

Macroinvertebrate Communities on Hard Substrates in Western Lake Erie: Structuring Effects of *Dreissena*

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Abstract. Of the approximately 140 non-indigenous species that have invaded the Great Lakes since the early 1800s, few have had greater effects on this ecosystem than the zebra and quagga mussel (*Dreissena polymorpha* and *D. bugensis*, respectively). In this study the effects of these bivalves on macroinvertebrates inhabiting hard substrates in western Lake Erie were quantified. Biomass, densities, diversity of macroinvertebrates, and particulate organic matter mass were measured on bricks with high and low *Dreissena* densities that were held at a depth of 3.5 m for 49 days in 1996. Total macroinvertebrate densities and biomass (excluding *Dreissena*) were two and five times greater on substrates with high *Dreissena* densities than when *Dreissena* were rare. These differences were largely attributed to the amphipod *Echinogammarus ischnus*, itself an invading species, which constituted 29 and 31% of total macroinvertebrate densities and biomass, respectively, on *Dreissena*-dominated substrates. *Dreissena* also stimulated increased macroinvertebrate diversity, causing a shift from a community dominated by the chironomid *Dicrotendipes neomodestus* to an assemblage characterized by increased densities and equitability of hydroids (Hydridae), the flatworm *Dugesia tigrina*, tubificid oligochaetes, leeches (*Alboglossiphonia heteroclita* and immature *Erpobdellidae*), limpets (*Ancylidae*), snails (*Physella integra* and *Amnicola limosa*), *Echinogammarus*, the microcaddisfly *Hydroptila waubesia*, and the chironomid *Microtendipes pedellus*. No taxon responded negatively to *Dreissena* in this study. In addition, particulate organic matter mass, an important food and habitat resource for benthic invertebrates, was two times greater on *Dreissena*-dominated substrates than on bricks with few *Dreissena*. Our results support hypotheses that *Dreissena* have strong effects on community dynamics and energy flow pathways in the Great Lakes.

INDEX WORDS: Community structure, species interactions, species diversity, structural complexity, benthic macroinvertebrates, *Dreissena*, particulate organic matter.

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Introduction

Biological communities in the Laurentian Great Lakes have been affected by introduced species and other anthropogenic influences since at least the 17th century, when Europeans first colonized the region (Mills et al. 1993). Benthic macroinvertebrates are valuable tools for monitoring these ecological changes because of their sensitivity to environmental conditions, and their short life cycles that make it possible to identify cause-and-effect relationships between environmental perturbations and species responses (APHA 1989). Macroinvertebrates have been used extensively and effectively in investigations of human pollution and other abiotic factors influencing Great Lakes communities (e.g., Barton 1988, Soster and McCall 1990, Nalepa 1991, Krieger and Ross 1993). However, until recently there have been few investigations of effects of exotic species and other biotic factors on macroinvertebrate distribution and abundance in the Great Lakes (but see Barton and Hynes 1976, Chilton et al. 1986), perhaps because of the difficulty of conducting manipulative experiments in this ecosystem. However, it is necessary to quantify strengths of species interactions for a complete understanding of community dynamics and important energy flow pathways.

Of the approximately 140 nonindigenous species to become established in the Great Lakes within the past two centuries (Mills et al. 1993), few have caused more concern for their effects on Great Lakes biota than the zebra mussel and quagga mussel (*Dreissena polymorpha* and *D. bugensis*, respectively). *Dreissena* are the first abundant sessile macroinvertebrates to inhabit rocky substrates in the Great Lakes, where they typically occur at densities of 2,000 to 50,000 individuals/m² (Leach Stewart and Haynes 1994, Ricciardi et al. 1997). Recent declines in phytoplankton and zooplankton biomass, and increases in biomass of submerged macrophytes, benthic algae, and benthic macroinvertebrates suggest that filter-feeding *Dreissena* redirect energy and nutrients from pelagic to benthic habitats (Stewart and Haynes 1994, Bridgeman et al. 1995, Fahnenstiel et al. 1995, Lowe and Pillsbury 1995, Skubinna et al. 1995). These shifts in the spatial distribution of resources may even have cascading effects on fishes (Leach 1993, Mitchell et al. 1996, Dermott and Kerec 1997). Because *Dreissena* are easily manipulated in field experiments, strengths of interactions among these mussels and other taxa can be quantified, and thus improve the understanding of *Dreissena* effects on Great Lakes food webs.

In this study, benthic macroinvertebrate community composition was analyzed and particulate organic matter mass on hard substrates with high and low *Dreissena* densities was measured. The primary objectives were to 1) quantify effects of *Dreissena* on biomass, densities, and diversity of sympatric benthic macroinvertebrates inhabiting hard substrates in a Great Lakes habitat, and 2) provide baseline data for evaluating future environmental changes on Great Lakes biological communities.

Materials and Methods

Study Area

The study site was in Fishery Bay near the southwest side of Gibraltar Island, Put-in-Bay, Ohio, USA (latitude = 41°39'30"N, longitude = 82°49'23"W). Benthic habitat at the study site was typical of nearshore zones in western Lake Erie, consisting of limestone/dolomite cobble among patches of smaller particles. This experiment was conducted using SCUBA at a depth of 3.5 m, where surfaces of rocks not buried in sediments were covered with a monolayer of *Dreissena*. Approximately 95% of *Dreissena* inhabiting the study site were zebra mussels, with quagga mussels constituting the remaining 5% of *Dreissena* individuals. The two species are collectively referred to as *Dreissena* in this study because of the difficulty distinguishing small individuals of these species.

Experimental Design

The experimental design consisted of two *Dreissena* treatments (low and high *Dreissena* densities; n = five replicates per treatment). Two red patio bricks (20 x 10 x 3 cm; 580 cm² surface area) were placed within each of ten 0.24-m² plots that were separated by a distance of 1 m. One brick from each replicate was used to sample the benthic macroinvertebrate community and the second brick was used to quantify benthic particulate organic matter mass. Bricks were preconditioned in wading pools containing dechlorinated water (30 days) before they were placed in plots on 25 June 1996. The following day, bricks in the high-*Dreissena* density treatment were inoculated by placing approximately 800 *Dreissena* individuals, 5 to 30 mm shell length, on them. These *Dreissena* had been collected from the study site and were lightly scrubbed and rinsed to remove associated invertebrates. Bricks in the low-*Dreissena* density treatment were not inoculated with mussels, but some *Dreissena* colonized the bricks during the experiment.

The duration of the 49-day experiment exceeded the 37-day colonization period that was previously found sufficient for densities of all non-colonial macroinvertebrates (minus *Dreissena*) to equal or exceed densities on rocks at the study site (Stewart *et al.* 1998a). Macroinvertebrate and particulate organic matter samples were collected at the end of the experiment by transferring bricks to polyethylene bags, and transporting them to the water surface. Macroinvertebrate samples were preserved in 10% buffered formalin. The formalin was later replaced with 70% ethanol. Benthic particulate organic matter samples were maintained in the dark within coolers filled with ice, and were frozen upon return to the laboratory.

Macroinvertebrate Sample Processing

Macroinvertebrate samples were processed by removing *Dreissena* from bricks, lightly scrubbing and rinsing shell and brick surfaces to remove invertebrates, and then sieving contents through a 60- μ m mesh. Macroinvertebrates were initially separated into coarse taxonomic groups using a stereomicroscope

(10X power), and were later identified to the lowest possible taxonomic level. Densities of taxa (number of individuals/m² brick surface area) were usually determined by counting all organisms in samples. Oligochaete, amphipod, and chironomid densities were derived from subsampling because of the large numbers of these organisms in samples. When subsampling was necessary, either 15 individuals, or 10% of the total number of individuals within each sample (whichever number was greater) were randomly selected, and they were identified to a lower taxonomic level. Densities and biomass of sponges and bryozoans were not quantified because the 49-day colonization period was probably insufficient for them to reach equilibrium densities. *Dreissena* biomass (dry mass with shell) was quantified after drying mussels at 60°C for 72 hours. Biomass of other macroinvertebrates was determined after drying representatives of each taxon at 60°C for 24 hours and ashing at 550°C for 24 hours to determine ash-free dry mass (g AFDM/m²; APHA 1989). For abundant taxa (e.g., amphipods), 100 individuals of each taxon were ashed per replicate, but fewer individuals were ashed when a taxon was rare.

Particulate Organic Matter Sample Processing

After each frozen particulate organic matter sample was thawed, *Dreissena* were removed from the brick. Brick and shell surfaces were scrubbed and rinsed in distilled water to remove attached organic matter, which was combined with the liquid component of the sample. The sample was then homogenized in a blender, and a subsample was removed for determination of benthic particulate organic matter AFDM (hereafter organic matter mass) using standard methods for determination of periphyton AFDM (APHA 1989). Organic matter mass (g AFDM/m² brick surface area) exclusive of invertebrates was obtained by subtracting total invertebrate biomass, determined from invertebrate samples, from the total mass of organic matter in particulate organic matter samples.

Data Analysis

Differences in *Dreissena* biomass, macroinvertebrate biomass (excluding *Dreissena*) and densities, and organic matter mass as a function of treatment were detected by two-sample t-tests. *Dreissena* effects on the relative abundance of other macroinvertebrate taxa were evaluated by determining the percent contribution of each taxon to the total number of macroinvertebrates (excluding *Dreissena*), and using t-tests to detect differences between the two treatments. Responses of invertebrate taxa (excluding *Dreissena*) that exhibited differences in densities or relative abundance between treatments were summarized using principal components analysis (PCA). Site scores (weighted averages of component loadings or "taxa" scores) were generated for the two principal components (PCs) that explained the most variation in invertebrate densities (Jongman *et al.* 1995). *Dreissena* effects on other invertebrates were then evaluated by 1) regressing each set of site scores on *Dreissena* biomass, and 2) using component loadings and strengths of correlations between *Dreissena* biomass and site scores to identify quantitative relationships among *Dreissena*

and other invertebrates (Jongman *et al.* 1995). *Dreissena* biomass rather than densities was used in these regressions because biomass is the best indicator of habitat and food resource levels that these mussels provide to other organisms.

Macroinvertebrate diversity was quantified in each treatment using two methods: taxonomic richness and Simpson's diversity index (Brower and Zar 1977). Taxonomic richness was simply the number of taxa present on each brick (including *Dreissena*), whereas Simpson's diversity accounted for both the number of taxa and how evenly individual macroinvertebrates were distributed among the taxa (Brower and Zar 1977). Simpson's diversity was calculated both including and excluding *Dreissena* as a member of the macroinvertebrate community. Two-sample *t*-tests were also used to identify between-treatment differences in taxonomic richness and Simpson's diversity.

Data transformations were made prior to conducting statistical analyses if raw data did not conform to normality and linearity assumptions. Data for invertebrate biomass and densities, and organic matter mass were \log_{10} -transformed, whereas *Dreissena* biomass was square-root transformed and relative abundance data were arcsine-square root transformed (Zar 1989, McClendon 1994). All statistical analyses were conducted using SYSTAT 5.2.1 (Wilkinson 1992), and effects were considered statistically significant at $p \leq 0.05$. When several univariate tests were conducted on the same data set simultaneously, Bonferroni-corrected critical *p*-values ($p = 0.05/\text{number of dependent variables}$) were used to maintain the probability of committing Type I errors at $p \leq 0.05$ (Scheiner 1993). Although Bonferroni-adjusted critical *p*-values were used as criteria for rejecting null hypotheses of no treatment effect, cases were recognized where statistically significant treatment effects would have been reported had the Bonferroni procedure not been used. This approach was used because Bonferroni-corrected critical *p*-values can be quite low and strict use of the Bonferroni procedure could result in failure to observe biologically significant responses. Unsummarized data for macroinvertebrate biomass and densities, and organic matter mass, are available upon request, and will also be reported in T.W. Stewart's Ph.D. dissertation.

Results

Macroinvertebrate Biomass and Densities

Final *Dreissena* densities in the high *Dreissena* density treatment ($7,508 \pm 415$ individuals/m², mean \pm 1 SE) were similar to densities recorded from our study site and elsewhere in the Great Lakes (Stewart and Haynes 1994, Ricciardi *et al.* 1997, Stewart *et al.* 1998b). Mussel densities in the high-*Dreissena* density treatment were 11 times greater than in the low *Dreissena* density treatment (683 ± 91 individuals/m²; *t*-test, separate variances $t = 15.6$, $df = 5.3$, $p < 0.001$; Table 1). In addition, *Dreissena* biomass was 40 times greater on bricks with high-*Dreissena* densities than in the low-*Dreissena* density treatment ($t = 12.9$, $df = 4.8$, $p < 0.001$; Fig. 1A).

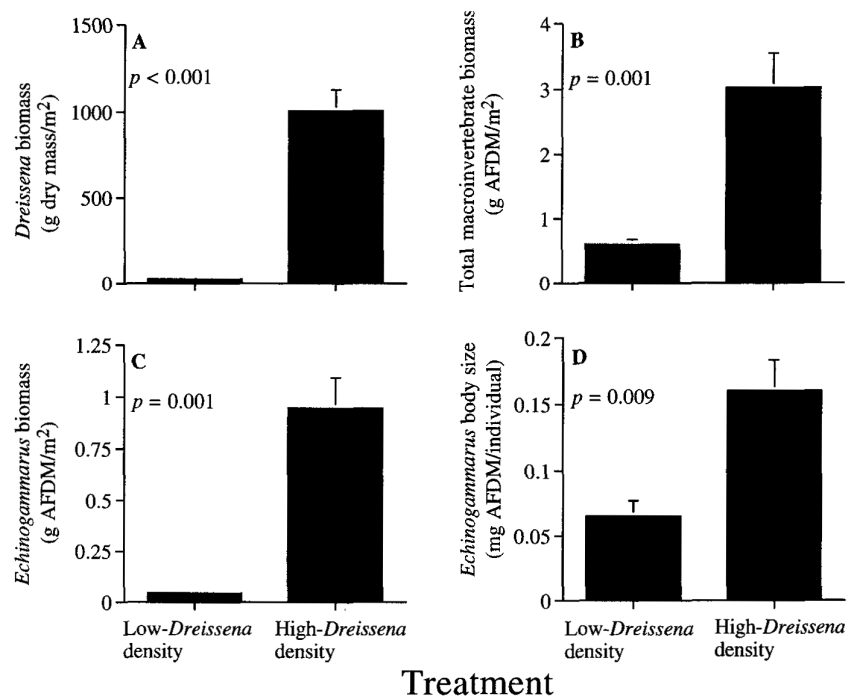


FIG. 1. *Dreissena* biomass (A), Total macroinvertebrate biomass minus *Dreissena* (B), *Echinogammarus ischnus* biomass (C), and mean *Echinogammarus* body size (D) in the two treatments (mean + 1 SE, expressed in terms of brick surface area). Significance values for treatment effects are provided in the upper left corner of each graph.

Total macroinvertebrate biomass (excluding *Dreissena*) was five times greater on inoculated bricks than on bricks with few *Dreissena*, indicating that *Dreissena* increased biomass of associated invertebrates ($t = 6.4$, $df = 5.2$, $p = 0.001$; Fig. 1B). This increase in total macroinvertebrate biomass was primarily due to the amphipod *Echinogammarus ischnus*, which constituted 31% of the total biomass of macroinvertebrates in the *high-Dreissena* density treatment, but only 7% of the biomass on substrates with low-*Dreissena* densities (Fig. 1C). *Echinogammarus* biomass was 22 times greater in the *high-Dreissena* density treatment than in the low *Dreissena* density treatment ($t = 7.8$, $df = 4.1$, $p = 0.001$; Fig. 1C). These differences resulted from increases in both *Echinogammarus* densities and body size on bricks with high densities of *Dreissena*. *Echinogammarus* densities were nine times greater on inoculated bricks than on bricks with few *Dreissena* ($t = 9.1$, $df = 6.1$, $p < 0.001$; Table 1), and mean *Echinogammarus* body size was 2.5 times greater on bricks with high densities of *Dreissena* than in the treatment with few *Dreissena* ($t = 3.8$, $df = 6.1$, $p = 0.009$; Fig. 1D). Finally, several other macroinvertebrate taxa also responded positively to *Dreissena*. Hydroids (Hydridae), the flatworm *Dugesia tigrina*, limpets (Ancylidae), and the chironomid *Microtendipes pedellus* were at least two times more abundant on substrates with high densities of *Dreissena* than on bricks with few mussels ($p < 0.001$; Table 1).

TABLE 1. Densities and relative abundance (percent contribution of each taxon to the total number of individuals, minus Dreissena) of macroinvertebrates in the two treatments (mean values with standard errors in parentheses). LD, HD = low-Dreissena density and high-Dreissena density treatments, respectively. Numbers in bold indicate differences between treatments exclusive of Bonnferroni adjustment of critical p-values ($p \leq 0.05$).

Taxon	Number of individuals/m ²		Percent of total	
	LD	HD	LD	HD
Cnidaria				
Hydridae ^a	789 (68)	1,664 (132)	9.7 (1.7)	8.3 (0.8)
Platyhelminthes				
<i>Dugesia tigrina</i> ^{a,b}	223 (13)	1,186 (176)	2.7 (0.3)	5.7 (0.6)
Annelida				
<i>Chaetogaster diaphanus</i>	413 (186)	715 (148)	4.4 (1.5)	3.5 (0.7)
<i>Nais</i> spp. (<i>N. breitscheri</i> , <i>N. communis</i> , <i>N. simplex</i>)	58 (31)	58 (36)	0.7 (0.3)	0.3 (0.2)
<i>Pristina leidy</i>	7 (7)	33 (33)	0.1 (0.1)	0.1 (0.1)
<i>Pristinella osborni</i>	153 (51)	276 (63)	1.9 (0.6)	1.4 (0.4)
<i>Stylaria lacustris</i>	7 (7)	50 (21)	0.1 (0.1)	0.3 (0.1)
<i>Vejdovskyella intermedia</i>	14 (14)	83 (64)	0.2 (0.2)	0.4 (0.3)
<i>Potamothrix moldaviensis</i>	0	18 (18)	0	0.1 (0.1)
<i>Potamothrix vejdoskyi</i>	62 (18)	32 (32)	0.7 (0.2)	0.2 (0.2)
immature Tubificidae	236 (82)	706 (113)	2.7 (1.0)	3.4 (0.5)
<i>Alboglossiphonia heteroclita</i>	0	101 (36)	0	0.5 (0.2)
immature Erpobdellidae	0	18 (6)	0	0.1 (<0.1)
Mollusca				
<i>Pisidium</i> sp.	7 (7)	11 (7)	0.1 (0.1)	0.1 (<0.1)
<i>Dreissena</i> spp. ^a	683 (91)	7,508 (415)		
Ancylidae (<i>Ferrissia</i> spp. and <i>Laevapex fuscus</i>) ^a	172 (23)	2,505 (504)	2.1 (0.4)	12.7 (2.9)
<i>Fossaria</i> sp.	21 (14)	22 (13)	0.2 (0.2)	0.1 (0.1)
<i>Gyraulus parvus</i>	4 (4)	22 (9)	0.1 (0.1)	0.1 (0.1)
<i>Physella integra</i>	40 (17)	245 (43)	0.5 (0.3)	1.2 (0.2)
<i>Amnicola limosa</i>	61 (12)	316 (39)	0.7 (0.2)	1.6 (0.2)
<i>Elimia livescens</i>	39 (18)	158 (44)	0.4 (0.2)	0.8 (0.2)
Arthropoda				
<i>Lebertia</i> sp.	187 (38)	197 (40)	2.3 (0.6)	1.0 (0.3)
<i>Limnesia</i> sp.	18 (14)	7 (7)	0.2 (0.2)	< 0.1
<i>Caecidotea</i> sp.	15 (7)	127 (58)	0.2 (0.1)	0.6 (0.3)
<i>Echinogammarus ischnus</i> ^a	687 (75)	6,168 (1,100)	8.0 (0.8)	29.4 (4.0)
<i>Stenacron</i> sp.	33 (11)	115 (28)	0.3 (0.1)	0.5 (0.1)
<i>Polycentropus ?cinereus</i>	90 (20)	93 (18)	1.0 (0.2)	0.5 (0.1)
<i>Hydroptila ?waubesiana</i>	43 (9)	104 (18)	0.5 (0.1)	0.5 (0.1)
<i>Ochrotrichia</i> sp.	7 (7)	4 (4)	0.1 (0.1)	< 0.1
<i>Oecetis</i> sp.	3 (3)	7 (4)	< 0.1	< 0.1
<i>Petrophila</i> sp.	0	4 (4)	0	< 0.1
<i>Procladius</i> sp.	37 (37)	28 (28)	0.3 (0.3)	0.2 (0.2)
<i>Thienemannimyia ?norena</i>	155 (40)	98 (41)	1.9 (0.6)	0.5 (0.2)
<i>Thienemannia</i> sp.	0	143 (75)	0	0.8 (0.4)
<i>Cricotopus ?bicinctus</i>	324 (119)	527 (177)	3.6 (1.3)	2.8 (1.0)
<i>Cryptochironomus</i> sp.	247 (104)	61 (39)	2.7 (1.2)	0.3 (0.2)
<i>Dicrotendipes neomodestus</i> ^b	4,317 (664)	3,464 (361)	48.9 (4.5)	17.0 (1.3)
<i>Microtendipes pedellus</i> ^a	0	798 (288)	0	4.1 (1.7)
<i>Pseudochironomus</i> sp.	143 (105)	113 (76)	1.6 (1.1)	0.5 (0.3)
<i>Rheotanytarsus</i> sp.	0	36 (36)	0	0.2 (0.2)
<i>Tanytarsus</i> sp.	62 (39)	36 (36)	0.7 (0.5)	0.2 (0.2)
Ceratopogonidae	0	4 (4)	0	< 0.1
Empididae	29 (9)	32 (16)	0.4 (0.1)	0.2 (0.1)
Total ^c	9,387 (766)	27,893 (1,743)		
Total minus <i>Dreissena</i> ^c	8,703 (811)	20,385 (1,355)		

^{a,b}Statistically significant differences in densities and relative abundance, respectively, after using the Bonnferroni procedure (0.05/number of taxa). Forty-three and 42 separate univariate t-tests, respectively, were conducted to identify differences in densities and relative abundance of taxa between treatments. ^c = Use of Bonnferroni procedure was not necessary.

Because we analyzed for treatment effects on 43 macroinvertebrate taxa, the critical value for rejecting the null hypothesis of no treatment effect on macroinvertebrate densities was very low after Bonnferroni adjustment of the critical p-value ($p < 0.0012$). If the Bonnferroni procedure was not used, densities of immature Tubificidae (oligochaetes), *Alboglossiphonia heteroclita* and immature Erpobdellidae (leeches), the snails *Physella integra* and *Amnicola limosa*, and the microcaddisfly *Hydroptila ?waubesiana*, were also greater on Dreissena-dominated substrates than on bricks with few mussels ($p \leq 0.04$; Table 1). Total macroinvertebrate densities in the high-Dreissena density treatment were also two and three times

greater than in the low-*Dreissena* density treatment (excluding and including *Dreissena*, respectively; $p < 0.001$; Table 1).

Diversity and Relative Abundance of Macroinvertebrates

In addition to causing changes in biomass and densities of macroinvertebrate taxa, *Dreissena* altered macroinvertebrate community composition by causing changes in the relative abundance of other macroinvertebrates (Table 1). Relative abundance of *Dugesia* and the chironomid *Dicrotendipes neo-modestus* increased and decreased, respectively, in the presence of *Dreissena* ($p < 0.001$; Table 1). If the Bonferroni procedure was not used (Bonferroni critical p -value $0.05/42 = 0.0012$), *Alboglossiphonia*, Ancyliidae, *Amnicola*, *Echinogammarus*, and *Microtendipes* also increased in relative abundance when *Dreissena* were abundant, whereas relative abundance of the net-spinning caddisfly *Polycentropus ?cinereus* declined as a function of increased *Dreissena* densities ($p < 0.035$; Table 1). However, absolute abundance (i.e., densities) of *Polycentropus* and *Dicrotendipes* did not differ in low- and high-*Dreissena* density treatments, suggesting that *Dreissena* had no net effects on these taxa ($p \geq 0.33$; Table 1).

This lack of adverse *Dreissena* effects on some invertebrates in combination with positive effects on other taxa resulted in increased taxonomic richness of macroinvertebrates on bricks with high *Dreissena* densities relative to those with few mussels ($t = 4.09$, $df = 6.7$, $p = 0.005$; Fig. 2A). Simpson's diversity was also greater in the high-*Dreissena* density treatment regardless of whether or not *Dreissena* was included as a member of the community ($t = 2.7$, $df = 6.5$, $p = 0.031$, and $t = 3.0$, $df = 7.6$, $p = 0.019$, respectively; Figs. 2B and 2C).

Ordination of Macroinvertebrate Taxa

The first two principal components of the principal components analysis explained 80% of the variation in macroinvertebrate densities (PC1 = 68%, PC2 = 12%; Fig. 3). *Dreissena* biomass was strongly correlated with PC1 (simple linear regression, $p < 0.001$, adjusted $r^2 = 0.99$) but was uncorrelated with PC2 ($p = 0.80$, adjusted $r^2 < 0.01$; Fig. 3). Thus, PCA results suggest that densities of taxa loading positively on PC1 were positively correlated with *Dreissena* biomass (Fig. 3). Indeed, all of these taxa were significantly more abundant on substrates with high *Dreissena* densities than on bricks with few *Dreissena* (Table 1). By contrast, *Dicrotendipes neomodestus* loaded negatively on PC1, suggesting that *Dreissena* had adverse effects on this chironomid (Fig. 3). However, *Dreissena* effects on *Dicrotendipes* were not statistically significant (t -test, $t = 1.04$, $df = 7.0$, $p = 0.33$; Table 1). Densities of the caddisfly *Polycentropus ?cinereus* were uncorrelated with *Dreissena* biomass (Table 1, Fig. 3).

Particulate Organic Matter

Potential causal mechanisms for increased benthic macroinvertebrate biomass, densities, and diversity on hard substrates colonized by *Dreissena* include: 1) shell-generated habitat,

and 2) increased particulate organic matter mass (Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998a). Indeed, organic matter mass was two times greater in the high-*Dreissena* density treatment than in the low-*Dreissena* density treatment ($t = 3.8$, $df = 7.8$, $p = 0.006$; Fig. 4), indicating that *Dreissena* do enhance concentrations of this valuable benthic resource on hard substrates in western Lake Erie.

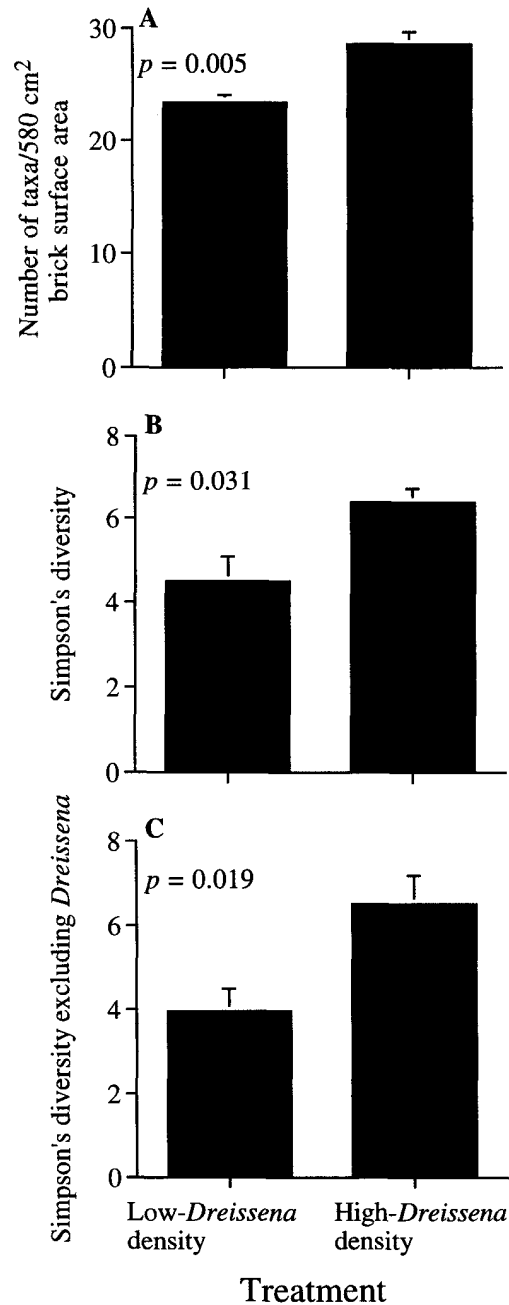


FIG. 2. Taxonomic richness (A), Simpson's diversity including *Dreissena* (B), and Simpson's diversity excluding *Dreissena* (C) in the two treatments (mean + 1 SE). Significance values for treatment effects are provided in the upper left corner of each graph.

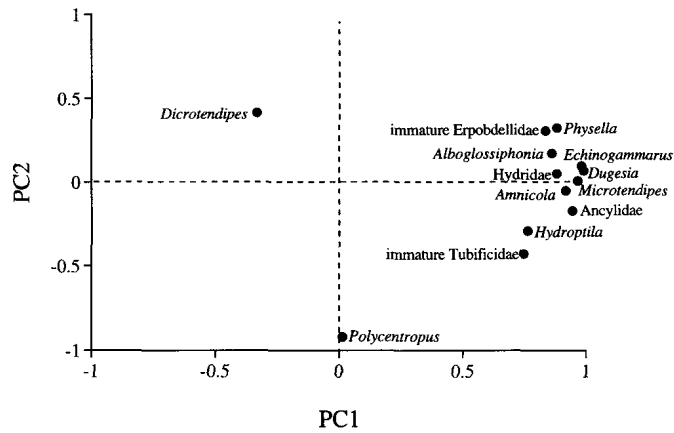


FIG. 3. PCA plot based on densities of invertebrate taxa that exhibited statistically significant differences in densities or relative abundance between treatments. The first two PCs explained 80% of the variation in invertebrate densities (PC1 = 68%, PC2 = 12%). Densities of taxa loading positively on PC1 were positively correlated with *Dreissena* biomass, whereas densities of the taxon loading negatively on PC1 were negatively correlated with *Dreissena* biomass.

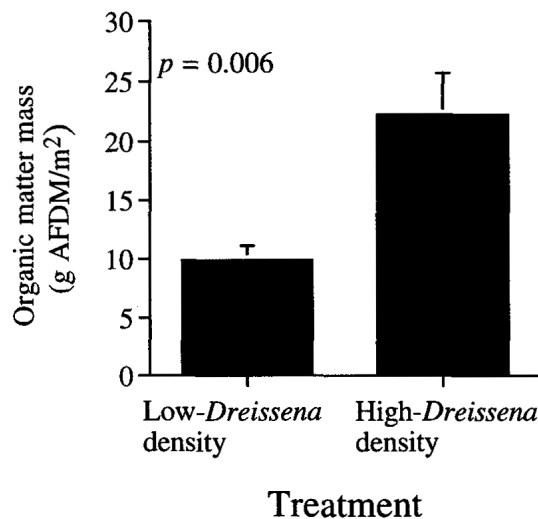


FIG. 4. Benthic particulate organic matter mass in the two treatments (mean + 1 SE). The significance value for treatment effect is provided in the upper left corner of the figure.

Discussion

Similarly to epifaunal sessile bivalves in marine rocky intertidal communities (Wootton 1994, Gosselin and Chia 1995), *Dreissena* are key structuring agents of benthic macroinvertebrate communities on hard substrates in freshwater habitats. *Dreissena* can exclude other taxa, including indigenous bivalves and the amphipod *Diporeia hoyi* from soft substrates through competition for food and space (Howell et al. 1996, Nalepa et al. 1996, Dermott and Kerec 1997). Occasionally, densities of gastropods, chironomids, and net-spinning caddisflies are also reduced on hard substrates in the presence of *Dreissena* (Dusoge 1966, Wisenden and Bailey 1995, Ricciardi et al. 1997). However, *Dreissena* generally cause increased biomass, densities, and diversity of co-occurring benthic macroinvertebrates by enhancing habitat and food resources (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a). *Dreissena* shells increase the colonizable benthic surface area available to other sessile invertebrates and grazers, and interstitial spaces between these shells likely provide associated invertebrates with refugia from predation, wave action, and other disturbances (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a). *Dreissena* also increase the quantity and possibly the quality of benthic particulate organic matter by filter-feeding and periodically depositing feces and nutrient- and energy-rich pseudofeces in benthic habitats (Izvekova and Lvova-Katchanova 1972, Roditi et al. 1997, Stewart et al. 1998a). Spaces between shells trap organic matter and inorganic particles that would otherwise be washed away by currents and wave action (Roditi et al. 1997). Pseudofeces, algae, and other forms of organic matter are important foods for benthic macroinvertebrates (Izvekova and Lvova-Katchanova 1972, Lamberti 1996). In addition, both organic and inorganic matter provide invertebrates with cover, substrate for clinging or attachment, and material for constructing protective cases (Izvekova and Lvova-Katchanova 1972; Lamberti 1996; Sheath et al. 1995, 1996). Although *Dreissena* modify effects of high flow velocity on organic matter mass by producing pseudofeces and feces that are retained between shells, turbulence created by filter-feeding inhibits settling or promotes removal of excessive organic matter when flow rates are low (Berg et al. 1996, T.W. Stewart, unpublished data). This may prevent mussels from being smothered by accumulating organic matter (Dermott and Kerec 1997), and may also favor limpets and other grazers that forage most effectively on substrates with moderate organic matter concentrations (Blinn et al. 1989). Thus, *Dreissena* likely have stabilizing effects on the benthic macroinvertebrate community, both through these regulatory effects on particulate organic matter, and by modifying effects of predators and other disturbances. Furthermore, structurally complex substrate created by *Dreissena* shells and increased particulate organic matter creates additional microhabitats, providing a likely explanation for increased macroinvertebrate diversity on substrates with high *Dreissena* densities. For example, organisms can obtain food and oxygenated water generated by filter-feeding mussels by occupying siphonal regions of shells. Alternatively, strong currents and predators may be avoided by inhabiting spaces between shells.

Effects on Macroinvertebrate Taxa

In this study, *Dreissena* caused a shift from a relatively depauperate macroinvertebrate community dominated by the chironomid *Dicrotendipes neomodestus* to a more diverse assemblage characterized by increased densities of hydroids, flatworms, oligochaetes, leeches, limpets and snails, amphipods, microcaddisflies, and the chironomid *Microtendipes pedellus*. Habitat created by shells is the primary mechanism for *Dreissena*-generated increases in hydroids (Hydridae), the flatworm *Dugesia tigrina*, limpets (Ancylidae), the snails *Physella Integra* and *Amnicola limosa*, gammarid amphipods, and the chironomid *Microtendipes pedellus* on hard substrates in the Great Lakes (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a). Sessile taxa, including hydroids and the microcaddisfly *Hydroptila waubesia*, appear to respond to increased hard benthic surface area provided by *Dreissena* shells. *Hydroptila* in particular had specific microhabitat preferences in our study, and was most often found within cases attached to the siphonal region of shells. This algivorous taxon (Wiggins 1996) probably obtains oxygen from microcurrents generated by *Dreissena*, and may also graze periphyton from shells. Limpets and snails probably also use *Dreissena* shells as substrate for grazing, whereas these gastropods also inhabit interstices between shells in response to predation pressure by fishes (Ricciardi et al. 1997, T.W. Stewart, unpublished data).

Amphipods are often the most abundant macroinvertebrates on hard substrates colonized by *Dreissena* (Stewart and Haynes 1994, Ricciardi et al. 1997, Stewart et al. 1998a), and this study was no exception. *Echinogammarus ischnus*, the amphipod that inhabited the substrates, is the latest of several recent invaders from the Black/Caspian Sea region to become established in the Great Lakes, following *Dreissena*, round gobies (*Neogobius melanostomus*), and tubenose gobies (*Proterorhinus marmoratus*) to North America (Jude et al. 1992, Ludyanskiy 1993, Witt et al. 1997). *Echinogammarus* is a common inhabitant of *Dreissena* beds in Europe (Ko'hn and Waterstraat 1990), and this amphipod has displaced *Gammarus fasciatus*, a pre-established amphipod taxon, from many *Dreissena*-dominated habitats in the Great Lakes (Witt et al. 1997). *Echinogammarus ischnus* has been the dominant amphipod on hard substrates at this study site since at least 1995. Amphipods reported as *Gammarus fasciatus* in Stewart et al. (1998a, b) were actually *Echinogammarus ischnus* (species identification verified by J. Witt, University of Guelph, Ontario, Canada).

Interstitial habitat provided by *Dreissena* shells is an important determinant of biomass, densities, and size-distributions of *Echinogammarus* and other gammarid amphipods in the Great Lakes (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a). Amphipods inhabiting similar interstitial habitat in fast-flowing water or wave-washed littoral zones may avoid costs of extreme hydrodynamic forces yet benefit from high oxygen concentrations (Barton and Hynes 1976, Olyslager and Williams 1993). In addition, spaces between substrate particles provide amphipods with protection from predators (Holomuzki and Hoyle 1990, Dahl and Greenberg 1996). Large, space-limited amphipods can displace smaller amphipods from inter-

stitial habitat (Adams et al. 1987), and in doing so may avoid fish which prey selectively on large individuals (Newman and Waters 1984, Holomuzki and Hoyle 1990). This may explain why amphipods inhabiting *Dreissena* beds or similar structurally complex substrates are often larger than amphipods on relatively homogenous substrates (Gee 1982, Adams et al. 1987). Indeed, response of *Echinogammarus* to shell-generated habitat in this study was likely influenced by predators. *Echinogammarus* and other amphipods are increasingly important components of crayfish and fish diets in the Great Lakes (Ricciardi et al. 1997, Stewart et al. 1998b). In addition, crayfish (*Orconectes rusticus*) reduce *Echinogammarus* densities on hard substrates in western Lake Erie that are colonized by *Dreissena* (Stewart et al. 1998b).

Like *Echinogammarus*, the chironomid *Microtendipes pedellus* occupied interstitial habitats in our study, and was most commonly collected from the shell-brick interface but also inhabited empty *Dreissena* shells. This microhabitat distribution suggests that *Microtendipes* uses mussel beds as a refuge from predation or other disturbances. *Microtendipes* is also a common associate of *Dreissena* in European waters (Walshe 1951), and was not collected in this study on substrates not inoculated with mussels. Thus, distribution of this large chironomid on hard substrates is clearly regulated by *Dreissena*. Finally, although increased densities of hydroids, the flatworm *Dugesia tigrina*, erpobdellid leeches, and the leech *Alboglossiphonia heteroclita* are likely due in part to shell-generated habitat provided by *Dreissena*, these carnivorous taxa also probably respond to increased prey densities on substrates with mussels (Dusoge 1966, Klemm 1991, Kolasa 1991, Slobodkin and Bossert 1991, Dermott et al. 1993, Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a). *Alboglossiphonia* and other glossiphoniid leeches may also prey on *Dreissena* (Smit et al. 1993, Ricciardi et al. 1997).

Although shell-generated habitat is the most important mechanism for increased biomass and densities of benthic macroinvertebrates on hard substrates, some taxa, including the snail *Physella* and the chironomid *Microtendipes*, also increase as a function of particulate organic matter produced by *Dreissena* (Ricciardi et al. 1997, Stewart et al. 1998a). *Physella*, *Microtendipes*, tubificid oligochaetes, and other algivore/detritivores (e.g., Oliver 1971, Brinkhurst and Gelder 1991, Brown 1991) probably use this organic matter as food. Organic and inorganic matter generated by *Dreissena* may also be used by *Microtendipes* and the microcaddisfly *Hydroptila waubesiana* for constructing cases, and as habitat for sediment-dwelling tubificids as well (Oliver 1971, Brinkhurst and Gelder 1991, Sheath et al. 1995).

Implications for Great Lakes Food Webs

Dreissena-mediated shifts in the spatial distribution of aquatic flora and fauna may affect Great Lakes fish communities. Reduced biomass of phytoplankton, zooplankton, and the burrowing amphipod *Diporeia hoyi* may adversely affect smelt (*Osmerus mordax*) and young salmonids, and these effects will probably cascade to predators of these small fishes (Dermott and Kerec

1997). However, several other important species of Great Lakes fishes, including yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), and freshwater drum (*Aplodinotus grunniens*) are consuming large numbers of gammarid amphipods, *Dreissena*, and other benthic invertebrates that have recently increased in abundance (Morrison *et al.* 1997, Ricciardi *et al.* 1997). Thus, substantial amounts of energy and nutrients redirected from pelagic to benthic habitats by *Dreissena* (Fahnenstiel *et al.* 1995, Mitchell *et al.* 1996) may still be channeled to these and other benthivorous fishes. This study was conducted 1 year before the study site was invaded by the round goby (J.G. Miner, personal observations), a potentially important predator of *Dreissena* and other benthic macroinvertebrates (Jude *et al.* 1992, Ghedotti *et al.* 1995). Thus, the results provide baseline data for evaluating impacts of this organism and other future environmental perturbations in the Great Lakes and other *Dreissena*-dominated benthic communities.

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