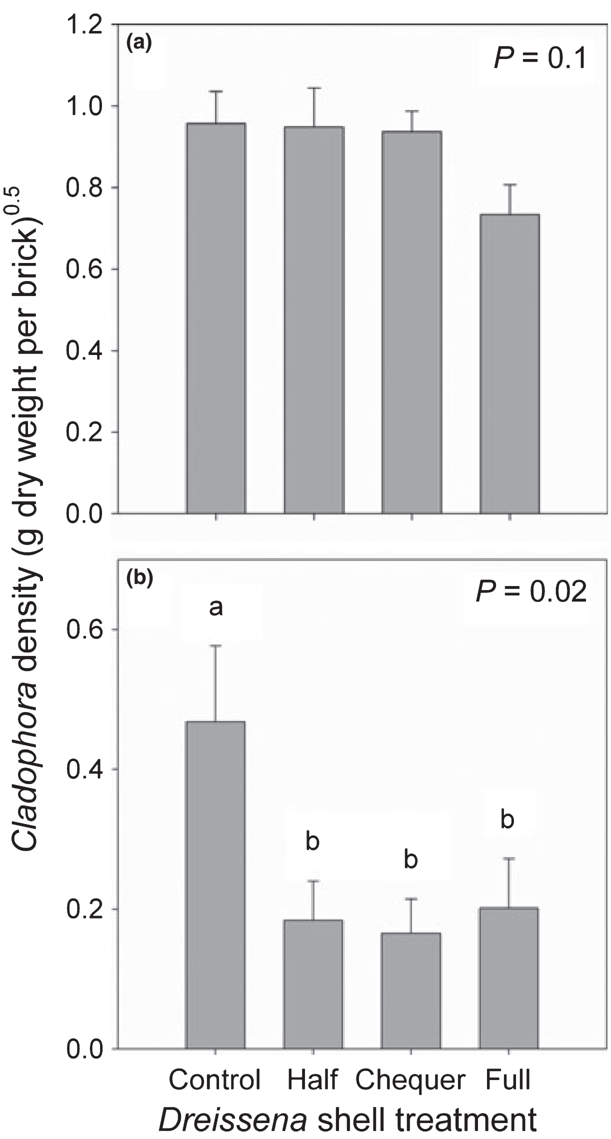

Fig. 3 Mean (± SE) *Cladophora* density on the four *Dreissena* shell treatments in (a) Experiment 2 and (b) Experiment 3. Letters denote significant differences between treatment levels (Tukey's tests, $P < 0.05$).

Table 1 Univariate analyses of community response variables for Experiment 2. *Cladophora* biomass and total macroinvertebrate abundance were square root transformed prior to analysis

		Total abundance			Richness			Diversity (*D*)			Evenness (E_D)		
Source of variation	d.f.	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Full model (ANCOVA)													
Dreissena (T)	3	6.44	0.62	0.61	15.39	1.51	0.23	3.40	1.70	0.19	0.007	0.58	0.63
Cladophora (Cov)	1	0.72	0.07	0.79	14.87	1.46	0.24	4.63	2.31	0.14	0.002	0.20	0.66
T x Cov	3	9.90	0.95	0.43	2.30	0.23	0.88	3.07	1.53	0.23	0.017	1.36	0.27
Residual	31	10.43			10.21			2.00			0.012		
Total	38												
Reduced model (ANOVA)													
Dreissena (T)	3	4.86	0.51	0.68	18.30	2.24	0.09	5.65	2.65	0.06	0.010	0.96	0.42
Residual	75	9.59			8.17			2.13			0.010		
Total	78												

model, the difference in Simpson's diversity index across *Dreissena* treatments was marginally insignificant (ANOVA, $P = 0.06$). This was probably driven by differences between control and full shell bricks, which had a mean (± SE) Simpson's diversity of 4.31 (±0.38) and 5.55 (±0.29), respectively.

Multivariate analyses indicated that the macroinvertebrate assemblage differed significantly among *Dreissena* shell treatments but this was not related to *Cladophora* biomass (PERMANOVA, Table 2; Fig. 2b). Pairwise comparisons detected a significant difference between the control and chequer shell treatments ($P = 0.009$). When *Cladophora* was removed from the model, the difference between control and full bricks became significant ($P = 0.009$). Five taxa consistently made large contributions to the dissimilarity between these *Dreissena* treatment levels (SIMPER, Table S3 in Supporting Information). These were the amphipods *Gammarus fasciatus* and *Echinogammarus ischnus*, the flatworm *Dugesia tigrina*, chironomids and the snail *Gyraulus deflectus*. The average Bray-Curtis dissimilarities between *Dreissena* treatment levels were lower than in Experiment 1.

Table 2 Permutational analysis of variance (PERMANOVA) for Experiments 2 and 3, based on Bray-Curtis dissimilarities using square root transformed taxon abundances. *P*-values generated by permutation (9999 iterations)

Experiment	Source of variation	d.f.	MS	Pseudo-*F*	*P*
2	*Cladophora* (Cov)	1	489.28	0.951	0.470
	Dreissena (T)	3	890.65	1.732	**0.009**
	Cov × T	3	549.61	1.069	0.365
	Residual (R)	31	514.40		
	Total	38			
3	*Cladophora* (Cov)	1	1288.80	2.141	**0.018**
	Dreissena (T)	3	799.41	1.328	0.115
	Cov × T	3	446.70	0.742	0.889
	Residual (R)	32	601.90		
	Total	39			

Experiment 3

A total of 45 non-dreissenid macroinvertebrate taxa were identified from experimental substrata, with a total of 32 taxa collected from both control and half shell bricks, and a total of 34 taxa collected from both chequer and full shell bricks (Table S1). Chironomids were the most abundant taxon, followed by *Gammarus fasciatus*, *Gyraulus deflectus*, *Dugesia tigrina* and *Echinogammarus ischnus*. Mean *Cladophora* biomass varied significantly among *Dreissena* treatment levels (ANOVA, $F = 3.64$, $P = 0.02$), being significantly higher on control bricks than on all other *Dreissena* shell treatments (Fig. 3b).

In univariate analyses, none of the *Dreissena* × *Cladophora* interaction terms explained a significant amount of variation in any of the community response variables, nor did *Cladophora* biomass when it was included as a covariate (Table 3). Regardless of whether these terms were included in the model, *Dreissena* treatment did not explain a significant amount of variation in total macroinvertebrate density, taxonomic richness, Simpson's diversity index or Simpson's evenness index.

Multivariate analyses indicated that the macroinvertebrate assemblage structure was related to *Cladophora* biomass but did not differ significantly among

Table 3 Univariate analyses of community response variables for Experiment 3. *Cladophora* biomass and total macroinvertebrate abundance were square root transformed prior to analysis

		Total abundance			Richness			Diversity (D)			Evenness (E_D)		
Source of variation	d.f.	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Full model (ANCOVA)													
Dreissena (T)	3	11.72	1.32	0.29	6.76	0.91	0.45	2.03	0.59	0.62	0.016	0.93	0.44
Cladophora (Cov)	1	1.49	0.17	0.69	0.80	0.11	0.75	1.48	0.43	0.52	0.009	0.53	0.47
T × Cov	3	7.11	0.80	0.50	11.20	1.50	0.23	1.13	0.33	0.80	0.006	0.34	0.79
Residual	32	8.91			7.47			3.42			0.017		
Total	39												
Reduced model (ANOVA)													
Dreissena (T)	3	11.72	1.37	0.27	6.76	0.89	0.46	2.03	0.64	0.59	0.016	0.99	0.41
Residual	36	8.55			7.60			3.17			0.016		
Total	39												

Dreissena shell treatments after accounting for this relationship (PERMANOVA, Table 2; Fig. 2c). This result was probably driven by negative correlations between *Cladophora* biomass and the abundance of two species, the amphipods *Gammarus fasciatus* (Spearman's rank correlation, $r_s = -0.381$, $P = 0.04$) and *Echinogammarus ischnus* ($r_s = -0.396$, $P = 0.03$), as well as positive correlations between *Cladophora* biomass and the abundance of three species: the snail *Physa gyrina* (Say) ($r_s = 0.449$, $P = 0.01$), the leech *Batracobdella phalera* (Graf) ($r_s = 0.434$, $P = 0.02$) and the oligochaete *Stylaria lacustris* (L.) ($r_s = 0.371$, $P = 0.04$). After sequential Bonferroni correction (Rice, 1989), none of these correlations remain significant. However, the risk of Type II error associated with this procedure argues against its use (Moran, 2003).

Discussion

Effect of Dreissena patch topography on benthic diversity

In our first experiment, substrata completely covered with *Dreissena* shells had higher total macroinvertebrate density and species richness, as well as lower Simpson's diversity and evenness indices, compared to control bricks lacking *Dreissena*. These findings are consistent with previous studies (Ward & Ricciardi, 2007) and support the hypothesis that some *Dreissena* impacts on macroinvertebrate communities are predictable across invaded sites. Despite higher species richness, full shell bricks had lower diversity and evenness indices than control bricks, owing to increased dominance by the amphipod *Gammarus fasciatus*, which accounted for more than 80% of all macroinvertebrates collected from full shell bricks. Gammarid amphipods frequently dominate macroinvertebrate assemblages on *Dreissena*-covered substrata, probably in response to mussel-generated interstitial habitat as well as to the provision of refugia from predation and hydrodynamic stress (Stewart & Haynes, 1994; Ricciardi *et al.*, 1997; Stewart *et al.*, 1998). Simpson's diversity remained relatively high in the half shell treatment, which contained patches of both *Dreissena*-modified and unmodified habitats. This reflected both high taxonomic richness and lower dominance by *G. fasciatus*. Interestingly, mean taxonomic richness tended to be highest on the half shell bricks, which were also colonised by the greatest total number of macroinvertebrate taxa (Fig. 1b, Table S1). This result contrasts with the assumption that the effect of *Dreissena* on benthic communities is a simple linear function of mussel density (e.g. Strayer & Smith, 2000; Mayer *et al.*, 2002) and further suggests that the spatial arrangement of mussel patches, along with mussel abundance (Horvath *et al.*, 1999; Strayer & Smith, 2000; Mayer *et al.*, 2002; Ricciardi, 2003) and size frequency distribution (Young *et al.*, 1996), modifies the impact. Factors that affect the arrangement of *Dreissena* patches, such as changes in settlement patterns or disturbance (e.g. mortality caused by sponge overgrowth; Ricciardi *et al.*, 1995), may therefore be important. That the same pattern was not observed in Experiments 2 and 3 indicates either that this result was site-specific, or the result is general but was obscured in subsequent experiments by *Cladophora*. We believe the latter explanation is more likely.

It has been predicted that ecosystem engineers should generally increase species richness at large (e.g. landscape) spatial scales that include both engineer-modified and unmodified habitat patches (Jones *et al*., 1997; Wright *et al*., 2002). This is purported to result from enhanced landscape-scale habitat heterogeneity, which should increase species richness if some species occur only in one habitat type (Wright *et al*., 2002; Badano *et al*., 2006). In our study, spatial scale was held constant while habitat heterogeneity (the number of different habitat types) was manipulated. Our results from the half shell treatment, where both modified and unmodified habitats were represented, support a positive relationship between habitat heterogeneity and species richness. This pattern arose in part because of the mechanism above: five taxa were present in the half shell treatment that otherwise occurred in either the control or full shell treatment but not in both (*E. ischnus*, heptageniid mayflies, polycentropodid caddisflies, tubificid oligochaetes and *Bithynia tentaculata* L.). An additional four taxa occurred only in the half shell treatment: valvatid snails and brachycentrid, hydrophychid and hydroptilid caddisflies. This suggests an added contribution of habitat diversity (generated by ecosystem engineers) to species richness at small spatial scales, arising from the preferential colonisation of heterogeneous (or patchy) habitats by some species. However, these four taxa were relatively rare, and it is unclear whether this pattern would hold at larger spatial scales or with greater sampling intensity.

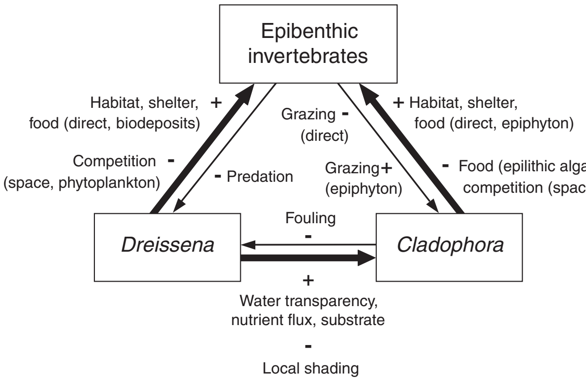

Fig. 4 Schematic illustration of the biotic interactions between *Dreissena*, *Cladophora* and epibenthic macroinvertebrates. Details of these interactions are discussed by Feminella & Resh (1991), Dodds & Gudder (1992), Vanderploeg *et al*. (2002) and Higgins *et al*. (2008).

Effect of Cladophora on benthic macroinvertebrates

A review of the literature on the effects of *Cladophora* on benthic invertebrates reveals mixed results (Fig. 4). In one study, *Cladophora* density was negatively correlated with diversity (H′) and evenness (J′) of stream macroinvertebrates, although it was positively correlated with *Baetis*, *Simulium* and chironomid abundance (Ellsworth, 2000). Elsewhere, *Cladophora* was associated with increased total density and taxonomic richness of stream invertebrates, although it negatively affected some dipteran taxa (*Blepharicera* and large-bodied *Simulium*), apparently via competition for substratum (Dudley, Cooper & Hemphill, 1986). Similarly, Hart (1992) found positive correlations between *Cladophora* cover and the abundance of chironomids, the mayfly *Stenonema*, and the stoneflies *Taeniopteryx* and *Isoperla*, as well as negative correlations with grazing caddisflies (*Leucotrichia* and *Psychomyia*) and the tipulid *Antocha*. Harrison & Hildrew (2001) reported a positive association between *Cladophora* and tube-dwelling chironomids (*Glyptotendipes pallens* (Meigen) and *Microtendipes pedellus* [de Geer)] in a lake littoral. In Lake Ontario, *Cladophora* was positively associated with gammarid amphipods and naidid oligochaetes, and negatively associated with chironomids (Barton & Hynes, 1978).

Some of the macroinvertebrates that commonly increase in abundance following *Dreissena* invasion, such as gammarid amphipods and snails (Ward & Ricciardi, 2007), are also expected to respond to *Cladophora*. In particular, a positive association has been documented between *G. fasciatus* and *Cladophora*, which may provide the amphipod with both food resources and interstitial habitat (Barton & Hynes, 1978; Stewart & Haynes, 1994; Van Overdijk *et al*., 2003; Palmer & Ricciardi, 2004). We detected a negative correlation between *Cladophora* and *G. fasciatus* in Experiment 3, but this was driven by the amphipod's positive response to *Dreissena* rather than avoidance of *Cladophora* (ANCOVA, effect of *Dreissena*: $F = 4.48$, $P = 0.01$, effect of *Cladophora*: $F = 1.03$, $P = 0.32$). We also found a negative association between *Echinogammarus ischnus* and *Cladophora*, which is consistent with the observation that this amphipod prefers substrata covered by *Dreissena* rather than *Cladophora* (Van Overdijk *et al*., 2003; Palmer & Ricciardi, 2004). Snails and other macroinvertebrates that graze on diatoms may avoid

Cladophora (Haynes *et al.*, 1999). The abundance of benthic diatoms, an important food source for grazers, declined with increasing biomass of filamentous green algae in Lake Huron following *Dreissena* invasion (Lowe & Pillsbury, 1995). *Cladophora* may inhibit the growth of epilithic microalgae by reducing light penetration (Feminella & Resh, 1991). In comparison with diatoms, *Cladophora* has lower nutritional value and is generally not a preferred food for freshwater grazers (Dodds & Gudder, 1992). However, epiphytic algae growing on *Cladophora* may be important for some grazers (Dodds, 1990).

In our study, *Cladophora* biomass did not explain variation in total macroinvertebrate density, taxonomic richness, Simpson's diversity index or Simpson's evenness index. However, *Cladophora* biomass explained a significant amount of variation in community composition in Experiment 3, when it was present at relatively low densities, but not in Experiment 2, when it occurred at relatively high densities. This suggests that the response of macroinvertebrates to *Cladophora* is nonlinear. Indeed, previous studies have demonstrated that macroinvertebrate responses to increasing habitat structure can be nonlinear (e.g. Stewart, Shumaker & Radzio, 2003). Furthermore, *Cladophora* has been shown to have significant effects on benthic macroinvertebrates at relatively low abundance; for example, Holomuzki *et al.* (1999) found that 4–13% cover of *Cladophora* on rocks was enough to nullify the effects of predatory stoneflies (Plecoptera) on drift of their larval hydropsychid prey. The *Cladophora* cover on substrata in Experiment 2 was typically much higher than 13% and reached 100% on some bricks (J. M. Ward, personal observation), which may have exceeded the range of *Cladophora* densities within which variation in its effect is most pronounced.

Is Cladophora obscuring the effect of Dreissena?

If the impact of *Dreissena* on benthic macroinvertebrates occurs mostly through the physical effects of interstitial habitat among the shells (an assumption supported by previous experiments comparing the effects of *Dreissena* shells to living mussels: Ricciardi *et al.*, 1997; Stewart *et al.*, 1998; Horvath *et al.*, 1999; Mörtl & Rothhaupt, 2003), then it follows that this effect will be reduced in systems where structurally complex habitat is not limiting. That is, in communities with abundant benthic algae such as *Cladophora*, the effect of the mussels should be less than in systems where structurally complex habitats are scarce (Gutiérrez *et al.*, 2003). These habitats may not have been limiting on control substrata colonised by *Cladophora*, where the alga probably provided some of the same benefits as mussel-engineered habitat to benthic fauna (Fig. 4), such as interstices and refugia from predation (Hart, 1992; Holomuzki *et al.*, 1999).

Our experiments were not designed to examine the effect of *Cladophora*; consequently, we lacked an adequate experimental control for both *Cladophora* and *Dreissena* effects. Neither Experiment 2 nor Experiment 3 had a treatment lacking both *Dreissena* and *Cladophora*, which we believe contributed to the lack of statistically significant effects on community response variables. In Experiment 2, control bricks (as well as other treatments) were heavily colonised by *Cladophora*, which may have reduced variation in habitat heterogeneity and structural complexity across *Dreissena* treatments. However, the significant effect of *Dreissena* shells on community structure, and the tendency for Simpson's diversity index to be higher on full versus control bricks in Experiment 2, indicates that some taxa responded to the habitat provided by *Dreissena* shells even in the presence of heavy *Cladophora* fouling. Here, *Dreissena* restructured the macroinvertebrate community without changing its total abundance. *Cladophora* and associated accumulation of fine sediment sometimes clogged the spaces between *Dreissena* shells and may have reduced the amount of shell-generated habitat available to macroinvertebrates (J. M. Ward, personal observation). Similarly, Jacobi (1987) found the density of macroinvertebrates associated with the brown mussel *Perna perna* (L.) was reduced when sediment covered the mussel shells and filled interstitial spaces.

In Experiment 3, *Cladophora* was most abundant on control bricks, possibly as a result of shading by mussel shells. It is also possible that grazing invertebrates inhibited *Cladophora* growth on *Dreissena* shells. *Cladophora* may deter grazers by chemical defences when it is mature but lacks these defences during its initial growth, and grazing insects have previously been shown to inhibit *Cladophora* establishment and growth in streams (Dudley & D'Antonio, 1991; Hart, 1992) and lakes (Harrison & Hildrew, 2001). However, we found no negative associations between the abundance of grazing macroinvertebrates and *Cladophora* and one grazer, the snail *Physa gyrina*, appeared to be positively associated with *Cladophora*. We also found positive associations between *Cladophora* and both the deposit-feeding oligochaete *Stylaria lacustris* and the predatory leech *Batracobdella phalera*. These species were probably responding to habitat structure and possibly to increased availability of food or prey.

Several studies in marine systems have compared benthic macroinvertebrate communities in habitats created by introduced bivalves and native macrophytes. Ferraro & Cole (2007) found that benthic macroinvertebrate communities inhabiting introduced oyster [*Crassostrea gigas* (Thunberg)] and native eelgrass (*Zostera marina* L.) habitats in Willapa Bay, Washington, were indistinguishable in terms of their total abundance, taxonomic richness and Bray-Curtis similarity. In another study, total macroinvertebrate density was higher in *Z. marina* beds compared to *C. gigas* beds, while the density of meiofauna did not differ between these habitats (Hosack *et al*., 2006). On biogenic reefs created by the native tube-building polychaete *Sabellaria alveolata* (L.), species richness was higher on reefs colonised by both oysters (*C. gigas*) and a green alga (*Ulva armoricana* Dion, Reviers & Coat) compared to reefs colonised by only the alga (Dubois *et al*., 2006). Elsewhere, the richness and identity of macroinvertebrates inhabiting a native mussel [*Aulacomya ater* (Molina)] bed and the macroalgae on its shell closely resembled that found in association with an exotic mussel (*Mytilus galloprovincialis* Lamarck) that was free of macroalgae, although the total density of associated macroinvertebrates was higher for the latter (Griffiths *et al*., 1992).

One additional line of evidence supports our hypothesis that *Cladophora* is responsible for the paucity of observed community-level impacts by *Dreissena* in Experiments 2 and 3. This comes from a survey of natural substrata (rocks, $n = 30$) spanning a range of *Dreissena* densities (0–2468 m^{-2}; mean, 1,086 m^{-2}), which was conducted concurrently and at the same site as Experiment 1. Unlike the artificial substrata in Experiment 1, on which *Cladophora* was essentially absent, natural substrata at the site were heavily colonised by *Cladophora* (range, 0–381 g dry weight m^{-2}; mean, 91 g dry weight m^{-2}). Linear regression analyses detected no statistically significant relationship between *Dreissena* density (square root transformed) and the total density (fourth root transformed, $r^2 = 0.01$, $P = 0.62$), taxonomic richness (fourth root transformed, $r^2 = 0.08$, $P = 0.14$), Simpson's diversity ($r^2 = 0.08$, $P = 0.13$) or Simpson's evenness ($r^2 = 0.01$, $P = 0.58$) of macroinvertebrates on the rocks. Thus, while *Dreissena* had highly significant effects on these community response variables on experimental substrata lacking *Cladophora* (Fig. 1), no effect was apparent on surrounding natural substrata that had abundant *Cladophora* cover.

Alternative explanations for reduced Dreissena effects at Pointe-du-Moulin

An alternative explanation for the results of our second and third experiments is that we lacked

Table 4 Comparison with other experiments that examined the effect of *Dreissena* shells on benthic macroinvertebrate communities. Results are for control (C) and *Dreissena* shell (S) treatments, the latter represented by the full shell treatment in this study (Experiments 1, 2 and 3). Taxonomic richness was standardized to the lowest level of identification common to all studies for each taxon

	Ricciardi *et al*. (1997)	Stewart *et al*. (1998)	Horvath *et al*. (1999)	Mörtl & Rothhaupt (2003)	This study		
					Expt 1	Expt 2	Expt 3
Study characteristics							
No. replicates (n)	10	5	7	9	10	20	10
Duration (days)	63	37	28	27	35	70	53
Years post-invasion	4	8	3	33	12	13	15
Results							
Total macroinvertebrate abundance (no. m^{-2})	C = 2152	C = 7700	C = 2967	C = 7796	C = 284	C = 3401	C = 1738
	S = 5930	S = 33 212	S = 7473	S = 15 133	S = 2032	S = 3811	S = 2732
Taxonomic richness (standardized)	C = 20	C = 11	C = 19	C ≥ 7	C = 13	C = 29	C = 22
	S = 22	S = 13	S = 24	S ≥ 7	S = 13	S = 28	S = 25

sufficient statistical power to detect *Dreissena* effects. Another possibility is that the time allowed for macroinvertebrates to colonise the experimental substrata was insufficient, preventing them from reaching equilibrium densities. However, the sample size and experimental duration in Experiments 2 and 3 equalled or surpassed that used in previously published experiments, as well as in our first experiment, which have consistently found significant effects of *Dreissena* shells on macroinvertebrate communities (Table 4). These explanations are therefore unlikely to account for our findings. Similarly, time since invasion, which could explain variation across sites if there are time lags in the impacts of *Dreissena* (Strayer *et al.*, 2006), is not a satisfactory explanation. Significant *Dreissena* effects were detected in Experiment 1, which was conducted 1–2 years earlier at a nearby site in the same system. Finally, some other aspect of the system besides *Cladophora* may have differed between the two sites. Anthropogenic disturbance differed greatly between Lachine and Pointe-du-Moulin, and may have influenced our results; in particular, this may have contributed to the relatively low abundance and diversity of macroinvertebrates in Experiment 1 (Table 4). However, the two experiments with anomalous results were conducted at a site where anthropogenic disturbance was limited. Here, macroinvertebrate densities on control substrata were comparable to those reported for other experiments conducted at lotic sites (Ricciardi *et al.*, 1997; Horvath *et al.*, 1999), and taxonomic richness equalled or surpasses that reported in other experimental studies (Table 4). Furthermore, the published studies summarised here were conducted in a diverse assortment of aquatic habitats, with different substrata, current velocities and fauna.

In conclusion, the results from our first experiment suggest that a patchy distribution of dreissenid mussels may be an important driver of benthic diversity at small spatial scales. If we had interpreted the results of Experiments 2 and 3 in the absence of other studies of the effect of *Dreissena* on benthic macroinvertebrates, we would have erroneously concluded that it has no effect. However, the results of many other studies, including some on the same system, corroborate a significant effect of *Dreissena*. This highlights the context-dependent nature of invasion impacts. Most studies of invasion examine the effects of an introduced species in isolation. As ecosystems become increasingly invaded, the co-occurrence of introduced engineers will become more common, and there is a need for studies investigating their interactive effects (Jones *et al.*, 1997; Altieri, Silliman & Bertness, 2007; Ferraro & Cole, 2007). The introduced ecosystem engineer, *Dreissena*, commonly occurs with native macroalgae such as *Cladophora*, and both are habitat modifiers that often comprise an interacting system (Fig. 4). The potential alteration of the effect of *Dreissena* by *Cladophora* illustrates the complexity of invasion impacts on biotic communities. Our results demonstrate that the interactions of habitat-modifying species can complicate efforts to predict the community-level effects of an invader.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Macroinvertebrate taxa collected from experimental substrata in the three experiments.

Table S2. Similarity percentages (SIMPER) analysis for Experiment 1, showing which taxa made the greatest percent contribution (δ %) to the Bray-Curtis dissimilarity between *Dreissena* shell treatment levels.

Table S3. Similarity percentages (SIMPER) analysis for Experiment 2, showing which taxa made the greatest percent contribution (δ %) to the Bray-Curtis dissimilarity between *Dreissena* shell treatment levels.

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