The impact of the zebra mussel (Dreissena polymorpha) on the availability of organic carbon and nutrients at the sediment surface of the Hudson River

by

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ABSTRACT

The rates at which zebra mussels (Dreissena polymorpha) have been observed to filter water in the Hudson River, coupled with the high population densities presently in the river, suggest that large amounts of suspended solids in river water may be deposited at the sediment surface as mussel feces and pseudofeces. To predict changes zebra mussels may cause in the benthic environment of the tidal freshwater portion of the Hudson River, mussel biodeposition was characterized using in situ incubations in chambers, with mussels that had reattached to artificial substrates. Biodeposits collected (which were actually a 40:60 mixture of mussel-generated biodeposits and passively-settled sediment) were analyzed for organic content, chlorophyll-a and phaeopigments, carbon and nitrogen, bacterial cell densities and bacterial production rates. Biodeposits were found to be significantly enriched, relative to control sediments from chambers without mussels, in all categories except bacterial cell densities. Mussel biodeposit mixtures were also found to be more easily resuspended relative to control sediments when subjected to a range of mixing energies. While these assays demonstrate that biodeposits are carbon and nutrient enriched, and that they contain organic matter of high nutritive value for bacteria, the propensity of biodeposits to resuspend is likely to moderate the ecological impact of this flux of nutrients and energy at the river bottom.

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INTRODUCTION

Zebra mussel populations in the tidal freshwater portion of the Hudson River have increased rapidly since this exotic species was first identified in the river in 1991. This bivalve is often one of the most abundant species, both in numbers and in biomass, in aquatic ecosystems where it is present (Wiktor 1963, Stanczykowska 1984, Stanczykowska and Lewandowski 1993, Stewart and Haynes 1994) and has been found in some cases to contribute up to 99% of benthic biomass (Stanczykowska et al. 1976). Researchers have also attributed to it a major role in influencing these ecosystems through its filter-feeding activities (Wiktor 1963, Stanczykowska and Lewandowski 1993).

The effects of zebra mussels may include changes both in pelagic and benthic ecosystems. Phytoplankton concentrations may be reduced when the filtration rate outpaces primary production (Nicholls and Hopkins 1993). This may deplete the food sources of pelagic food chains, while sometimes having the effect of increasing water transparency (Holland 1993) and thereby altering relative abundance of phytoplankton species and increasing benthic photosynthesis (Pillsbury and Lowe 1994, Stewart and Haynes 1994). Some effects of zebra mussels may be considered desirable as a way of counteracting eutrophication (Reeders and Bij de Vaate 1992, Mackie and Wright 1994) and as a way of removing pollutants in the water column that are adsorbed onto particulate matter (Noordhuis et al. 1992, Reeders and Bij de Vaate 1992).

At the benthic level, large quantities of processed seston--both organic and inorganic--may be deposited as the mussel eliminates feces or undigested pseudofeces (Stanczykowska et al. 1976). The mussels also accumulate phosphorus and nitrogen in their tissues and shells (Stanczykowska and Lewandowski 1993), providing a large amount of biomass at the lake or river bottom for predators. Furthermore, the substrate may be changed by the dense covering of the shells of live mussels and the accumulation of the shells of dead mussels (Wiktor 1963), thereby providing a more extensive and complex habitat for benthic macroinvertebrates (Stewart and Haynes 1994). Wiktor (1963) estimated that each 1000 mussels added 1.5 m^2 of net surface area to the substrate,

which further accelerates the sedimentation rate since deposits which might have been resuspended are better retained in the pores between shells.

Zebra mussels produce pseudofeces as a waste product in addition to feces; in fact, pseudofeces may be the predominant form of zebra mussel waste products in a turbid environment like the Hudson River estuary. Pseudofeces consist of undigested filtered solids which are agglutinated with mucus and are expelled through the mussel's inhalant siphon following an abrupt closure of the valves (Morton 1969). Two explanations have been proposed for the formation of pseudofeces (Sprung and Rose 1988). One is that the mussel needs to clear its gills of excess filtered matter when concentrations of suspended solids become high. Kiorboe and Mohlenberg (1981) state that a threshold concentration of particulate matter exists above which pseudofeces are produced. They report a value for Mytilus edulis only, which is about 1 mg dry weight (DW) L^{-1}, and suggest that because natural particle concentrations in estuaries and other neritic waters are generally between 5-20 mg L^{-1}, large amounts of pseudofeces are likely to be produced by bivalves in these waters. Suspended organic particles in estuaries and rivers are often greatly diluted by inorganic matter, a fact which raises the question of whether bivalves are able to select particles based on their food quality. Some research has shown that bivalves are capable of particle selection (Kiorboe and Mohlenberg 1981, Ten Winkel and Davids 1983), which suggests a second explanation for pseudofeces--they are produced when bivalves reject particles by selectively trapping them in mucus.

Regardless of which view is correct, zebra mussels have been observed to produce large amounts of pseudofeces in Hudson River water (Roditi, personal observation). Given the relatively high concentrations of suspended particulate matter typical of Hudson River water, we hypothesized that much, if not most, zebra mussel biodeposits would be in the form of undigested and mucus-bound pseudofeces. Izvekova and Lvova-Katchanova (1972) found these waste products have higher bacterial densities than the seston and contain a detritus-bacterial complex rich in nutritional value. However, few other studies have attempted to characterize zebra mussel pseudofeces, so little information is available on this subject.

While some chemical, biological, and quantitative aspects of bivalve biodeposits have been studied in marine ecosystems (Jordan and Valiela 1982, Tsuchiya 1980, Smith and Frey 1985) and in lakes (Wiktor 1963, Izvekova and Lvova-Katchanova 1972, Stanczykowska 1976), findings from these studies are difficult to apply to a riverine ecosystem because the composition of seston in rivers is different and contains a large fraction of inorganic matter. Also, the water column is well mixed by river flow and tides in estuarine systems, which tends to resuspend sediments.

Earlier filtration experiments (Roditi et al. submitted) using mussels collected from the Hudson River and incubated in Hudson River water showed that mussels clear suspended phytoplankton and seston (approximately 80% inorganic) from river water non-selectively, at approximately 2.8 ± 0.2 L mussel^{-1} day^{-1} (shell length = 13 mm). If we apply these rates to a mussel density of 30,000 mussels m^{-2} (estimated density in rocky areas as of September 1994--Strayer, personal communication), and we estimate a mean total suspended solids value of 10 mg DW L^{-1} (a conservative value since year-round it is closer to 20 mg DW L^{-1}), we estimate that 1 m^2 of mussels can filter a volume equivalent to a column of water 84 m high daily, and process 840 g DW of solids, much of which may be biodeposited at the sediment surface. Thus, the potential ecological effects of biodeposition are considerable.

We hypothesized that the zebra mussel biodeposits would more closely resemble seston than solids from other river sources, such as river sediment, for two reasons. First, as stated above, zebra mussels clear particles from Hudson River water nonselectively and at very high rates. This suggests there may be a large flux to the benthos of the same assemblage of particles present in the water column. Secondly, because concentrations of suspended solids in Hudson River water are relatively high, it appeared that most of the biodeposited matter would be in the form of undigested pseudofeces, and the organic matter might thus be in a relatively undegraded form.

This study looks at selected biological, chemical, and physical characteristics of the biodeposits produced by zebra mussels in the tidal freshwater portion of the Hudson River with the objective of helping to predict changes zebra mussel populations may

induce in benthic communities in the Hudson River and elsewhere.

METHODS

Experimental design: Microcosms were designed for in situ incubations. Zebra mussels were collected from the Hudson River at Poughkeepsie, removed from stones and allowed to reattach to artificial plastic substrates in trays of aerated river water. The substrate was a rigid plastic mesh, approximately 47 cm by 32 cm, with sufficient surface area for mussels to attach to. Sediments could settle through the mesh and accumulate without being resuspended by turbulence. Substrates were placed horizontally in plastic basins measuring 49 cm by 34 cm, with a height of 22 cm. Basins were covered with lids. Two openings (4 cm by 17 cm) were cut in both long sides of each container to allow water to flow through the microcosms. Each basin was weighted by a cast iron grating to which a solid concrete block was fastened. This combination was raised off the river bottom by about 25 cm on steel supporting legs fastened to the cast iron grating. The final set-up was further weighted with a cinderblock at each of 4 corners, and attached to shore by rope.

Two microcosms were used in each incubation, one containing mussels and the other as a control. Approximately 575 mussels with a mean shell length of approximately 17 mm were placed in the mussel chamber. In the control, pebbles of approximately mussel size were placed on an identical substrate to simulate the roughness of the mussels in case hydrodynamic effects were important. Each incubation lasted approximately 24 h, after which sediments were collected. One hour after collection, surface water was decanted from each sediment and subsequently sediments were well-shaken before analysis. River water and sediments were also collected at the site of incubations. River sediments were collected from a depth of 2.5-3 m below the water surface at low tide.

Chemical assays: Organic content of sediments was determined by drying samples at 60° C for 48 h then measuring weight loss upon combustion at 450° C for 4 h. Chlorophyll-a and phaeopigments in river water samples were measured following the methods of Holm-Hansen and Riemann (1978). Total suspended weight of water samples

was determined after filtration on pre-tared 0.4-μm Nuclepore filters, followed by oven-drying for 48 h at 60°C. Chlorophyll-a and phaeopigment content of sediments were determined as described above after suspending a small amount of sediment in deionized water and then filtering water samples. Chlorophyll-a was used as a measure of live algal abundance and phaeopigments as a measure of degraded or digested algal abundance. Some calculations make an estimate of algal biomass, which is approximated by multiplying chlorophyll values by 100 (chlorophyll x 50 = organic C; organic C x 2 = biomass). Nitrogen content was measured using a Carlo Erba NA 1500 CNS analyzer. Sediments were oven-dried (48 h at 60° C), then pulverized by mortar and pestle before analysis in the CNS analyzer.

Biological assays: Bacteria were counted following the methods of Hobbie et al. (1977). Sediments were diluted in deionized water, blended in a Waring blender for 4 minutes, then sonicated. The dilution was then stained with acridine orange and filtered onto 0.2-μm Nuclepore filters stained in Irgalan black. Bacterial production was measured by rate of uptake of labelled ^{3}H-thymidine into bacterial DNA according to the methods of Findlay et al. (1984). Incubations lasted 36 and 54 minutes. Five live replicates and two replicates killed with formalin as controls were used for both biodeposit sediments and control sediments.

Physical assay: Volumes of biodeposit mixture and control sediment containing equal amounts of solid matter (DW) were evenly distributed in a petri dish in a 1-L beaker filled with 0.7 L deionized H_2O. A Nalgene suspended stirring bar was centered over the sediment. An initial water sample was taken, then the magnetic stirrer setting was raised by increments, with 4 minutes allowed at each setting before a 10-mL water sample was drawn at the beaker's 400-mL mark. Light absorbance was used as a measure of suspended-solid concentration; absorbance was measured at 660 nm in 1x1-cm cuvettes with a Shimadzu UV 160 spectrophotometer. A linear relationship is assumed between light absorbance at 660 nm and the amount of suspended solids in the water. As magnetic stirrer settings have not been converted into conventional energy units, results should be used for comparison only.

Mixing model: The sediments obtained in chambers with mussels are a mixture of mussel waste products and passively trapped material. The dilution of biodeposits with non-biodeposit material can be corrected for with the control data. The difference, after subtracting the control chamber sediment from mussel chamber sediments, should be the quantity of sediment biodeposited by mussels. By knowing the ratio of passively deposited sediment to biodeposits in mussel chambers, the characteristics of pure biodeposits can easily be estimated algebraically. These calculations are made, but it should be remembered that they are generated mathematically by a mixing model and are not actual results. In this paper these calculated values are referred to as pure biodeposits, and the sediments actually collected from mussel chambers are referred to as biodeposit mixtures. Statistical analyses were performed on values before any results were adjusted for dilution. Since the biodeposit mixtures contained roughly 60% passively settled solids (presumably the same sediments as those accumulating in the control chamber), the values used for statistical analysis here are likely to underestimate actual differences between sediments.

RESULTS

Considerable amounts of sediment accumulated in control chambers, thus passive settling occurred in the absence of mussels. However, sediment accumulated more rapidly in chambers with mussels, and after 24-hour incubations, these chambers contained on average 39% more sediment than the control (Table 1). If we assume that passive settling was caused by the chambers themselves, which were identical in both treatments, then simple subtraction of the control sediment from mussel-chamber sediments should yield the quantity of sediment generated by mussel filtration or biodeposition. This computation yields a deposition rate of 2.3 ± 0.4 mg mussel^{-1} h^{-1}. It is difficult to determine ambient concentrations of suspended solids in river water during these incubations because the values were variable even within a 24-hour period. However, a mean value of 9.8 mg DW L^{-1} (SD =3.4) is obtained from five measurements made over a one-week period during the incubations. This value can be used to indirectly

estimate a filtration rate of 230 mL mussel^{-1} h^{-1}.

Chemical assays: Mean organic content of biodeposit mixtures was significantly higher (t-test, $p<0.05$) than in the control sediment. Pure biodeposits, according to the mixing model, had an organic content of 9.5%, which is 22% richer in organic matter than the control. If river sediment, control sediment, biodeposit mixtures, pure biodeposits and seston are arranged in this order, they form a gradient of increasing organic content (Fig.1).

Chlorophyll-a was used to estimate live algal abundance, as explained above. The biodeposit mixture contained significantly more live algal biomass than the control sediment. Pure biodeposits were estimated to consist, by weight, of 3.9% live algae, which is approximately four times the value for the control sediment. Again, if river sediment, control sediment, biodeposit mixtures, pure biodeposits and seston are arranged in this order, they form a gradient of increasing live algal content (Fig. 2).

The degraded or digested algal content of these sediments, determined by phaeopigment concentration, follows a similar pattern to chlorophyll-a content. If a ratio is made of detrital algae to live algae (phaeopigments to chl-a) for the above sediment and seston types, in the same order, a gradient of decreasing ratios is formed, with river sediment having the highest ratio (about 4 to 1) and seston having the lowest (roughly a 1 to 1 ratio; Fig. 3). Differences between control sediments and biodeposit mixtures were statistically significant (t-test, $p<0.05$).

Nitrogen content of biodeposit mixtures was significantly higher than that of control sediments. The model-generated N value for pure biodeposits was 0.53%--an enrichment of almost 40% over the control value of 0.38%. C:N ratio of biodeposits was also significantly lower than the control (Fig. 4).

Biological assays: Measurements of bacterial densities and bacterial production were made in control sediments and biodeposit mixture sediments collected from two incubations. Whereas mean bacterial densities in biodeposit mixture sediments were not significantly higher than those in control sediments, they appear slightly higher in biodeposit mixtures; however, the data were variable. If bacterial densities in both

sediment types are compared to typical values for river sediment and seston in the Hudson River (Austin and Findlay 1989), we can see that bacterial densities of biodeposit and control sediments fall roughly in between those of river sediment and seston, and do not differ much from each other (Fig. 5).

Bacterial production in biodeposit mixtures was significantly higher than in control sediments; growth rates were $1.0\text{x}10^{8}\pm5.2\text{x}10^{5}$ and $0.74\text{x}10^{8}\pm1.3\text{x}10^{5}$ cells g^{-1} OM h^{-1} in biodeposit mixture and control sediments, respectively. The model-generated value for growth in pure biodeposits was $1.5\text{x}10^{8}\pm0.2\text{x}10^{8}$ cells g^{-1} OM h^{-1} (error values are standard errors).

Physical assay: At all settings of the magnetic stirrer, more of the biodeposit mixture than the control sediment was resuspended (Fig. 6). The critical point at which there was a sudden, large increase in the amount of the sediment resuspended was above setting 2.5 in the case of the biodeposit mixture and above setting 3.5 for the control sediment.

DISCUSSION

We hypothesized that large-scale filter-feeding by zebra mussels would have the effect of coupling pelagic resources to the benthos, and would produce a flux of material at the river bottom resembling seston. The results of this study support this hypothesis.

In this study, seston was found to be richer than river sediment in chlorophyll-a and to have a higher ratio of live to detrital algae; previous findings show seston to be richer than sediment in organic content (Findlay, personal communication) and bacterial densities, and to have higher bacterial growth rates (Austin and Findlay 1989). If the control and biodeposit mixture sediments are ranked--along with river sediment and seston--in order of increasing organic content and chlorophyll-a, and in order of decreasing ratio of phaeopigments to chlorophyll-a, a predictable gradient is formed in which mussel

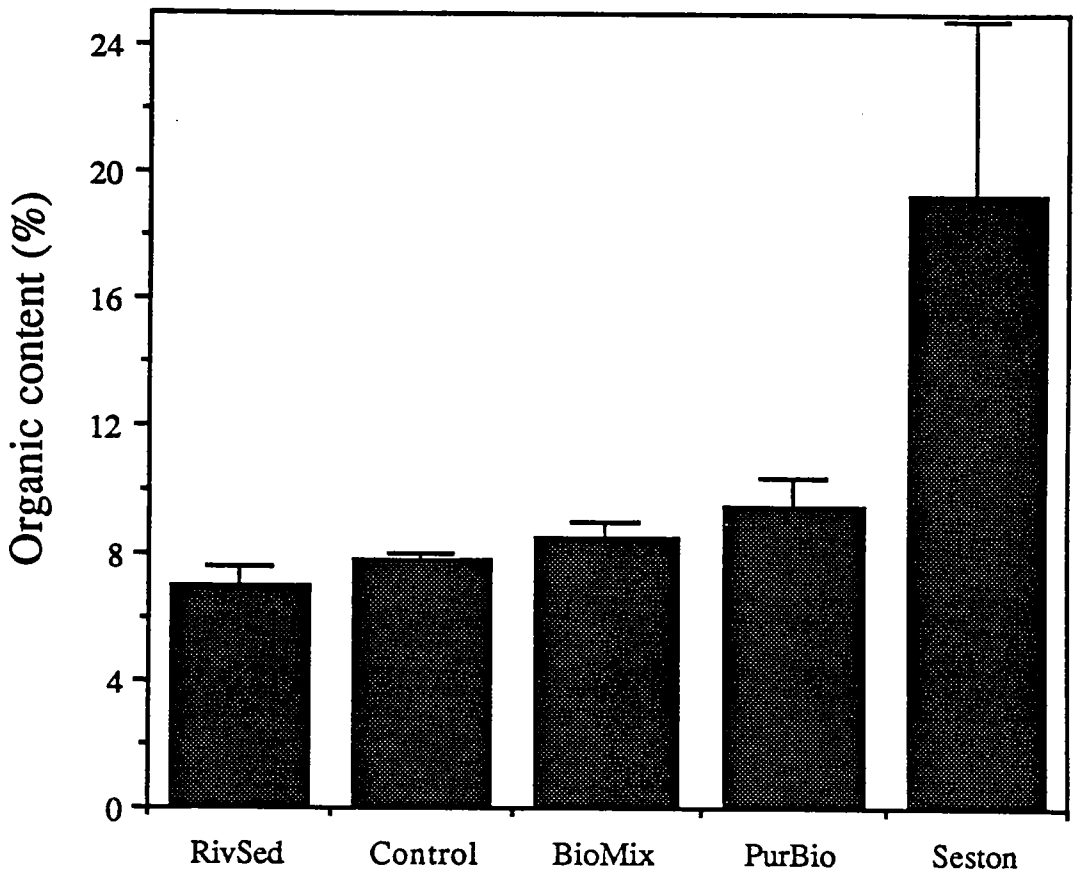

Figure 1. Percent organic content of various sediments and seston. RivSed=river sediment, Control=control sediment, BioMix=biodeposit mixture, PurBio=pure biodeposits and Seston=seston. Vertical bars show standard deviations. The biodeposit mixture (BioMix) was statistically higher in organic content than the control (Control) (t-test, $p<0.05$).

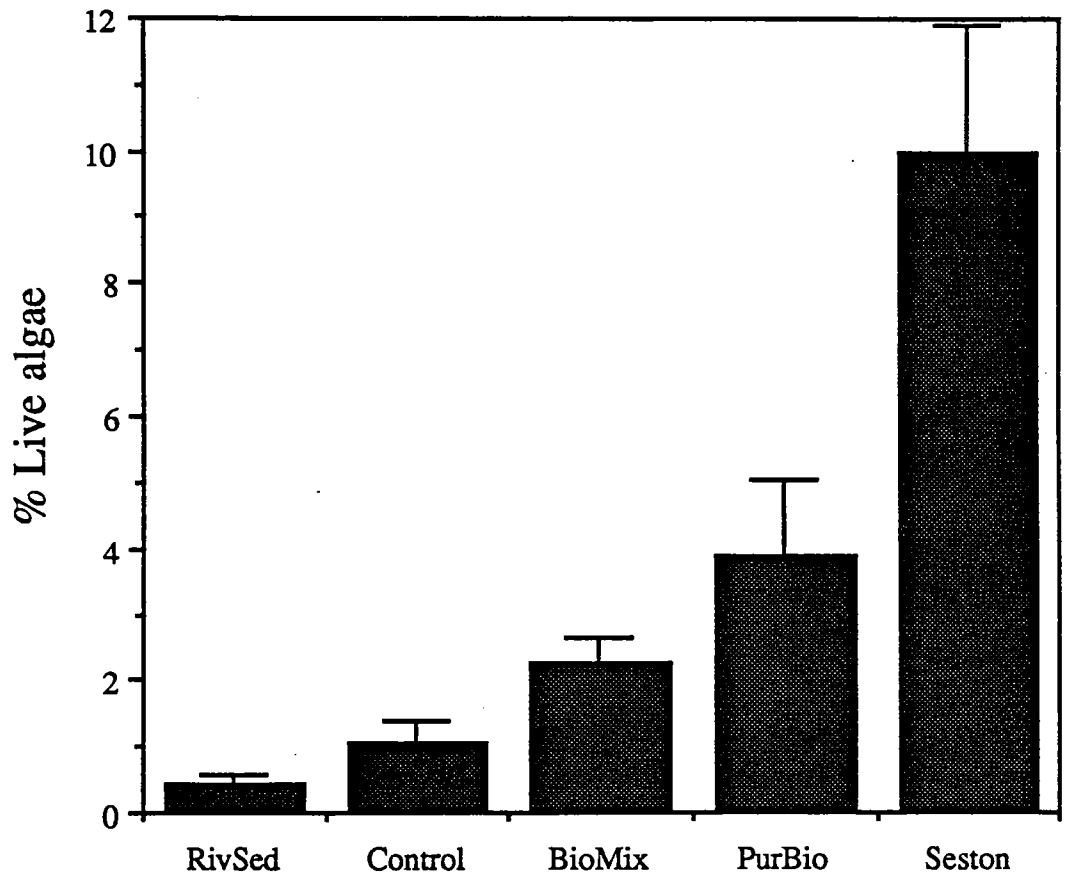

Figure 2. Estimated percentage of various sediments and seston consisting of live algae. Algal biomass is estimated by multiplying chl-a by 100. Vertical bars show standard deviations. The biodeposit mixture (BioMix) was statistically higher in live algae than the control (Control) (t-test, $p<0.05$).

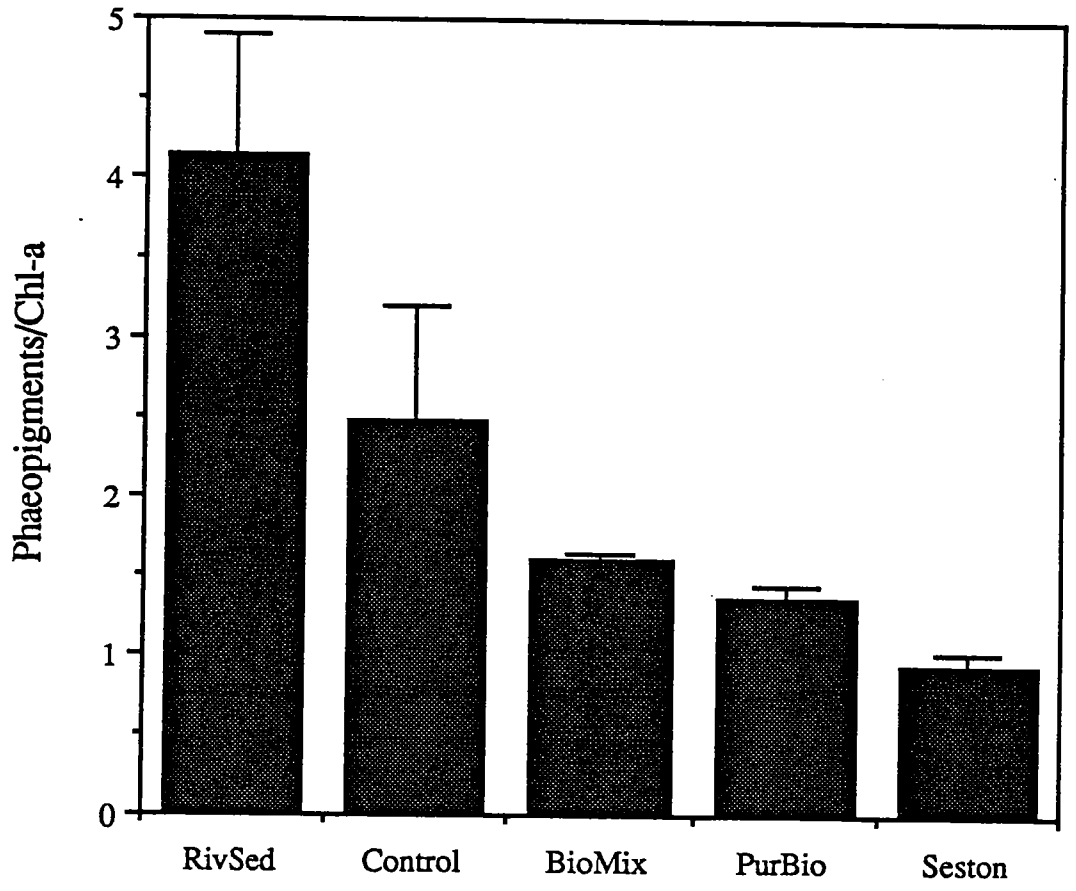

Figure 3. Ratio of detrital algae to live algae in various sediments and seston. Ratio is expressed as ratio of phaeopigments to chlorophyll-a. Vertical bars show standard deviations. The biodeposit mixture (BioMix) ratio was statistically lower than the control (Control) (t-test, $p<0.05$).

biodeposits are consistently closest to seston in their values (Figs. 1-3).

While C:N ratios typical for Hudson River seston were not obtained for comparison in this study, presumably they are low compared to the various sediment types studied here. If this is the case, then again biodeposit mixtures would be ranked closest to seston. Compared to control sediments, biodeposit mixtures were enriched by approximately 8% and 16% in carbon and nitrogen, respectively; consequently the C:N ratio was lower for the biodeposit mixtures. If the C:N ratio is taken as an index of food quality, the organic matter of biodeposits should be of higher quality as a food source for bacteria and benthic protozoans and deposit feeders than the organic matter in either the control sediments or the river sediments (both have a C:N ratio of 9.7; Fig. 4).

Table 1. Quantity of sediment in experimental and control chambers, biodeposition rates and implied filtration rates: filtration rate estimates used a mean suspended solids concentration of 9.8 mg DW L^{-1}. Incubations are approximately 24 hours in length. Error values are standard errors.

Incubation date	Sediment with mussels (g DW)	Sediment without mussels (g DW)	Estimated biodeposit content (%)	Biodeposition rate (mg $ind.^{-1}$ day^{-1})	Estimated filtration rate (L $ind.^{-1}$ day^{-1})
7/26	79.7	48.5	39	58	5.9
7/28	81.5	55.9	31	43	4.4
8/4	64.6	33.4	48	55	5.6
8/12	99.7	62.0	38	65	6.6
mean	81.4 ± 7.2	50.0 ± 6.2	39 ± 3	55 ± 5	5.6 ± 0.5

Results of the bacterial production assays are consistent with this hypothesis. The rate at which cells are produced, per gram of organic matter, is higher in the biodeposit mixture than in control sediments by approximately 35%. Mixing model calculations yield a theoretical production value for pure biodeposits which is approximately 97% higher than the control. Since a larger starting population may incorporate more thymidine without necessarily growing more rapidly per cell, production was also

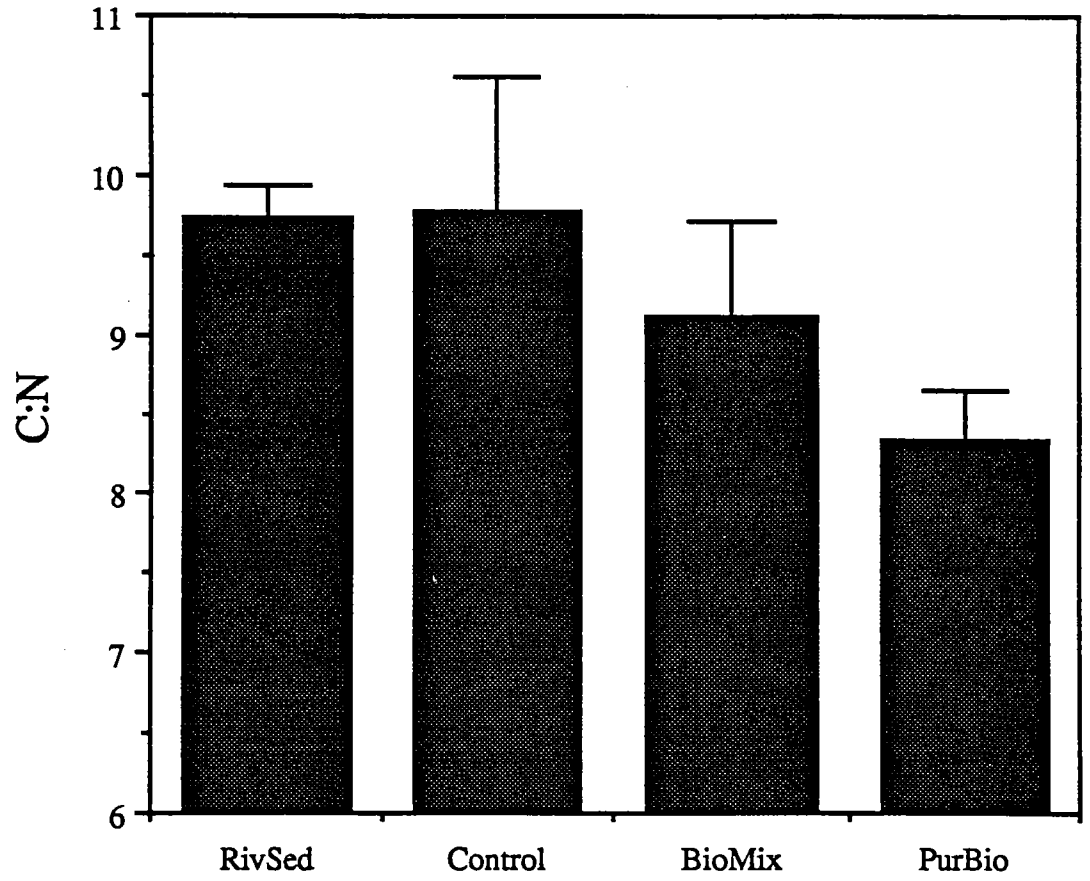

Figure 4. Ratio of carbon to nitrogen by weight in various sediments and seston. Vertical bars show standard errors. The biodeposit mixture (BioMix) C:N ratio was statistically lower than the control (Control) (t-test, $p<0.05$).

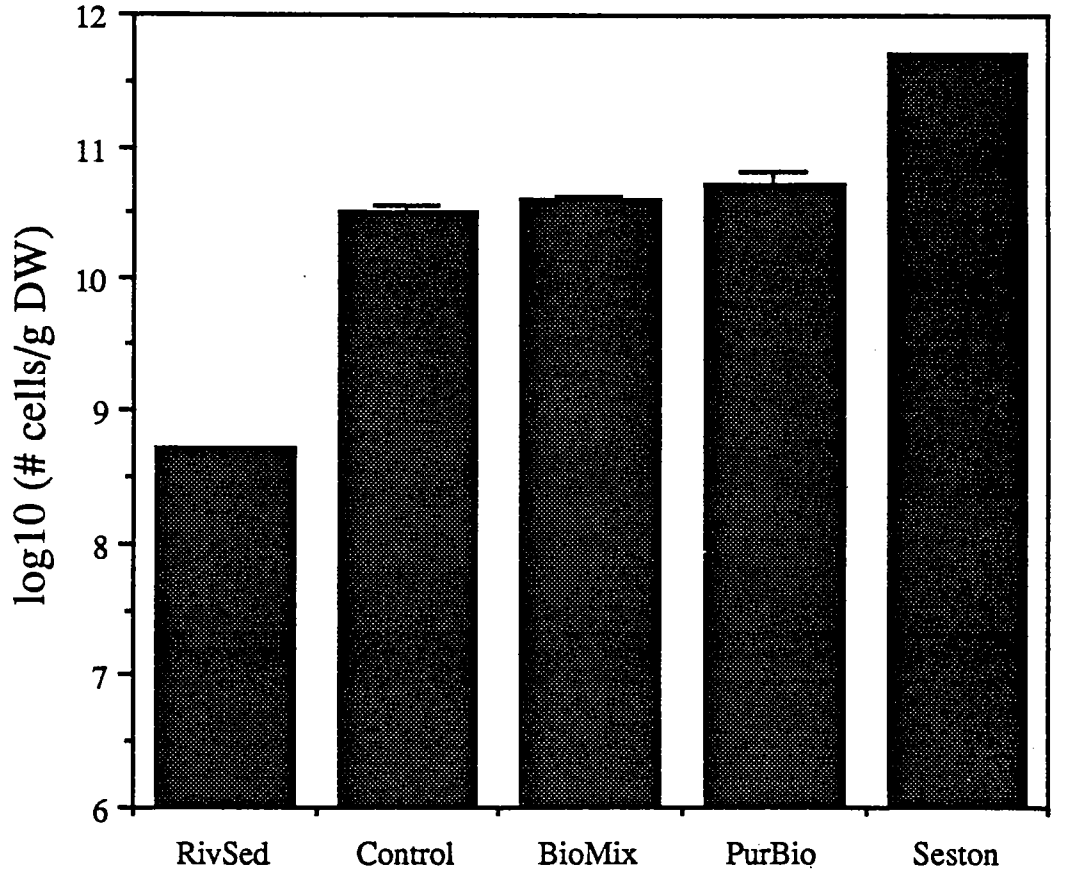

Figure 5. Bacterial densities in various sediments and seston. Vertical bars show standard errors. Differences between the biodeposit mixture (BioMix) and the control (Control) were not statistically significant. River sediment (RivSed) and seston (Seston) values are from Austin and Findlay 1989.

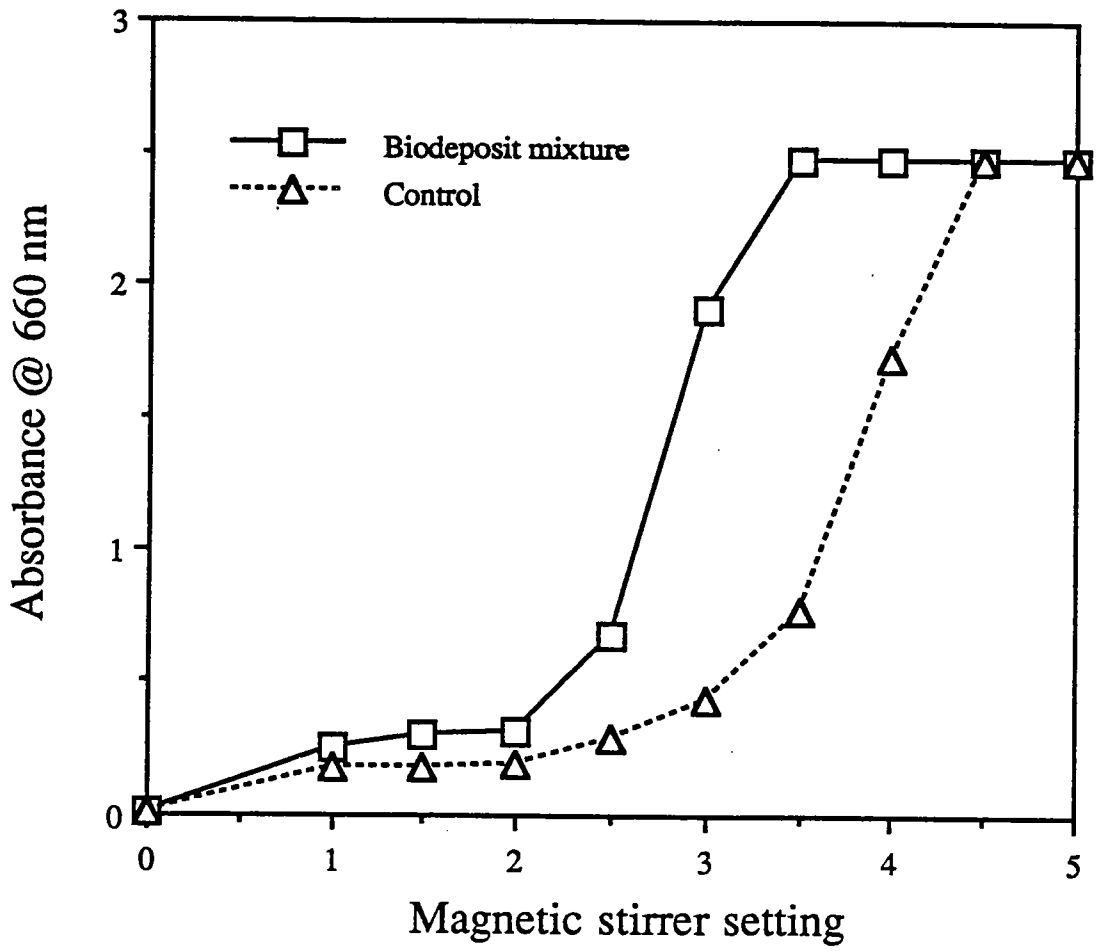

Figure 6. Suspension of control sediments and biodeposit mixtures as a function of mixing intensity. Higher stirrer settings indicate more vigorous mixing. A linear correspondance is assumed between light absorbance at 660 nm and concentration of suspended solids. Saturation of the spectrophotometer is reached at 2.47.

expressed as turnover time. Mean turnover times for control sediments, biodeposit mixtures and pure biodeposits are 231 days, 201 days and 168 days, respectively. While these times suggest bacteria in biodeposits are growing at a faster rate than in control sediments, a comparison with turnover times typical of seston and river sediments--on the order of several days and 20 days, respectively (Austin and Findlay 1989)--reveals how low these rates are. Given that biodeposit sediments are quite similar to seston in ways discussed above, it is surprising that turnover times are not closer to those of seston, or at least shorter than those of river sediment. It is possible that the protocol of the incubation with labelled thymidine needs to be adjusted for use with these sediments. We suggest using our figures for comparison between sediment types, not as absolute values.

We were also surprised to find that bacterial densities were not greatly enriched in the biodeposits, if at all. Other work (Izvekova and Lvova-Katchanova 1972) found zebra mussel pseudofeces were more rich in bacteria than the original seston, although it is difficult to compare their results to ours because their cell numbers are expressed per unit volume of material, and it is not clear how much solid matter corresponds to these volumes. A comparison of our cell densities to typical sediment and seston values (Fig. 5) shows that cell counts in biodeposits and control sediments fall somewhere between seston and river sediments, and are not significantly different from one another. The reason for this may be that most bacterial biomass in the water column is not attached to particulate matter (Findlay, personal communication). The clearance efficiency of zebra mussels for particles below about 1μm drops rapidly (Sprung and Rose 1988), so suspension feeding by mussels may not filter out bacteria. Greater bacterial densities may occur as bacteria quickly colonize the more nutritive sediment and grow more rapidly in it; however, the 24-hour in situ incubations used here may not have provided sufficient time for colonization and growth to occur.

We also hypothesized that, given high ambient concentrations of suspended solids in the Hudson River, pseudofeces production by mussels would be high. This hypothesis is supported by the high chlorophyll-a content (Fig. 2) and low ratio of phaeopigments to chlorophyll-a (Fig. 3) of the biodeposit mixture; both results suggest that much of the

biodeposit sediments have not been digested by mussels.

Results from the pigment assays also support our claim that excess sediment in chambers with mussels was caused by filtration by mussels and not by a difference in passive settling caused by mussel shells. Since silts and clays, because of their greater density, are more prone to passive settling than phytoplankton cells, a factor which increases the rate of passive settling should enrich the deposits in silts and clays relative to algae. The opposite trend occurred in chambers with mussels--algal cells were deposited more rapidly than in the control.

The fact that biodeposits--which presumably consist mostly of undigested pseudofeces--contain less live algae by weight than seston (fig. 2) may support the view that this material consists of undesirable particles that the mussel rejects. However, if particle selection is occurring, mussels are not selective enough to produce pseudofeces that contain little live algae. Also, because algal cells are less dense than the inorganic component of sediments, the lower amount of live algae in biodeposits relative to seston may partly be explained by a loss from the experimental chamber to resuspension during the incubations. The supernatant of biodeposit mixtures, which was decanted following each sediment collection, was visibly greener than that of control sediments.

Estimates currently place zebra mussel densities in the Hudson River (as of September 1994) at 30,000 mussels m^{-2} in rocky areas and 700 mussels m^{-2} riverwide (Strayer, personal communication). Biodeposition characteristics obtained from this study can be applied to these densities to gain insight into the ecosystem-scale implications of these processes. If we use our mean biodeposition rate of 55 mg DW $mussel^{-1}$ day^{-1} (Table 1), and we estimate the N, C, and chlorophyll-a content of this matter using values estimated for pure biodeposits, we get the following results: riverwide, zebra mussels will cause an estimated flux of 38.5 g DW of matter per m^2 per day, containing 0.2 g N, 1.7 g organic C and 1.5 g of live algal biomass. In rocky areas, zebra mussels will cause an estimated flux of 1.65 kg DW of matter per m^2 per day, containing 8.7 g N, 72.8 g organic C and 64.4 g of live algal biomass.

Obviously, these values correspond to theoretical quantities of solids filtered out

of the water column by mussels, and they do not account for the resuspension of matter that is bound to occur to varying degrees in a river environment. The latter omission highlights the importance of understanding how easily biodeposits are resuspended if the ecosystem effects of biodeposition by zebra mussels are to be known. This leads to the last assay of this study.

Resuspension of both control and biodeposit mixture sediments, at different mixing energies, showed that for conditions of equal mixing energy, more biodeposit mixture sediments were resuspended than control sediments (Fig. 6). Also, the threshold energy at which major resuspension occurred was lower for the biodeposit mixture sediments than control sediments. It would be desirable to convert into conventional energy units the energy introduced by the magnetic stirring bar, and to estimate mixing energies of river processes such as tides. This would allow us to relate the river energies to the critical resuspension energies determined in this experiment, and thus estimate whether resuspension will occur on a tidal cycle.

As mentioned earlier, mussel beds greatly increase the surface area available for retaining sediments (Wiktor 1963). The resuspension measured in this experiment was from a flat surface, and is therefore an overestimate. However, it will be technically difficult to model this process realistically, and thus make a realistic estimate of how long biodeposits are available to deposit feeders and benthic protozoans. The sediment retention mechanisms employed by the biota, such as the mucus nets of deposit feeders, are an additional factor which will determine how ecologically significant the flux of nutrients and energy to the river bottom is. Both the amount and nature of the biodeposits remaining on the river bottom will depend critically on the energy regime of the specific parts of the river, the roughness of the bottom, and the nature of the structures, including the biological structures, available to retain particles on the bottom.

A study in Lake Ontario (Stewart and Haynes 1994) has shown that, over a period coinciding with declining fertility of the Lake Ontario ecosystem, many benthic macroinvertebrate taxa have increased in abundance since the arrival of zebra mussels. These authors attribute this change partly to an increased flow of energy to benthic

environments. We predict a similar pattern will occur in the Hudson River based on the results of the assays in this study; however, further studies of patterns of resuspension in different parts of the Hudson River will be important in fine-tuning this prediction.

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