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Effects of the zebra mussel on nitrogen dynamics and the microbial community at the sediment-water interface

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ABSTRACT: A flow-through experiment was conducted on intact cores of sediments from Saginaw Bay, Lake Huron, to examine how trophic interactions between filter-feeding bivalve mussels and microbial populations could affect nitrogen dynamics at the sediment-water interface. The zebra mussels used in this experiment removed a large proportion of protozoa and phytoplankton from the overlying water, particularly heterotrophic nanoplankton (up to 82%), while bacterial populations showed less change. A 3-fold decrease in the protozoan to bacterial carbon ratio corresponded to a 2.5-fold increase in relative ammonium removal rates as estimated from the dark loss of ^{15}N-ammonium. Excretion by the bivalves also increased net ammonium flux to the water, thus elevating the total calculated areal ammonium removal rates to about 6-fold over rates observed in the control treatment. These data suggest that filter-feeding bivalves may significantly affect nitrogen transformation rates near the sediment-water interface by excreting ammonium and altering the microbial food web structure at the sediment-water interface.

KEY WORDS: Nitrogen · Microbial food web · Sediment-water interface · Bivalve mussels

INTRODUCTION

The sediment-water interface is a region of active biological and biogeochemical processes, such as labile organic matter biodegradation and ammonium production in shallow coastal systems. Under such conditions, kinetic diffusion-reaction models based on equilibration of ammonium between the sediments and pore water do not adequately predict actual ammonium flux into overlying waters (Ullman & Aller 1989). If oxygen is present, as often is the case in shallow waters, a portion of ammonium may be oxidized to nitrate (Ward 1986). In turn, the nitrate may be completely or partially denitrified to nitrogen gas in adjacent sites (Seitzinger 1988). Understanding the mechanisms that control the extent of N transformations at the sediment-water interface is important, because these processes can affect the amount of mineralized N that is ultimately available to primary producers or lost through denitrification.

Trophic cascades involving bacterivorous protozoa can affect community N regeneration rates (Suzuki et al. 1996) and bacterial community structure in the water column (Jürgens & Güde 1994). Furthermore, planktonic bacterivorous protozoa can inhibit the biogeochemical process of nitrification, directly by reducing

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bacterial numbers and indirectly by forcing bacteria to grow in colonies, whereas predation by larger zooplankton diminishes these effects (Lavrentyev et al. 1997). The important role of the bottom-dwelling protozoa in consuming heterotrophic bacterial production (e.g. Bak et al. 1995) supports the idea that similar cascading trophic effects on nitrogen transformation may take place at the sediment-water interface. Here, microorganisms are involved in complex interactions with other benthic organisms that have significant effects on nitrogen transformations (Dame et al. 1984, 1991, Henriksen & Kemp 1988).

One of these organisms is the zebra mussel *Dreissena polymorpha*, an invasive filter-feeding bivalve that alters the structure of food webs in shallow areas by filtering particles (e.g. Nalepa et al. 1995) and excreting nutrients (Gardner et al. 1995b, Binelli et al. 1997). In this study, we examined how trophic interactions, induced by zebra mussels, can modify the microbial food web structure and nitrogen transformations at the sediment-water interface.

Studying trophic interactions and nutrient transformations involving microorganisms at the sediment-water interface presents methodological difficulties. The use of a ^{15}N tracer is necessary to study N dynamics because of close coupling between ammonium regeneration, nitrification, and denitrification. The mass analysis techniques for ^{15}N require large sample volumes and involve multi-step sample preparations that increase the risk of contamination. The physical, chemical and biological nature of the sedimentary matrix is impossible to replicate in the laboratory; yet, the maintenance of this structure is crucial to many benthic processes (Miller-Way & Twilley 1996). The necessity to maintain sediment integrity during an experimental incubation limits the application of conventional size-fractionation and dilution techniques that are commonly used to modify food web structure in planktonic studies. Further, the presence of meroplanktonic protozoa, which are able to migrate freely between sediments and the water column, may greatly diminish the effects of experimental manipulations with inlet water in such studies.

The purpose of this study was to examine how trophic interactions between filter-feeding bivalve mussels and microbial populations could change nitrogen dynamics in controlled experimental systems using intact sediments. To simulate a trophic cascade, we used the zebra mussel as a 'biological particle filter' in a sediment core continuous flow cell. We used this approach in combination with high performance liquid chromatographic analysis of ammonium concentration and atom % ^{15}N to test the hypothesis that cascading trophic effects involving bacterivorous protists affect nitrogen transformation at the sediment-water interface.

MATERIAL AND METHODS

Material for this study was collected from Saginaw Bay, a large (about 82 km long and 42 km wide) bay extending off the western edge of Lake Huron. The shallow (1 to 3.5 m depth) inner bay receives large inflows of enriched waters from the Saginaw River. Since 1991, the zebra mussel has heavily infested the inner bay (Nalepa et al. 1995).

Intact cores of sediments and the overlying water were collected by SCUBA divers from a site near Au Gres Point (43° 56' N, 83° 52' W) on June 30, 1995. These samples were taken using 76 mm internal diameter plastic tubes. Simultaneously, several pebbles colonized by the zebra mussel were collected for experimental additions. Several 20 l carboys of surface water from the same site were collected to supply a flow-through system. The samples were transported to the laboratory in insulated coolers within a few hours after collection.

The sediments were placed in a system consisting of the cores (in the original collection tubes), a clear polycarbonate vessel with intake lake water, a Technicon peristaltic pump, and an outflow collection vessel (Fig. 1). This laminar flow system is an improved and larger version of the flow-cell described earlier (Gardner et al. 1991). It was designed with an O-ring seal and plunger that could be lowered to the desired position without disturbing the surface sediments. The overflow tube released water as the plunger was positioned but was closed during operation. Water was pumped over the sediment surface at a rate of 1 ml min^{-1}.

The pebbles holding the zebra mussels were of different size and shape and had large amounts of periphyton on them. Mussels were removed from the pebbles by cutting the byssal threads with a razor blade

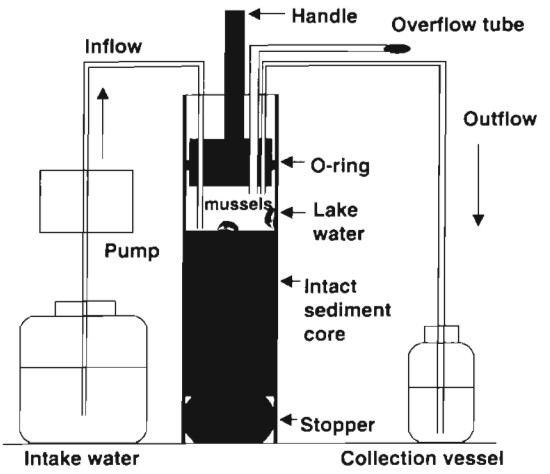

Fig. 1. The continuous flow through system. The diameter of the core was 76 mm. The flow rate for the unfiltered water was 1 ml min^{-1}

and rinsed with bay water to remove periphyton before they were used in the experiment. Two adult mussels, shell length 22.3 mm ± 0.69 SE, were added to each triplicate core. By the time the system had reached steady state, the zebra mussels remained either on the top of the sediments or attached to the side of the core tube above the sediment surface. Thus, they were positioned to filter overlying water rather than pore water. All zebra mussels remained alive during the experiment and were still filtering water at the end of the incubation.

The cores and the inflow water from the sample site were incubated in an indoor Percival incubator that was set for a 12:12 h light:dark cycle and held at ambient temperature (21°C). The inlet water was held under fluorescent lights to ensure phytoplankton growth. Triplicate cores with mussels and triplicate controls without mussels were each assembled and wrapped in aluminum foil to prevent light penetration and make it possible to differentiate between removal by nitrification/denitrification and algal uptake. Large quantities of light (both visible and UV lengths) can inhibit nitrification via photooxidation of bacterial cytochrome *c* (Bock et al. 1989).

The concentrations of NH_4^+ and nitrates (equals $NO_2^- + NO_3^-$) were monitored over time. Ammonium concentrations and $^{15}NH_4^+$ isotope ratios were respectively measured via 2 high performance liquid chromatography methods (Gardner & St. John 1991, Gardner et al. 1995a). Concentration of nitrates was measured using a standard colorimetric technique (Strickland & Parsons 1972) with a Technicon autoanalyzer.

After the system had been maintained at steady state (based on the concentrations of dissolved nutrients) for 3 d, ^{15}N-ammonium isotope (10 µM final concentration) was added into the container with inflow water and mixed thoroughly. The additions of 10 µM $^{15}NH_4^+$ were selected to provide concentrations of ammonium comparable to those produced in the sediments. Some ammonium (approximately 40% for the example in Table 1) was removed by organisms in the water before the water was passed over the cores. Of the water coming out of the cores, the labeled ammonium constituted 20 to 54% of the total ammonium. Note, the actual concentration of dissolved $^{15}NH_4^+$ in the water varied from day to day because of biological uptake after spiking. After allowing the system to equilibrate over night with the added $^{15}NH_4^+$, we performed 3 sequential ^{15}N-incubation intervals and measured ammonium concentration and atom % ^{15}N within each interval to increase statistical robustness of the experiment.

Concentrations of $^{15}NH_4^+$ (i.e. NH_4^+ concentration × atom % ^{15}N) were measured in the inflow waters and outflow waters, which were sampled at about the same time. We believe that phytoplankton uptake during passage across the dark core should not have exceeded that occurring in the inlet water held under light/dark conditions. Therefore, the observed differences in $^{15}NH_4^+$ concentrations between the inflow and outflow waters were assumed to result from microbial processes at or near the sediment-water interface.

Results from the flow-through core system, without (incubation Days 2, 3, and 4) and with (incubation Days 5, 6, and 7) $^{15}NH_4^+$ additions, were used to calculate ammonium removal rates. Successive results from each core were averaged before (n = 3) and after (n = 3) addition of $^{15}NH_4^+$ to yield core-specific ammonium concentration and isotope ratio values. The core-specific values were than averaged among replicate core treatments to calculate mean values and standard errors (SE) for the zebra mussel and control treatments, respectively, before and after $^{15}NH_4^+$ additions. We assumed that the same percentage of ammonium was removed, whether it was released from the sediments, excreted by organisms, or added to the inlet water as $^{15}NH_4^+$. Net areal ammonium flux (N_{net}, µmol N m^{-2} h^{-1}) was calculated as follows:

$$N_{net} = (N_O - N_I) \times \text{flow rate/core surface area} = (N_O - N_I) \times 13.3 \quad (1)$$

where N_O and N_I were ammonium concentrations (µM) in the outflow and inflow waters, respectively, during Days 2, 3 and 4, before the addition of $^{15}NH_4^+$. The flow rate was 0.060 l h^{-1} and the surface area of the core was 0.0181 m^2. Total ammonium flux (N_{total}, µmol N m^{-2} h^{-1}), i.e. N_{net} corrected for estimated removal, was then calculated as:

$$N_{total} = N_{net} \times {}^{15}N_I / {}^{15}N_O \quad (2)$$

where $^{15}N_I$ and $^{15}N_O$ are the concentrations of $^{15}NH_4^+$ (i.e. total ammonium concentration × atom % $^{15}NH_4^+$) in the inflow and outflow waters, respectively. Note, this calculation is based on the assumption that the NH_4^+ originating from the sediments or benthos was removed at the same relative rate as the added $^{15}NH_4^+$. Finally, the amount of the removed ammonium ($N_{removed}$) on an areal basis (µmol N m^{-2} h^{-1}) was calculated as:

$$N_{removed} = N_{total} \times ({}^{15}N_I - {}^{15}N_O)/{}^{15}N_I \quad (3)$$

The concentrations of bacteria, phytoplankton, and protozoa in the inflow and outflow water were measured at the beginning and the end of $^{15}NH_4^+$ incubations. Bacteria preserved with 1% (final concentration) formaldehyde were counted on acriflavine-stained filters (Bergstrom et al. 1986). Nanoplankton were preserved with ice-cold glutaraldehyde (1% final concentration) and counted using DAPI/FITC double staining (Sherr et al. 1993). Microplankton preserved with freshly prepared acid Lugol's iodine (1% final concentration) were counted in settling chambers. Microbial

cell linear dimensions were measured using an eyepiece micrometer (magnification up to 1250×) and their biovolumes were calculated by approximating geometric solids. Allometric relationships (Norland 1993) were used to estimate bacterial biomass from their cell volume and then an average of these estimates was calculated. Protozoan biomass was estimated assuming carbon contents of 0.15 and 0.19 pg C μm^{-3} for living and preserved cells, respectively (Putt & Stoecker 1989). Algal biovolumes were converted to carbon using the allometric equation for phytoplankton (Montagnes et al. 1994).

Under steady state, successive determinations of ^{15}N dark losses and microbial parameters were averaged to obtain a single value for each flow-through chamber, and then a mean and standard error were calculated for triplicate experimental treatments and control.

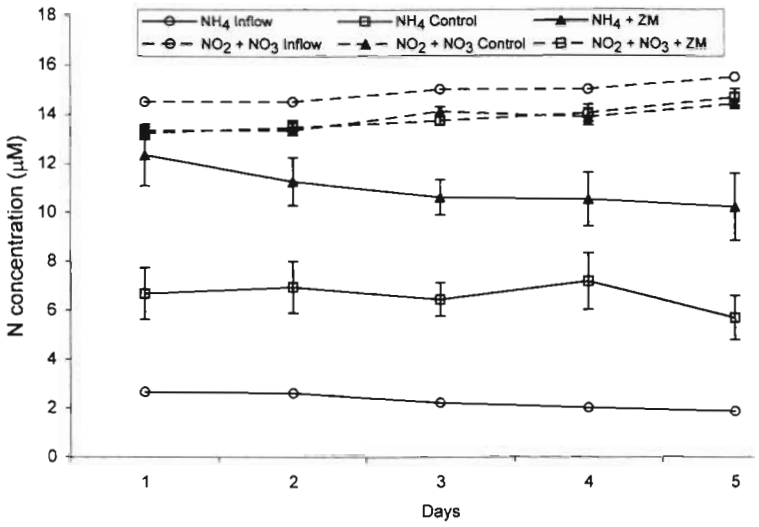

Fig. 2. Dynamics of ammonium (——) and nitrates (— — —) during the initial phase of the experiment (before the addition of $^{15}NH_4^+$). Mean and standard error values are calculated for 3 replications at each time point

At the end of the incubation, triplicate samples of sediments were collected from each core to estimate abundance of benthic protozoa. Benthic protozoa were counted in several 100 µl subsamples of non-preserved sediments, which were diluted 1:10 with 0.2 µm filtered lake water (Finlay et al. 1979). Heterotrophic nanoflagellates, preserved with 1% (final concentration) glutaraldehyde, were extracted from the sediments using isopycnic centrifugation in silica gel gradients (Epstein 1995) and counted via epifluorescence microscopy as described above.

RESULTS

After some initial oscillation of nutrient concentrations in control and experimental cores with added zebra mussels over the first 24 h, the flow-through system stabilized (Fig. 2). The concentration of NH_4^+ in both triplicate outflows remained significantly higher than in the inflows throughout the experiment, indicating a positive flux of NH_4^+ from the sediments and benthic organism excretion. Mean net ammonium production rate (117 ± 18 [SE], µmol N m^{-2} h^{-1}) was significantly higher in the zebra mussel treatments than in the control treatments (59 ± 16 [SE], µmol N m^{-2} h^{-1}). Conversely, the concentration of nitrates was slightly higher in the inflows than in both outflows, which did not differ from each other. Sequential measurements of ammonium production rates in individual cores consistently varied less than the mean results obtained from replicate cores (data not shown). Likewise, variability among cores was greater for the concentrations and fluxes of total ammonium produced by natural mineralization processes than for the ^{15}N-labeled ammonium that had been added on both an absolute and relative basis (Table 1).

The mean percentage of $^{15}NH_4^+$ removed as the spiked water moved over the sediment cores was 10 ± 2.0 (SE) % for the control treatments as compared to 26 ± 9% for the zebra mussel treatments. The mean total ammonium flux and removal rate, calculated by Eqs. (2) & (3), respectively, were 68 ± 18 and 7.3 ± 2.5 µmol N m^{-2} h^{-1} for the control treatment sediments as compared to 169 ± 30 and 46 ± 12 µmol N m^{-2} h^{-1} for the zebra mussel treatments.

The biomass of phytoplankton was largely formed by nanoplankton-sized diatoms, cryptophytes, and *Chlamydomonas* sp. It slightly increased in the control due to the large *Cymbella* sp. and *Pediastrum* sp. that may

Table 1. Total NH_4^+ and $^{15}NH_4^+$ (= total concentration times atom % ^{15}N) concentrations (±SE) in inflow water and outflow waters for each time point (T6, T7, and T8) in the $^{15}NH_4^+$-addition experiments. All concentrations are expressed as µM N

	T6		T7		T8	
	Total	$^{15}NH_4^+$	Total	$^{15}NH_4^+$	Total	$^{15}NH_4^+$
Inflow	5.9	4.4	6.7	5.7	5.9	4.7
Control						
Mean	10.3	4.2	11.0	5.9	9.6	3.3
SE	1.2	0.1	1.1	0.2	1.2	0.2
Zebra mussel						
Mean	15.8	3.7	15.4	4.7	13.2	2.6
SE	1.6	0.2	1.7	0.4	1.6	0.2

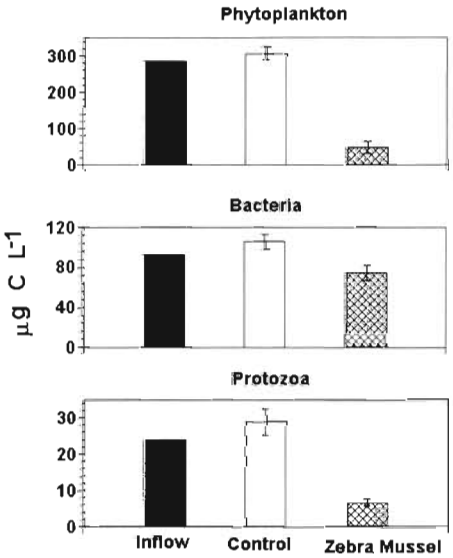

Fig. 3. Mean biomass (±SE) of microorganisms during ^{15}N incubations

have been flushed from the sediments. All groups of phytoplankton, with the exception of the colonial cyanobacterium *Merismopedia* sp., drastically decreased in the zebra mussel treatments (Fig. 3).

In the control, there was no appreciable change in biomass and species composition of the ciliate assemblage, which consisted mainly of oligotrichs and *Urotricha* spp. The occurrence of the benthic scuticociliate *Uronema* sp. in the outflow water did not significantly affect the total ciliate biomass. However, in the treatments with zebra mussels, there was a ca 2-fold decline in protozoan biomass. The most dramatic change was observed for heterotrophic nanoflagellates (HNAN). Their biomass decreased by 82% in the zebra mussel treatments.

Bacterial biomass showed a similar trend to that of protozoa but in much smaller proportion. The observed changes were mainly accounted for by large (>1 µm) and chain-forming rod- and vibrio-shaped cells that represented ca 25% of the total bacterial biomass in the inflow, >40% in the control outflow, and <8% in the zebra mussel outflow.

The ratio of protozoan to bacterial carbon-based biomass decreased from 27.3 ± 2.45 (SE) in the control to 8.72 ± 1.39 in the zebra mussel treatments. The ratio of HNAN to bacterial biomass declined even stronger, 0.16 ± 0.03 in the control versus 0.03 ± 0.01 in the zebra mussel treatments. As mentioned above, the percentage of ^{15}N lost during the passage of water through the core treatments was also significantly higher in the grazed treatments than in the control.

The total biomass of benthic protozoa (µg C ml^{-1}), sampled in the sediments at the end of the experiment, did not significantly differ between the treatments, 0.53 ± 0.07 (SE) in the control versus 0.70 ± 0.08 in the zebra mussel cores. However, the proportional contribution of the small scuticociliate *Uronema* sp. was nearly twice as high in the latter treatment, where it comprised ca 60% of the protozoan biomass in the sediments. In the control, the more diverse protozoan assemblage was reflected in the quantitative presence of large ciliates, such as *Spirostomum minus*, *Loxodes* sp., and *Oxytricha* sp., and a substantial contribution from HNAN. The ciliate *Saprodinium* sp. occurred in both treatments.

DISCUSSION

A steady-state response in our experiments, where ammonium and nitrate fluxes remained stable over time, supported the observation of Miller-Way & Twilley (1996) that continuous flow systems can maintain near-initial experimental conditions throughout incubation. Net production and changes in atom % ^{15}N were measurable in all of the cores. Variability of the $^{15}NH_4^+$ concentrations and fluxes among cores at a given time point were consistently lower than those for the total ammonium concentrations. These results indicate that the ratio of ammonium removal to production rates in the nepheloid layer was not greatly affected by the magnitude of total ammonium concentration or production rate, at least within the ranges of data that were examined here. Net sediment-water ammonium fluxes reported here are similar to those previously measured in Saginaw Bay (Ullmman & Aller 1989).

Both ammonium flux and nitrification rate increased significantly in the presence of the zebra mussels. Interestingly, even though total NH_4^+ fluxes were higher, the percentage of the total ammonium flux that was taken up increased by 2.5-fold in the zebra mussel treatments as compared to results from the control treatments. Thus, the presence of zebra mussel not only affected absolute ammonium removal rates but also increased the percentage of regenerated ammonium that was removed. Increased ammonium removal rates partially counterbalanced increased ammonium production rates in the presence of the zebra mussel. Positive shifts in the NH_4:NO_3 ratio have been reported to trigger blooms of non-nitrogen-fixing cyanobacteria, such as *Microcystis* (Blomqvist et al. 1994).

Given the drastic decrease in phytoplankton biomass that was observed in the zebra mussel outflow, the increased dark loss of $^{15}NH_4^+$ in this treatment was likely more the result of enhanced nitrification than of algal uptake. The lack of corresponding changes in nitrate concentrations can be explained by coupled nitrate losses to denitrification that may have occurred close to the sediment-water interface (Gardner et al. 1987, Henriksen & Kemp 1988). The zebra mussel can

stimulate the development of benthic microalgae in Saginaw Bay (Lowe & Pilsbury 1995), but we expect that N uptake by these organisms may have been small during the prolonged dark incubation. The occurrence of the benthic ciliate *Saprodinium* sp. indirectly suggests that anoxic conditions conductive to denitrification may have existed in certain regions of sediments in this experiment.

The mechanisms underlying the zebra mussel effects on microbial nitrogen transformations in this study appear to be different from those reported for other macrobenthos. In our experiments, the zebra mussels remained either on the top of the sediments or attached to the side of the core tube above the sediment surface. Thus, they were positioned to filter overlying water rather than pore water. The fact that the sediments were firm sand rather than clay prevented the mussels from penetrating extensively into the sediment matrix. Unlike many other sediment-dwelling macrofauna, which aerate sediments via their bioturbation activities (Pelegri & Blackburn 1995, Rysgaard et al. 1995, Svensson & Leonardson 1996), the zebra mussel does not burrow into the sediments, but forms dense beds on solid substrates at the sediment surface.

In Saginaw Bay, the zebra mussel deposits large amounts of feces and pseudofeces at the sediment surface (Nalepa et al. 1995) and significantly enhances N-cycling rates by excreting ammonium (Gardner et al. 1995b). However, the concentrations of NH_4^+ were not limiting to microorganisms even in the absence of zebra mussel, as indicated by the positive net NH_4^+ flux from the control cores. Under nitrogen-limited conditions, which are more typical for marine systems, nitrification may be enhanced by NH_4^+-rich fecal pellets placed on the sediment surface (Henriksen & Kemp 1988).

Our results are consistent with the idea that cascading trophic phenomena could directly affect the transformation and fate of mineralized nitrogen at the sediment-water interface. The zebra mussel filtering process appeared to selectively remove algae and bacterial grazers from the overlying water. This observation corresponds well to the results of earlier studies, where the mussel drastically reduced the abundance of phyto- and protozooplankton (Leach 1993, Lavrentyev et al. 1995, Bastviken et al. 1998, Findlay et al. 1998). The size-based prey selectivity of filter-feeding mussels appears to determine their cascading effects on bacteria. Having a typical filtration rate of ca 50 ml mussel^{-1} h^{-1} (Reeders & de Vaate 1990), the zebra mussel is capable of filtering particles from 0.7 to 450 µm (Jørgensen et al. 1984), but maximum retention occurs in the size range from 5 to 35 µm (Sprung & Rose 1988). Heterotrophic nanoflagellates, the major bacterivorous organisms in Saginaw Bay (Lavrentyev et al. 1997), fall within this size category.

Bacterial biomass did not differ significantly between the control and the treatments with zebra mussels, despite a strong decline in protozoan abundance in the latter treatments. Combined with the observed changes in bacterial size structure, this fact implies that mussels may have removed a certain proportion of the bacterial population from the overlying water. However, in the latter treatment, a decrease in the protozoan to bacterial biomass ratio, possibly reflecting the degree of bacterivory, corresponded to an increase in the dark ^{15}N loss. This result suggests that a sharp reduction in HNAN numbers allowed bacterial activity to increase. In Saginaw Bay, the zebra mussel grazed a certain proportion of the bacterial population, but their overall effect on bacterial production in the water column in Saginaw Bay was stimulating (Cotner et al. 1995). Protozoa can selectively graze metabolically active bacteria (del Georgio et al. 1996, López-Amorós et al. 1998). Although some bivalve mussels are capable of assimilating bacterial food due to their flexible digestive system (Dech & Luoma 1996), it is unlikely that a similar level of selectivity can occur in them.

The potential cascading trophic effect of *Dreissena polymorpha* on the microbial community appears to be similar to those described for planktonic heterotrophic (Jürgens & Güde 1994) and nitrifying bacteria (Lavrentyev et al. 1997). Although we did not measure bacterivory rates in these experiments, our earlier experiments in Saginaw Bay (Lavrentyev et al. 1997) identified HNAN as major consumers of bacteria. Moreover, we found that HNAN were capable of efficiently removing nitrifying bacteria, even when these bacteria were present at very low concentrations.

The effects of bivalve activities appear to be more complex in the sediments than in the overlying water. It is reasonable that the organic-rich feces and pseudofeces deposited by the zebra mussel at the sediment surface could have stimulated the growth of heterotrophic bacteria in sediments that, in turn, may have caused the observed shift toward a predominance of scuticociliates in microbenthic community. These specialized bacterivorous ciliates have much higher specific grazing rates upon bacteria than do HNAN (e.g. Šimek et al. 1994). However, the lack of direct measurements of bacterial biomass in sediments inhibits further speculation at this point.

Trophic links between microorganisms and bottom-dwelling invertebrates are not unique to the zebra mussel and the freshwater environment. The estuarine bivalve *Mytilus edulis* affected microzooplankton-sized ciliates (Riemann et al. 1990) and preyed upon bacterivorous heterotrophic flagellates (Kreeger & Newell 1996). The oyster *Crassostrea gigas* has been

recently found to assimilate ciliates and flagellates (Dupuy et al. 1999).

Combined with these observations, the results of our study suggest a new interpretation of previously published data on the effects of marine invertebrates on the nitrification process. For example, in the Chukchi Sea, the large bivalve *Macoma calcera* stimulated nitrification despite the fact that it excreted directly to the water column through its exhalant siphon with little irrigation effect in the sediments (Henriksen et al. 1993). One explanation that agrees with these results is that the bivalves could have stimulated nitrification by filtering out bacterivorous protozoa that would otherwise graze nitrifying bacteria.

Another marine study found that sponges positively affected nitrification rates (Diaz & Ward 1997). The difference in accumulation of nitrite and nitrate in the presence of different species of sponges in that study led to the conclusion that bacteria directly associated with the sponges caused that nitrification. However, these data are also interesting with respect to our hypothesis regarding cascading trophic effects on the nitrification process. Filter-feeding sponges could reasonably reduce the numbers of bacterivorous protozoa, which could otherwise graze down both suspended and surface-associated nitrifier cells.

Although we did not attempt to represent all actual complex processes at the sediment-water interface in our laboratory study, we believe that these data offer some preliminary insight into the effects that bivalves such as the zebra mussel may have on nitrogen dynamics in nature. The cascading trophic effects could be quantitatively important to the transformations and fluxes of nitrogen in certain sediment-water environments (e.g. shallow productive areas of lakes, estuaries, and the coastal ocean). Conducive features include both an environment favorable for active microbial processes (e.g. nitrification) and the presence of dense populations of bivalve mussels or other suspension-feeding invertebrates that can exert 'top-down' effects on microbial food web components. The above example of zebra mussel affecting microbial food web composition, as well as the fate of nitrogen at the sediment-water interface, points to the need for more research on the effects of cascading trophic effects on biogeochemical cycles at both regional and global scales.

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