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Characteristics of zebra mussel (*Dreissena polymorpha*) biodeposits in a tidal freshwater estuary

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With 2 figures and 2 tables in the text

Abstract: Zebra mussels are now a major component of the benthos in the tidal freshwater Hudson River. Their filtering activity has had a wide range of ecosystem-level effects. Zebra mussel biodeposits (feces and pseudofeces) were sampled in in situ chambers containing mussels attached to artificial substrates. The biodeposits collected were analyzed for organic matter (OM), chlorophyll-a, phaeopigments, C, N, bacterial cell densities, and bacterial production rates. Relative to control sediments (sediments passively collecting in the chambers), biodeposits were significantly enriched in all measures except bacterial cell densities. Biodeposits were estimated to contain 9.5 % OM and 3.9 % live algae by weight, while values in passive deposits were 7.8 % and 1.1 %, respectively. The C : N ratio of biodeposits was estimated at 8.3, and bacterial production was estimated at 14.6×10^7 cells $gOM^{-1}\,h^{-1}$, while passive deposit values were 9.8 and 7.4×10^7 cells $gOM^{-1}\,h^{-1}$, respectively. When subjected to a range of mixing energies, biodeposit mixtures (feces, pseudofeces and passive deposits) were resuspended at a bed stress that was approximately 50 % lower than the bed stress required to resuspend the passive deposits. Although biodeposits were shown to be enriched in the above measures, their resuspension by water currents in a system like the tidal freshwater Hudson River will reduce their residence time at the river bottom, possibly reducing their ecological impact on the benthos.

Introduction

The zebra mussel often is the most abundant macrofaunal species in some aquatic ecosystems (WIKTOR 1963, STANCZYKOWSKA 1984, STEWART & HAYNES 1994), and this species may have a major influence on particle fluxes and nutrient cycles in these ecosystems through its filtration of the water column (MACISAAC et al. 1992, HOLLAND 1993, NICHOLLS & HOPKINS 1993, FAH-

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NENSTIEL et al. 1995, CARACO et al. 1997). The benthic effects of zebra mussels are not well studied, however. Large quantities of processed seston (both organic and inorganic) may be deposited in zebra mussel beds as feces or pseudofeces, coupling pelagic energy and nutrients to benthic food webs (STANCZYKOWSKA et al. 1976, STANCZYKOWSKA & LEWANDOWSKI 1993, KLERKS et al. 1996).

Pseudofeces consist of undigested filtered solids which are bound with mucus and expelled periodically through the mussel's inhalant siphon (MORTON 1969). Zebra mussels produce large amounts of pseudofeces in Hudson River water (RODITI, unpubl.), and pseudofeces may be the predominant form of zebra mussel waste particles produced in turbid environments like the Hudson River estuary. In a European river, 90 % of zebra mussel waste particles were observed to be pseudofeces (REEDERS & BIJ DE VAATE 1992) and pseudofeces production has been observed to increase with increasing suspended sediment (MACISAAC & ROCHA 1995). Given the relative high concentrations of suspended solids (SS) in Hudson River water (FINDLAY et al. 1991) we hypothesized that much of zebra mussel biodeposits would be in the form of pseudofeces.

IZVEKOVA & LVOVA-KATCHANOVA (1972), in one of the only studies characterizing this material, found pseudofeces had higher bacterial densities than seston and contained a detritus-bacterial complex rich in nutritional value for the chironomid larvae they studied. KLERKS et al. (1996) examined the effects of zebra mussels on sediment deposition rates and on the organic content and % silt and clay of the biodeposits, using flow-through aquaria in the lab and in situ sediment traps; findings showed that mussels accelerated deposition rates in both lab and in situ treatments and increased organic content in lab flow-through aquaria.

Earlier filtration experiments (RODITI et al. 1996) using mussels collected from the Hudson River and incubated in Hudson River water showed that mussels cleared suspended phytoplankton and inorganic seston from river water non-selectively, at 2.8 ± 0.2 L mussel^{-1} day^{-1} (shell length = 13 mm). If we apply these rates to a mussel density of 17,000 mussels m^{-2} (estimated density in rocky areas in September 1993; STRAYER et al. 1996), and a mean SS value of 16.9 mg dry mass (DM) L^{-1} (FINDLAY et al. 1991), we estimate that 1 m^2 of mussels can filter ~48 m^3 of water daily, and process ~811 g DM of solids, much of which may be biodeposited at the sediment surface (these may be overestimates since a perfectly-mixed water column is unlikely; FRÉCHETTE et al. 1989, O'RIORDAN et al. 1993). Thus, biodeposition by zebra mussels may significantly alter sediments at the river bottom, potentially altering community structure of the benthos (BRINKHURST 1974, COLE et al. 1988, ALLAN 1995).

While some chemical and biological aspects of bivalve biodeposits have been studied in marine ecosystems (JORDAN & VALIELA 1982, TSUCHIYA 1980,

SMITH & FREY 1985) and in lakes (WIKTOR 1963, IZVEKOVA & LVOVA-KATCHANOVA 1972, STANCZYKOWSKA et al. 1976), findings may not be applicable to river ecosystems because the composition of seston in rivers is different and includes a large fraction of inorganic matter derived from erosion and resuspension. Also, the water column is well mixed by river flow and tides in estuarine systems, which tends to resuspend sediments.

In situ chambers were used in this study due to the difficulty of sampling biodeposits directly from mussel beds. Surface sediments are resuspended frequently due to tidal currents, and it would be difficult to find field sites that are alike in all respects except for the presence and absence of mussels. We thus deployed microcosms in the field which exposed mussels to ambient river water and retained biodeposits.

We expected that zebra mussel biodeposits would be distinct from existing river sediment for two reasons. Firstly, as stated above, zebra mussels clear particles from Hudson River water non-selectively. This suggests there will be a flux to the sediment surface of the same assemblage of particles present in the water column, much of which would not settle gravitationally. Secondly, because concentrations of SS in Hudson River water are relatively high, it appeared that most of the biodeposited matter would be in the form of undigested pseudofeces and therefore the organic fraction would be relatively undigested and, again, would resemble the organic fraction suspended in the water-column.

This is the first comprehensive survey of the biological, chemical, and physical characteristics of biodeposits produced by zebra mussels in situ. Our objective was to describe changes that zebra mussel populations cause in a range of sediment characteristics in the tidal freshwater portion of the Hudson River.

Methods

Experimental design

Zebra mussels were collected from the Hudson River at Poughkeepsie, NY, and allowed to reattach to artificial substrates consisting of rigid plastic mesh surfaces measuring 47 cm by 32 cm. Sediments could settle through the mesh and accumulate without being resuspended by river flow or tidal current. Plastic substrates were placed in covered plastic basins measuring 49 cm by 34 cm, with a height of 22 cm (Fig. 1). Both long sides of each container had 4 cm by 17 cm openings to allow water to flow through. Each basin was kept perpendicular to the river current, so that water flowed directly through the openings, and fastened securely about 25 cm above the river bottom.

Two microcosms were used in each field incubation, one with mussels and the other as a control without mussels. Two microcosms only were deployed due to their

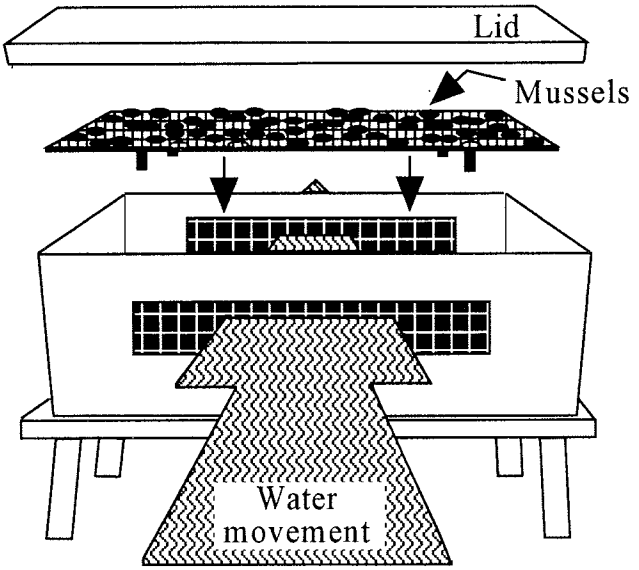

Fig. 1. Chamber deployed in the Hudson River to collect zebra mussel biodeposits; two chambers were used – one a control with only gravel "mimics" of zebra mussels, and one with approximately 575 mussels (mean shell length = 17 mm). Mussels reattached to rigid plastic mesh surfaces (47 cm by 32 cm) which were placed within plastic enclosures (49 cm by 34 cm by 22 cm high) shown above. Both long sides of each enclosure had a 4-cm by 17-cm opening to allow flow through. Biodeposits settled through the rigid mesh surface and accumulated during 24-hour incubations. The apparatus was 25 cm above the river bottom, with its upper surface a minimum of 1 m below water surface at low tide.

large size and the difficulty of moving them in the field. Replication was in series, over 4 dates and variability in measures over these dates was low and results were highly repeatable. Approximately 575 mussels with a mean shell length of 17 mm were placed in the mussel chamber (the resulting microcosm density of 3800 mussels m^{-2} is low relative to populations in rocky areas). In the control, gravel of approximately the same size as the mussels was placed on an identical substrate to simulate the surface texture of the mussel treatment. Sediments were obtained from 24-hour incubations on four separate dates through July and August, 1994. One hour after collection, surface water was decanted from each chamber and sediments were mixed well for analysis. Assays were conducted on sediments collected on 2 to 4 of these collection dates, referred to here as replicate sediments. River water and in situ sediments were 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

The organic content of sediment was determined by drying samples at 60 °C for 48 h then measuring weight loss on combustion at 450 °C for 4 h. Chlorophyll-a and phaeo-

pigments in river water samples were measured according to HOLM-HANSEN & RIEMANN (1978). SS of water samples was determined by filtration on tared 0.4-μm Nuclepore filters, followed by oven-drying for 48 h at 60 °C. The chlorophyll-a and phaeopigment content of sediment was determined as described above after diluting in deionized water and then filtering water samples. To estimate algal biomass (AFDM), we multiplied chlorophyll values by 100 (chlorophyll × 50 = organic C; organic C × 2 = biomass; CARACO et al. 1997). To estimate nitrogen content, sediments were oven-dried (48 h at 60 °C), then pulverized and analyzed in a Carlo Erba NA 1500 CNS analyzer.

Biological assays

Bacteria were counted according to 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 with Irgalan black. Bacterial production was measured by rate of uptake of labeled ^{3}H-thymidine into bacterial DNA according to the methods of FINDLAY et al. (1984). Incubations lasted 36 and 54 minutes. Five live subsamples and two subsamples killed with formalin as controls were drawn from biodeposit sediments and control sediments obtained on 2 dates.

Physical assay

We compared the relative ease of resuspension of biodeposits and sediments trapped in control chambers. Volumes of biodeposit mixture (including feces, pseudofeces and passive deposits) and control sediment, each containing equal amounts of solid matter (DM), were evenly distributed in Petri dishes in separate 1-L beakers filled with 0.7 L deionized H_2O. A suspended stirring bar was centered over each sediment type for mixing without direct contact. An initial water sample was taken, then the rate of stirring 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 to measure SS, with absorbance measured at 660 nm in 1 × 1-cm cuvettes with a Shimadzu UV 160 spectrophotometer.

Biodeposit dilution model

The sediments in chambers with mussels were a mixture of mussel biodeposits and solids that settled passively. The dilution of biodeposits with non-biodeposit solids can be corrected for by using the data from the control chambers. Subtraction of control sediments from mussel chamber sediments should yield the quantity of sediment biodeposited by mussels. Using the ratio of passively deposited sediment to biodeposits in mussel chambers, and the known characteristics of passively deposited sediment, the characteristics of pure biodeposits were estimated algebraically. We refer to these calculated values as "pure biodeposits", and the sediments actually collected from mussel chambers as "biodeposit mixtures".

Statistical analyses (1-tailed paired t-test, $p < 0.05$) compared control sediments with biodeposit mixtures only. Because the biodeposit mixtures contained roughly 60 % passively settled solids, the values used for statistical analysis here are likely to underestimate actual differences between pure biodeposits and passively-deposited sediment.

Results

Sediment accumulated more rapidly in chambers with mussels, compared to chambers with gravel "mimics" (t-test, $p < 0.05$). Mussel chambers contained on average 39 % more sediment than controls (Table 1). From these data, we estimate a deposition rate of 2.3 ± 0.4 mg mussel^{-1} h^{-1}. While SS in river water varied during these incubations, a mean value of 9.8 mg DM L^{-1} (SD = 3.4) was obtained from five measurements made over a one-week concurrent period. This SS value can be used to indirectly estimate a filtration rate of 230 mL mussel^{-1} h^{-1}, which is close to filtration rates predicted by Roditi et al. (1996) and Kryger & Riisgård (1988), both of which predicted an average of 170 mL mussel^{-1} h^{-1} for this size distribution of mussels. Therefore, these chambers provide a reasonable estimate of zebra mussel biodeposition rate under field conditions.

Chemical assays

Biodeposit mixtures were significantly higher than passively deposited sediments in organic content, algal biomass, phaeopigments, and nitrogen (t-test, $p < 0.05$; Table 2). According to our biodeposit dilution model, pure biodeposits had an organic content 22 % higher than passively deposited sediments. Pure biodeposits were estimated to consist of 3.9 % live algae by weight, which is approximately four times the value for passively deposited sediments.

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

Incubation date	Sediment with mussels (g DM)	Sediment without mussels (g DM)	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

Table 2. Characteristics of passive deposits (sediment in control chambers), zebra mussel biodeposits, calculated pure zebra mussel biodeposits (using a biodeposit dilution model), seston and field sediments. Values are means over all trials, with standard errors in parentheses (n = 2 to 6). Statistical comparisons were made between passive deposits and biodeposits (columns 1 and 2); asterisks show statistically significant differences (t-test, $p < 0.05$). Characteristics of calculated pure biodeposits, seston and field sediment (columns 3 through 5) may be most relevant understanding processes in the river and are shown for comparison.

	Passive deposits	Biodeposits	Calculated pure biodeposits	Seston	Field sediment
% loss on ignition	7.8 (0.1)	8.5 (0.2)*	9.5 (0.5)	19.3 (1.6)	7.0 (0.3)
% C	3.6 (0.04)	4.0 (0.03)*	4.4 (0.1)	na	3.5 (0.1)
% N	0.38 (0.02)	0.44 (0.02)*	0.53 (0.02)	na	0.36 (0.01)
C:N[a]	9.8 (0.4)	9.1 (0.3)*	8.3 (0.2)	7.1[b]	9.7 (0.1)
% live algae	1.1 (0.2)	2.3 (0.3)*	3.9 (0.8)	10.0 (0.9)	0.45 (0.07)
phaeopigments: chlorophyll	2.5 (0.5)	1.6 (0.03)*	1.4 (0.1)	0.94 (0.04)	4.1 (0.4)
bacterial density (10^{10} cells gDM^{-1})	3.2 (0.7)	4.0 (0.5)	5.3 (0.9)	83[c]	0.50 (0.03)
bacterial production (10^7 cells $gOM^{-1}hr^{-1}$)	7.4 (0.02)	10.0 (1.0)*	14.6 (2.1)	68[c]	4[d]

[a] by mass
[b] typical summer value, 1986–1988, COLE (pers. comm.)
[c] FINDLAY, unpublished
[d] SINSABAUGH & FINDLAY (1995)

Furthermore, biodeposit mixtures had a lower phaeopigments : chlorophyll-a ratio than passively deposited sediments (t-test, $p < 0.05$). Pure biodeposits contained almost 40 % more N than passive deposits, and the C : N ratio of biodeposits was also significantly lower than the control (t-test, $p < 0.05$). For all these constituents, river sediment, passively deposited sediment, biodeposit mixtures, pure biodeposits, and seston form a gradient of increasing content (Table 2).

Biological assays

Mean bacterial densities in biodeposit mixtures were not significantly higher than those in passively deposited sediments (t-test, $p < 0.05$; Table 2). Bacterial densities in both sediment types fell roughly between typical values for river sediment and seston in the Hudson River (AUSTIN & FINDLAY 1989, FINDLAY et al. 1991). Bacterial production in biodeposit mixtures was significantly higher than in passively deposited sediments; the model-generated growth rate in pure biodeposits was twice that in the passive sediments (Table 2).

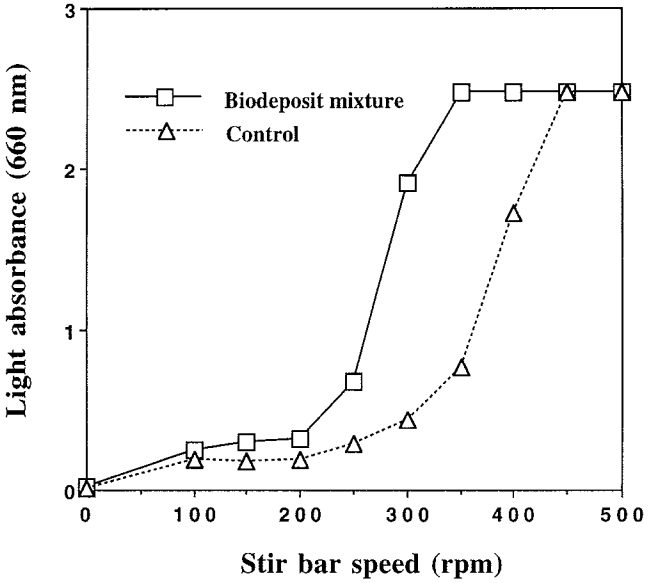

Fig. 2. Resuspension of control sediments and biodeposit mixtures as a function of stir bar speed. A suspended stir bar was placed over sediment in a petri dish, under 0.7L of water. Light absorbance (OD660) of overlying water was measured as an index of sediment resuspension. The highest value possible on the spectrophotometer is 2.47.

Physical assay

At all rates of magnetic stirring, more of the biodeposit mixture was resuspended than the passively-deposited sediment (Fig. 2). The critical stir bar speed at which there was a sudden increase in the amount of sediment resuspended was above 250 rpm in the case of the biodeposit mixture and above 350 rpm for the passively-deposited sediment. To approximate the bed stress we assumed quadratic drag and determined the drag coefficient based on a Reynolds number calculated from the maximum water velocity and the water depth. The resulting bed stress values using a drag coefficient relation from SABERSKY et al. (1971) were 4.1 dynes cm^{-2} and 7.4 dynes cm^{-2} at 250 and 350 rpm, respectively.

Discussion

The problem of characterizing effects of zebra mussel biodeposition on river sediment can be divided into 2 parts: first, characterization of biodeposits, and second, determination of the effects of local hydrodynamics on resuspension of biodeposits. In this study we undertook the first part, and we also compared resuspendability of biodeposit and non-biodeposit sediments.

Our results support the hypothesis that filter-feeding by zebra mussels brings high quality pelagic resources to the river bottom. By any of several measures (content of OM, N, algae), zebra mussel biodeposits were of substantially higher quality for benthic consumers than control sediments. In contrast, bacterial densities were not greatly enriched in the biodeposits. This finding differed from that of IZVEKOVA & LVOVA-KATCHANOVA (1972); the latter study found zebra mussel pseudofeces to be enriched in bacteria relative to seston. A comparison of our cell densities to typical sediment and seston values (Table 2) shows that cell counts in biodeposits and control sediments fell somewhere between seston and river sediments, and were not significantly different from each other. The reason for this may be that most bacterial biomass in the water column is not attached to particulate matter and is less than 1 μm in size (FINDLAY, unpubl.). The clearance efficiency of zebra mussels for particles below about 1 μm drops rapidly (SPRUNG & ROSE 1988, LEI et al. 1996), so suspension feeding by mussels may not filter out most bacteria.

COTNER et al. (1995) found that zebra mussels fed on bacterial-sized particles (0.36 and 0.91 μm) and they reduced bacterial abundances in overlying water. Clearance rates of the 0.91-μm particles were 5–37 % of those for phytoplankton particles. These results are not inconsistent with our findings. While the bacterial densities in passive deposits and biodeposit mixtures were not statistically different (possibly because mixing of passive deposits with biodeposits reduces the signal to noise ratio), a clearance efficiency for bacteria of 4–9 % of seston clearance rates would be consistent with the bacterial densities we measured (Table 2). The higher bacterial growth rates measured in biodeposits suggest that over time bacteria may increase rapidly in number as they quickly colonize the nutritive biodeposits and grow more rapidly in them; however, our 24-hour incubations may not provide the time for colonization and growth to occur.

Measurement of biodeposition must account for passive settling of particles. Our control chambers deployed with gravel "mimics" of zebra mussels acted as sediment traps. However, the consistently greater mass of material in the zebra mussel chambers shows this technique can be used to collect biodeposit mixtures under field conditions. Sixty percent of the "biodeposit mixture" consists of these particles which settled passively. If this process favored the settling of denser particles, which are likely to be mineral particles, it should have diluted sediments in mussel chambers with silts and clays and made our hypothesized sediment enrichment in mussel treatments more difficult to detect. However, these "mixed biodeposit" sediments were still significantly enriched (t-test, $p<0.05$) relative both to control sediments and natural river sediments in sites without mussels.

We also hypothesized that, given the relatively high SS load in Hudson River water, pseudofeces production would be high. This hypothesis is sup-

ported by the high chlorophyll-a content and low phaeopigment : chlorophyll-a ratio (Table 2) of the biodeposit mixture; both results suggest that much of the biodeposit sediments has not been digested by mussels and is pseudofeces rather than feces. The fact that biodeposits contain less live algae by weight than seston (Table 2) may indicate that some degree of pre-ingestive particle sorting is occurring; however, if this is so, mussels are still not selective enough to produce pseudofeces that contain little live algae.

Our biodeposition rates (55 ± 5 mg DM mussel^{-1} day^{-1}; mean mussel size = 17 mm and SS = 9.8 mg DM L^{-1}) are low compared to other studies. KLERKS et al. (1996) observed a biodeposition rate of 164 mg DM mussel^{-1} day^{-1} with approx. 50 mg L^{-1} SS in overlying water (mussel size = 17.5–22.5 mm). REEDERS & BIJDE VAATE (1992) observed a biodeposition rate of approx. 100 mg DM mussel^{-1} day^{-1} with 87 mg L^{-1} SS in overlying water (mussel size = 19 mm). However, if we consider the low SS in overlying water during our study relative to other studies and express our results in terms of the volume of water mussels cleared, our biodeposition rates are relatively high. Our study yields 5.6 L mussel^{-1} day^{-1}, versus approx. 3.3 L mussel^{-1} day^{-1} (KLERKS et al. 1996) and 1.2 L mussel^{-1} day^{-1} (REEDERS & BIJDE VAATE 1992). This may be due to declining pumping rates at higher SS values (SPRUNG & ROSE 1988).

In September 1993, zebra mussel densities in the Hudson River were 17,000 m^{-2} in rocky areas and 1200 mussels m^{-2} riverwide (STRAYER et al. 1996). Using these numbers with our mean biodeposition rate of 55 mg DM mussel^{-1} day^{-1} (Table 1), and the N, C, and chlorophyll-a contents of pure biodeposits from Table 2, we estimate that, riverwide, zebra mussels will cause a gross deposition of 66 g DM per m^2 per day, containing 0.3 g N, 2.9 g organic C and 2.6 g of live algal biomass. In rocky areas, zebra mussels will cause an estimated gross biodeposition of 940 g DM per m^2 per day, containing 4.9 g N, 41 g organic C and 36 g of live algal biomass.

These calculations, of course, are not adjusted for resuspension of biodeposits from the river bottom. We have shown that biodeposits are resuspended at a bed shear stress which is approximately 50 % lower than the bed stress which resuspends control sediments, further suggesting that net biodeposition must be lower than the gross rates above. The amount of biodeposits actually retained on the bottom and made available to the benthic biota will depend 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 & HAYNES 1994) has shown that 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 due to zebra mussel biodeposits. We predict a similar pattern will occur in the Hudson River based on the results of

our study; however, further studies of patterns of resuspension in different parts of the Hudson River will be important in fine-tuning this prediction.

Acknowledgements

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