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Selective feeding by three native North American freshwater mussels implies food competition with zebra mussels

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Abstract

We examined the ability of three species of native North American freshwater mussels (*Margaritifera margaritifera*, *Amblema plicata*, and *Pyganodon cataracta*) to preferentially ingest or reject various phytoplankton species and nonliving particles. Our objective was to: (1) determine the particle preferences of the native mussels, (2) determine whether native mussels are able to differentiate between nutritious and less nutritious particles, and (3) compare sorting abilities and particle preferences to those of the invasive zebra mussel (*Dreissena polymorpha*). Native mussels selected and preferentially ingested the unicellular cyanobacteria *Microcystis* over most other phytoplankton species. However, despite their ability to select between phytoplankton, they did not select against cattail (*Typha*) detritus. Our results suggest that native mussels (1) prefer particles (*Microcystis*) that may no longer be abundant in some systems, such as the Hudson River, (2) must compete with zebra mussels for the same preferred food types (*Microcystis*), and (3) are unable to differentiate between nutritious (phytoplankton) and less nutritious (*Typha* detritus) particles. We suggest that native mussels must compete with zebra mussels for many of the same food types and are less efficient than zebra mussels at differentiating between nutritious and less nutritious particles. This indicates that there is an additional mechanism, other than direct physical interference, contributing to native mussel mortalities following zebra mussel invasions.

Introduction

The introduction and spread of zebra mussels (*Dreissena polymorpha*) (Pallas) throughout the eastern United States and Canada has caused major biotic and abiotic changes in freshwater ecosystems (MacIsaac, 1996). Zebra mussels can reach extremely high densities and are very efficient filter feeders (Reeders et al., 1989; Roditi et al., 1996; Baker et al., 1998), reducing phytoplankton biomass by as much as 90% (Holland, 1993; Leach, 1993; Fahnensteil et al., 1995; Caraco et al., 1997). In addition, zebra mussels are capable of efficiently sorting particles for ingestion (Baker et al., 1998), and may be responsible for the shifts in phytoplankton community structure that some systems have experienced (Heath et al., 1995; Vanderploeg et al., 1996). In the Hudson River, for example, the phytoplankton community has shifted from prevalence of the cyanobacterium *Microcystis* to dominance by diatoms (Smith et al., 1998), and despite a reduction in phytoplankton biomass, nonliving particles have persisted (Caraco et al., 1997; Strayer et al., 1999). Selective feeding by zebra mussels, especially for *Microcystis*, in combination with resuspension of diatoms, clay, and detrital material from feces and pseudofeces, can explain the changes that have taken place in the Hudson River (Baker et al., 1998; Bastviken et al., 1998).

Populations of native North American mussels (Family Unionidae) have been in decline over the last

several decades owing to habitat destruction, loss of fish hosts, and exploitation (Bogan, 1993). The introduction of zebra mussels poses another threat to native mussels, including many federally listed species. Species-specific declines in condition and increases in mortality rates of native mussels have been dramatic and well documented for many bodies of water since zebra mussels became established (Gillis & Mackie, 1994; Nalepa, 1994; Strayer & Smith, 1996). Zebra mussels attach byssally to hard surfaces, including the shells of native mussels, and the interference of attached zebra mussels with feeding and movement has been proposed as the cause of native mussel mortalities (Mackie, 1991; Schloesser & Kovalak, 1991). In contrast, native mussel mortalities can occur even when actual attachment of zebra mussels to native mussels is light or absent. In the St. Lawrence River, declines in native mussel populations have been associated with mean infestation rates of as few as 10 zebra mussels per native mussel (Ricciardi et al., 1996). In the Hudson River, where densities of native mussels had dropped by 36–90%, only 30% of the native mussels were infested (Strayer & Smith, 1996). These observations indicate that some mechanism, in addition to direct physical interference, is involved in native mussel mortalities.

We offer the following hypotheses: (A) zebra mussels effectively compete with native mussels for the same food types; and (B) as a result of zebra mussel filtering activities, phytoplankton communities have shifted to particles that are either undesirable to native mussels or are of low food quality. In this study, we (1) examine the ability of three native North American freshwater mussels to sort food particles, (2) determine their particle preferences, and (3) compare particle preferences among the three species of native mussel and zebra mussels.

Methods

Mussels

Specimens of freshwater mussels were collected from a variety of locations: 10 specimens of *Margaritifera margaritifera* (Linneaus), were collected from Peach Brook, Newberry, Vermont, in June, 1998; 15 specimens of *Amblema plicata* (Say) were collected from the Sunrise River, a tributary of the St. Croix River, Minnesota, in August 1998; and 10 specimens of *Pyganodon cataracta* (Say) were collected from Big Fresh Pond, Long Island, New York, in October 1998. Specimens of *M. margaritifera* used in the experiments were between 21 and 78 g total wet mass (shell included); *A. plicata* between 198 and 364 g; and *P. cataracta* between 21 and 85 g. Due to the declining and threatened status of freshwater mussel populations, the same mussel specimens were used repeatedly in experiments, through June 1999. Mussels were maintained in a 350-l recirculating system at 21 °C and were provided with a sand substrate in which to burrow. Mussels were fed a daily ration of cultured phytoplankton and preserved diatoms (Diet C, Coast Seafoods, Co., Bellevue, Wash). Mussels remained healthy over the 8 – 12 month period as indicated by (1) mussel wet weights did not change significantly and some mussels increased in weight, (2) clearance rates for a 'control' particle suspension of *Crucigenia* did not change significantly over time, and (3) there were few deaths. Prior to experiments, mussels were scrubbed of fouling materials and starved for 24 h. Sample sizes varied depending on number of mussels collected, the number of mussels open and feeding during a particular experiment, and the cell count of the cultured phytoplankton available. Zebra mussel data presented here for comparative purposes are from Baker et al., 1998.

Particles

Phytoplankton cultures were obtained from the University of Texas Culture collection and grown in freshwater enrichment medium WCL1 (Guillard, 1983; Guillard & Hargraves, 1993). Cultures were grown at 22 °C, under a 16:8 h light:dark regime. Species of phytoplankton cultured for use in the experiments included: *Microcystis aeruginosa* (LB 2386; spherical, 4 μm) (Cyanophyceae), *Micractinium* sp. (LB 2614; spherical, 6 μm), *Crucigenia tetrapedia* (63; disk-shaped, 5 $\times$ 11 μm), and *Scenedesmus quadricauda* (LB 614; four cells stacked, total 25 $\times$ 10 μm) (Chlorophyceae), and *Cyclotella meneghiniana* (LB 2455; barrel-shaped, 18 $\times$ 16 μm) (Bacillariophyceae). Cells were measured using an ocular micrometer.

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 remove particles greater than 20 μm; 90% of the particles in the de-

trital suspension were $\leq$3.5 μm, as measured by a Coulter Multisizer. *Typha* detritus stock suspensions were made 1 day before use and were refrigerated overnight.

Particle selection

A series of experiments was performed, comparing selection for the cyanobacterium *Microcystis aeruginosa* against selection for other particles common to the Hudson River. We chose *Microcystis* as a constant particle type because (1) it was prevalent in the Hudson River prior to zebra mussel invasion, and (2) zebra mussels preferentially ingest unicellular *Microcystis* over almost all other particle types (Baker et al., 1998). Particle suspensions were prepared by diluting phytoplankton cultures and/or detrital particle stock solutions with filtered (0.45 μm) water to total concentrations of 10^5 particles ml^{-1}. Combinations of two particle types were provided in nearly equal proportions. Individual mussels were placed in jars containing 3000 ml of the particle suspension. No sediment for burrowing was provided. To keep particles homogeneously in suspension, jars were gently aerated throughout the measurements. Experiments were conducted in a dimly lit room. 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 were not allowed to decline below 50% of the starting value. Biodeposits were removed from the jars as they were produced by the mussels; feces were discarded and pseudofeces were collected for analysis. Three control jars, without mussels, were run concurrently.

Abundances of the two particle types in the water samples and the pseudofeces were 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 from each other by chlorophyll fluorescence (>650 nM) and phycoerythrin fluorescence (560–590 nm) emissions, forward scatter (a measure of size), and 90° side scatter. Nonliving particles (*Typha* detritus) were differentiated from phytoplankton cells based on their lack of pigmentation. The volume of sample analyzed was determined gravimetrically.

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

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

Where P is the proportion of the particle of interest in the pseudofeces (abundance of particle A/total particle abundance) and S is the proportion of the particle of interest in the suspension (abundance of particle A/total particle abundance) (Jacobs, 1974; Bayne et al., 1977). The electivity index can range from –1.0 to 1.0; a positive EI for a given particle type indicates that it is preferentially ingested (particle type is depleted in the pseudofeces, compared to suspension), a negative EI indicates rejection (particle type is enriched in the pseudofeces compared to suspension), and zero indicates the absence of active selection. Electivity indices were compared to zero using one-sample, two-tailed, nonparametric Wilcoxon signed-rank tests to test the null hypothesis that electivity of a particular particle type was equal to zero (no sorting).

Sorting efficiency was calculated to better illustrate the efficiency of particle selection (Iglesias et al., 1992; Macdonald & Ward, 1994):

$$SE = 1–(P/S)$$

Sorting efficiency represents the percentage of depletion of a particle type in the pseudofeces compared with the suspension.

Clearance rates

Particle depletion data from the selectivity experiments were used to calculate clearance rates (ml h^{-1}). In addition, clearance rates were also determined for suspensions of single-particle types. In both types of experiments, biodeposits were immediately removed to prevent resuspension. Therefore, the clearance rate referred to here represents gross clearance rate (removal from suspension by both ingestion and pseudofeces production), rather than net clearance rate (pseudofeces allowed to become resuspended, permanent removal by ingestion only). In suspensions of two particle types, clearance rate refers to total clearance rate and includes both particle types.

The abundance of particles in the water samples was determined using a Coulter Multisizer II, equipped with a 100 μm aperture tube (see http://www.beckmancoulter.com). Samples were diluted with electrolyte solution and gently agitated. Counts were corrected for dilution and background

count. Clearance rates were calculated according to Coughlan (1969). Rates were corrected for particle abundance changes in the controls and for the time that each individual mussel was open. Clearance rates were standardized to a dry mass of 2 g using the allometric exponent for freshwater bivalves of 0.88 (Kryger & Riisgärd, 1988). A dry mass of 2 g represents the mean dry mass of the mussels used in these experiments; therefore, clearance rates are standardized to approximately one individual mussel. *Dreissena* data shown were standardized to an animal of 15 mg.

Two analyses of variance were performed for each mussel species to test the null hypotheses that there were no effects of particle type or particle combination on clearance rates. If a null hypothesis was rejected, Dunnett's multiple comparison test was used to identify specific clearance rates that differed from the clearance rate of *Microcystis* alone. Statistical analyses were conducted using JMP version 3.2.6 software (SAS Institute Inc., 1999). A significance level of 0.05 was used.

Results

Particle selection

At the end of the experiments, proportions of particles were no different in the experimental jars with native mussels than they were in control jars. This indicates that the native mussels removed particles of different types and sizes from suspension with equal efficiency. Analyses of pseudofeces, however, revealed that all three native species sort particles for ingestion or rejection once the particles have been removed from suspension. Most particle combinations tested resulted in significant EIs (Fig. 1A–C).

The native mussels preferentially ingested the unicellular cyanobacterium, *Microcystis*, over nearly all other particles (Fig. 1A–C). Sorting efficiencies indicate that pseudofeces were depleted of *Microcystis* by up to 54%, compared with the suspension. However, there was no significant sorting between *Microcystis* and *Typha* in *M. margaritifera*, *A. plicata*, or *P. cataracta* (Fig. 1A–C). In addition, *P. cataracta* showed no significant sorting between *Microcystis* and the similarly sized green phytoplankton, *Micractinium* (Fig. 1C).

The native mussels generally strongly rejected (EI = 0.4) species of green phytoplankton with larger cell sizes, such as *Crucigenia* and *Scenedesmus*, in favor of unicellular *Microcystis* (Fig. 1A–C). A smaller green, *Micractinium* was weakly (EI = 0.25) rejected in favor of *Microcystis* by all three species of native mussel (Fig. 1A–C). *M. margaritifera* and *P. cataracta* significantly rejected the diatom, *Cyclotella*, in favor of *Microcystis* (Fig. 1A, C). *A. plicata*, however, strongly rejected *Microcystis* in favor of *Cyclotella* (Fig. 1B). As indicated above, phytoplankton cells were not preferentially ingested over nonliving vascular plant detrital particles (Fig. 1A–C); in all three native species, there was no significant sorting between *Typha* detritus and unicellular *Microcystis*.

During experiments, we observed the consistency and integrity of pseudofeces, as well as the location of expulsion. Pseudofeces consisting primarily of *Typha* detritus, *Micractinium*, or *Cyclotella*, were generally ejected from the pedal gape, rather than from the inhalent siphon. This was especially true for specimens of *M. margaritifera* and *P. cataracta*. Pseudofeces of *Typha* detritus or the small green phytoplankton, *Micractinium*, emerged as narrow mucus strings. Pseudofeces of the green, *Crucigenia*, emerged as compact balls, while those of the large green, *Scenedesmus*, emerged as voluminous mucus strings. These pseudofeces were particularly dense, remaining intact for min to h. Pseudofeces consisting primarily of the diatoms *Cyclotella* or *Thalassiosira* sp. (LB 2054; barrel-shaped, 15 $\times$ 13 μm) also emerged as voluminous mucus strings but their consistency was more diffuse.

Clearance rates

Relative clearance rates of single-particle type suspensions appeared to differ within and between mussel species. However, only clearance rates of three of the particle types differed significantly from those of *Microcystis* suspensions (Fig. 2A–C). In *M. margaritifera*, clearance rates of single-species suspensions of the diatom *Cyclotella* and the large green *Scenedesmus*, were significantly lower than those of *Microcystis* (Fig. 2A). *P. cataracta* also cleared *Scenedesmus* at rates significantly lower than those of *Microcystis* suspensions (Fig. 2C). In *A. plicata*, the clearance rates of *Typha* detritus suspensions were significantly greater than those of *Microcystis* suspensions (Fig. 2B). All other single-particle type clearance rates were not significantly different than those of *Microcystis* suspensions (Fig. 2A–C).

Total clearance rates of suspensions of two particle types combined also appeared to differ between and within mussel species (Fig. 3A–C). Relative clearance

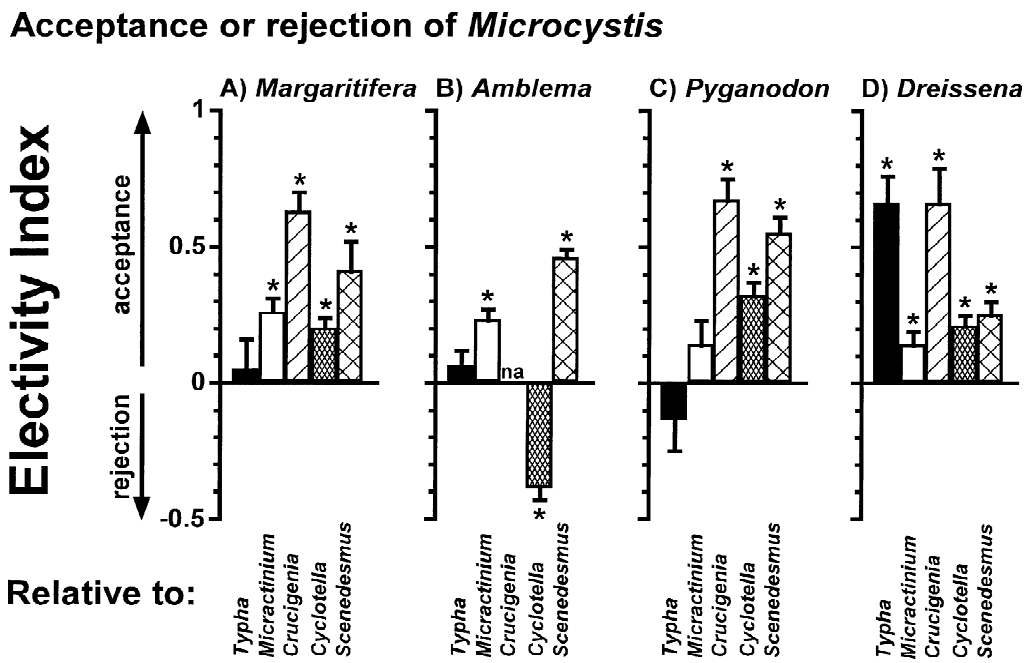

Figure 1. Electivity indices for the blue-green *Microcystis*, relative to the particles listed across the bottom, by the bivalves (A) *Margaritifera margaritifera*, (B) *Amblema plicata*, (C) *Pyganodon cataracta*, and (D) *Dreissena polymorpha* (Baker et al., 1998). Particle types are listed in order of ascending size. A positive EI indicates selection of *Microcystis* relative to the particle type listed on the bottom. A negative EI indicates a rejection of *Microcystis* and therefore selection of the particle type listed on the bottom. * Indices significantly different than zero ($p < 0.05$).

rates of the individual particle types within a given combination suspension, however, did not differ (no significant change in suspended particle proportions, indicating no selective retention prior to pseudofeces formation on the gills/palps). Only clearance rates for three of the combination suspension types differed significantly from those of *Microcystis* alone. In *M. margaritifera*, addition of the small green *Micractinium*, the diatom *Cyclotella*, or the large green *Scenedesmus*, to suspensions of *Microcystis*, significantly lowered total clearance rates (Fig. 3A). *P. cataracta* also cleared suspensions of *Scenedesmus* and *Microcystis*, combined, at a significantly lower rate than suspensions of *Microcystis* alone (Fig. 3C). Clearance rates of all other particle type combinations were not significantly different than those of *Microcystis* alone.

Total clearance rates appeared to be unrelated to the desirability of the particle types, as measured by selectivity indices comparing mixed food types in suspension and in the pseudofeces. For example, although *Crucigenia* was strongly rejected by *P. cataracta* when paired with *Microcystis* (Fig. 1C), total clearance rates for suspensions of *Crucigenia* and *Microcystis*, combined, were no less than that of *Microcystis* alone (Fig. 3C). In addition, the three native mussel species differed in their response to particle suspensions. For example, all three species strongly rejected *Scenedesmus* when paired with *Microcystis* (Fig. 1A–C), however, only in *M. margaritifera* and *P. cataracta*, were total clearance rates for suspensions of *Scenedesmus* and *Microcystis*, combined, significantly lower than those of *Microcystis* alone (Fig. 3A, C).

Discussion

We examined the particle sorting abilities and ingestion preferences of three species of native North American freshwater mussels and compared them to those of the zebra mussel, *Dreissena polymorpha,* under identical controlled conditions. Native mussels were capable of sorting particles and, under experimental conditions, native mussels and zebra mussels preferred similar food types, preferentially ingesting *Microcystis* (4 μm) over most other phytoplankton species ($\geq$6 μm). However, despite their ability to select between phytoplankton, the native mussels that we examined did not select against *Typha* detritus ($\leq$3.5 μm). Our results are consistent with the hypo-

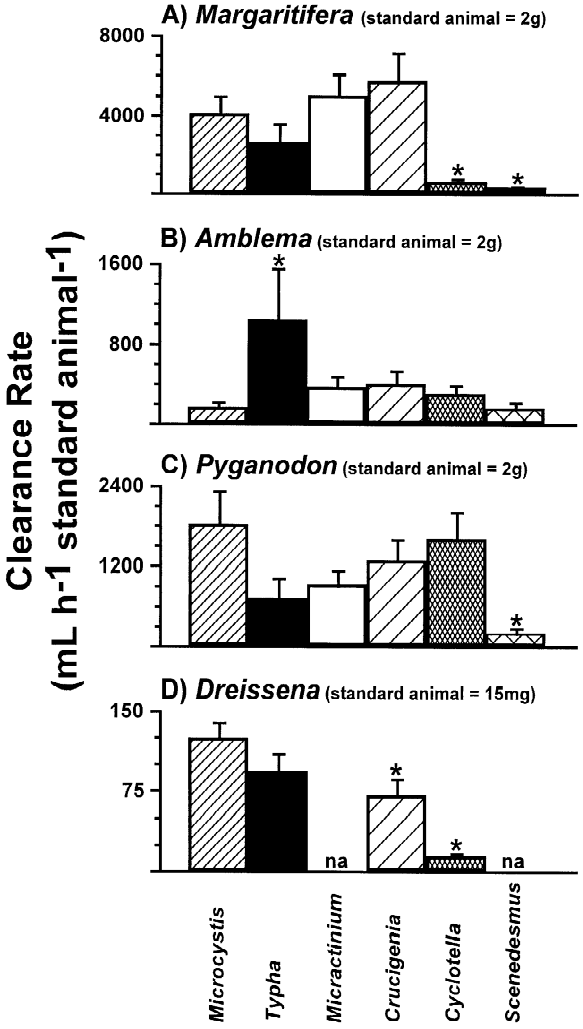

Figure 2. Clearance rates of single-particle type suspensions, standardized to an animal of 2 g dry tissue mass: (A) *Margaritifera*, (B) *Amblema*, and (C) *Pyganodon*, or standardized to an animal of 15 mg dry tissue mass: (D) *Dreissena* (Baker et al., 1998). * Clearance rates of particle type significantly different than that of *Microcystis* (far left bar) ($p < 0.05$).

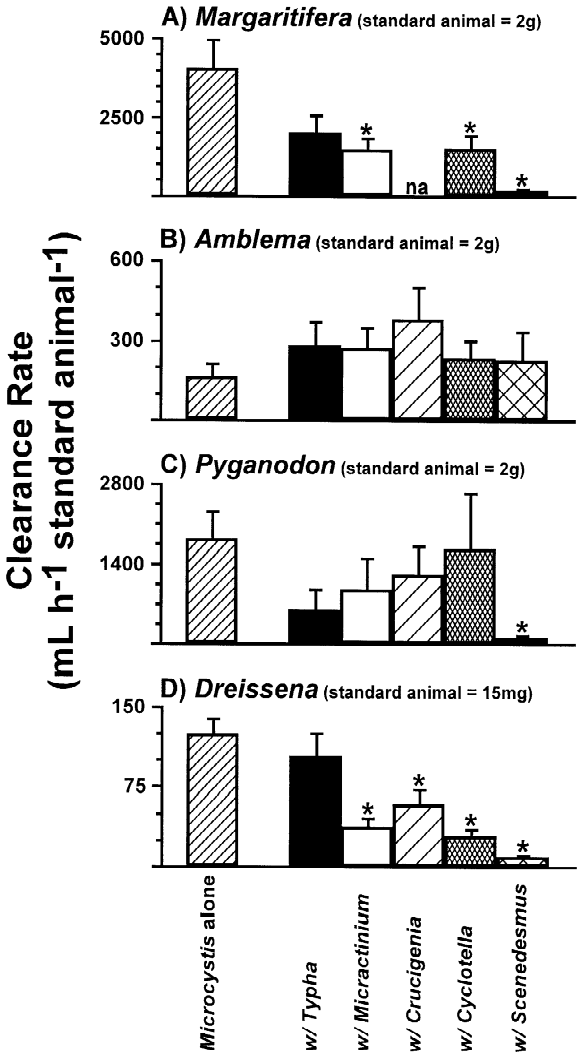

Figure 3. Clearance rates of single-particle type suspensions of *Microcystis* (far left bar) and total clearance rates of suspensions of particle types paired with *Microcystis* (right hand bars). Clearance rates standardized to an animal of 2 g dry tissue mass: (A) *Margaritifera*, (B) *Amblema*, and (C) *Pyganodon*, or standardized to an animal of 15 mg dry tissue mass: (D) *Dreissena* (Baker et al., 1998). * Clearance rates of paired suspensions significantly different than that of *Microcyctis* alone.

theses that native mussels (1) prefer particles that are no longer abundant in the Hudson River (*Microcystis*), (2) must compete with zebra mussels for the same preferred food types (*Microcystis*); and (3) are unable to differentiate between nutritious (phytoplankton = 4 μm) and less nutritious (*Typha* detritus, $\leq$3.5 μm) particles. These characteristics, in combination with the very high clearance rates of zebra mussels, may result in the reduced availability of preferred and nutritious food items, which may severely affect native mussels.

These results contribute to an understanding of the mechanisms underlying the decline in abundance and diversity of native mussel populations in the Hudson River estuary since its invasion by the zebra mussel, where colonial and unicellular cyanobacteria, especially *Microcystis*, have nearly disappeared from the river (Smith et al., 1998), declining from 36 to 4% of the total number of cells (Marshall, 1988; Smith et al., 1998). While zebra mussels reject large gelatin-

ous colonies of *Microcystis* (Bastviken et al., 1998), they preferentially ingest unicellular *Microcystis* over most other particles and increase clearance rates in the presence of *Microcystis.* Therefore, zebra mussels appear to be responsible for the decline of *Microcystis* in the Hudson River (Baker et al., 1998; Bastviken et al., 1998). In the current study, we found that, like zebra mussels, native mussels also preferentially ingest the unicellular cyanobacterium, *Microcystis*, over nearly all other phytoplankton species. Native mussels, however, appeared to be less efficient at selecting *Microcystis* than are zebra mussels; native mussel sorting efficiencies indicated that their pseudofeces were depleted of *Microcystis* by 4 – 54%, while sorting efficiencies of zebra mussels indicate that their pseudofeces are depleted of *Microcystis* by 14 – 67%, compared with the suspension. These results confirm previous suggestions that decline in native mussel population density and body condition are the result of inadequate food supply (Strayer et al., 1999). Given that (1) native mussels and zebra mussels prefer the same phytoplankton but have lower sorting efficiencies (this study), (2) the preferred cyanobacterium is now scarce in the Hudson River (Smith et al., 1998), and (3) zebra mussel biomass in the River is many times that of native mussels (Strayer et al., 1996), we suggest that the potential for exploitation competition between zebra mussels and native mussels is high. The consumption of a resource, (phytoplankton, in general, and *Microcystis,* in particular) by large populations of zebra mussels reduces its availability to the native mussels.

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, compared to a drop in phytoplankton biomass of 90% (Cole et al., 1991; Caraco et al., 1997; Strayer et al., 1999). Thus, the relative abundance of nonphytoplankton material has dramatically increased, diluting the remaining phytoplankton and presumably resulting in a reduction in overall food quality. Many bivalves are able to compensate for reductions in food quality, and thereby maintain energy intake, by altering filtration rate, ingestion rate, sorting efficiency, or absorption efficiency (Iglesias et al., 1992; Hawkins et al., 1996; Navarro et al., 1996). Bivalves differ, however, in their abilities to regulate these responses (Hawkins et al., 1990; Navarro & Iglesias, 1993). In a previous study, we found that zebra mussels efficiently sort and reject *Typha* detritus (Baker et al, 1998). Zebra mussels appear able to compensate for decreases in seston quality by selecting desirable particles for ingestion, thereby optimizing energy intake. The three species of native mussels we examined, however, did not select between *Typha* detritus and *Microcystis*. The apparent inability of native mussels to select between nutritious and less nutritious particles, when combined with a relative increase in non-nutritious material in suspension, will result in decreases in food quality of ingested material and long-term energy intake. A reduction in energy intake per unit of ingested material, if not compensated for, will eventually lead to a decline in body condition, growth, and reproduction. Declines in condition and abundance of native mussels, while zebra mussels continue to thrive, may be explained by differences in their abilities to compensate for poor food quality.

This study, along with our previous study of zebra mussels, demonstrates the fact that clearance rates of single particle types are not necessarily representative for a given bivalve. In zebra mussels for example, the clearance rates of particles, even those that are not preferred, generally increase 1.2-fold to 6-fold with the addition of *Microcystis* to the suspension (Baker et al., 1998). This was not always the case for the native mussels we examined. Clearance rates by the native mussel *M. margaritifera* did increase 2.5-fold ($p = 0.0557$) when *Microcystis* was included in suspensions of *Cyclotella*. In all other combinations with *Microcystis*, however, clearance rates remained similar to that of the single particle type or declined, often dramatically. In *M. margaritifera* and *A. plicata*, clearance rates declined by 71% ($p \leq 0.0001$) and 73% ($p = 0.015$) when *Microcystis* was included in suspensions of *Micractinium* and *Typha*, respectively. In contrast, zebra mussels appear able to compensate for particle mixtures by not only efficiently selecting desirable particles from the mixture but by also greatly increasing filtration rates when desirable particles are available, thereby optimizing energy intake.

Previous studies have indicated that the subfamily Ambleminae is less sensitive to zebra mussel infestation than are other subfamilies, such as Anodontinae and Lampsilinae (Haag et al., 1993; Strayer & Smith, 1996; Baker & Hornbach, 1997). In the current study, *Amblema plicata* differed from the other two native mussels in selecting the diatom *Cyclotella* over *Microcystis*. In systems such as the Hudson River, where diatoms now dominate the phytoplankton community, this would appear to be advantageous. In addition, although *A. plicata* did not select between

Typha detritus and *Microcystis*, it had a relatively high clearance rate for suspensions of *Typha*. This suggests that *A. plicata* may gain some nutritional value from detritus. Cellulosic detritus may be an important source of carbon in some populations of bivalves (Crosby et al., 1989; Langdon & Newell, 1990). If this is the case for *A. plicata*, the high clearance rate for *Typha* represents another advantage in systems where the relative abundance of nonphytoplankton material has increased. Indeed, *A. plicata* has fared better than other native mussel species in systems invaded by zebra mussels (Haag et al., 1993).

In summary, we examined the ability of three species of native North American freshwater mussels to sort food particles, determined their particle preferences, and compared their preferences to those of zebra mussels. We also determined their clearance rates. Our results suggest that native mussels must compete with zebra mussels for many of the same food types and are less efficient than zebra mussels at differentiating between nutritious and less nutritious particles. This supports previous evidence that observed declines in native mussel population density and body condition are the result of inadequate food supply and suggests an additional mechanism, other than direct physical interference, for native mussel mortalities following zebra mussel invasions.

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