

# Can Dreissenid Attachment and Biodeposition Affect Submerged Macrophyte Growth?

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## ABSTRACT

The dreissenid mussels (zebra mussel, *Dreissena polymorpha* and quagga mussel, *D. bugensis*) have the ability to attach to submerged macrophytes, thereby decreasing light available to the plant through shading or weighing down the leaves. Through production of feces and pseudofeces, dreissenid mussels may also relocate nutrients from the water column to the sediments in proximity to the submerged macrophytes. Although indirect effects of mussels on macrophytes by increasing water clarity are well documented, few studies have investigated these direct effects. In this study, comparisons of leaves with and without mussels showed lower photosynthetic activity (measured as quantum yield) and lower chlorophyll concentrations in Eurasian water milfoil (*Myriophyllum spicatum* L.) leaves with zebra mussels, but not in eelgrass (*Vallisneria spiralis* L.) leaves with zebra mussels, suggesting the impact of shell attachment is species-specific. The zebra-mussel effect was apparently not mediated by changes in plant nutrient status but likely by shading. Experimental field manipulations of zebra mussels in Oneida Lake, NY, designed to test the importance of nutrient relocation, revealed no effect of dreissenid mussels on eelgrass growth. Because submerged macrophyte abundance generally increases after dreissenid invasions in North American lakes, the direct effects of dreissenid mussels on submerged macrophyte communities through attachment and nutrient relocation appeared to be less important than the positive indirect effects associated with increased light penetration.

**Key words:** Eurasian water milfoil, eelgrass, *Dreissena*, chlorophyll and protein, feces and pseudofeces, Oneida Lake.

## INTRODUCTION

The dreissenid mussels (zebra mussel, *Dreissena polymorpha* and quagga mussel, *D. bugensis*) affect submerged macrophytes in freshwater ecosystems through both direct and indirect pathways (Zhu et al. 2006). The indirect effects of dreissenids through increasing light penetration in the water column have been relatively well studied (Skubinna et al. 1995, Mayer et al. 2002, Chu et al. 2004, Lammens et al. 2004, Zhu et al. 2006,

2007). Direct effects associated with the presence of *Dreissena* on or near plants may be important, but have received little attention. The goal of this study was to investigate potential negative effects of the physical presence of dreissenid mussels on submerged macrophytes and potential positive effects of biodeposition of nutrients from the water column to the sediments.

Dreissenid mussels can aggregate on macrophytes, but stem and leaf structure of different plant species may affect the number of *Dreissena* supported. In a Polish lake, more than 2000 individual zebra mussels m<sup>2</sup> were found on *Chara* spp. and coontail (*Ceratophyllum demersum* L.), and ca. 1000 m<sup>2</sup> on starry stonewort (*Nitellopsis obtusa*), but less than 200 m<sup>2</sup> on Eurasian water milfoil (*Myriophyllum spicatum* L.) and American waterweed (*Elodea canadensis* Michx.) (Lewandowski and Ozimek 1997). In Oneida Lake, NY, about 86% of individual Eurasian water milfoil plants were colonized by zebra mussel juveniles with as much as 40% of the plant surface covered by zebra mussels (Zhu 2006). While the attachment may benefit dreissenid mussels for dispersal, it can decrease the growth rate of submerged macrophytes by weighing them down (Buchan and Padilla 2000) or by direct shading. Light is an important factor controlling the photosynthesis and growth of submerged macrophytes; consequently, any fouling organism that blocks light may have dramatic impacts on the plant community.

On the other hand, dreissenid mussels may benefit submerged macrophytes by increasing nutrient availability for the plants. Rooted submerged macrophytes usually absorb significant levels of nutrients, such as nitrogen (N) and phosphorus (P), from the sediments (Barko and Smart 1981). For example, most N and P of eelgrass (*Vallisneria spiralis* Michx.) and up to 99% of P fixed by Eurasian water milfoil may be taken up by the roots (Carignan and Kalff 1980, Rogers et al. 1995). Oppositely, non-rooted macrophytes such as *Chara* and coontail generally absorb nutrients from the water column (Wetzel 1983). Dreissenid mussels can affect the balance of water-column and sediment nutrients by relocating N and P from plankton and seston to the sediments through the production of feces and pseudofeces (Roditi et al. 1997, Madon et al. 1998). Through this process, dreissenid mussels may be redirecting a significant proportion of nutrients to nearshore areas in the Laurentian Great Lakes (Hecky et al. 2004). Additionally, *Dreissena* that settle on plant leaves may excrete inorganic nutrients that can be absorbed by leaf or stem tissue for both rooted and non-rooted macrophytes. Therefore, a potentially important direct effect of dreissenid mussel activity is the conversion of particulate (both inorganic and organic) forms of nutrients to dissolved inorganic forms via decomposition and resuspension. This process may benefit submerged macrophytes (e.g., Reusch et al. 1994).

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Submerged macrophyte communities are important to lake ecosystems because they affect physical, chemical and biological components in the system. Specifically, submerged macrophytes can directly or indirectly alter the physical and chemical environment by shaping light, temperature, and nutrient dynamics (Carpenter and Lodge 1986). They also define the littoral zone, provide physical living or nursery habitats for many zooplankton, invertebrates, and fish, and play a significant role shaping the structure and dynamics of pelagic and benthic food webs in rivers and lakes (Jeppesen et al. 1998). Therefore, it is important to understand the response of submerged macrophytes to ecological changes such as the invasion of dreissenid mussels.

We used four indices (photosynthetic electron transport, chlorophyll concentration, protein content, and specific leaf mass) to assess the response of Eurasian water milfoil and eelgrass to natural *Dreissena* colonization of stems and leaves (light occlusion effect) and the response of eelgrass to the placement of *Dreissena* clusters at their stem bases (added-nutrient effect). These two macrophytes were selected because they have different growth forms. Eurasian water milfoil has long stems and feather-like leaves and dreissenid mussels are abundant on both leaves and stems of this species, whereas dreissenid mussels usually attach sparsely on the base of the ribbon-like leaves of eelgrass that emerge in clusters along a rhizome (Smith and Barko 1990). We hypothesized that dreissenid mussels will inhibit the growth of submerged macrophytes by impeding light absorption when shells are directly attached to the plant, but will promote plant growth when the shells are only near the plant base by increasing nutrient availability through biodeposition of feces and pseudofeces. We assessed mussel effects on photosynthesis by monitoring the quantum yield (or efficiency) of photosynthetic electron transport (Genty et al. 1989) and by measuring leaf chlorophyll content. Changes in total chlorophyll content can reflect changes in both nutrient (especially N) status and light levels during growth (Evans 1989). In order to help separate any mussel-related light *vs.* nutrient effects on leaves, we also measured leaf protein content, as most nitrogen in plants is in proteins, and so increases with plant N status (e.g., Dashti et al. 1997). In addition, changes in specific leaf mass (SLM) were also measured to assess the direct effects of dreissenid attachment and nutrient relocation on leaf structure (e.g., an increase in leaf thickness with mussel attachment).

## MATERIALS AND METHODS

In the observational study, leaves of Eurasian water milfoil and eelgrass were collected by species in pairs, comprised of an individual with attached zebra mussels and an individual without mussels within close proximity of each other, at 14 locations in Oneida Lake, NY, in late July of 2003. Skin divers collected samples in 1-2 meters of water at midday (1300-1500 h), when there was full sunlight. The quantum yield of photosynthetic electron transport was measured on the middle portion of recently fully expanded leaves immediately after collection from mussel-free plants or after removing attached mussels for plants with mussels (as described below). Additional leaves of both species were covered with ice in a dark box and transported to the lab for chlorophyll, pro-

tein, and biomass analyses. Eurasian water milfoil with mussels was very densely covered with shells and we therefore had to remove shells from leaf areas in order to conduct measurements. Leaves of eelgrass were never covered with *Dreissena* (stems were the attached parts) and we were therefore able to take all measurements described below from areas that had at no time been covered by shells.

In the controlled experiment, 14 similar patches of eelgrass that were free of zebra mussels were selected in the nearshore of Oneida Lake, NY. Each patch included about 10 individuals in an area of 0.25 m<sup>2</sup>. The 14 patches were divided into seven pairs located within 2 m of each other and at similar depth. In one of the two patches in each pair, we placed five rocks with a total of approximately 1000 zebra mussels on the sediments adjacent to the plant stems; in the other patch in each pair, we placed five similarly sized uncolonized rocks. The experiment started on July 23, 2003, and lasted 30 days. Leaf samples in each patch were collected for chlorophyll, protein, quantum yield, and biomass analyses after 3, 6, 9, 16, 24, and 30 days.

## Photosynthesis

Quantum yield (or efficiency) of photosynthetic electron transport of detached leaves was monitored under steady-state light using a pulse-amplitude-modulated chlorophyll fluorometer (model OS1-FL, Opti-Sciences, Tyngsboro, MA). Quantum yield was calculated as  $[F_m' - F_s] / F_m'$ , where  $F_m'$  is maximum chlorophyll fluorescence during a saturating light pulse (>4000 mmol PAR m<sup>-2</sup> s<sup>-1</sup>) and  $F_s$  is basal fluorescence prior to the saturating light pulse (Genty et al. 1989). When measured in light-adapted leaves at equal light intensity and temperature, quantum yield is proportional to the rate of net photosynthesis (Genty et al. 1989). Quantum yield was recorded for all plant leaves incubated in lake water under ambient sunlight for 30 minutes at midday. All individual plants were measured under similar light levels, corresponding to the light conditions before harvest (1191-1400 mmol PAR m<sup>-2</sup> s<sup>-1</sup> at water surface). Due to mussel removal, quantum yield for plants with mussels might be overestimated, thereby underestimating the zebra mussel effect.

## Specific Leaf Mass, Chlorophyll, and Protein

Measurements of the fresh weight (FW) and the silhouette-area of leaves were used to calculate specific leaf mass (SLM; FW per unit leaf area). SLM was only measured in eelgrass, because of the technical difficulty of measuring area of the very fine leaves of Eurasian water milfoil.

Chlorophyll concentration was determined on 1-cm-long segments of eelgrass cut from the mid-length region, after incubation in 1 mL dimethyl sulfoxide (DMSO) in the dark at 60°C for 2 h prior to extract total pigment. The same procedure was followed for three whole leaves of Eurasian water milfoil using 1.5 mL DMSO. After extraction in DMSO, chlorophyll *a* and *b* were determined by using the equations of Barnes et al. (1992) and a spectrophotometer (model DU 640, Beckman Coulter, Inc., Fullerton, CA). Total chlorophyll content was calculated as the sum of chlorophyll *a* and *b*.

Total leaf protein was extracted by grinding leaf tissue (0.1 g) with a mortar and pestle in liquid N<sub>2</sub>, then in an extraction buffer (1 mL) containing 1% sodium-dodecyl-sulfate, 100 mM Tris pH 8.0, 10 mM dithiothreitol, and protease inhibitors (for details of the buffer, see Heckathorn et al. 2004). Extracted protein was heated for 2 min at 75-85°C and then centrifuged at 21,000 × *g* for 2 min to remove insoluble debris. Protein concentration of each sample was determined in triplicate by the Coomassie dye-binding method of Ghosh et al. (1988), using bovine serum albumin as a standard and using a desktop scanner and the software Scion Image (Scion Corporation, Frederick, MD) to perform densitometry.

### Statistical Analysis

Paired *t*-tests were used for comparisons of quantum yield, chlorophyll concentrations, SLM, and protein content in Eurasian water milfoil and eelgrass in the observational study. While in the controlled experiment, two-way ANOVA (repeated measures) was used to investigate the effects of dreissenid mussels and time on the four growth indices of eelgrass (Kuehl 2000). All analyses were conducted by using the general linear model procedure of SAS 9.0 (SAS Institute, Cary, NC).

## RESULTS AND DISCUSSION

Since their invasions to North America in the late 1980s, dreissenid mussels have increased water clarity and promoted the process of benthification (Mills et al. 2003). Benthification alters ecosystem function in part through effects on submerged macrophytes, including increased species richness, increased depth of maximum colonization and increased coverage (Skubinna et al. 1995, Mayer et al. 2002, Zhu et al. 2006, 2007). These changes have generally been attributed to the indirect ecological impacts of dreissenid mussels through increased water clarity and light penetration. Direct pathways, addressed in this study, are also potentially important.

### Observational Study

The results from the observational study revealed the responses of Eurasian water milfoil and eelgrass to direct attachment of zebra mussels differed. Decreased quantum yield, chlorophyll *a* concentration, and total chlorophyll concentration were observed in Eurasian water milfoil when zebra mussels were present on the leaves and stems (*t* test, *df* = 13, *t* = 3.90, *p* = 0.002; *t* = 2.46, *p* = 0.029; and *t* = 2.39, *p* = 0.032 respectively, Figures 1 and 2A). However, the ratio of chlorophyll *a* to *b* did not change in this species (4.51 *vs.* 4.36, for without and with mussels respectively; *df* = 13, *t* = 1.11, *p* = 0.285); hence, the decreases in chlorophyll indicate a decrease in the number of photosynthetic reaction centers, rather than decreases in sub-components of reaction centers. In contrast, a marginally significant increase in quantum yield was found in eelgrass with the presence of zebra mussels (Figure 1, *t* test, *df* = 13, *t* = -2.00, *p* = 0.067) and no changes were observed in chlorophyll concentrations (Figure 2B, *t* test, *df* = 13, *t* = -0.07, *p* = 0.945 for chlorophyll *a*; *t* =

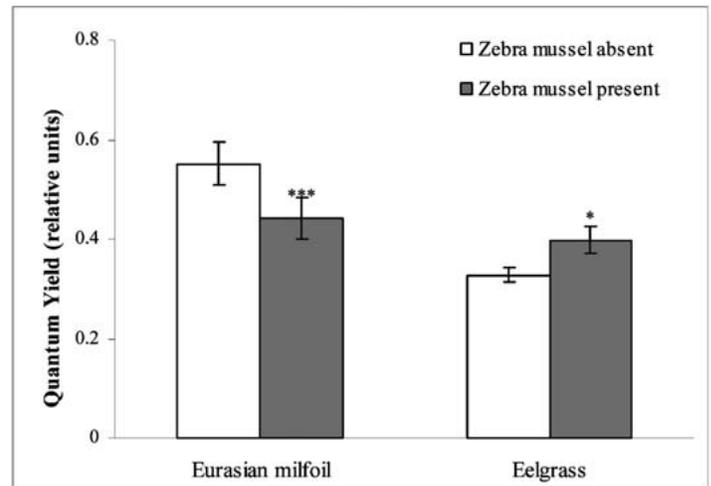


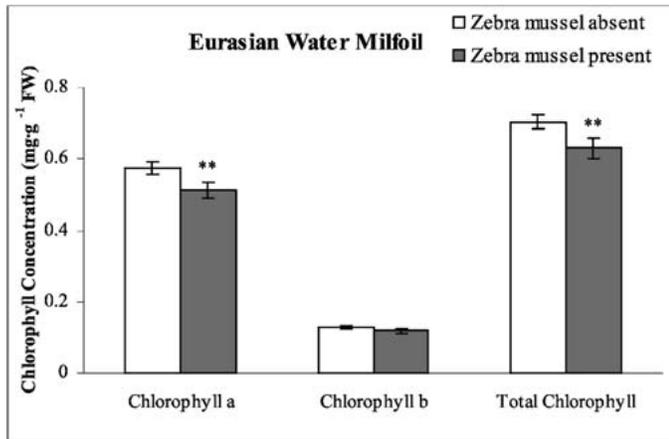
Figure 1. Dreissenid attachment effects on quantum yield in Eurasian water milfoil and eelgrass collected from natural habitats in Oneida Lake, NY. \* denotes significance at  $\alpha = 0.10$  and \*\*\* denotes significance at  $\alpha = 0.01$  in paired *t* test. Error bars represent  $\pm 1$  SE.

0.35, *p* = 0.731 for chlorophyll *b*; and *t* = 0.02, *p* = 0.982 for total chlorophyll). In addition, SLM of eelgrass was not affected by the dreissenid attachment (Figure 3A, *t* test, *df* = 13, *t* = 0.47, *p* = 0.646). Although there was a tendency towards higher protein content with the presence of zebra mussels in both species, it was not statistically significant for either species (Figure 3B, *t* test, *df* = 13, *t* = -1.33, *p* = 0.207; and *t* = 1.00, *p* = 0.336). Thus, decreases in chlorophyll content in Eurasian water milfoil were not related to decreases in leaf protein status.

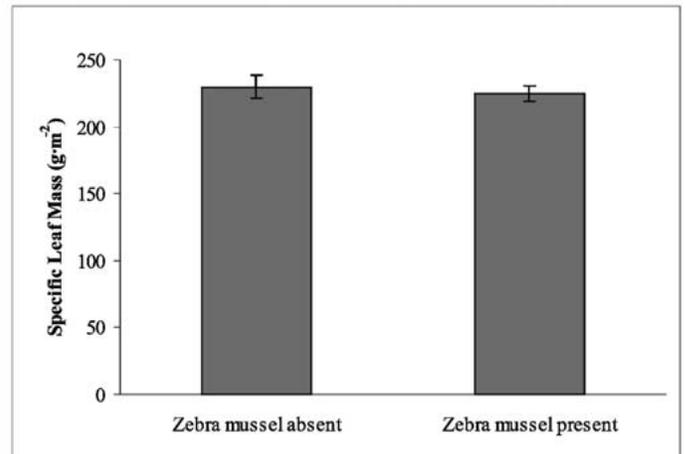
Decreases in quantum yield and chlorophyll concentration in Eurasian water milfoil when zebra mussels were present was apparently not due to nutrients. Instead, it suggests the effect of light occlusion because both variables index the photosynthetic ability of submerged macrophytes and Dreissena covered the measured areas for plants with mussels. Zhu (2006) also showed 86% of individuals and an average of 40% of leaf surface of each individual Eurasian water milfoil plant were covered by zebra mussels in Oneida Lake. This indicates the negative impacts are mainly due to decreases in leaf surface light capture instead of decreases in photosynthetic potential. It is possible that protein content did not change with dreissenid attachment because protein content is determined by nutrient availability to the plant and not by a process that is light limited in macrophytes (Dashti et al. 1997). The slight, although not statistically significant, increase in protein content for both plants with dreissenid attachment could be due to nutrient excretion from the mussels in the forms of feces and pseudofeces (Reusch et al. 1994).

The responses to dreissenid attachment were also species-specific. There was no negative impact of mussels on eelgrass growth, and in fact there was a positive, though marginally statistically significant effect in photosynthetic capacity. Harley and Findlay (1994) found that the maximum light-saturated values of photosynthesis were not different between Eurasian water milfoil and eelgrass, indicating similar photosynthetic capacity of both species. Therefore, different re-

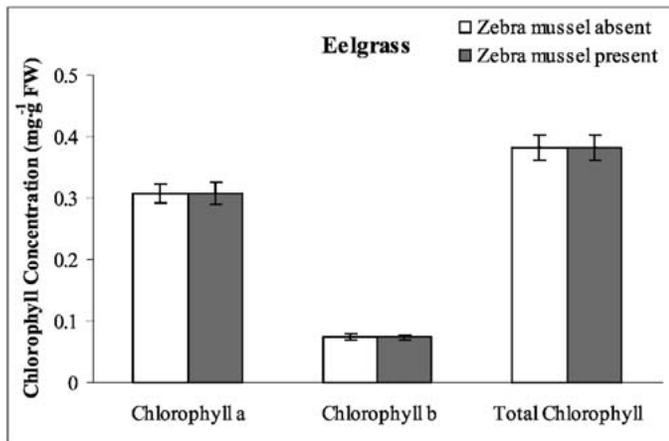
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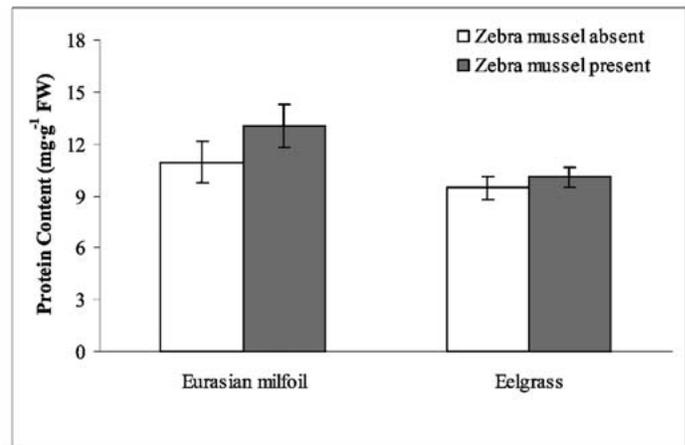


Figure 2. Dreissenid attachment effects on concentrations of chlorophyll *a*, chlorophyll *b*, and total chlorophyll in A. Eurasian water milfoil and B. eelgrass collected from natural habitats in Oneida Lake, NY. \*\* denotes significance at  $\alpha = 0.05$  in paired *t* test. Error bars represent  $\pm 1$  SE.

Figure 3. Dreissenid attachment effects on A. specific leaf mass of eelgrass and B. leaf protein content in Eurasian water milfoil and eelgrass collected from natural habitats in Oneida Lake, NY. No significance was present at  $\alpha = 0.10$  in paired *t* test. Error bars represent  $\pm 1$  SE.

sponses in growth of these two species reflect the true effect of dreissenid mussel attachment. Thus, the effect of zebra mussels on submerged macrophytes depends on the species of plant affected. The strength of an impact is likely dependent on the morphology of plants and the attachment position of the mussels. Canopy-forming Eurasian water milfoil usually extends its stems and leaves both laterally and vertically and their feather-shaped leaves are good substrates for dreissenid veligers and juveniles (Smith and Barko 1990). Therefore the zebra mussels attached on both leaves and stems of Eurasian water milfoil, blocking light for photosynthesis. This negative impact may have contributed to the decrease in frequency of occurrence of this invasive species in Oneida Lake, although other factors may have been more important, such as biological control by a native weevil *Euhrychiopsis lecontei* and a naturalized moth *Acentria ephemera*

(Johnson et al. 2000, Zhu et al. 2006). In contrast, eelgrass rises vertically from the bottom and usually grows in near-shore shallow water, where there is more wave action (Wetzel 1983). Only a few adult zebra mussels were found on the base of eelgrass leaves. It is likely that the difference in response to attached dreissenid mussels between the two species is due to plant morphology and the density of mussel colonization.

### Controlled Experiment

The controlled experiment was designed to directly test the possibility that mussels affect plants via deposition of nutrients next to plants. We expected that bottom-associated dreissenid mussels would promote submerged macrophyte growth by increasing nutrient availability through producing feces and pseudofeces (Reusch et al. 1994, Hecky et al. 2004).

TABLE 1. SUMMARY OF P-VALUES FROM ANOVA FOR REPEATEDLY MEASURED VARIABLES FROM THE CONTROLLED EXPERIMENT TO TEST DREISSENID BIODEPOSITION EFFECTS ON EELGRASS IN ONEIDA LAKE, NY.

	ANOVA model	<i>Dreissena</i> effect	Time effect	Interaction
Quantum yield (relative units)	0.001***	0.190	0.001***	0.605
Total chlorophyll (mg·g <sup>-1</sup> FW)	0.106	0.152	0.130	0.364
Specific leaf mass (g·m <sup>-2</sup> )	0.505	0.240	0.300	0.629
Protein content (mg·g <sup>-1</sup> FW)	0.006***	0.526	0.001***	0.171

\*\*\*Significance at the level  $\alpha = 0.01$ .

However our results did not support this hypothesis; there were no significant dreissenid effects on quantum yield, total chlorophyll concentration, SLM, or protein content with presence of zebra mussels placed adjacent to eelgrass (Table 1). The ANOVA models were significant for quantum yield and protein content due to the significant time effects, which indicate that yield and protein changed through time. Nonetheless, there were no significant time effects on total chlorophyll or plant biomass.

The mussel density used in the experimental manipulation was comparable to that of Oneida Lake, NY in recent years (~4000 individuals m<sup>-2</sup>; Zhu 2006), suggesting that dreissenid mussels currently do not affect eelgrass growth in meso- and eutrophic lakes such as Oneida. This insignificant biodeposition effect is likely due to three factors. First, the sediment is already nutrient rich and additional nutrient input from zebra-mussel deposition would not affect plant growth. This is very likely because Oneida Lake is a eutrophic-mesotrophic lake (Zhu et al. 2006). Secondly, the experimental sites were close to the shore where wave action contributes to faster resuspension and transports nutrients from feces and pseudofeces away from the experimental sites (e.g., Madon et al. 1998). This will dilute the nutrient concentration, diminishing the nutrient effects on plant growth. Finally, high background natural variability may have made experimental assessments difficult. For example, plants in the 14 patches were not at the exact same growing conditions at the beginning of the experiment and sediment nutrients may vary from site to site. However nutrient relocation by *Dreissena* has been proposed for very large systems such as the Great Lakes (Hecky et al. 2004) where shorelines receive very high wave activity. One difference between our study and observations from the Great Lakes is the spatial scale of colonization. It is possible that large area of *Dreissena* coverage are required in order to draw and retain nutrients at levels high enough to promote plant growth. Our results suggest that at least at a localized scale biosedimentation of nutrients by *Dreissena* does not affect plant growth.

We have shown that direct effects of zebra mussels on submersed macrophytes are measurable in the field, and that the effect varies between two species with different growth morphology. This is mainly due to the fact that very few mussels were attached on eelgrass leaves (just stems), but high numbers distributed all along Eurasian water milfoil leaves and stems. The direct negative effect of leaf colonization demonstrated in this study may oppose the indirect effect of increased water clarity. The significant increases in species richness and abundance of macrophytes associated with dreissenid mussel colonization in many systems, including Onei-

da Lake and Lake Ontario (Mayer et al. 2002, Chu et al. 2004, Zhu et al. 2006, 2007), suggests that the indirect positive effects are stronger than this direct negative effect. However, the magnitude of the direct effect varies among species and may contribute to the observed shifts in macrophyte composition and increased diversity observed in Oneida Lake since the zebra mussel invasion (Zhu et al. 2006). This study also suggests that at least on a small spatial scale in meso- and eutrophic systems plants do not increase growth because of *Dreissena* nutrient deposition. We have thus been able to narrow the potential mechanisms underlying observed responses of macrophyte communities to *Dreissena* introduction, which can help to inform aquatic plant management decisions in North American lakes.

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