

Zebra mussel colonisation of soft sediments facilitates invertebrate communities

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SUMMARY

1. We examined the effect of zebra mussel colonisation on invertebrate communities inhabiting soft sediments in two bays along the Vermont shoreline of Lake Champlain, U.S.A.
2. In summer 2001, we conducted manipulative experiments (addition and removal of zebra mussel colonies) with respective controls to assess the effect of colonies on invertebrate abundance, richness, and position within sediments (within colony versus underlying colony) and compared these data to comparative studies of natural communities in summer 2002.
3. Split core samples were taken two months after the manipulation and the following year so that we could quantify individuals and species inhabiting zebra mussel colonies separately from those in sediments underlying zebra mussel colonies and adjacent sediments lacking zebra mussels.
4. Zebra mussel-covered sediments supported more abundant and richer invertebrate communities than adjacent sediments lacking zebra mussels.
5. Abundance and richness patterns in zebra mussel-addition and removal treatments closely paralleled those in natural communities.
6. Despite severe oxygen depletion at the interface of underlying sediments and overlying zebra mussel colonies, most infaunal invertebrates responded positively to zebra mussel colonisation either by remaining in sediments underlying zebra mussel colonies or by migrating into zebra mussel colonies.

Keywords: facilitation, invertebrate communities, soft sediments, zebra mussels

Introduction

One of the most dramatic effects of invasive aquatic species is their physical alteration of ecosystems (Crooks, 2002a). The establishment of exotic species may alter ecosystems by affecting resource availability (Vitousek *et al.*, 1987), redirecting energy flow through food webs (Savidge, 1987), changing disturbance regimes (Chapuis, Bousses & Barnaud, 1994), and/or by modifying the physical structure of the ecosystem

itself (Simberloff, 1991; Bertness, 1994; Crooks & Khim, 1999). While the adverse effects of invasive species are frequently highlighted, these species may serve as additional food resources (Reusch, 1998; Crooks, 2002b) or facilitate native species through direct, indirect, or commensal relationships (Crooks, 1998; Posey, 1998). One example of an indirect facilitation is the physical alteration of benthic substrates by the zebra mussel, *Dreissena polymorpha* (Pallas) (Botts, Patterson & Schloesser, 1996).

Zebra mussels provide both habitat complexity and a rich supply of organic material to benthic invertebrates (Stewart & Haynes, 1994; Stewart, Miner & Lowe, 1998). Dreissenid mussels form very dense

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colonies and may completely cover both hard (Ricciardi, Whoriskey & Rasmussen, 1997 and references therein) and soft substrates (Dermott & Munawar, 1993; Berkman, Garton & VanBloem, 1994; Coakley *et al.*, 1997; Dermott & Kerec, 1997; Berkman *et al.*, 1998; Bially & MacIsaac, 2000). *Dreissena* shells increase structural complexity of hard and soft substrates. The creation of interstitial spaces among shells provides refugia from predation and protection from disturbances such as wave action. The deposition of nutritionally and energetically rich pseudofaeces and faeces in benthic habitats can increase both the quality and quantity of particulate organic matter available to other benthic invertebrates (Roditi, Strayer & Findlay, 1997; Thayer *et al.*, 1997; Stewart *et al.*, 1998).

Benthic invertebrate diversity and biomass are typically higher on hard substrates colonised by zebra mussels than on hard substrates lacking zebra mussels (Stewart & Haynes, 1994; Stewart *et al.*, 1998). Ricciardi *et al.* (1997) reported increases in biomass for a wide array of taxa including Gastropoda, Trichoptera, Ephemeroptera, Diptera, Hirudinea, and Oligochaeta. However, positive effects of zebra mussels on benthic invertebrate species are not universal. A few invertebrate species, including polycentropodid caddisflies, large pleurocerid snails, and plumatellid bryozoans had reduced abundances on hard substrates colonised by zebra mussels than on bare substrates (Ricciardi *et al.*, 1997).

Fewer studies have examined how benthic invertebrate communities in soft sediments respond to zebra mussel colonisation (e.g. Botts *et al.*, 1996; Bially & MacIsaac, 2000). Responses of benthic invertebrates to zebra mussel colonisation of soft sediments have been more mixed than on hard substrates. For example, Bially & MacIsaac (2000) reported that sediment covered by zebra mussel colonies supported between 4.6 and seven times as many taxa and between two and four times as many individuals than sediments lacking zebra mussel colonies. In contrast, declines of infaunal invertebrate species have been also been reported following zebra mussel colonisation of soft sediments. In the Great Lakes, declines in *Diporeia hoyi* populations, a major food source for commercial fish, have been attributed to zebra mussel colonisation of soft sediments (Nalepa *et al.*, 2000). Reduced densities of gastropods, chironomids, and caddisflies have also been observed in

sediments colonised by zebra mussels (Wisenden & Bailey, 1995; Ricciardi *et al.*, 1997). Clearly, additional studies are needed to clarify effects of zebra mussels on soft sediment invertebrate communities.

We examined how the colonisation of soft sediments by zebra mussels affects benthic invertebrates in Lake Champlain. Unlike previous studies, we artificially manipulated the presence or absence of zebra mussel colonies and measured the response of both infaunal and epifaunal invertebrates over time. We also used a modified sampling technique compared with other studies to determine the position of invertebrates within zebra mussel colonies on soft sediments. Burks *et al.* (2002) found degraded interstitial water quality in zebra mussel colonies. Vertical gradients in water quality were attributed to the chemical degradation of pseudofaeces and faeces produced by zebra mussels as well as decreased water flow within the colony itself. As many benthic invertebrates are intolerant of degraded water quality, one would expect to see sharp contrasts in the distribution of invertebrates within zebra mussel colonies. We hypothesised that few if any invertebrates would occupy sediments beneath zebra mussel colonies.

Methods

Site characteristics

Colonisation of Lake Champlain, U.S.A, by zebra mussels began in 1993 in the southern end of the lake. Benthic surveys revealed little or no colonisation of soft sediments until 2000. Surveys conducted after 2000 found widespread colonisation of soft sediments in many bays along the Vermont shoreline (unpublished data). For this experiment, all sampling was conducted in two shallow bays along the Vermont shoreline of Lake Champlain. Appletree Bay is relatively exposed and subject to strong wind and wave action and characterised by a sandy bottom. Hawkins Bay has a muddy bottom and is somewhat sheltered. To quantify sediment characteristics in each bay, we sampled sediments in areas colonised by zebra mussels and adjacent areas lacking zebra mussels using a core sampler with a 7.7 cm diameter and 12 cm depth. In the laboratory, sediments were separated from zebra mussels/shell fragments and dried for 48 h at 70 °C. Each sediment sample was sieved with a

standard set of sediment sieves (0.06, 0.12, 0.25, 0.5, 1.0, and >2.0 mm in diameter). Each sediment size class was weighed to the nearest 0.1 mg and expressed as the percentage of the whole sample weight. The size classes were then averaged across samples for each sediment type (bare sediment versus zebra mussel covered sediments) and site.

To account for possible differences in zebra mussel density and colony thickness among sites, we sampled each bay in 2001 and 2002 using corers (13.5 cm high \times 10.2 cm diameter). Ten core samples were taken in areas colonised by zebra mussels in both Appletree and Hawkins bays. Zebra mussel density (number per core sample), minimum and maximum size (greatest anterior to posterior shell length), and colony thickness (depth in centimetres of zebra mussels in corer) were recorded.

We used scuba and a YSI probe to measure dissolved oxygen (DO) (mg mL^{-1}) *in situ* at the interface between overlying zebra mussel colonies and underlying sediments as well as at the bare sediment/water column interface. To measure DO at the sediment/water column interface, we gently pushed the DO probe 2 cm into the sediment. We measured DO at the sediment/zebra mussel interface by carefully sliding the probe between the zebra mussels and underlying sediments. In each case, we waited for the probe to stabilise (approximately 2 min) before recording the oxygen level. Measurements were replicated between 15 and 20 times in each substrate type in each bay.

Addition/removal experiment

We added and removed zebra mussels in both Appletree and Hawkins bays and compared corresponding changes in benthic invertebrate abundance and richness. Galvanised steel tubs (28 cm high \times 53 cm diameter) with their bottoms removed were buried to a depth of 10 cm at a water depth of 5–6 m in each bay. Tubs were arranged in blocks of four tubs with each block straddling a zebra mussel colony on soft sediment (two tubs) and adjacent soft sediment lacking zebra mussels (two tubs). For each block, we randomly selected a tub in the zebra mussel-covered sediment and removed all of the zebra mussels (henceforth referred to as removal treatment). The removed zebra mussels were placed in a dive bag, vigorously shaken to remove as many macro-inverte-

brates as possible, and added to a randomly-selected tub in the same block in bare sediment (addition treatment). Unmanipulated tubs in each block served as bare sediment and zebra mussel control treatments. Seven blocks of four tubs each were placed in each of the two bays for a total of 28 experimental units per field site. The tubs were placed in Appletree and Hawkins bays on 17 July and 30 August 2001, respectively.

To compare changes in invertebrate abundance and richness, we used core samplers constructed from polyvinyl chloride (PVC; 13.5 cm high \times 10.2 cm diameter) with removable ends made of 0.05 mm Nitex[®] mesh cloth (Wildlife Supply Company, Saginaw, MI, U.S.A.). Each core was pushed into the sediment to a depth of 10 cm. In tubs with zebra mussels, we separated invertebrates living within the zebra mussel colony from those living underneath the colonies by taking two separate cores in the same spot, one containing the zebra mussel layer, one containing the sediment directly beneath the first core. Samples were taken from control tubs (unmanipulated) on the day the treatments were established and again in all tubs after 2 months (12 September and 22 October 2001 for Appletree and Hawkins bays, respectively).

All samples were washed through a 0.05 mm mesh screen in the field to remove small and fine sediments before being preserved in 70% ethanol. Invertebrates were separated from sediment and zebra mussels using a series of stacked mesh sieves (4 mm, 1 mm, and 500 μm). Contents retained on each sieve were sorted under a dissecting microscope at 40 \times magnification. Species richness, invertebrate abundance, and zebra mussel density were determined for each sample. Invertebrates were identified to the lowest practical taxonomic resolution, using Merritt & Cummins (1997) and Thorp & Covich (2001). Although taxonomic precision varied by group, we refer to taxon richness as species richness throughout the paper.

Comparison samples

To further document natural patterns of infaunal invertebrate abundance and richness as well as increase temporal coverage, we sampled each bay a second time in 2002. We also increased our sampling area by taking multiple core samples of bare sediment and zebra mussel-covered sediment. Each sample

consisted of three cores within a 0.25 m² quadrant. The cores were processed and the invertebrates (excluding zebra mussels) were separated and identified as described above. We combined the data from all cores within a single sample area. These data provide a comparison of invertebrate communities a year after the termination of the addition/removal experiment.

Data analysis

Species richness and abundance were the response variables in all analyses. Abundance data were square root transformed to achieve normality prior to analyses. Zebra mussels were not included in the macro-invertebrate abundance or richness variables. Treatment (addition, removal, zebra mussel control, and bare sediment control), position (sediment layer, zebra mussel layer), and site (Appletree and Hawkins' bays) were categorical variables. We analysed overall patterns of species richness and abundance using MANOVAS. If there were significant differences, we then analysed the treatment effects on species richness and abundance using ANOVA.

We used a two-way ANOVA to test for effects of treatment, site, and treatment by site interactions on the response variables in whole samples (zebra-mussel layer and underlying sediments combined and bare-sediment samples). We subsequently performed a one-way ANOVA to test for treatment effects on the response variables in whole samples for each bay. We used an *a priori* linear contrast in the one-way ANOVA to test for differences between the group of treatments with zebra mussels present and the group of treatments lacking zebra mussels for both Appletree and Hawkins bays.

To compare the communities underlying zebra mussel colonies with communities in bare sediment and communities in zebra mussel colonies with underlying communities, we reanalysed the data with the zebra-mussel layer and the sediment layer of each zebra-mussel sample considered as separate treatments in the analysis. We used one-way ANOVA followed by *post hoc* analyses (Tukey's) comparing the abundance and richness of invertebrate communities in bare sediments and sediments underlying zebra mussel colonies as well as invertebrate communities in sediments underlying zebra mussel colonies to the invertebrate community within zebra mussel colonies.

Finally, we examined the effect of zebra mussel colonisation on the nine most abundant invertebrates obtained in each bay. Differences in the abundance of these nine species between zebra mussel colonies and adjacent sediments lacking zebra mussels were analysed using *t*-tests for both 2001 and 2002 samples.

Results

Site characteristics

Sediment in Appletree Bay was largely composed of sand grains between 0.12 and 0.5 mm diameter while sediment in Hawkins Bay was dominated by silt and mud with the majority of grains between 0.06 and 0.12 mm diameter. Particle size was not significantly different between sediment underlying zebra mussel colonies and adjacent bare sediment for either Appletree or Hawkins bays (ANOVA, $P > 0.05$).

Zebra mussel density and colony thickness increased in both Appletree and Hawkins bays from 2001 to 2002 (Fig. 1). In Appletree Bay, zebra mussel density was on average 31 312 individuals m⁻² in 2001 and 45 656 individuals m⁻² in 2002. Mean zebra mussel densities were 38 172 individuals m⁻² in 2001 and 67 096 individuals m⁻² in 2002 in Hawkins Bay. Colony thickness ranged from 2 to 3 cm thick and increased in both bays between 2001 and 2002. On average, zebra mussels ranged in size from 5.8 to 24.6 mm in length in Appletree and Hawkins bays. Zebra mussel density increased (ANOVA, $F = 45.31$, d.f. = 1, $P < 0.0001$) as did colony thickness (ANOVA, $F = 5.52$, d.f. = 1, $P < 0.05$) increased significantly

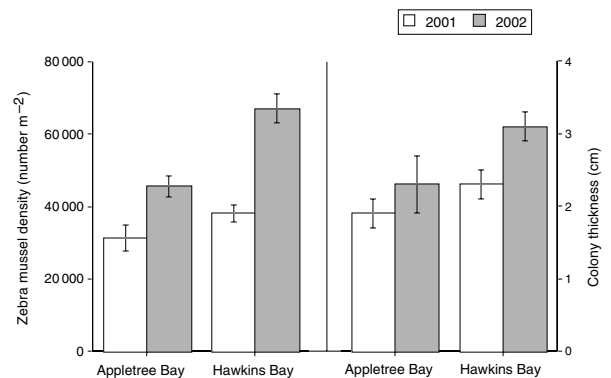


Fig. 1 Mean zebra mussel density and colony thickness in Appletree and Hawkins bays in 2001 and 2002. $n = 10$ for each bay and year (± 1 SE shown).

between 2001 and 2002 in both Appletree and Hawkins bays. However, zebra mussel density was greater in Hawkins Bay than in Appletree Bay (ANOVA, $F = 19.38$, d.f. = 1, $P < 0.0001$) as was colony thickness (ANOVA, $F = 4.67$, d.f. = 1, $P < 0.05$).

Dissolved oxygen was significantly higher in bare sediment than in sediments underlying zebra mussels in both Appletree and Hawkins bays (ANOVA, $F = 40.2$, d.f. = 1, $P < 0.001$). In Appletree Bay, mean (± 1 SE) DO was 7.6 ± 0.2 mg mL⁻¹ in bare sediment and 2.2 ± 0.4 mg mL⁻¹ in sediment underlying zebra mussels. In Hawkins Bay, mean DO was 7.4 ± 0.2 mg mL⁻¹ in bare sediment and 1.8 ± 0.6 mg mL⁻¹ in sediment underlying zebra mussels. There was no difference in DO concentration between Hawkins and Appletree bays.

Addition/removal experiment

Overall, both macro-invertebrate abundance and richness were greater in sediments colonised by zebra mussels than in adjacent sediments lacking zebra

mussels in both Appletree and Hawkins bays (Fig. 2). Average invertebrate abundance and richness were 2.5 times and 1.4 times greater respectively in zebra mussel covered sediments than in bare sediments in Appletree Bay at the beginning of the experiment. In Hawkins Bay, zebra mussel covered sediments initially supported on average 3.8 times more individuals and 2.2 times more species than bare sediments.

The addition and removal of zebra mussel colonies had a significant effect on both invertebrate abundance (ANOVA, $F = 14.58$, d.f. = 3, $P < 0.001$) and richness (ANOVA, $F = 17.75$, d.f. = 3, $P < 0.001$) (Table 1). The addition of zebra mussels to bare sediment increased both macro-invertebrate abundance and richness while zebra mussel removal decreased abundance and richness (Fig. 2). Appletree Bay supported a significantly richer community than Hawkins Bay (ANOVA, $F = 6.91$, d.f. = 1, $P < 0.01$; Table 1), although there was no difference with respect to abundance. There was a significant interaction between bay and treatment (MANOVA, $F = 3.68$, d.f. = 6, $P < 0.01$; Table 1); the addition of zebra mussels produced a dramatic increase in abundance and richness in Appletree Bay and a smaller response in Hawkins Bay (Fig. 2).

The *a priori* linear contrast comparing all zebra mussel treatments (zebra mussel controls and zebra mussel additions) to all treatments lacking zebra mussels (bare sediment control and zebra mussel removal) showed that the presence of zebra mussels increased both abundance ($t = 4.78$, d.f. = 24, $P < 0.001$) and richness ($t = 4.47$, d.f. = 24, $P < 0.001$) in Appletree Bay as well as abundance ($t = 6.86$, d.f. = 24, $P < 0.001$) and richness ($t = 8.00$, d.f. = 24, $P < 0.001$) in Hawkins Bay.

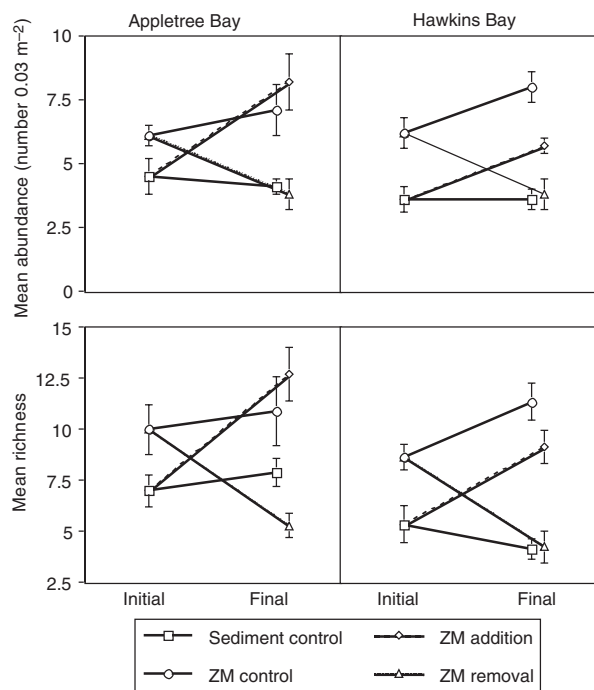


Fig. 2 Effect of treatment on macroinvertebrate abundance and richness inhabiting soft sediments in Appletree and Hawkins bays. Abundance and richness are plotted for zebra mussel addition, removal, and corresponding control treatments. Abundance data were square root transformed to achieve normality. $n = 7$ for each treatment (± 1 SE shown).

Position of invertebrates within substrate

In general, both abundance and richness were far greater within zebra mussel colonies than in sediments underlying zebra mussel colonies or in bare sediment alone in both Appletree and Hawkins bays (Fig. 3). In Appletree Bay, position within substrate had a significant effect on both abundance (ANOVA, $F = 24.54$, d.f. = 2, $P < 0.001$) and richness (ANOVA, $F = 21.10$, d.f. = 2, $P < 0.001$). Interestingly there was no significant difference between the number of individuals in bare sediments compared with sediments underlying zebra mussels although richness

Table 1 Effect of zebra mussel addition and removal on macroinvertebrate abundance and richness. A. MANOVA testing for effects of treatment (addition/removal), site, and treatment by site interaction on abundance and richness in Appletree and Hawkins bays in 2001. B. Two-way ANOVA examining the effects of treatment, site, and site by treatment interaction on macroinvertebrate abundance and richness

| (A) Source of variation | | | | |
|-------------------------|--------------------|------------|---------------|-----------|
| | d.f. | Error d.f. | Wilks' lambda | F |
| Site | 2 | 102 | 0.911 | 4.993** |
| Treatment | 6 | 204 | 0.622 | 9.094*** |
| Site × treatment | 6 | 204 | 0.742 | 3.677** |
| (B) Source of variation | | | | |
| | Dependent variable | d.f. | MS | F |
| Site | Abundance | 1 | 3.106 | 0.956 |
| | Richness | 1 | 63.088 | 6.914** |
| Treatment | Abundance | 3 | 47.375 | 14.579*** |
| | Richness | 3 | 161.932 | 17.747*** |
| Site × treatment | Abundance | 3 | 21.203 | 6.525*** |
| | Richness | 3 | 42.364 | 4.643** |
| Error | Abundance | 103 | 3.250 | |
| | Richness | 103 | 9.124 | |

Statistical significance is denoted as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

was significantly greater in bare substrates than in sediments underlying zebra mussels (Fig. 3). Position within substrate also had a significant effect on abundance (ANOVA, $F = 9.69$, d.f. = 2, $P < 0.001$) and richness (ANOVA, $F = 15.85$, d.f. = 2, $P < 0.001$) in Hawkins Bay. In contrast to Appletree Bay, there were no differences in abundance or richness between bare sediments and sediments underlying zebra mussel colonies.

Comparison samples

Samples taken a year after the termination of the experiment in immediately adjacent areas yielded qualitatively similar results as our manipulative experiments. Zebra mussel-covered sediments supported over three times more species in Appletree Bay and nearly twice as many species in Hawkins Bay than adjacent sediments lacking zebra mussels (Fig. 4). Likewise, zebra mussel-covered sediments contained two and three times more individuals than adjacent bare sediments in Appletree Bay and Hawkins Bay, respectively (Fig. 4). Zebra mussel presence increased both abundance (ANOVA, $F = 115.32$, d.f. = 1, $P < 0.001$; Table 2) and richness (ANOVA,

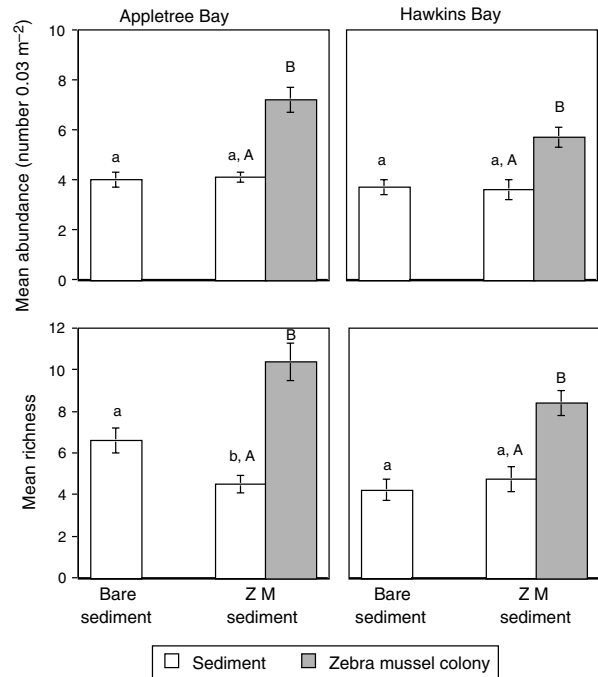


Fig. 3 Mean abundance and richness of macroinvertebrates with respect to position within substrate. Abundance (square-root transformed) and richness are plotted with respect to substrate type (bare sediment versus zebra mussel dominated sediment) and position within substrate (within sediment versus within zebra mussel colony). $n = 14$ for all categories with the exception of underlying sediment in Appletree Bay where $n = 12$, (± 1 SE shown). Letters denote significant differences between the following comparisons: bare sediment versus sediment underlying zebra mussel colonies (lower case) and sediment underlying zebra mussel colonies versus overlying zebra mussel colonies (upper case) (Tukey's, $P < 0.05$).

$F = 57.67$, d.f. = 1, $P < 0.001$; Table 2). Position within substrate had significant effects on abundance (ANOVA, $F = 36.22$, d.f. = 2, $P < 0.001$) and richness (ANOVA, $F = 13.96$, d.f. = 2, $P < 0.001$) in Appletree Bay. Similarly, position within substrate affected abundance (ANOVA, $F = 32.44$, d.f. = 2, $P < 0.001$) and richness (ANOVA, $F = 4.42$, d.f. = 2, $P < 0.05$) in Hawkins Bay. In contrast to 2001, abundance was significantly greater in the sediments underlying zebra mussel colonies than in adjacent bare sediments for both Appletree and Hawkins bays (Fig. 5). Richness was greater on average in sediments underlying sediments underlying zebra mussels than in adjacent bare sediments in Appletree Bay (Figs 3 & 5). In Hawkins Bay, richness was not significantly different among substrate types, in contrast to the previous year's data (Figs 3 & 5).

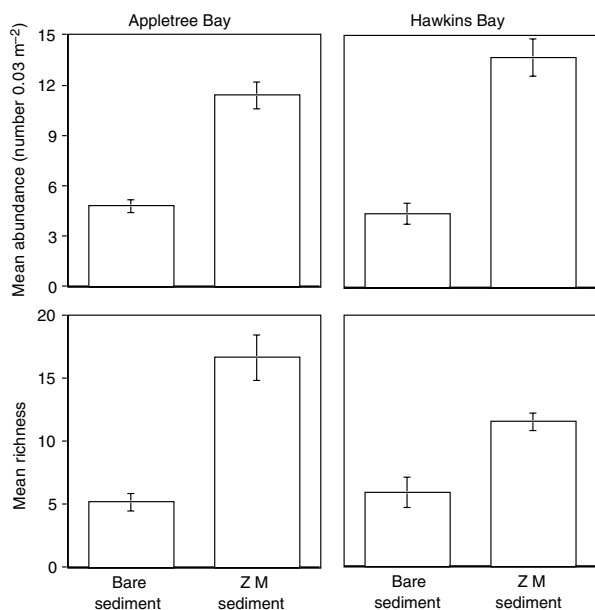


Fig. 4 Overall effect of natural zebra mussels on macroinvertebrate abundance and richness. Abundance (square-root transformed) and richness are plotted versus substrate type (bare sediment, sediment colonised by zebra mussels) for Appletree and Hawkins bays in 2002. $n = 8$ for each substrate type (± 1 SE shown).

Table 2 Effect of zebra mussels on macroinvertebrate abundance and richness in 2002 in Appletree and Hawkins bays. Multivariate and univariate analyses are presented for abundance and diversity with site and zebra mussel presence (bare sediment versus sediment colonised by zebra mussels) as the independent variables and abundance and richness as the dependent variables

| Source of variation | d.f. | Error d.f. | Wilks' lambda | F |
|-------------------------------------|--------------------|------------|---------------|-----------|
| Multivariate test | | | | |
| Site | 1 | 26 | 0.67 | 6.45** |
| Zebra mussel presence | 1 | 26 | 0.185 | 57.32*** |
| Site \times zebra mussel presence | 1 | 26 | 0.57 | 9.65*** |
| Source of variation | Dependent variable | d.f. | MS | F |
| Univariate tests | | | | |
| Site | Abundance | 1 | 10.10 | 2.29 |
| | Richness | 1 | 36.06 | 3.70 |
| Zebra mussel presence | Abundance | 1 | 508.09 | 115.32*** |
| | Richness | 1 | 562.77 | 57.67*** |
| Site \times zebra mussel presence | Abundance | 1 | 11.07 | 2.51 |
| | Richness | 1 | 65.44 | 6.71* |
| Error | Abundance | 27 | 4.41 | |
| | Richness | 27 | 9.76 | |

Statistical significance is denoted as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

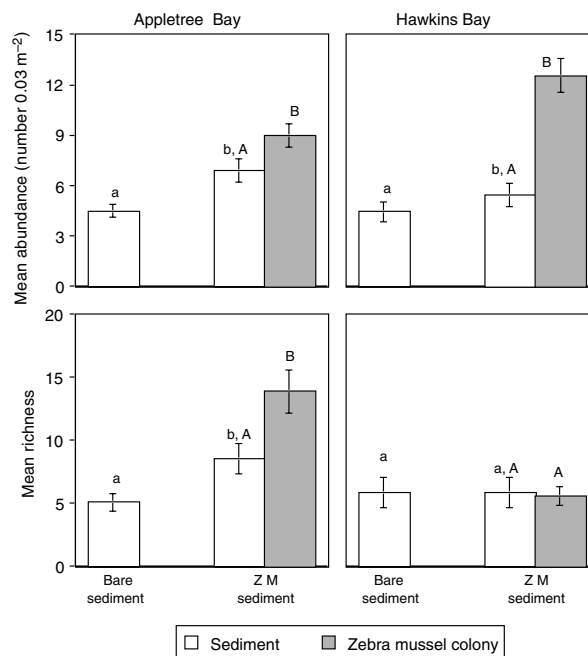


Fig. 5 Effect of natural zebra mussels on macroinvertebrate abundance and richness inhabiting soft sediments with respect to position within substrate. Abundance (sqrt transformed) and richness are plotted with respect to substrate type (bare sediment versus zebra mussel dominated sediment) and position within substrate (within sediment layer versus within zebra mussel colony). Letters denote significant differences between the following comparisons: bare sediment versus sediment underlying zebra mussel colonies (lower case) and sediment underlying zebra mussel colonies versus overlying zebra mussel colonies (upper case) (Tukey's, $P < 0.05$). $n = 8$ for all locations (± 1 SE shown).

Dominant species

Among the nine most abundant species in Hawkins and Appletree bays, the majority had higher abundance in soft sediments with zebra mussels than in bare sediments (Tables 3 & 4). At the end of the experiment, only the abundance of *Oecetis* sp. (Trichoptera: Leptoceridae) in Appletree Bay and *Ablabesmyia* sp. (Diptera: Chironomidae) in Hawkins Bay were significantly lower in areas colonised by zebra mussel than in adjacent bare sediment (Tables 3 & 4).

Comparison samples taken the year after the termination of the experiment reveal a slightly different pattern of abundance in the nine most dominant species. *Oecetis* sp. in Appletree Bay occurred in greater abundance in sediments colonised by zebra mussels than in adjacent sediments lacking zebra mussels (Table 3). In Hawkins Bay, there were significantly fewer individuals of *Hexagenia* sp.

Table 3 Effect of zebra mussel presence on the nine numerically dominant macroinvertebrate species in Appletree Bay. Data for 2001 manipulations are based on samples from the addition/removal experiment. Data for 2002 natural samples are from samples taken immediately adjacent areas to the previous year's experimental site within Appletree Bay. The data in 2002 were obtained using a core sample area three times larger than in the manipulation experiment. Significant differences determined using independent *t*-tests

| Taxon | 2001 Manipulations | | | 2002 Natural samples | | |
|-------------------------------|--------------------|---------------|----------|----------------------|---------------|----------|
| | Sand | Zebra mussel | <i>P</i> | Sand | Zebra mussel | <i>P</i> |
| Coleoptera: Elmidae | | | | | | |
| <i>Dubiraphia</i> sp. | | No difference | | - | + | 0.040 |
| Diptera: Chironomidae | | | | | | |
| <i>Ablabesmyia</i> sp. | | No difference | | | No difference | |
| <i>Paratendipes</i> sp. | - | + | 0.015 | - | + | 0.012 |
| Ephemeroptera: Ephemeridae | | | | | | |
| <i>Ephemer</i> sp. | | No difference | | - | + | <0.001 |
| Trichoptera: Lepidostomatidae | | | | | | |
| <i>Lepidostoma</i> sp. | | No difference | | - | + | 0.008 |
| Molannidae | | | | | | |
| <i>Molanna</i> sp. | | No difference | | | No difference | |
| Leptoceridae | | | | | | |
| <i>Oecetis</i> sp. | + | - | 0.027 | - | + | 0.002 |
| Oligochaeta | | No difference | | + | - | <0.001 |
| Mesogastropoda: Hydrobiidae | | | | | | |
| <i>Gillia altilis</i> | | No difference | | - | + | <0.001 |

Table 4 Effect of zebra mussel presence on the nine numerically dominant macroinvertebrate species in Hawkins Bay. Data from 2001 manipulations were obtained from the addition/removal experiment. Data for 2002 natural samples are from samples taken immediately adjacent to the previous years experimental site within Hawkins Bay. The data in 2002 were obtained using a core sample area three times larger than the previous year. The dashed line indicates that no species were present in the samples. Significant differences determined using independent *t*-tests

| Species | 2001 Manipulations | | | 2002 Natural samples | | |
|-----------------------------|--------------------|---------------|----------|----------------------|---------------|----------|
| | Sand | Zebra mussel | <i>P</i> | Sand | Zebra mussel | <i>P</i> |
| Diptera: Chironomidae | | | | | | |
| <i>Ablabesmyia</i> sp. | + | - | 0.029 | | No difference | |
| <i>Paratendipes</i> sp. | - | + | 0.043 | | No difference | |
| <i>Ceratopogonidae</i> sp. | | No difference | | - | | |
| Ephemeroptera: Ephemeridae | | | | | | |
| <i>Hexagenia</i> sp. | | No difference | | + | - | 0.019 |
| Mesogastropoda: Hydrobiidae | | | | | | |
| <i>Gillia altilis</i> | | No difference | | | No difference | |
| Amphipoda: Gammaridae | | | | | | |
| <i>Gammarus</i> sp. | - | + | <0.001 | - | + | <0.001 |
| Isopoda: Asellidae | - | + | <0.001 | - | + | 0.002 |
| Ostracoda | | No difference | | | No difference | |
| Oligochaeta | - | + | <0.001 | | No difference | |

(Ephemeroptera: Ephemeridae) in sediments colonised by zebra mussels than in adjacent sediment lacking zebra mussels (Table 4).

Discussion

The colonisation of soft sediments by zebra mussels has profound effects on benthic invertebrate commu-

nities. In Appletree and Hawkins bays, these effects were characterised by multifold increases in invertebrate abundance and richness. Although Appletree and Hawkins bays differ with respect to sediment particle size, wave action, zebra mussel density, and colony thickness, both macroinvertebrate abundance and richness were greater in mussel-dominated sediments than bare sediments. The similar responses of the

macroinvertebrate communities in physically very different bays supports the conclusion that the colonisation of soft sediments by zebra mussels is responsible for changes observed in the benthic community. This conclusion is supported by our manipulative field experiments as well as by observations in natural communities; zebra mussel colonies significantly increased macroinvertebrate abundance and diversity (Fig. 2).

We predicted that degraded interstitial water quality would inhibit invertebrate communities in interstitial spaces between shells and in sediments underlying zebra mussel colonies. Despite decreased oxygen availability and Burks *et al.*'s (2002) evidence of degraded water quality within interstitial spaces of zebra mussel colonies, we found that invertebrate abundance and richness responded positively to zebra mussel colonisation both within zebra mussel colonies and in underlying sediments. Upon termination of our experiment in 2001, invertebrate abundance was significantly higher within zebra mussel colonies compared with sediments directly beneath the colony and adjacent bare sediments (Fig. 3). There were no general differences in abundance or richness between adjacent bare sediments and sediments underlying mussel colonies (Fig. 3) contrary to our predictions. Only richness in Appletree Bay was significantly lower in sediments underlying zebra mussels than in adjacent bare sediments. Interestingly, both abundance and richness were greater in sediments underlying zebra mussels than in adjacent bare sediments in 2002 (Fig. 5). One explanation for these unexpected results is that water flow created by *Dreissena* filter-feeding promotes the removal of excess organic matter and aids in the abatement of severely degraded water quality that would inhibit most infaunal invertebrates (Berg, Fisher & Landrum, 1996). Berg *et al.*'s (1996) suggestion that multi-layered zebra-mussel colonies could draw oxygenated water down into interstitial spaces aiding invertebrate respiration is not supported by our DO data. Invertebrates clearly colonise zebra mussel colonies and sediments underlying zebra mussel colonies despite reduced DO and degraded water quality within zebra mussel colonies.

Most of the nine numerically dominant species found in soft sediments increased in response to the presence of zebra mussels (Tables 3 & 4). *Oecetis* (Trichoptera: Leptoceridae) was one of the few species

with lower density in the presence of zebra mussels (Table 3). However, this response was only evident in 2001. In fact, the following year significantly more *Oecetis* were found in the presence of zebra mussels than in adjacent bare sediments (Table 3). This shifting pattern of abundance was also evident for other species including *Oligochaeta* (Table 3), *Ablabesmya* (Diptera: Chironomidae; Table 4), and *Hexagenia* (Ephemeroptera: Ephemeridae; Table 4). These fluctuations might represent natural temporal or seasonal patterns in abundance. While it is possible that zebra mussel colonisation might lead to the decline of some invertebrates that typically inhabit soft sediments (e.g. *Diporeia*, Nalepa *et al.*, 2000), the overall pattern of invertebrate abundance and richness from this study reinforces earlier findings that zebra mussels facilitate benthic invertebrate communities in soft sediments (Botts *et al.*, 1996; Bially & MacIsaac, 2000).

Facilitation of benthic invertebrate communities is well documented in marine (Gallagher, Jumars & Trueblood, 1983; Gosselin & Chia, 1995) and freshwater environments (Diamond, 1986; Englund, 1993; McCabe & Gotelli, 2003). Spatially complex habitats support richer faunal communities in aquatic systems by providing a greater number of available niches (Hart, 1978; Minshall, 1984; O'Connor, 1991). Fouling organisms have long been known to play important roles in structuring marine benthic invertebrate communities (e.g. Paine, 1974; Suchanek, 1986; Seed, 1996). For example, blue mussel settlement produces large, spatially complex patches that provide habitat for a diverse array of species on rocky shores (Lintas & Seed, 1994). The introduction of Dreissenid species to North America established the first dominant macro-fouling organism in freshwater communities (Ricciardi *et al.*, 1997). A series of studies on zebra mussels have revealed their importance as facilitators of benthic invertebrates (Stewart & Haynes, 1994; Botts *et al.*, 1996; Bially & MacIsaac, 2000).

Dreissena colonisation results in increased surface area and spatial heterogeneity of benthic substrata. Zebra mussel colonies trap sediments and organic particles, both important food and habitat resources for benthic invertebrates (Stewart *et al.*, 1998). Filtration by zebra mussels removes large quantities of particulate organic matter from the water column. Much of this particulate organic matter is eventually deposited on sediments as faecal and pseudofaecal material. Zebra mussel colonisation of soft substrates

also facilitates species that depend on firm, stable substrata for colonisation, such as hydroids, sponges, turbellarians, gastropods, and leeches (Botts *et al.*, 1996). Many of the species found within zebra mussel colonies in this study are typically associated with hard substrata (scrapers, grazers, and predatory insect larvae). Most of these species are absent in typical soft sediment habitats. In effect, zebra mussels have altered soft substrates to provide habitat for both infaunal and typical epifaunal species. In particular, epifaunal amphipods and isopods are now dominant species (Table 4) in terms of abundance where before they were relatively rare or absent altogether.

In conclusion, we have demonstrated that zebra mussels increase both the abundance and richness of benthic invertebrate communities in soft sediments. These increases are likely because of an increase in habitat complexity (Stewart *et al.*, 1998), stability (Bially & MacIsaac, 2000), and increased food resources such as detritus from pseudofaeces and faeces as well as increased prey availability (Ricciardi *et al.*, 1997). This study is the first to explicitly examine the impact of zebra mussels on macroinvertebrate communities in soft sediments using manipulative experiments. The data indicate that zebra mussels do not serve as a barrier to typical infaunal invertebrates as we originally predicted. In fact, most infaunal macroinvertebrates migrate into the zebra mussel colony from underlying sediments. The colonisation of soft substrates also leads to influx of epifaunal species such as amphipods and isopods that are typically associated with hard substrates and/or other complex habitats such as submerged vegetation. As a result, the colonisation of soft substrates by zebra mussels results in more diverse and dense macro-invertebrate community than previously existed.

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