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SELECTIVE FEEDING AND BIODEPOSITION BY ZEBRA MUSSELS AND THEIR RELATION TO CHANGES IN PHYTOPLANKTON COMPOSITION AND SESTON LOAD

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ABSTRACT We examined the ability of zebra mussels (*Dreissena polymorpha*) to preferentially ingest or reject various phytoplankton species and nonliving particles. Our objective was to determine if preferential ingestion by zebra mussels could explain the changes observed in the Hudson River since their invasion: (1) decline of cyanobacteria, *Microcystis* in particular, (2) rise to dominance by diatoms, and (3) very small change in total seston load. We found that zebra mussels are capable of efficiently sorting and rejecting particles. Not only were clearance rates higher when the cyanobacterium *Microcystis* was present in suspension, but *Microcystis* was preferentially ingested over almost all other particle types tested. Diatoms were generally rejected as diffuse pseudofeces which were easily resuspended, even in still water. The rejection of cattail (*Typha*) detritus by zebra mussels corresponds to the rejection by oysters (*Crassostrea virginica*) of cord grass (*Spartina*) detritus particles (Ward et al. 1998). Pseudofeces of clay or detritus particle types were also very diffuse. In a few cases, however, clay or detritus particles, rather than phytoplankton cells, were preferentially ingested by zebra mussels. The interaction of selective feeding by zebra mussels with resuspension of diffuse biodeposits by tidal mixing may explain the differential decline of phytoplankton groups and nonliving particles in the Hudson River.

KEY WORDS: Zebra mussels, particle selection, clearance rates

INTRODUCTION

Suspension-feeding organisms, such as bivalves, can influence the function of ecosystems to a great extent. In dense populations, bivalves can dominate total ecosystem metabolism (Murphy and Kremer 1985, Boucher-Rodoni and Boucher 1990, Dame et al. 1992), nutrient cycling (Jordon and Valiela 1982, Dame et al. 1991, Asmus et al. 1995), and grazing of primary producers (Cloern 1982, Officer et al. 1982). Grazing of primary producers moves energy through ecosystems by coupling pelagic and benthic processes; organic materials are removed from suspension and are deposited on the bottom as feces or pseudofeces, or excreted back to the water column (Dame and Patten 1981, Newell and Field 1983, Smaal and Prins 1993). In many estuarine and coastal systems, bivalves effectively control phytoplankton biomass, harvesting up to 100% of the phytoplankton primary production (Carlson et al. 1984, Asmus et al. 1990, Gerritsen et al. 1994).

The introduction and spread of the zebra mussel (*Dreissena polymorpha*) (Pallas) has added a previously absent guild of organisms to North American freshwater ecosystems. Though native bivalves and other organisms certainly contribute to phytoplankton grazing (Strayer et al. 1994, Cahoon and Owen 1996, Caraco et al. 1997), zebra mussels are fouling organisms that can attain extremely high densities and have the capacity to filter large quantities of water (Reeders et al. 1989, Roditi et al. 1996). As a result of their great clearance rates, phytoplankton biomass has decreased by over 60% in many systems in which zebra mussels have become established (Holland 1993, Leach 1993, Fahnenstiel et al. 1995). Phytoplankton biomass in the Hudson River, New York, has dropped by 90% since zebra mussels invaded in 1991 (Caraco et al. 1997). In some systems, phytoplankton composition has also changed since invasion (Heath et al. 1995, Vanderploeg et al. 1996). The Hudson River phytoplankton community has shifted from prevalence of cyanobacteria to diatoms (Smith et al. in press). Despite the massive reduction in phytoplankton biomass in the Hudson River, water transparency has increased by only 12%, owing to the persistence of nonliving particles (Caraco et al. 1997, Strayer et al. in press). This is in contrast to other systems in which transparency has increased by 33–100% (Holland 1993, MacIsaac and Rocha 1995).

Studies on marine bivalves have demonstrated their ability to sort particles based on size (Vahl 1972, Stenton-Dozey and Brown 1992, Defossez and Hawkins 1997) and quality (MacDonald and Ward 1994, Arifin and Bendell-Young 1997, Ward et al. 1997). However, the capacity to sort and preferentially ingest particles varies among bivalve species (Møhlenberg and Riisgård 1978, Prins et al. 1991, Ward et al. 1998). It is evident that drops in phytoplankton biomass are the result of zebra mussel filtration, but it is less clear to what extent zebra mussels are directly responsible for changes in phytoplankton community composition. In this study we examined preferential ingestion by zebra mussels of various Hudson River phytoplankton species and nonliving particles. Our objective was to determine if differential ingestion and rejection by zebra mussels could explain the observed changes in the Hudson River phytoplankton community and the lack of change in turbidity. In addition, we examined the effect of suspension complexity on sorting, and compared selection of phytoplankton species with information on assimilation efficiencies. This is the first study to determine zebra mussel particle preferences by directly examining pseudofecal composition by means of flow cytometry.

MATERIALS AND METHODS

Mussels

Specimens of *Dreissena polymorpha* were collected from the Hudson River at Tivoli, New York, or from the Huron River, Ann Arbor, Michigan. Mussels were maintained in 40 L aquaria at

16°C and fed a daily ration of cultured phytoplankton plus a mixture of preserved diatoms (Diet C, Coast Seafoods, Co., Quilcene, Wash). Partial water changes (ca. 20%) were performed on alternating days; freshwater was prepared according to Sprung (1987).

Particles

Phytoplankton cultures were obtained from the University of Texas Culture Collection and grown in a modified f/2 media (Guillard and Hargraves 1993); working stock solutions were added to distilled water, rather than seawater, resulting in 0 ppt salinity. Cultures were grown at room temperature, under a 16:8 h light and dark regime. Species of phytoplankton that are typically found in the Hudson River were cultured for use in experiments: *Cyclotella meneghiniana* (LB 2455; barrel-shaped, 18 X 6 μm), freshwater-acclimated *Thalassiosira sp.* (LB 2054; barrel-shaped, 15 X 13 μm) (Bacillariophyceae), *Micractinium sp.* (LB 2614; spherical, 6 μm), *Crucigenia tetrapedia* (63; disk-shaped, 5 X 11 μm), *Scenedesmus quadricauda* (LB 614; four cells stacked, total 25 X 10 μm) (Chlorophyceae), and *Microcystis aeruginosa* (LB 2386; spherical, 4 μm) (Cyanophyceae). Cells were measured using an ocular micrometer.

Nonliving particles of detritus and clay were also used in the experiments. Dead cattail (*Typha sp.*) leaves from the previous growing season were collected from a marsh on the Hudson River for use as detrital material. Leaves were washed of debris, and processed in a blender with distilled water for 5 min. The resulting suspension was sieved through a nylon screen to include particles less than 20 μm; 90% of the particles were ≤3.5 μm, as measured by a Coulter Multisizer. Clay suspensions were produced by adding kaolin (hydrated aluminum silicate, Fisher Scientific, Co., Pittsburgh, PA) to distilled water and agitating vigorously. All clay particles were ≤20 μm and 90% of the particles were ≤2.5 μm. Both *Typha* detritus and clay suspensions were made 1 day before use in experiments and were refrigerated overnight.

Particle Selection

A series of particle selectivity experiments was performed. Zebra mussels were scrubbed and allowed to purge themselves for 24 h before experiments. Particle suspensions were prepared by diluting phytoplankton cultures and/or nonliving particle stock solutions with filtered (0.45 μm) Hudson River freshwater to total concentrations of 10^5 particles mL^{-1}. Combinations of two or three particle types were provided in nearly equal proportions. Individual mussels were placed in beakers in 200 mL of the particle suspension. Ten experimental beakers and two or three control beakers, without mussels, were run concurrently. To keep particles homogeneously in suspension, beakers were gently aerated throughout the measurements. The behavior of the mussels, whether open or closed, was carefully monitored. Water samples of 1 mL each were taken at the beginning of the experiments and after 30–90 min. Particle concentrations did not decline below 65% of the starting value. Biodeposits were removed from the beakers as they were produced by the mussels; feces were discarded and pseudofeces were collected for analysis. Following experiments, the mussels were measured, the tissues were removed from the shells, and the tissue dry mass was determined by oven drying at 60°C for 24 h.

The abundance of particle types in water samples and pseudofeces was determined using a FACScan portable flow cytometer (Becton Dickson, San Jose, CA) equipped with a 15 mW, 488 nM argon laser. Samples of both water and pseudofeces were agitated vigorously before analysis to disrupt any aggregations. Phytoplankton cells were differentiated by chlorophyll fluorescence (>650 nm) and phycoerythrin fluorescence (560–590 nm) emissions, forward scatter (a measure of size), and 90° side scatter. Nonliving particles were differentiated from phytoplankton cells based on their lack of pigmentation, as well as forward and side scatter. The volume of sample analyzed was determined gravimetrically.

The proportions of particle types in the samples were determined from the flow cytometry data. To examine the degree of acceptance or rejection of particle types, we calculated a modified electivity index (EI) as follows:

$$EI = -[(P - S) / ((P + S) - (2 * P * S))]$$

where P is the particle ratio in the pseudofeces and S is the particle ratio in the suspension (Jacobs 1974, Bayne et al. 1977). Electivity index can range from −1.0 to 1.0. A positive EI for a given particle type indicates preferential ingestion (depletion of the particle type in the pseudofeces compared with the suspension), and a negative EI indicates rejection (enrichment of the particle type in the pseudofeces compared with the suspension). Electivity indices were compared with zero using a one-sample, two-tailed, nonparametric Wilcoxon signed-rank test. These analyses test the null hypothesis that electivity of a particular particle type is equal to zero (no sorting).

To better illustrate the efficiency of particle selection, sorting efficiency (Iglesias et al. 1992, MacDonald and Ward 1994) was calculated:

$$SE = 1 - (P/S)$$

This index, which ranges from 0 to 1, represents the percentage enrichment or depletion of a particle type in the pseudofeces compared with the suspension.

Clearance Rates

Particle depletion data from the above selectivity experiments were used to calculate clearance rates ($mL\ h^{-1}$). Some clearance rates were determined separately from the selectivity experiments. These experiments were conducted in the same manner as the selectivity experiments except as follows. Fifteen experimental beakers and three control beakers were run concurrently. Feces and pseudofeces were removed from the beakers as they were produced by the mussels; both were discarded. The abundance of particles in the water samples was determined using a Coulter Multisizer II, equipped with a 75 μm aperture tube, and set to draw 500 μL. Samples were diluted with electrolyte solution and gently agitated. Counts were corrected for dilution and background count.

Particle depletion data from either the flow cytometer or Coulter Multisizer was used to calculate clearance rates according to Coughlan (1969). Clearance rates were corrected for particle abundance changes in the controls and for the time that each mussel was open. Clearance rates were standardized to a 15 mg dry tissue mass (corresponding to a mussel of approximately 20 mm in length) using the allometric exponent for bivalves of 0.88 (Kryger and Riisgård 1988).

Analyses of variance were performed for groups of experiments with at least one common particle type to test the null hypotheses that there were no effects of particle combination on clearance rates. If a null hypothesis was rejected, Dunnett's multiple comparison test was used to identify specific two-particle

clearance rates that differed from the clearance rate of the common particle alone. Statistical analyses were conducted using JMP version 3.1.6 software (SAS Institute Inc. 1994). A significance level of 0.05 was used.

RESULTS

Particle Selection

At the end of all experiments, proportions of provided particles were not significantly different in the experimental beakers with zebra mussels than they were in control beakers. This indicates that zebra mussels removed different particle types and particle sizes from suspension with equal efficiency. Analyses of pseudofeces, however, showed that zebra mussels sort particles for rejection or ingestion once they have entered the mantle cavity, on the gills and/or labial palps. Most particle combinations tested resulted in significant EIs (Fig. 1). Though there was a tendency for smaller particles to be accepted for ingestion over larger particles, this was not always the case (Fig. 1).

The cyanobacterium, *Microcystis,* was preferentially ingested over nearly all other particles (Fig. 1C). Sorting efficiencies indicate that pseudofeces were depleted of *Microcystis* by up to 67%, compared with the suspension. There was no sorting between clay and *Microcystis* (Fig. 1C).

Zebra mussels generally rejected species of green phytoplankton with larger cell sizes. *Scenedesmus* was rejected in favor of other particles (Fig. 1C, 1F). *Crucigenia* was rejected in favor of *Microcystis* and nonliving particles (Fig. 1D), although there was no sorting between *Crucigenia* and a smaller green, *Micractinium,* or a diatom, *Thalassiosira* (Fig. 1D). *Micractinium* was rejected in favor of *Microcystis* (Fig. 1C) but was preferentially ingested over a large diatom, *Cyclotella* (Fig. 1F).

Diatoms were either rejected or there was no sorting between them and other particles (Fig. 1E, 1F). Only *Scenedesmus* was rejected in favor of a diatom (Fig. 1F). *Thalassiosira* was rejected in favor of *Microcystis* (Fig. 1E), and there was no sorting between *Thalassiosira* and *Crucigenia* (Fig. 1D), or the larger diatom, *Cyclotella* (Fig. 1E). *Cyclotella* was rejected in favor of *Microcystis* and *Micractinium,* and the degree of rejection relative to *Typha* detritus was nearly significant as well ($p = .062$) (Fig. 1F). There was no sorting between *Cyclotella* and clay particles (Fig. 1F).

Phytoplankton cells were not always preferentially ingested over nonliving particles (Fig. 1A, 1B). Clay particles were preferentially ingested over *Crucigenia,* and there was no sorting between clay and *Microcystis* or *Cyclotella* (Fig. 1A). *Typha* detritus was rejected in favor of *Microcystis,* but was preferentially ingested over *Crucigenia,* and nearly significantly accepted over *Cyclotella* (Fig. 1B).

The sign (either positive or negative) and magnitude of the electivity index for a given particle type depended on the complexity of the suspension. For example, in paired suspensions, *Microcystis* was preferentially ingested over both diatoms *Thalassiosira* and *Cyclotella* (Fig. 1C), and there was no sorting between the two diatoms when paired with each other (Fig. 1E, 1F). In suspensions of these three particle types together, however, the EI for *Cyclotella* shifted to positive (acceptance) (Fig. 2A). Similar shifts from significant rejection to acceptance (although not significant) occurred for *Micractinium* (Fig. 2B) and for *Crucigenia* (Fig. 2C) in suspensions with *Microcystis* and *Scenedesmus.*

During experiments, we also observed the consistency and integrity of pseudofeces. Pseudofeces consisting mainly of large green cells were ejected as compact balls that remained intact for long periods of time, min to h. Pseudofeces consisting mainly of diatoms or clay particles were ejected as diffuse, nondiscrete masses from the inhalent siphon, or were ejected as a particulate cloud from the byssal gape. These types of pseudofeces dispersed into the water column within a few sec, even in still water. Cultures were successfully started from the resuspended cells.

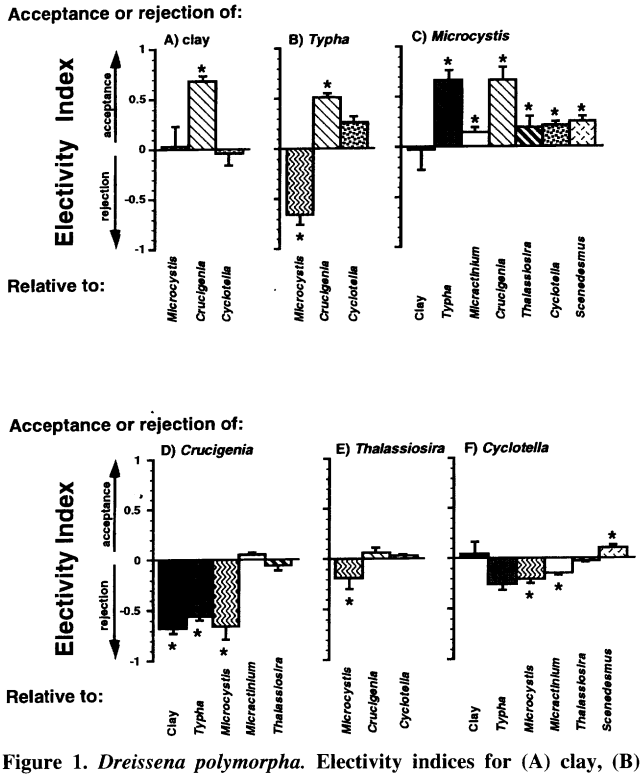

Figure 1. ***Dreissena polymorpha.*** **Electivity indices for (A) clay, (B)** ***Typha*** **detritus, (C)** ***Microcystis,*** **(D)** ***Crucigenia,*** **(E)** ***Thalassiosira,*** **and (F)** ***Cyclotella*** **relative to particle types listed across the bottom. Particle types are listed in order of ascending size. A positive EI indicates selection of the particle type in the heading. A negative EI indicates a rejection of the particle type in the heading (and therefore selection of the particle type listed on the bottom).* Indices significantly different than zero ($p < .05$). (Means ± SE, n = 10).**

Clearance Rates

The clearance rate of *Microcystis* alone was greater than that of the other single-particle type suspensions (Fig. 3). Total clearance rates of suspensions with different particle types combined also differed (Fig. 3A–F), even though relative clearance rates of the individual particle types within a given suspension did not (as shown by no significant change in suspended particle proportions). Total clearance rates appeared to be unrelated to the desirability of the individual particle types in suspension. For example, although *Thalassiosira,* and especially *Typha,* were rejected when paired with *Microcystis* (Fig. 1C), clearance rates for suspensions of these particles with *Microcystis* were not less than that of *Microcystis* alone (Fig. 3C). Clearance rates of combinations of particle types were generally equal to or less than that of the common particle types alone (Fig. 3A–D). Diatoms were an exception to this, however. Addition of *Microcystis* to suspensions of *Thalassiosira,* and addition of *Micractinium* or clay to suspensions of *Cyclotella,*

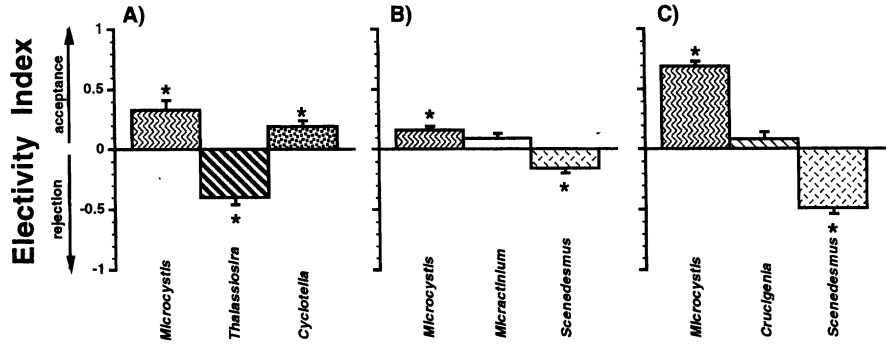

Figure 2. *Dreissena polymorpha.* **Electivity indices for individual particle types in suspensions of three particle types. A positive EI indicates selection of the particle type, a negative EI indicates a rejection of the particle type. Suspensions of (A)** *Microcystis, Thalassiosira,* **and** *Cyclotella,* **(B)** *Microcystis, Micractinium,* **and** *Scenedesmus,* **and (C)** *Microcystis, Crucigenia,* **and** *Scenedesmus.** **Indices significantly different than zero ($p < .05$). (Means ± SE, n = 10).**

increased clearance rates above that of the diatoms alone (Fig. 3E, 3F).

DISCUSSION

Our study is the first to determine zebra mussel selection of phytoplankton species by directly examining pseudofeces by means of flow cytometry. We found that zebra mussels are capable of efficiently sorting particles. Our results are consistent with the changes in phytoplankton community composition that have occurred in the Hudson River estuary since invasion by the zebra mussel. The main phenomena in need of explanation were (1) the decline of cyanobacteria, *Microcystis* in particular, (2) the rise to dominance by diatoms, and (3) the very small change in total seston load, which is dominated by clay particles. The interaction of selective feeding by zebra mussels with resuspension of diffuse biodeposits by river mixing, due in part to tidal forces, may explain the differential decline in phytoplankton groups that has occurred in the Hudson River.

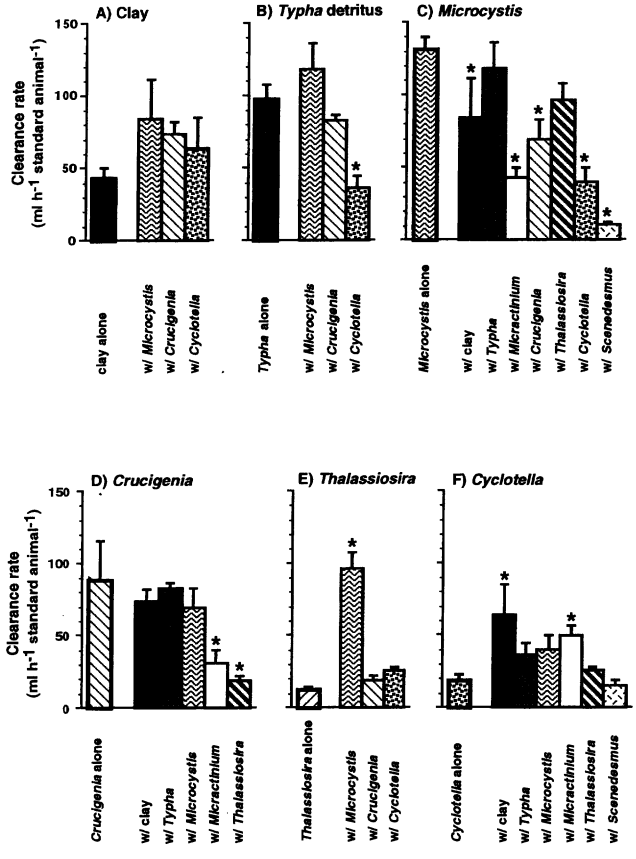

Figure 3. *Dreissena polymorpha.* **Clearance rates of single-particle type suspensions and pairs of particle types, standardized to an animal of 15 mg dry tissue mass. Clearance rates of combination suspensions were compared with those of the common particle types alone: (A) clay, (B)** *Typha* **detritus, (C)** *Microcystis,* **(D)** *Crucigenia,* **(E)** *Thalassiosira,* **and (F)** *Cyclotella.** **Clearance rates significantly different than the common particle type alone ($p < .05$). (Means ± SE, n = 15).**

Before invasion of the Hudson River by zebra mussels, colonial and single-celled cyanobacteria, especially *Microcystis aeruginosa* and *Microcystis* sp., often reached summer bloom densities of over 10^7 cells L^{-1} (Howells and Weaver 1969, Marshall 1988). Since then, cyanobacteria have nearly disappeared from the river (Smith et al. in press), decreasing from 36 to 4% of the total number of cells (Marshall 1988, Smith et al. in press). Similarly, Noordhuis et al. (1992) documented the absence of cyanobacteria blooms in Dutch ponds following zebra mussel stocking. Consistent with the disappearance of cyanobacteria from the Hudson River and from the Dutch ponds, we found that not only were zebra mussel clearance rates higher when *Microcystis* was present in suspension, but also that *Microcystis* was preferentially ingested over almost all other particle types tested. Our results corroborate those of other workers. Bastviken et al. (1998) indirectly measured selection in short-term microcosm experiments by comparing gross (no resuspension of feces and pseudofeces) and net (feces and pseudofeces resuspended) clearance rates for different phytoplankton. They found that single-celled *Microcystis* is among those phytoplankton cleared most efficiently from Hudson River water by zebra mussels.

In some lake systems, however, zebra mussels are reported to promote *Microcystis* blooms (Vanderploeg et al. 1996) or have no effect on *Microcystis* abundance (Lavrentyev et al. 1995), suggesting that *Microcystis* is not a preferred food. Blooms of cyanobacteria have been observed in Lake Erie, Saginaw Bay, and Oneida Lake since zebra mussels invaded (Health et al. 1995, MacIsaac 1996, Vanderploeg et al. 1996), and microcosm experiments in Saginaw Bay show that zebra mussels have no effect on the abundance of *Microcystis* (Lavrentyev et al. 1995). In these cases, there may be mechanical or chemical inhibition of clearance of *Microcystis* by zebra mussels. For example, *Microcystis* in Saginaw Bay is primarily in the form of large, gelatinous colonies (Lavrentyev

et al. 1995) which appear to mechanically disturb filtering in some bivalves (Kamermans 1992, Smaal and Twisk 1997). In addition, some strains of *Microcystis aeruginosa* are toxic to bivalves, zooplankton, and fish, causing mortalities or reduced feeding activity (Birger et al. 1978, Keshavanath et al. 1994, Shaw et al. 1997). However, we have found that clearance rates of a toxic strain of single-celled *Microcystis* (LB 2385) were no different from those of a nontoxic strain (LB 2386) (Baker and Levinton unpublished data). It is unclear what proportion of *Microcystis* in the Hudson River occurred as colonies or was toxic, prior to the zebra mussel invasion.

Total phytoplankton cell densities have decreased since the invasion of the Hudson River by zebra mussels, but the proportion of diatoms has increased from 14 to 76% of the total number of cells (Marshall 1988, Smith et al. in press). Species of diatoms appear to have been affected unequally; there was a tendency for smaller genera to decline in relative abundance whereas larger diatom genera were unchanged or increased (Smith et al. in press). We found that diatoms were generally excluded from ingestion and rejected as diffuse pseudofeces. In addition, clearance rates for suspensions with diatoms, especially *Cyclotella,* were lower than those for other suspensions. Bastviken et al. (1998) also found that diatoms were cleared at net rates lower than those of other phytoplankton. These observations are consistent with the increase in relative diatom abundance in the Hudson River since the zebra mussel invasion.

Though less dramatic than the relative increase in diatoms, the proportion of green phytoplankton has also increased in the Hudson River (Smith et al. in press) from 2 to 5% since zebra mussels invaded (Marshall 1988, Smith et al. in press). Again, smaller cells tended to decline, while larger cells, such as *Scenedesmus,* increased in relative abundance (Smith et al. in press). In our study, zebra mussels generally rejected larger species of green phytoplankton from ingestion. For example, *Scenedesmus* was always rejected and clearance rates were very low when suspensions included this species. Preliminary rejection of particles such as *Scenedesmus* appears to take place on the gills, before reaching the labial palps. Using endoscopic examination and video recording, we have observed that when zebra mussels are fed *Scenedesmus* and *Microcystis* together, *Scenedesmus* moves toward the labial palps in a mucus string above the ventral food groove, while *Microcystis* moves deep within the groove and, presumably to the mouth (Baker et al. 1998).

There has been very little change in the amount of nonphytoplankton material in the Hudson River since the invasion of zebra mussels (Caraco et al. 1997). The concentration of suspended particulate matter, such as silt and detritus, is only 15% lower than the average annual load of 20 mg L^{-1} (Cole et al. 1991, Caraco et al 1997, Strayer et al. in press), compared to a drop in phytoplankton biomass of 90% (Caraco et al. 1997). Given this, we might expect that such particles are not removed from suspension by zebra mussels. However, we found that zebra mussels removed different particle types and particle sizes, including clay and detritus, from suspension with equal efficiency, as indicated by the lack of change in suspended particle proportion. This is not surprising, given that zebra mussels retain even 1 μm particles with greater than 90% efficiency (Sprung and Rose 1988, Roditi et al. 1996, Baker and Levinton, unpublished data). In a few cases, clay or detritus particles, rather than phytoplankton cells, were preferentially ingested by zebra mussels. We observed that pseudofeces of detritus, and especially clay particles, were easily resuspended, even in still water. This, combined with the vigorous tidal flow of the Hudson estuary, would explain the modest drop in seston concentrations.

The changes that have taken place in the Hudson River—disappearance of cyanobacteria, increase in relative abundance of diatoms, and lack of change in turbidity—are not always typical of systems invaded by zebra mussels. For example, in Lake Erie, there has been a proportional decline in all major groups of phytoplankton (Nicholls and Hopkins 1993). In lakes and slow-moving rivers, there have been concomitant drops in turbidity, resulting in transparency increases of from 33 to 100%, presumably due to removal of clay and detritus from the water column (Holland 1993, MacIsaac and Rocha 1995). These proportional declines in particle types are consistent with observations that zebra mussels do not preferentially remove particles from suspension (Roditi et al. 1996, Bastviken et al. 1998). What then, is the underlying cause of the disproportional changes in the Hudson River? It appears that the Hudson River is sufficiently turbulent and tidally mixed to resuspend bottom material (Cole et al. 1992, Caraco et al. 1997). Therefore, particles deposited on the bottom as feces or pseudofeces are likely to be resuspended to the water column. We found that large diatoms and nonliving particles were generally rejected and that pseudofeces consisting of the these particles were very diffuse. Biodeposits of this type would be particularly susceptible to resuspension. Our study helps explain why diatoms have become the dominant phytoplankton in the Hudson River, why there has been very little change in turbidity, and why cyanobacteria, which is preferentially ingested, has disappeared since the invasion of zebra mussels.

In our study, selectivity of phytoplankton species differed, depending on the complexity of the offered suspension. For example, *Cyclotella* was preferentially ingested relative to *Thalassiosira* in combinations of three particle types, but was not preferentially accepted when paired with *Thalassiosira* only. This implies that the phytoplankton assemblage that exists before invasion is important in determining the effects that zebra mussels will have on future phytoplankton species composition. Therefore, we might expect different trajectories of phytoplankton populations in different water bodies, depending on the starting conditions. When modeling the effects of bivalve grazing on phytoplankton species composition in a given body of water, it may be necessary to include contextual selectivity measurements, as well as species-specific phytoplankton growth rates.

Our results show a general hierarchy of selectivity for nonliving particles and phytoplankton species, modulated by the specific composition of the phytoplankton species presented to the mussels. The rejection of *Typha* detritus by zebra mussels corresponds to the rejection by oysters of cord grass (*Spartina*) detritus as particles of relatively little nutritive content (Ward et al. 1998). Clay particles were ingested to a surprising degree. Previous studies (Sornin et al. 1988, Gatenby et al. 1996) show that clay may enhance bivalve growth and this may apply to zebra mussels as well.

The hierarchy of selectivity might be expected to correspond to assimilation efficiency, but few data exist to test this hypothesis. Unpublished data (H. Roditi, personal communication) show the following order of assimilation efficiency for zebra mussels: *Microcystis* > *Thalassiosira* > *Chlorella.* If we assume that selectivity of *Chlorella* is similar to our results for other green phytoplankton, then the order of assimilation efficiency corresponds generally to

our order of selectivity by *D. polymorpha*. This provides evidence that selectivity does have a reward in the degree of assimilation.

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