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Clearance and Processing of Algal Particles by Zebra Mussels (*Dreissena polymorpha*)

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ABSTRACT. *The exotic zebra mussel,* Dreissena polymorpha *Pallas, has become a dominant member of nearshore benthic communities in the Laurentian Great Lakes. Suspension-feeding bivalves such as the zebra mussel filter algal particles from the water column and either reject them as pseudofeces, digest them, or egest them as feces. We used laboratory experiments to compare clearance and particle processing of two green algal species by zebra mussels. The effect of algal concentration on clearance rate of* Chlamydomonas reinhardtii *varied between large and small mussels. When mussels were fed* Pandorina morum, *clearance rate declined with increasing algal concentration. Mussel size affected clearance of* C. reinhardtii *but not* P. morum. *On a diet of* P. morum, *pseudofeces production was constant across algal concentrations. When fed* C. reinhardtii, *mussels increased pseudofeces production as algal concentration increased once a threshold was crossed. Below this threshold, no pseudofeces were produced. Measured clearance rates tended to be as high or higher than those previously reported, indicationg that incipient limiting concentrations vary with the types of particle processed. Absorption efficiencies were similar for both algal species. Our results show that particle processing by zebra mussels depends on the types of particles present in the water column and the size structure of the mussel population. To accurately determine the impacts of zebra mussels on the trophic structure of ecosystems and the cycling of contaminants, investigators must use realistic algal assemblages and account for the size structure of mussel populations.*

INDEX WORDS: *Zebra mussel, clearance rate, algae, contaminant cycling, suspended particles.*

INTRODUCTION

Since its introduction in 1985, the exotic zebra mussel (*Dreissena polymorpha* Pallas) has become a dominant member of the nearshore benthic communities of the Laurentian Great Lakes. Recent studies have reported densities greater than 100,000 individuals • m^{-2} in Lakes Erie and St. Clair (Griffiths *et al.* 1991, MacIsaac *et al.* 1991). Native bivalves are considerably less abundant in these systems, with average densities of 10 individuals • m^{-2} or less (McCall *et al.* 1979, Nalepa and Gauvin 1988). Thus, the explosive growth in abundance of *D. polymorpha* has greatly increased the biomass of benthic suspension feeders in these aquatic systems.

Filtration of the water column by bivalves often represents an important mechanism for processing suspended particles, including algae. Bivalves remove suspended particles from the water column and return some portion to the environment in altered forms (Bayne and Newell 1983). These altered forms differ in size, density, and composition from the originally filtered particles. Pseudofeces are particles that are taken into the mantle cavity,

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processed, but not ingested. Instead, these particles are coated with mucus and ejected via the inhalant siphon or along the ventral mantle margin. These pseudofecal particles are basically clumps of finer particles and the increase in relative size and/or density through aggregation make them less likely to be suspended than the individual constituent particles. In contrast, fecal pellets are made up of nondigestible remnants of absorbed materials and substances that have passed unabsorbed through the gut. These pellets are expelled via the exhalant siphon. Not only are fecal pellets larger and more dense than ingested particles, but they have often been altered chemically via digestion processes in the gut. The processing of suspended particles by bivalves is often important in determining trophic interactions and contaminant cycling in marine and freshwater systems (e.g., Asmus and Asmus 1991, Geyer *et al.* 1982, Fisher *et al.* 1993, Leach 1993).

Determining the importance of particle processing by a suspension-feeding species requires quantifying the rate at which particles are cleared from the water column, the proportion of cleared particles that are packaged as pseudofeces, the proportion absorbed by the filtering organism, and the proportion egested as feces. A number of studies have examined the rate at which zebra mussels clear particles from the water column. Clearance rates have been shown to vary with size of mussels (Morton 1971, Reeders and Bij de Vaate 1990, Bunt *et al.* 1993), concentration of particles (Dorgello and Smeenk 1988, Sprung and Rose 1988), and type of particle (Ten Winkel and Davids 1982, Reeders and Bij de Vaate 1990). Production of pseudofeces generally does not occur below a concentration threshold termed the incipient limiting concentration (Sprung and Rose 1988), although reports of pseudofeces production below this level have been noted (Walz 1978). Feces production and absorption of ingested algae by *Dreissena polymorpha* have only been reported for a single algal species (Walz 1978).

We used a series of laboratory experiments to compare clearance and processing of two common green algal species. *Chlamydomonas reinhardtii* Dangeard is a spherical unialgal species, while *Pandorina morum* Bory is colonial, with each colony composed of a number of spherical cells of similar size (7.61 μm ± 0.51 standard error, n = 25) and shape to an individual *C. reinhardtii* (7.41 ± 0.13 μm, n = 67). We examined clearance rates, absorption efficiencies, and production of pseudofeces and feces by zebra mussels from a population in western Lake Erie. We measured the effects of algal species, algal concentration, and mussel size on each of these factors and relate these results to the potential roles of zebra mussels in the processing of suspended particles and the fate of aqueous contaminants.

METHODOLOGY

Zebra mussels were collected from the vicinity of Kelly's Island, western Lake Erie in April, 1992. Mussels were held in aquaria filled with carbon-filtered tap water for a minimum of 10 days at 10°C and were fed a diet of Tetra-Min® fish food at a rate of 3.3 g • 1,000 mussels^{-1} • day^{-1}. Earlier studies indicated that mussels remain healthy for several months when held under these conditions (Fisher *et al.* 1992). A minimum of 48 hours before an experiment, individuals were transferred to a 40-L aquarium containing a modified hard Standard Reference Water (hSRW) at 22°C and allowed to reattach to gravel. The hSRW had a pH of 8.3 (±0.2 range), alkalinity of 3 mM (150 mg • L^{-1} as $CaCO_3$), and hardness of 180 mg • L^{-1} as $CaCO_3$ (U.S. Environmental Protection Agency 1975). One molar HCl or NaOH was used as needed to adjust pH. The hSRW was modified by the substitution of Na_2HPO_4 for K_2HPO_4 because of the toxicity of potassium to zebra mussels (Fisher *et al.* 1991). Mussels were starved for 24 hours before an experiment. Monocultures of both algal species were raised in 9:1 Bold's Basal Medium (Nichols and Bold 1965) under fluorescent lights using 16 hours:8 hours light:dark at 23°C.

On the day of an experiment, mussels and all attached gravel were transferred to 1,000 mL beakers containing approximately 500 mL of 22°C hSRW. Beakers were placed in a lighted, 22°C incubator for at least 1 hour prior to initiation of experiments. We observed no production of feces or pseudofeces during this period. Following the acclimation period, mussels that gaped with siphons extended were used for the experiments. These mussels and all attached gravel were transferred to clean 1,000 mL beakers (1 mussel per beaker) containing 525–550 mL of 22°C hSRW.

Experiments were begun by adding measured volumes of algae to the beakers. Algae were added to create two concentration classes (high and low) for each algal species. However, we were unable to carefully control these levels and thus, algal concentrations approximated continuous distributions that ranged from 1.0 to 18.0 μg • mL^{-1} for *Chlamy-*

domonas reinhardtii and 0.5 to 24.5 μg • mL^{-1} for *Pandorina morum*. These concentrations are equal or greater than the range of total algae concentration in Lake Erie (Makarewicz and Bertram 1991). Beakers containing only hSRW and algae were used as controls for gravitational settling. The number of replicates (individual mussels) varied with each experiment. No experiments were conducted on mixed cultures of algae. Following addition of algae, a 25–50 mLwater sample (Time 0) was withdrawn from each beaker and algal biomass or cell density was measured. The volume of the sample was adjusted to ensure that the sample contained enough algae to be measured while leaving 500 mL of water in the beaker during the experiment. Biomass was determined by filtering the sample through preweighed 0.45 μm filters, drying for at least 24 hours at 60°C and then weighing the filter papers. Cell density was determined using a Model Z_{BI} Coulter Counter. Beakers were returned to the incubator after removal of the Time 0 sample. Mussels were allowed to filter for 3 hours except when large mussels were exposed to low algal concentrations, in which case experiments lasted only 1 hour so that algae were not depleted. Algal concentration was measured again at the end of the filtering period. The first few sets of experiments also contained beakers with mussels but without algae to account for any nonalgal debris released by the mussels. However, the amount of debris released was never measurable, so this control was deleted in later experiments. In addition, algal cell division was monitored in separate beakers using a Coulter Counter to determine total particle concentration and found to be insignificant during the 3-hour filtering experiments. Following exposure to algae, mussels were transferred to beakers without algae; pseudofeces and feces were collected from the experimental chambers and from the clean beakers containing mussels every 24 hours for 72 hours. Feces and pseudofeces were easily distinguished: feces were compact, brown pellets while pseudofeces were loose, bright green bundles. Each particle type was removed by pipet, physically sorted and quantified using the same technique as that used for determining algal biomass. In order to obtain measurable quantities of each of these classes, particles were pooled for 3 mussels. At the end of 72 hours, most feces and all pseudofeces had been expelled. Mussels were removed from beakers and total shell length of each individual was determined.

Algal clearance rates for individual mussels were calculated as

$$CR = [(\ln C_0 - \ln C_t) - (\ln C'_0 - \ln C'_t)] \times V / t \quad (1)$$

where CR = clearance rate (mL • min^{-1}), C_0 = algal concentration of the beaker containing a mussel at the start of the experiment (μg • mL^{-1}), C_t = algal concentration of the beaker containing a mussel at the end of the experiment (μg • mL^{-1}), C'_0 = algal concentration of the control beaker at the start of the experiment (μg • mL^{-1}), C'_t = algal concentration of the control beaker at the end of the experiment (μg • mL^{-1}), V = experimental volume (mL), and t = time (min) (Coughlin 1969). Total biomass of algae cleared was determined using the equation

$$BCA = [(C_0 - C_t) - (C'_0 - C'_t)] \times V \quad (2)$$

where BCA = biomass of algae cleared from the water column (μg). This model requires that the following assumptions be met: 1) the reduction in concentration over time is due only to gravitational settling and filtering by the mussel; 2) pumping rate of the mussel is constant; 3) the proportion of particles retained by the mussel is constant; 4) the test suspension remains homogeneous throughout the experiment.

Pseudofeces production was expressed as the percentage of cleared algae (%P) converted to pseudofeces with equation (3).

$$\% P = (P / BCA) \times 100 \quad (3)$$

where P = pseudofeces produced (μg). Absorption efficiency was calculated as

$$A = \{[BCA - (P + F)] / (B - P)\} \times 100 \quad (4)$$

where A = absorption efficiency (%) and F = feces produced (μg).

Mussels were divided into two size classes: small (10–15 mm total length) and large (20–25 mm). Analysis of covariance (ANCOVA) of natural log-transformed data (Abacus Concepts 1989) was used to examine the effects of mussel size (large vs. small) and algal concentration (the covariate) on clearance rate. T-tests (Mann-Whitney tests if normality was uncertain) were used to determine if pseudofeces production and absorption efficiency varied between algal concentrations and between mussel sizes for each algal species tested. Linear regression was used to determine if there were relationships between pseudofeces production, absorption efficiency, and algal concentration within each mussel size class when algal concentration classes were not discreet.

RESULTS

Early experiments were evaluated using the cell density method while the algal biomass method was used for later experiments. These two methods produced equal estimates of clearance rate for large mussels fed *Chlamydomonas reinhardtii* (t-test, $p > 0.05$) and average biomass of *C. reinhardtii* cells (3.72×10^{-5} μg • cell^{-1} ± 2.16×10^{-6}, n = 15) did not change over time (one-way ANOVA, $p > 0.05$). Therefore, results for the cell density method were converted to a biomass basis and combined with results for experiments measuring biomass directly. However, average biomass of *Pandorina morum* colonies varied greatly, presumably due to alterations in the average number of cells per colony. Because of these fluctuations, results for *P. morum* experiments are reported using only the biomass method of measuring consumption.

Mussels Fed *Chlamydomonas reinhardtii*

The ANCOVA revealed a significant (algal concentration) * (mussel size) interaction (Table 1), indicating that the effects of algal concentration on clearance rate depended on the size of mussel. Clearance rate as a function of algal concentrations from 1.07 to 17.88 μg • mL^{-1} did not produce a significant regression for large mussels ($p = 0.15$, n = 98). A similar result was found for small mussels fed *Chlamydomonas reinhardtii* at concentrations varying between 0.03 and 3.11 μg • mL^{-1} ($p = 0.09$, n = 18). The percent of cleared algae converted to pseudofeces by large mussels was positively correlated with *C. reinhardtii* concentrations in the range of 1.17 to 7.74 μg • mL^{-1} (Fig. 1). Because the dependent variable is a percentage, the relationship is best described using an arcsin transformation of the dependent variable

$$\arcsin(\%P/100) = (6.05 * \text{conc.}) - 7.71$$

where conc. = μg of algae • mL^{-1} ($p < 0.05$, $r^2 = 0.727$, n = 10). This relationship leads to the prediction that the threshold below which pseudofeces are not produced is 1.27 μg • mL^{-1} (approximately 34,000 cells • m L^{-1}). Absorption efficiency of large mussels was 80.5% (± 4.0, n = 11) and did not vary with algal concentration (t-test, $p > 0.05$). Only two experiments gave successful estimates of pseudofeces production and absorption efficiency by small mussels. Pseudofeces production varied from 29.3 to 73.2% and absorption efficiencies were 81.8 and 97.0% for *C. reinhardtii* concentrations greater than 12 μg • mL^{-1}.

Mussels Fed *Pandorina morum*

There was no (algal concentration) * (mussel size) interaction for mussels feeding on *Pandorina morum* (Table 1). Clearance rate was not significantly related to mussel size ($F = 0.07$, 1 df, $p = 0.80$), but was a function of algal concentrations between 0.59 and 24.4 μg • mL^{-1} (Fig. 2). This relationship is described by the equation

TABLE 1. Analysis of covariance table for zebra mussels fed **Chlamydomonas reinhardtii** *or* **Pandorina morum.** *The dependent variable is ln(clearance rate). Mussel size classes were large (20–25 mm total length) or small (10–15 mm). Algal concentration was continuously distributed from 0.03 to 17.88 μg • mL^{-1} for* **C. reinhardtii** *and 0.59 to 24.4 μg • mL^{-1} for* **P. morum.** *Clearance was measured as mL • individual^{-1} • minute^{-1}.*

	df	Sum of Squares	Mean Square	F	P-value
Mussels fed *Chlamydomonas reinhardtii*					
Mussel Size	1	0.013	0.013	0.014	0.9063
ln(Algal Concentration)	1	1.349	1.349	1.491	0.2246
Size * ln(Algal Concentration)	1	5.434	5.434	6.005	0.0158
Error	112	101.349	0.905		
Mussels fed *Pandorina morum*					
Mussel Size	1	0.058	0.058	0.082	0.7762
ln(Algal Concentration)	1	7.558	7.558	10.691	0.0022
Size * ln(Algal Concentration)	1	0.026	0.026	0.036	0.8497
Error	42	29.692	0.707		

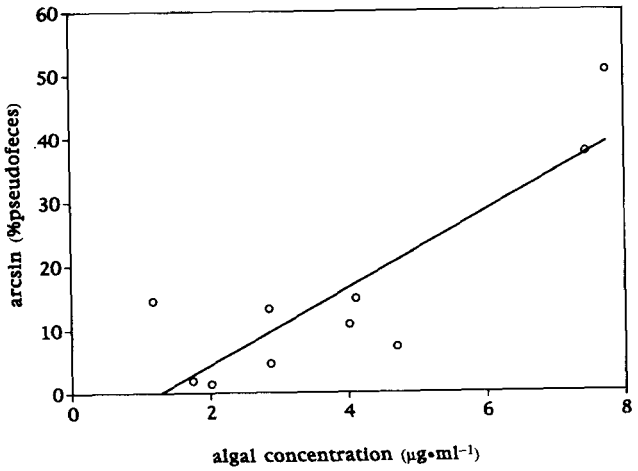

FIG. 1. Relationship between percentage of cleared algae converted to pseudofeces (%P) by large (20–25 mm) zebra mussels to **Chlamydomonas reinhardtii** *concentration. Y-axis values represent arcsin transformations of %P. The regression is significant at $p < 0.05$ ($n = 10$, $r^2 = 0.727$).*

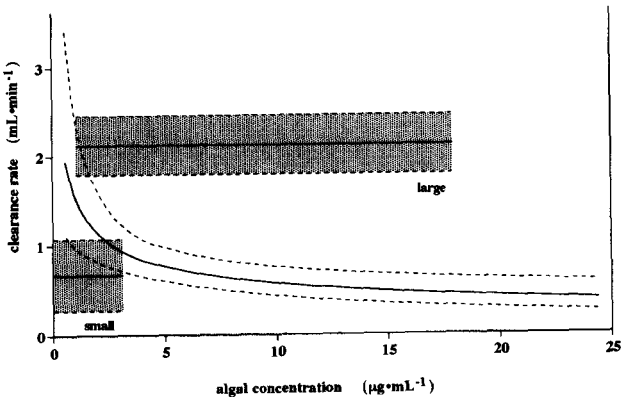

FIG. 2. Relationship between clearance rate of zebra mussels and concentration of Pandorina morum (regression line and 95% confidence bands) and mean clearance rate of large and small mussels filtering **Chlamydomonas reinhardtii** *(shaded bars). The regression is significant at $p < 0.01$ ($n = 46$, $r^2 = 0.249$). Heights of shaded bars represent the mean (central line) and 95% confidence interval (upper and lower edges) for clearance. Width of region along the X-axis represents the range of* **C. reinhardtii** *concentrations measured. Regions of overlap between 95% confidence limits are algal concentrations where rate of clearance for the two algal species was not significantly different.*

$$\ln(CR) = 0.433 - [0.432 * \ln(C_0)]$$

and is statistically significant ($p < 0.01$, $r^2 = 0.249$, $n = 46$). Proportion of cleared algae converted to pseudofeces did not vary over algal concentrations from 0.8 to 12.6 µg • mL^{-1} for large mussels (arcsin-transformed regression, $p > 0.08$, $n = 11$) and averaged 22.5 % (± 3.6). Absorption efficiency for large mussels exposed to high *P. morum* densities was 96.2% (± 1.3, $n = 3$) and 81% (± 5.0, $n = 6$) at low densities. These values were significantly different (Mann-Whitney test, $p < 0.05$, $n = 9$). Almost no pseudofeces or feces were collected from small mussels.

Between-species Comparisons of Algal Clearance Rates

We calculated 95% confidence intervals for the mean of natural log-transformed clearance rates for large and small mussels fed *Chlamydomonas reinhardtii*. These intervals were compared to 95% confidence bands generated for the regression of ln(clearance rate) on ln(*Pandorina morum* concentration) (Fig. 2). Regions of overlap in the confidence intervals were considered nonsignificant. For large mussels, clearance rates for *C. reinhardtii* were significantly greater than those for *P. morum* at algal concentrations greater than 2.93 µg • mL^{-1}. For small mussels, clearance rates for *P. morum* were significantly higher than for *C. reinhardtii* at algal concentrations less than 3.71 µg • mL^{-1}. As noted earlier, pseudofeces production by large mussels was a function of algal density when mussels were fed *C. reinhardtii*, but was independent of density when they were fed *P. morum*. Absorption efficiency of large mussels was constant at low algal densities (below 5 µg • mL^{-1}), averaging approximately 81% for both food types.

DISCUSSION

Processing of algal particles by zebra mussels was highly variable, depending on a number of factors including the algal species, concentration of particles, and size of the zebra mussels. Several other studies have measured clearance of *Chlamydomonas* by zebra mussels. Small mussels (14–17 mm) cleared an average of about 0.18 mL • min^{-1} when fed *Chlamydomonas eugametos* (Dorgello

and Smeenk 1988), approximately a third of the clearance rate that we measured for 10–15 mm mussels. For large mussels, our rates fall within the range noted by Sprung and Rose (1988) for 25–30 mm mussels fed *C. reinhardtii* (0.83 to 4.17 mL • min^{-1}). In general, clearance rate should be independent of particle concentration until a threshold (the "incipient limiting concentration") is crossed (Sprung and Rose 1988). Above this level, clearance rate should decline with increasing particle concentration and pseudofeces production should begin. This level is a function of particle type and mussel size (Morton 1971, Reeders and Bij de Vaate 1990). When fed *Chlamydomonas*, the incipient limiting concentration for zebra mussels has been reported to be as low as 0.60 μg • mL^{-1} for 25–30 mm individuals (Sprung and Rose 1988) and as high as 3.44 μg • mL^{-1} for 14–17 mm mussels (Dorgello and Smeenk 1988). Our finding that clearance rate was independent of *C. reinhardtii* concentration for small mussels agrees with the latter study, since maximum concentration in our experiments was 3.11 μg • mL^{-1}. Further evidence that this was below the incipient limiting concentration was the lack of pseudofeces production by small mussels. However, our results for large mussels contradict the former study, since we did not find a relationship between *C. reinhardtii* concentration and clearance rate over a range of concentrations up to 15 times greater than those reported (Sprung and Rose 1988), and pseudofeces production did not begin until algal concentrations were more than twice as great as in previous studies.

It is possible that these differences represent population-specific attributes, since these earlier studies were conducted using European populations of zebra mussels, while our measured values are similar to other reports of clearance rates of North American zebra mussels. Clearance rate varied between 0.07 and 0.63 mL • min^{-1} for small mussels (mean length < 0.92 mm) filtering natural seston from Saginaw Bay, Lake Huron (Fanslow *et al.* 1995). For this population, mean clearance across all seasons was between 0.45 and 0.60 mL • min^{-1} except when seston levels were very high in the inner bay during 1992, at which time it was approximately 0.16 mL • min^{-1}. The clearance rates we measured are very comparable to the results from Lake Huron. Our estimates of clearance rates are considerably higher than pumping rates reported for juvenile Lake Erie zebra mussels that fall within the same size range as our small size class (Bunt *et al.* 1993). The higher values we observed can be explained by the use of larger mussels and algal cultures rather than natural seston.

Algal concentration significantly affected clearance rate when mussels were fed *Pandorina morum*, implying that the incipient limiting concentration had been exceeded and that this level should be less than 0.60 μg • mL^{-1}, the minimum value of the incipient limiting concentration reported for *Chlamydomonas* (Sprung and Rose 1988). At *Chlorella* sp. concentrations below 0.64 μg • mL^{-1} (assuming a dry weight of 6.4 x 10^{-6} μg • $cell^{-1}$ (Nalewajko 1966)), a constant clearance rate of 1.67 mL • min^{-1} was measured for 22 mm mussels (Mikheev and Sorokin 1966, cited in Walz 1978). This value declined to 0.17–0.33 mL • min^{-1} for higher algae concentrations, indicating that the incipient limiting concentration was above 0.64 μg • mL^{-1}. A similar study reported clearance rates of 0.89 mL • min^{-1} for 21–25 mm quagga mussels (*Dreissena bugensis*) fed *Chlorella* sp. at concentrations of 0.52 μg • mL^{-1} and 0.16 mL • min^{-1} for concentrations of 6.27 μg • mL^{-1} (Zolotareva *et al.* 1978). In both of these studies, the incipient limiting concentrations appear to be less than 1 μg • mL^{-1}, similar to our estimate for *P. morum* and much less than our estimate for *C. reinhardtii*. Estimates of clearance rate of natural suspended particles were a negative exponential function of particle concentrations between 5 and 80 μg • mL^{-1}, with maximum clearance rates of approximately 2.83 mL • min^{-1} at particle concentrations of less than 10 μg • mL^{-1} (Reeders *et al.* 1989). In this case, the incipient limiting concentration was therefore, less than 5 μg • mL^{-1}. Our calculated clearance rates are comparable to those from previous studies and follow the general pattern of a constant maximum clearance rate up to some threshold level beyond which clearance rate declines as a function of algal concentration. It appears that zebra mussels feeding on *P. morum* reach this threshold at biomass concentrations similar to those fed other algal species, while incipient limiting concentrations for *C. reinhardtii* are higher. This result is consistent with the observation that *C. reinhardtii* is cleared with "maximum efficiency" by zebra mussels (Sprung and Rose 1988).

Mussel size affected the clearance of *Chlamydomonas reinhardtii* but not *Pandorina morum*. Clearance rate increased as a function of size when zebra and quagga mussels were fed *Cryptomonas* sp. (Bunt *et al.* 1993), *Chlorella* sp. (Zolotareva *et al.* 1978, Kryger and Riisgård 1988) and *Nitzschia actinastroides* (Walz 1978). Because the average

size of a *P. morum* colony is considerably larger than the size of individual *C. reinhardtii* cells, the lack of a positive correlation between mussel length and clearance of *P. morum* is not readily explained. Sample sizes (21 small mussels, 25 large mussels) were moderate but variability was quite high (coefficients of variation > 0.50 for each group). This high variability may have obscured any size-related effects. Large mussels were able to clear *C. reinhardtii* at a faster rate than *P. morum* at high algal concentrations, presumably due to higher handling costs associated with the colonial alga. For small mussels, both algal species were cleared at similar rates at high concentrations, but *P. morum* was cleared more rapidly at low concentrations. Particle sizes of both species may be large enough that they have equally great handling costs for small mussels. If this is the case, the number of particles, rather than the algal biomass, will determine clearance rate at low algal concentrations. The smaller numbers of *P. morum* particles at any given biomass concentration may account for the higher clearance rates.

Turbulence created by the pumping action of zebra mussels may inhibit gravitational settling of algae. Thus, a control that does not include turbulence will overestimate the amount of gravitational settling in the experimental chambers and may result in estimates of clearance rate that are less than the actual values. Our use of flagellated green algae should have minimized this problem and indeed, most of the time (72%) gravitational settling was zero in the control chambers.

The production of pseudofeces may be explained as a mechanism for clearing excess particles, or as a means for rejecting certain particle types (Sprung and Rose 1988). In the former case, pseudofeces production should be positively correlated with particle concentration, once a threshold level is crossed. In the latter situation, production of pseudofeces should begin when some minimum concentration of undesirable particles is encountered. In our study, the relationship between proportion of ingested algae converted to pseudofeces and algal concentration was a function of the algal species being filtered. When zebra mussels were fed *Chlamydomonas reinhardtii,* pseudofeces production increased rapidly with increased algal concentration once a threshold level was crossed. This level was higher than the incipient limiting level for *C. reinhardtii* reported in earlier studies (Sprung and Rose 1988). Additional experiments at concentrations below this threshold confirm that pseudofecal production does not occur at these low *C. reinhardtii* concentrations (K.A. Bruner, pers. comm., The Ohio State University, Columbus, OH). These results indicate that pseudofeces production was due to excess particle concentration, especially if one accepts the assertion that pseudofeces production is simply a function of particle concentration when mussels are fed *Chlamydomonas* (Sprung and Rose 1988).

Percent of filtered particles ejected as pseudofeces was constant across algal concentrations when mussels were filtering *Pandorina morum*. This means that total pseudofeces production increased with increasing particle concentration and decreasing clearance rate. This pattern of pseudofeces production by zebra mussels closely resembled that of *Mytilus edulis* L., with a constant proportion of filtered particles being ejected as pseudofeces across algal concentrations (Foster-Smith 1975), although the plateau for *M. edulis* was much higher (70–80% of cleared algae) than that for *Dreissena polymorpha* (22.5%). We conclude that the pattern of pseudofeces production varies with different algal species, but it is not clear whether differences in handling of various algal species is due to size, biological characteristics (such as presence of a gelatinous sheath) of the algal species, or methods employed for particle processing (Ward *et al.* 1993).

In Lake Erie, total phytoplankton abundance in 1985 varied between 0.6 and 1.8 $\mu g \cdot mL^{-1}$ (Makarewicz and Bertram 1991). Throughout most of the growing season, these levels were below those causing pseudofeces production for *C. reinhardtii* and above those for *P. morum*. In 1993, zebra mussels transferred directly from Lake Erie to laboratory containers produced little, if any, pseudofeces (D. Arnott, pers. comm., Miami University, Oxford, OH). It is very likely that pseudofeces production by zebra mussels is low under typical conditions in Lake Erie and that its production varies with seasonal succession of the algal assemblage.

Large mussels at low *Pandorina morum* concentrations and across all *Chlamydomonas reinhardtii* concentrations had similar absorption efficiencies (80–81%). These treatment groups are the only ones for which reasonable numbers of replicates were obtained (6 and 11, respectively). All other groups contained three or fewer replicates and had very high absorption efficiencies. These high values may reflect difficulties in collection and weighing of feces. Absorption efficiencies of around 80% are typical for mussels when feeding on pure algal sus-

pensions (Bayne and Newell 1983). Zebra mussels fed *Nitzschia actinastroides* absorbed only 24.7% of ingested algae (Walz 1978), but this low value may be due to the large amounts of nondigestable silica in diatoms.

Processing of suspended particles by zebra mussels differs for *Chlamydomonas reinhardtii* and *Pandorina morum*. Clearance rates and the threshold for onset of pseudofeces production are higher for *C. reinhardtii* than for *P. morum*. This indicates that the former is a more efficiently processed food item. Evidence for particle size selectivity by zebra mussels is contradictory. Studies have shown zebra mussels to equally prefer algal particles of any size greater than 5μm diameter (Sprung and Rose 1988) or to prefer particles between 20 and 30 μm diameter (Ten Winkel and Davids 1982). Thus, either *C. reinhardtii* and *P. morum* should have been equally preferred or *P. morum* should have been favored because colonies of the latter, although variable, were always greater than 20 μm diameter (20.71 ± 1.40 μm diameter, n = 28), while cells of the former were less than 8 μm diameter (7.41 ± 0.13 μm, n = 67). The mucilaginous sheathes enclosing the colonies of *P. morum* may account for the decrease in clearance rates and low pseudofeces production threshold, since algae with gelatinous layers are less preferred food for zebra mussels (Ten Winkel and Davids 1982). Because clearance and pseudofeces production differ among algal species, it is clear that the net effect of zebra mussels on trophic interactions and contaminant cycling is dependent on the algal assemblage present in the system. Both size structure and species composition of the algal community are important factors.

Ecotoxicological Implications

Zebra mussels have become an important component of aquatic foodchains in several of the Great Lakes because of their prodigious filtering capacities and because their populations constitute a significant fraction of the biomass in these lakes (MacIsaac *et al.* 1992, Dermott *et al.* 1993). In addition to their trophic impacts in the lakes, it is likely that the mussels are influencing the cycling of contaminants such as polychlorinated biphenyls (PCBs) and polynuclear aromatic hydrocarbons (PAHs), which readily sorb to particles including algae (Fisher *et al.* 1993, deKock and Bowmer 1993, Swackhamer and Skoglund 1993). Zebra mussels can affect contaminant cycling in at least two ways. First, the mussels themselves can become contaminated via filtration and assimilation of contaminated particles. Second, contaminated zebra mussel tissue, pseudofeces and fecal products can serve as sources of contamination for higher trophic levels (Bruner *et al.* 1994). Factors which govern the accumulation and distribution of contaminants within the mussel are thus critical to understanding zebra mussel-mediated trophic transfer of contaminants.

The ability of zebra mussels to accumulate hydrophobic contaminants (e.g., PCBs and PAHs) from algal cells has recently been established (Bruner *et al.* 1994). However, the exposure levels of zebra mussels to these chemicals will vary with the medium and factors that affect filtering rates. Our data suggest that large mussels filtering *Chlamydomonas reinhardtii* will experience greater exposure to contaminated algae than smaller mussels at any concentration of *C. reinhardtii*. In contrast, exposure to zebra mussels filtering *Pandorina morum* will be regulated more by the concentration of algae than by the size of the mussel. In addition, exposure of zebra mussels to contaminants sorbed to *P. morum* may be relatively greater than for an equivalent biomass of *C. reinhardtii* since colonies of the former are enclosed within a gelatinous coating which will readily concentrate nonpolar contaminants (Bruno *et al.* 1982). Clearly, realistic estimates of filtering rates using natural algal assemblages will provide more insight into the role of zebra mussels in contaminant cycling.

The processing of filtered algae will also affect the ability of zebra mussels to serve as a source of contaminants for aquatic foodchains. Approximately 20% of filtered *Pandorina morum* biomass is converted to pseudofeces, regardless of the exposure concentration. In contrast, pseudofeces formation from *Chlamydomonas reinhardtii* was concentration-dependent with a threshold value (1.27 $\mu g \cdot mL^{-1}$) below which no pseudofeces were produced. Species-specific differences in the relationship between algal biomass and pseudofeces production is important because concentrations of some PCBs and PAHs increase in pseudofeces relative to the algae that are the source of the pseudofeces (Reeders and Bij de Vaate 1992). Thus, detritivorous invertebrates could experience elevated exposure to these nonpolar contaminants from feeding on pseudofeces and feces. Recent studies have shown that gammarid amphipods that feed upon PCB-contaminated zebra mussel feces have an absorption efficiency of greater than 80% (Bruner *et al.* 1994). Thus, any factor which tends

to increase fecal contamination may dramatically increase exposure of benthic detritivores to hydrophobic chemicals. These increases in benthic exposure would not be anticipated in the absence of zebra mussels, since it is the processing of individual algal particles into highly digestible aggregates (feces and pseudofeces) that makes the algal detritus an attractive food source for benthic detritivores. Realistic hazard assessment must therefore include information about the rates of filtering for different particle types and the subsequent processing of filtered particles by the zebra mussel to gauge the likely effects of zebra mussels on contaminant cycles.

The establishment of the zebra mussel in the Great Lakes has had, and will continue to have, profound ecological consequences. It is clear, however, that size distributions of mussel populations and characteristics of algal assemblages have a significant influence on overall lake particle dynamics. This, in turn, affects how contaminants are distributed and their movement throughout aquatic systems. To better understand contaminant dynamics, future studies should use realistic algal assemblages while accounting for the size structure of mussel populations.

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