

Effects of sediment source and flow regime on clam and sediment transport

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ABSTRACT: Erosion and transport of juvenile benthic invertebrates, including bivalves, has the potential to alter patterns of distribution and abundance during the early postsettlement period. Field observations indicate that there is often great spatial variability in rates of transport of juvenile bivalves. Differences in transport among sites may arise from both physical and biological causes, including variation in water flow, sediment grain size, and the local biological community. In this study, an experiment was conducted in a laboratory flume to examine the effect of sediment source (4 subtidal sites in the Navesink River estuary, New Jersey, USA) and flow velocity on rates of transport of juvenile *Mya arenaria* and *Gemma gemma*. Rates of erosion of *M. arenaria* were significantly related to sediment volume eroded, suggesting that dispersal at high flow speeds is linked to bedload transport. Sediment erosion and clam transport was lower for sediment cores from the 2 sites where the sediment was covered by a mat of amphipod *Ampelisca abdita* tubes. Reduction of the tube mat resulted in a small but significant increase in sediment erosion. The results of this study and comparison of shear velocities between the laboratory and the field suggest that both the presence of an amphipod mat and low shear velocities will result in low rates of transport of sediment and juvenile clams in the field.

KEY WORDS: Juvenile dispersal · Recruitment · Bivalves · Sediment transport · Amphipod tubes

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INTRODUCTION

Understanding the processes that generate patterns of recruitment of benthic invertebrates requires knowledge not only of patterns of larval supply and settlement (Butman 1987, Snelgrove & Butman 1994), but also of early postsettlement mortality (reviewed by Hunt & Scheibling 1997) and juvenile dispersal (reviewed by Günther 1992, Palmer et al. 1996). Post-larval dispersal of macrofauna is likely to be particularly important in soft-bottom habitats because juveniles often live close to the sediment surface, where they are susceptible to erosion by currents and waves. Although the existence of juvenile invertebrate dispersal has been recognized for at least 50 yr (e.g. Baggerman 1953, Smith 1955), it has received much less attention than larval dispersal, and there are critical gaps in our knowledge of this process.

Juvenile bivalves and the sediment they are living in may be resuspended and transported in the water column or may travel along the bottom as bedload (Commito et al. 1995b, Turner et al. 1997). This dispersal is generally influenced both by physical factors and by behaviour. Burrowing is important in maintaining position in the sediment and avoiding erosion, at least at flow speeds less than the sediment's critical erosion velocity (Roegner et al. 1995), and in some cases also at higher velocities (Lundquist et al. 2004). Some bivalves disperse actively by producing threads that increase their drag and, therefore, their likelihood of resuspension into the water column (Sigurdsson et al. 1976, Cummings et al. 1993). Regardless of whether bivalves actively promote or resist the initiation of transport, their subsequent dispersal will be under the control of tidal or wind-driven currents and waves. On intertidal flats, the significance of storms and wind-driven cur-

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rents has been demonstrated by positive relationships between wind conditions and flux of sediment and bivalves in sediment traps (Emerson & Grant 1991, Commito et al. 1995b, Armonies 1996, Turner et al. 1997) and abundance of individuals drifting in the water column (Armonies 1992). Intertidal (Hunt & Mullineaux 2002) and subtidal (Olivier & Retière 1998) studies have found that bivalve transport also varies with tidal conditions and may be influenced by local topography (Rankin et al. 1994).

Field observations indicate that there is a great deal of spatial variability in rates of bivalve transport (e.g. Hunt & Mullineaux 2002). Differences among sites in transport of juvenile bivalves may be generated by both physical and biological factors, particularly those that influence sediment erosion. For example, studies of juvenile *Mya arenaria* indicate that erosion rate often increases with increasing shear velocity (Roegner et al. 1995, Dunn et al. 1999, Gulmann et al. 2001) and that disturbance of the sediment by mud snails *Ilyanassa obsoleta* (Dunn et al. 1999) and shrimp *Cranogon septemspinosa* (Hunt 2004) increases rates of sediment transport and, consequently, juvenile *M. arenaria* transport. Sediment erodability is known to be affected by a number of factors, including variation in water flow (and consequently shear stress on the bottom), sediment grain size and the local biological community. Sediment grain size, which often varies with flow speed, alters the critical erosion velocity of sediments, with larger grain sizes eroding at higher velocities (Miller et al. 1977). In the intertidal zone, sediment stability is increased by organisms like microphytobenthos that cause adhesion of grains (e.g. Sutherland et al. 1998) and decreased by bioturbators such as deposit-feeding bivalves (e.g. *Macoma balthica*) and grazers (e.g. *Hydrobia ulvae*) (reviewed by Widdows & Brinsley 2002). Sediment erodability often varies temporally and spatially due to variations in the balance between biostabilizers and bioturbators (Widdows & Brinsley 2002). Biogenic structures such as animal tubes, pits and mounds, macroalgae and seagrasses will influence flow and affect the erosion rate of sediment (Paterson & Black 1999). For example, tubes created by polychaetes can have either a stabilizing (e.g. Luckenbach 1986, Thrush et al. 1996) or destabilizing effect (Eckman et al. 1981), depending on tube density (Jumars & Nowell 1984a, Friedrichs et al. 2000).

The experiment described in this paper forms part of a larger study whose overall goal is to develop an understanding of the magnitude and scale of transport of juvenile bivalves in an estuary in New Jersey, USA. This larger project combines field observations of hydrodynamic conditions and rates and distances of bivalve dispersal with laboratory flume experiments and modelling. In this study, I used a laboratory flume

to examine the effect of sediment source (4 subtidal sites in the Navesink River, New Jersey) and flow velocity on rates of transport of juvenile *Mya arenaria*, which were added to natural sediment cores, and *Gemma gemma* naturally occurring in the cores. Both *M. arenaria* and *G. gemma* are known to disperse as juveniles (e.g. *M. arenaria*, Baggerman 1953; *G. gemma*, Commito et al. 1995a). This dispersal appears to occur primarily through bedload transport (*M. arenaria*, Emerson & Grant 1991; *G. gemma*, Rankin et al. 1994), although juveniles of both species can produce drifting threads (*M. arenaria*, Sigurdsson et al. 1976) and have been found in the water column (*M. arenaria*, Möller 1986; *G. gemma*, Sellmer 1967).

The 4 study sites differ greatly in flow velocity, sediment grain size and their biological communities, including the ambient density of bivalves and the amphipod *Ampelisca abdita*. The tubes (3.5 cm long, 2 to 3 mm wide, protruding up to 1 cm above the sediment, Mills 1967) of this common amphipod, which occurs in the intertidal and shallow subtidal zones of many estuaries from Florida to Maine (Mills 1967), may 'armour' the sediment and influence rates of erosion of sediment and associated macrofauna. By adding equal numbers of *Mya arenaria* to sediment from each of the sites and exposing these cores to the same sequence of flow speeds in the laboratory, this experiment allowed me to separate the effects of flow velocity and sediment source (sites differing in sediment grain size and macrofauna) on rates of transport of juvenile bivalves.

MATERIALS AND METHODS

Study sites. The study sites were located in the Navesink River, an estuary just south of Sandy Hook, New Jersey. Despite its small size (approx. 10 km in length), this estuary has features typical of many estuaries in the Mid-Atlantic Bight and Long Island Sound. The Navesink is shallow, generally <2 m MLW with a centre channel up to 5 m deep. This estuary is flood-tide dominated and has strong horizontal gradients in physical characteristics (Chant & Stoner 2001). The tide is semi-diurnal with a range of 1.4 m. Seasonal temperatures range from near 0°C, with winter ice cover, to over 30°C in mid-summer, while salinities can range from 0 to 35 ppt (Stoner et al. 2001).

Sediment was collected from 4 subtidal sites (Fig. 1), which span a gradient of sediment grain sizes and flow speeds in the estuary (Table 1). Sediment grain size was estimated from a small core (diameter 6.35 cm, depth 2 cm) collected at each site, which was frozen and later analysed by standard dry-sieving techniques (Folk 1965). The sediments from Sites 1 and 3 were coarse sand (mean grain sizes 500 and 450 µm respec-

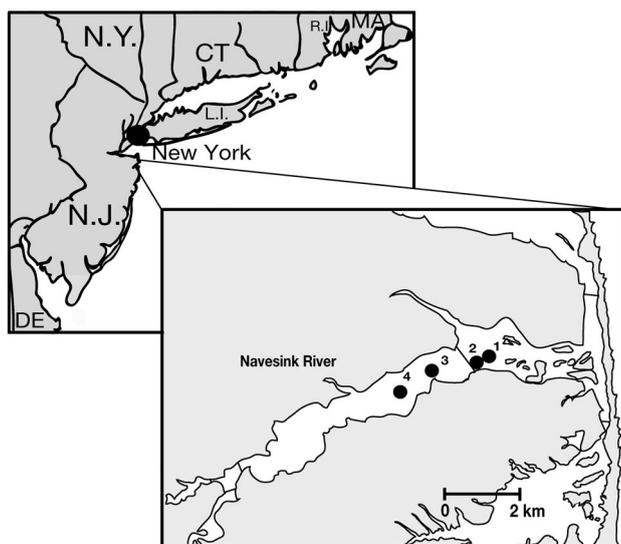


Fig. 1. Location of study sites in the Navesink River estuary, New Jersey. The estuary is 10 km long

tively), while those at Sites 2 and 4 were considerably finer (200 and 100 μm respectively) (Table 1). The silt/clay content (<63 μm) of the sediment was <1% at Sites 1, 2 and 3, but 31.5% at Site 4. Sediment organic content, determined from the change in weight of sediment ashed at 600°C for 24 h, ranged from 0.5% at Site 1 to 11.7% at Site 4 (Table 1).

Current meters mounted 1 m above the bottom showed that maximum currents at Site 1 in June 2003 were 67 cm s^{-1} on the flood tide and 47 cm s^{-1} on the ebb, while maximum currents at Site 4 were <20 cm s^{-1} (Fugate & Chant 2005). Fugate & Chant (2005) estimated that shear velocity at Site 1 varied from near 0 to over 2.0 cm s^{-1} on each tidal cycle; maximum shear velocities exceeded 3.0 cm s^{-1} on spring flood tides (Table 1). Maximum shear velocities also reached 3.0 cm s^{-1} at Site 3. In contrast, at Sites 2 and 4, shear velocities reached a maximum of only 0.8 and 1.5 cm s^{-1} respectively.

Table 1. Physical characteristics of the 4 sites in the Navesink River, New Jersey. Shear velocities are estimated from current metre moorings in June 2003 (Fugate & Chant 2005, D. C. Fugate & R. J. Chant unpubl. data), while sediment characteristics were measured in July 2002

Site	Depth MLW (m)	Shear velocity (cm s^{-1})	Grain size Mean (μm)	ϕ	Silt/clay (%)	Organic content (%)
1	3.3	0–3	500	1.0	0.01	0.5
2	1.2	0–0.8	200	2.3	0.52	2.2
3	3.3	0–3	450	1.2	0.10	1.1
4	2.9	0–1	100	3.3	31.5	11.7

Rates of sediment transport may vary among sites due to differences in both shear velocity and sediment stability. To determine the influence of sediment source and shear velocity on rates of transport of bivalves and sediment, cores were collected from the Navesink on 22 July 2002 for use in a flume experiment. Four or 8 (Site 2; see below) large cores (diameter 11.9 cm, depth 5.5 cm) were collected at each of the 4 sites by scuba divers. In addition, 4 small cores (diameter 6.35 cm, depth 2 cm) were collected from each site to be preserved in 80% ethanol for later determination of the ambient density of juvenile bivalves and crustaceans. Polychaetes and a variety of meiofauna, including nematodes, ostracods and foraminifera, also were common but were not enumerated or identified to the species level.

Each large core was transferred underwater to a plastic Rubbermaid container (diameter 14.2 cm, depth 5.5 cm), and the small gap between the acrylic cylinder used to take the core and the container was filled with sediment from that site. The cylinder was then removed from the container, and the container was capped with a lid. Once the containers of sediment for a site were collected and capped, they were carefully brought to the surface by the divers. The large sediment cores were transferred to the laboratory within a few hours and uncapped. No evidence of mortality or sediment disturbance was observed. Cores were maintained in a recirculating seawater system for 5 to 14 d until they were used in the experiment.

Clams. To standardize the number of clams in each core, juvenile *Mya arenaria* were added to the cores during the experiment. *M. arenaria* were chosen because, although juvenile *M. arenaria* were not very abundant in the Navesink in 2002 (H. L. Hunt et al. unpubl. data), they are at times the most abundant benthic invertebrate in this estuary (average density at 84 stations in the Navesink and Sandy Hook estuary in July 1997 was 27 000 ind. m^{-2} , Stehlik & Meise 2000). Juvenile (1.30 ± 0.23 mm) *M. arenaria* were obtained from Sandy Cove Hatcheries in Harrington, Maine, USA, where they had been reared on downwellers. Clams were held on 180 μm mesh in plastic containers filled with 1 μm filtered seawater in a controlled environment room (20°C). The containers were aerated and the seawater was changed every third day. Clams were fed daily with *Isochrysis* sp. and *Tetraselmis suecica*. These algae were obtained from the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP) at Bigelow Laboratories, Maine and cultured in sterilized seawater enriched with Kent ProCulture F/2 algal culture medium. All clams used in the experiments were checked to ensure that they were alive (moving actively or siphon extended).

Fall velocities of preserved clams and of sediments from the 4 sites were measured at 32.5 ppt in an acrylic cylinder (diameter 13 cm, height 30 cm) in a constant temperature bath. Individual clams and sediment grains were released below the sediment surface, and the length of time of their fall was recorded. Measurements were made on 6 clams of each species and on 6 grains from the median size class of the sediment from each site. Subsequent trials have shown that live *Mya arenaria* and *Gemma gemma* of the size used in this experiment do not produce threads to retard their fall and decrease their settling velocity in a settling cylinder. Fall velocities of dead clams are 5% lower than those of live clams, likely due to a 4% decrease in size (H. L. Hunt unpubl. data), although there also may be a small change in density upon preservation in ethanol.

The flume. The experiments were carried out in the racetrack flume at the Institute of Marine and Coastal Sciences, Rutgers University (<http://marine.rutgers.edu/flume/racetrk.html>; modelled after the flume in Nowell et al. 1989). The flume is oval in shape, with a working channel 6.2 m long and 0.7 m wide. Flow is driven by a set of paddles spanning the entire length of the return channel and is computer controlled. Flow speed is measured with a 2-axis (measuring the downstream horizontal and vertical components of the velocity) laser Doppler velocimeter (LDV). Flow velocities were measured in the centre of the channel at 21 heights above the bottom (ranging from 1.5 to 12.5 cm) to obtain a vertical profile of flow speeds, and shear velocities, u_* , were estimated from the slope of this profile in the log layer (as predicted by the 'law of the wall', Vogel 1994). Four points, those above 5 cm, were above the log layer (as determined graphically) and were not used in the calculation of u_* . The flume was filled with 32 ppt, 20°C filtered (5 µm) seawater to a depth of 14 cm.

Experimental set-up. This experiment was designed to examine transport of juveniles at flow speeds above the critical erosion velocity of the sediment. In previous flume experiments, I found little to no dispersal of juvenile *Mya arenaria* over a period of 4 to 5 h in the absence of sediment transport ($u_* < 0.97 \text{ cm s}^{-1}$, Hunt 2004 and unpubl. data). However, low-flow dispersal may be more prevalent under certain conditions, such as on an unsuitable substrate. Because the critical erosion velocity of juvenile *M. arenaria* and *Gemma gemma* is less than that of the sediment (Roegner et al. 1995, H. L. Hunt unpubl. data), juveniles have the potential to disperse at low flow speeds by not burrowing into the sediment. This study only addressed dispersal at flow speeds above the critical erosion threshold for sediment transport.

At the start of each experimental run, one of the large sediment cores was inserted flush with the flume

bottom in a test section 5.4 m from the upstream end of the working section of the flume. A slot trap (depth 17.5 cm, width 1.5 cm, cross-stream 44 cm) was located 27 cm downstream of the core to collect clams and sediment that had been transported as bedload. Sediment and clams rolled along the bottom and were collected by the trap. For those runs where *Mya arenaria* in both the core and the trap were enumerated (Sites 1 and 3, see section on *Gemma gemma*), $94.9 \pm 4.6\%$ of the *M. arenaria* added to the flume were recovered in either the core or the trap, indicating that the trap collected almost all dispersing clams. No clams were observed to produce threads and be resuspended into the water column.

For cores from Site 4, a small aquarium net (1 mm mesh) was positioned 60 cm downstream of the trap to collect the pieces of amphipod mat that sometimes were transported in the water column (this material was preserved with that from the trap). This net did produce some local disturbance of the flow but did not appear to alter the erosion of sediment from the core. After the sediment core was placed in the flume, 150 (9500 ind. m^{-2}) juvenile *Mya arenaria* were dropped onto the sediment surface and allowed to burrow for 30 min to standardize the number of clams occurring in each core. This burial time was chosen based on previous flume experiments with juvenile *M. arenaria* (Dunn et al. 1999, Hunt 2004). All clams burrowed within this time (most within 5 min) or attached firmly to the amphipod tubes (the tube mat prevented burrowing into the sediment for cores from Sites 2 and 4). The density of clams used is representative of high field densities (e.g. Stehlik & Meise 2000, Hunt et al. 2003). Because of the low abundance of juvenile *M. arenaria* in the Navesink at the time of the experiment (mean per site $< 78 \text{ ind. m}^{-2}$), there was estimated to be < 1 naturally occurring *M. arenaria* per core. Four replicates were run for each site, with the exception of Site 3, which had 3 replicates due to the use of 1 core during a preliminary run while setting up the experiment.

The sediment cores were exposed to increasing flow speeds in 30 min increments. A 30 min exposure time is representative of the time scale of variation of current speeds in the Navesink (R. J. Chant et al. unpubl. data). The shear velocities were selected to represent conditions in the Navesink River. Water velocity was increased gradually from a starting velocity of 34 cm s^{-1} (shear velocity, $u_* = 1.4 \text{ cm s}^{-1}$). This initial velocity is one at which only a small amount of sediment ($< 2 \text{ g}$) and juvenile clams were eroded (see 'Results'). Based on observations of dead clams (H. L. Hunt unpubl. data), I expected that any clams that had not burrowed or attached to the sediment would have been eroded at this first flow speed. After 30 min of exposure to that speed, flow in the flume was stopped and the trap was emptied of sediment

and clams (*Mya arenaria* that were added and any naturally occurring bivalves). Flow was then increased in increments of 4 or 5 cm s⁻¹ at 30 min intervals to a maximum flow speed of 47 cm s⁻¹ ($u_* = 1.9$ cm s⁻¹), for a total of 4 velocities (see Table 4). It was not possible to adjust the height of the sediment–water interface of the core as erosion occurred. At high flow speeds for sediment where considerable erosion occurred, this would result in some alteration in near-bottom flow dynamics and an underestimation of the erosion rate.

The effect of reducing the amphipod mat was tested using sediment from Site 2. Forceps were used to pull entire tubes vertically out of the sediment, removing all of the tubes visible at the surface of 4 additional cores from this site. Little disturbance of the Site 2 sediment was observed as a result of this removal. Tubes that did not protrude above the sediment surface were not removed. Juvenile *Mya arenaria* were added to the cores and subjected to the same series of flow speeds as the undisturbed cores.

At the end of each run, the sediment in the core container and the contents of the trap from each flow increment were sieved, separately, on a 106 µm sieve. Core and trap contents were preserved in 80% ethanol and stained with Rose Bengal. The trap contents were then sieved on a 500 µm sieve and examined under a dissecting microscope to enumerate any bivalves (*Mya arenaria* that had been experimentally added as well as any naturally occurring bivalves >500 µm in shell length). The dry weight of sediment collected in the trap was later measured. For Sites 1 and 3, where the gem clam *Gemma gemma* was abundant, the clams remaining in the cores at the end of the runs were also counted so that the total number of *G. gemma* present (eroded into the trap and still present in the core) could be determined for each run.

Data analysis. If necessary (as determined by Cochran's test with $\alpha = 0.05$), weights were $\ln(x + 1)$ -transformed and proportions were arcsine-transformed prior to analysis to satisfy the assumption of homogeneity of variances. Each core was exposed to multiple flow speeds. Consequently, the proportion of clams eroded and the weight of sediment eroded were summed sequentially over the flow speeds. One-way ANOVA was used to compare cumulative erosion among sites after the first 2 shear velocities and after all 4 shear velocities. Reduction of the amphipod mat was tested using a 1-tailed *t*-test comparing cores for Site 2 with and without a reduction in the cover of tubes.

RESULTS

In July 2002, the biological communities varied considerably among the sites and included a variety of

juvenile bivalve species (Table 2). *Gemma gemma*, the most common bivalve, was abundant at Site 1 and, less so, at Site 3. The amphipod *Ampelisca abdita* was particularly abundant at Sites 2 and 4 (Table 2) and created dense mats of tubes. This amphipod is generally very abundant in the middle reaches of the Navesink, with densities reaching >80 000 ind. m⁻² (Stoner et al. 2001), considerably higher than those recorded in this study. A variety of other epifauna also were common at the sites: mud crabs *Panopeus herbstii* and *Rithropanopeus harrisii*, mud snails *Ilyanassa obsoleta* and hermit crabs *Pagurus longicarpus* (Site 1) (Table 2).

Based on the higher fall velocities of sediment from Sites 1 and 3 (Table 3), it was predicted that sediment from these sites would be eroded at higher shear velocities than sediment from Sites 2 and 4. However, the large percentage of silt/clay at Site 4 (Table 1) could impart cohesive properties to the sediment at this site and increase its critical erosion velocity. The presence of biogenic structures (amphipod tubes) also had the potential to affect the erosion of sediment and clams from the cores collected at Sites 2 and 4 (Table 2). For all sites, the ratio of fall velocity to u_* was greater than 1, suggesting that material in transport would move as bedload, saltating or rolling within a few grain diameters of the bottom, rather than being resuspended in the water column (Jumars & Nowell 1984b). As predicted, most sediment and clams were transported as bedload, with the exception of pieces of amphipod tube that broke off and were resuspended into the water column and collected in the net.

For the cores from all 4 sites, little sediment erosion occurred at the 2 lowest velocities (Fig. 2), and total weight of sediment eroded over shear velocities of 1.4 and 1.6 cm s⁻¹ did not differ significantly among sites ($F_{3,11} = 2.80$, $p = 0.09$). Erosion of sediment occurred at the 2 highest flow velocities at Sites 1 and 3, resulting in totals of >100 g of sediment eroded; the total weight of sediment eroded at Sites 2 and 4 was <10 g. Summed over the 4 flow velocities, total weight of sediment eroded differed significantly among sites ($F_{3,9} = 34.2$, $p < 0.001$) and was significantly greater at Sites 1 and 3 than at Sites 2 and 4 (Tukey-Kramer HSD, $p < 0.05$). The maximum depth of erosion was estimated to be 0.6 cm (Sites 1 and 3).

Patterns of erosion of *Mya arenaria* were similar to those of the sediment for each of the sites, with the exception of greater erosion of *M. arenaria* at Site 4. The total proportion of *M. arenaria* eroded over all 4 flow speeds was only 7.8% at Site 2, but >39% at the other sites. At Sites 1 and 3, rates of erosion were high at both 1.7 and 1.9 cm s⁻¹. In Site 2 cores, erosion of *M. arenaria* was low at all velocities. For Site 4, erosion of *M. arenaria* occurred at moderate levels at all velocities as pieces of the amphipod tube mat, to which

Table 2. Densities (ind. m⁻²; mean ± SE) of bivalves, crustaceans (amphipod *Ampelisca abdita*, mud crabs *Panopeus herbstii* and *Rithropanopeus harrisi*, and hermit crab *Pagurus longicarpus*) and the gastropod *Ilyanassa obsoleta* in core samples collected on 22 July 2002

Site	Bivalve	Bivalve species	<i>A. abdita</i>	Mud crabs	<i>P. longicarpus</i>	<i>I. obsoleta</i>
1	4.3 ± 2.2 × 10 ⁴	<i>Gemma gemma</i> (99%) <i>Lyonsia hyalina</i> <i>Mya arenaria</i> <i>Petricola</i> sp.	310 ± 260	0	156 ± 180	0
2	1.6 ± 1.2 × 10 ³	<i>Gemma gemma</i> (71%) <i>Lyonsia hyalina</i> <i>Petricola</i> sp. <i>Tellina agilis</i> <i>Mya arenaria</i>	3.1 ± 1.8 × 10 ³	1.3 ± 1.1 × 10 ³	0	5.5 ± 6.9 × 10 ²
3	8.0 ± 7.2 × 10 ³	<i>Gemma gemma</i> (99%) <i>Tellina agilis</i>	780 ± 900	1.6 ± 1.8 × 10 ²	0	0
4	0		1.9 ± 1.6 × 10 ³	9.4 ± 6.8 × 10 ²	0	0

clams were attached, occasionally broke off. Summed over the first 2 shear velocities, the total proportion of *M. arenaria* eroded did not differ significantly among sites ($F_{3,11} = 1.92$, $p = 0.19$). However, when summed over all 4 flow speeds, sites differed significantly ($F_{3,9} = 7.11$, $p = 0.01$), and the total proportion of *Mya* eroded was significantly greater at Sites 1 and 3 than at Site 2, while Site 4 did not differ significantly from either group (Tukey-Kramer HSD, $p < 0.05$).

Differences in rates of erosion of *Mya arenaria* among sediment from the 4 sites could result from differences in the erosion of the sediment or the burrowing behaviour of the clams. To determine if clam erosion was related to the weight of sediment eroded, the relationship between the total (summed over the flow speeds) amount of *M. arenaria* and sediment eroded in each replicate was examined (Fig. 3). There was a strong linear relationship between the proportion of *M. arenaria* eroded and the weight of sediment eroded ($r^2 = 0.665$, $F_{1,13} = 25.8$, $p = 0.0002$). The slope of this relationship appeared to differ at Site 4, where most of

the material eroded was relatively light pieces of amphipod mat. When Site 4 was analysed separately, a stronger relationship between the proportion of *M. arenaria* and sediment weight was detected both for Site 4 ($r^2 = 0.986$, $F_{1,2} = 145.3$, $p = 0.0068$) and for the other sites (Sites 1, 2 and 3; $r^2 = 0.919$, $F_{1,9} = 102.78$, $p < 0.001$). Rates of sediment and clam erosion were still low when the amphipod mat was reduced (Fig. 4). However, summed over the 4 shear velocities, reduction of the amphipod mat did result in a small but significant increase in the weight of sediment eroded (1-tailed t -test: $t_6 = 2.20$, $p = 0.03$). In contrast, there was no detectable difference in the proportion of *M. arenaria* eroded from the cores when the amphipod mat was reduced (1-tailed t -test: $t_6 = 1.30$, $p = 0.12$).

Gemma gemma occurred naturally in the sediment from Sites 1 and 3, but was less abundant at Site 3. The *G. gemma* were comparable in size to the *M. arenaria* (1.12 ± 0.53 mm vs. 1.30 ± 0.23 mm), although there was a larger size range of *G. gemma* (0.33 to 2.8 mm) compared to *M. arenaria* (0.9 to 1.9 mm). For a given size, *G. gemma* have a thicker shell and a higher fall velocity than the similarly sized *M. arenaria* (Table 3). Like the proportion of *M. arenaria*, the proportion of *G. gemma* collected in the trap from the cores from Sites 1 and 3 was greater at shear velocities of 1.7 and 1.9 cm s⁻¹ than at 1.4 and 1.6 cm s⁻¹ (Fig. 2). The proportion of *G. gemma* eroded did not differ significantly between Sites 1 and 3, both after 1.4 and 1.6 cm s⁻¹ ($t_5 = 0.23$, $p = 0.83$) and summed over all 4 velocities ($t_5 = 0.59$, $p = 0.58$). There was no significant relationship between the total (summed over the flow speeds) amount of *G. gemma* and sediment eroded ($r^2 = 0.087$, $F_{1,5} = 0.48$, $p = 0.63$) (Fig. 3). For both *M. arenaria* and *G. gemma*, 40 to 63% of individuals in cores from Sites 1 and 3 eroded over the 4 shear velocities. The proportion of *G. gemma* and *M. arenaria* eroded from cores at Sites

Table 3. Mean (±1 SD) fall velocities of *Mya arenaria*, *Gemma gemma* and the sediments from the 4 sites. Sediment grains used were from the most abundant size fraction of the sediment, with the exception of Site 4. Because the sediment used was previously preserved and sieved, the sediment represents the largest size fraction at Site 4 (>125 µm) and overestimates the average fall velocity for this site

Species/sediment	Size (mm)	Fall velocity (cm s ⁻¹)
Site 1	0.420–0.500	8.86 ± 0.82
Site 2	0.125–0.180	2.26 ± 0.17
Site 3	0.354–0.420	5.10 ± 0.44
Site 4	0.125–0.250	2.23 ± 0.10
<i>M. arenaria</i>	1.56 ± 0.29	3.24 ± 0.38
<i>G. gemma</i>	1.65 ± 0.78	6.17 ± 2.22

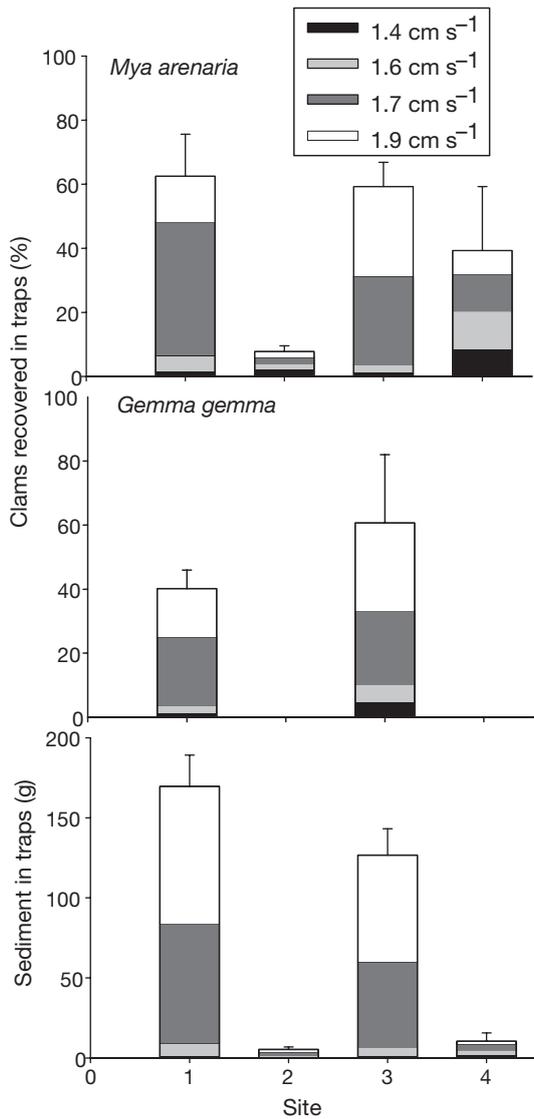


Fig. 2. Mean (+SE, n = 3 or 4) percentage of *Mya arenaria* and *Gemma gemma* and weight of sediment (g) eroded into traps from cores from 4 sites in the Navesink River over a sequence of exposure to 4 shear velocities in the flume experiment

1 and 3 did not differ significantly between the 2 species (paired *t*-test: $t_6 = 1.67$, $p = 0.15$), although a greater proportion of *M. arenaria* than *G. gemma* were eroded in 6 of 7 runs.

DISCUSSION

Sediment erosion

In the presence of amphipod tubes (Sites 2 and 4), the erosion rate of the sediment could not be predicted from its grain size. Based on grain size, sediment from Sites 2 and 4 would be predicted to have a lower ero-

sion threshold than that of the coarser grains at Sites 1 and 3 (predicted critical shear velocity for quartz grains of sizes 500, 200 and 100 μm : 1.7, 1.4 and 1.0 cm s^{-1} from Miller et al. 1977). Contrary to these predictions, rates of erosion of sediment from Sites 2 and 4 were low even at shear velocities $>1.7 \text{ cm s}^{-1}$ and were an order of magnitude less than at Sites 1 and 3. Effects of biota can outweigh the effects of the physical characteristics of the sediment. For example, Lelieveld et al. (2003) found that the critical shear velocity of initiation of motion of intertidal sediments from an estuary in New Zealand increased with decreasing grain size. This inverse relationship was correlated with indicators of microalgal biomass and mucilage content. In this study, the low rates of erosion at Sites 2 and 4 are

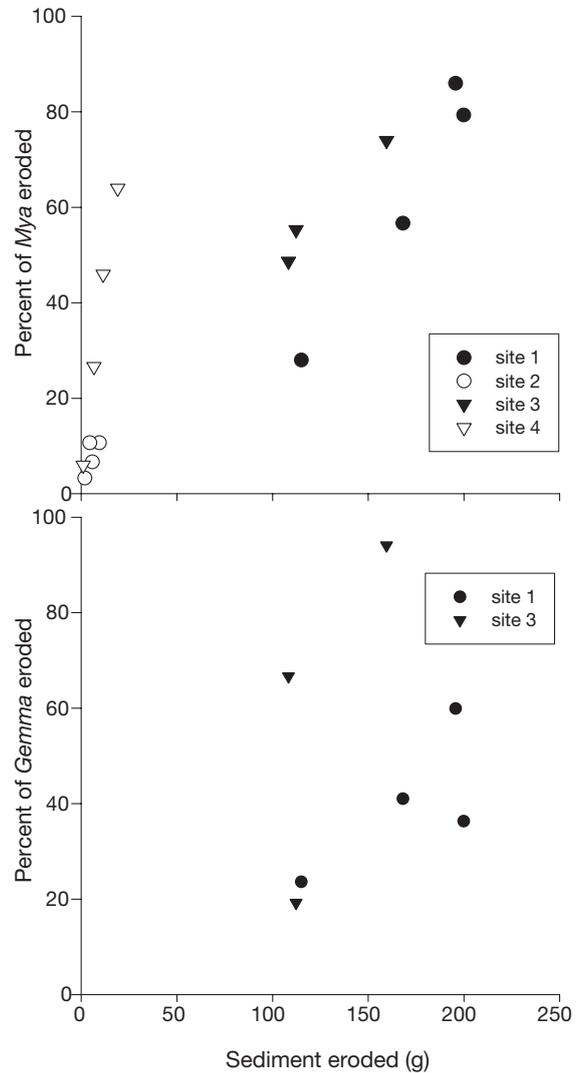


Fig. 3. Relationship between the total percentage of *Mya arenaria* and *Gemma gemma* eroded into traps and the total weight of sediment eroded (summed over the 4 shear velocities) in the flume experiment for cores from 4 sites in the Navesink River

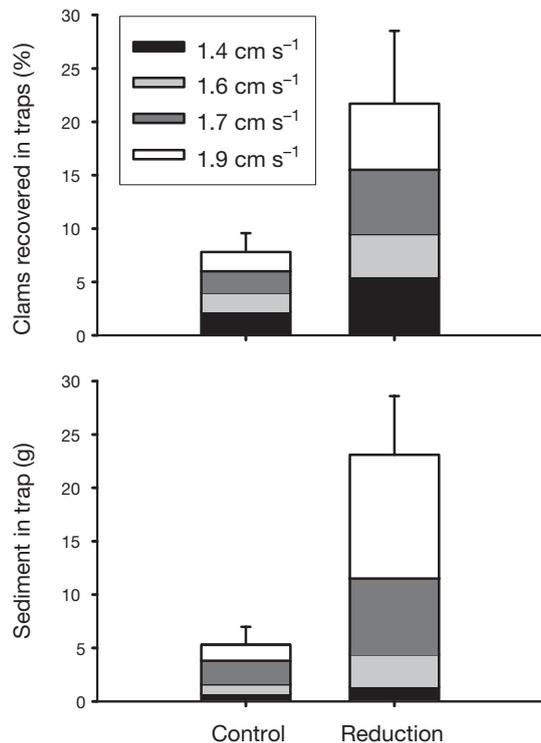


Fig. 4. Mean (+SE, $n = 4$) percentage of *Mya arenaria* and weight of sediment eroded into traps from cores from Site 2 over a sequence of exposure to 4 shear velocities in the flume experiment. Control cores were undisturbed, while the reduction treatment cores had all visible amphipod tubes removed from the sediment surface

most likely due to armouring of the sediment surface by mats of tubes created by the amphipod *Ampelisca abdita*. Polychaete worm tubes have often been noted to stabilize sediment (Fager 1964, Luckenbach 1986, Thrush et al. 1996), although they can also have destabilizing effects at low densities (Eckman et al. 1981, Friedrichs et al. 2000). *A. abdita* tubes are flattened and flexible and may have effects more similar to macroalgae. Macroalgae and seagrasses are known to have effects on flow and sediment transport (e.g. Gambi et al. 1990). For example, Romano et al. (2003) found that a mat of *Enteromorpha intestinalis* reduced current velocities by 10 to 56% and sediment erosion by 60 to 90%.

Ampelisca abdita tubes covered essentially 100% of the bottom at Sites 2 and 4 (amphipod densities of 31 000 and 19 000 m^{-2} , Table 2). Other amphipods, some of which may be tube building, also were abundant at these sites (densities of 98 000 and 57 000 m^{-2}). Blanketing of the sediment by organisms alters the fluid momentum on the bed (Jumars & Nowell 1984a). The stabilizing effect of the tubes probably did not occur solely through blanketing. Reduction of the amphipod mat by removing tubes

visible on the surface increased the rate of sediment erosion, but it still remained lower than that of the sediment from the other sites. Although tubes protruding above the sediment were removed, other tubes later became visible once the sediment eroded down around them, and these may have stabilized the sediment. It is likely that these remaining tubes were dense enough to reduce the fluid momentum to the bed as the sediment eroded down around the tubes. Amphipod tubes may make it difficult for clams that do burrow to disperse due to the reduced flow velocity amongst the tubes. The amphipod tubes also may be reducing sediment transport by affecting inter-particle adhesion (see Jumars & Nowell 1984a for a review of effects of organisms on sediment transport). The sites also differed in other macrofauna (e.g. bivalve species, crabs, snails), and interactions with these species may have influenced rates of dispersal of juvenile bivalves.

Relationship between clam transport and sediment erosion

Behaviour undoubtedly plays a role in preventing or promoting transport of juvenile bivalves such as *Mya arenaria*. Clams would be eroded at a much lower velocity if they did not burrow into the sediment (Roegner et al. 1995). Dead *M. arenaria* and *Gemma gemma* of the size used in this experiment are transported at shear velocities <1.2 $cm\ s^{-1}$ (H. L. Hunt unpubl. data). Over a broad range of sediments there was a very tight relationship between the weight of sediment and the proportion of *M. arenaria* eroded (Fig. 3). Less information was available for *G. gemma* than for *M. arenaria*, and no relationship was detected between the weight of sediment and the proportion of *G. gemma* transported at Sites 1 and 3, possibly due to the smaller range of sediment erosion. Previous field studies on *M. arenaria* (Emerson & Grant 1991) and *G. gemma* (Comito et al. 1995a) found positive relationships between the number of clams and the amount of sediment collected in bedload traps. At the shear velocities employed in this study, clams and sand grains rolled along the bottom as bedload and were collected in the trap. For Sites 2 and 4, where the surface was covered with tubes, *M. arenaria* often adhered to the tubes with byssal threads rather than burrowing into the sediment (which was covered by the mat of tubes); as a result, the clams eroded when pieces of the tube mat eroded.

The relationship between sediment and clam transport at high flow speeds in this study contrasts with the pattern of dispersal of species of juvenile bivalves that actively promote resuspension by using threads or emerging on the sediment surface (e.g. Sigurdsson et

al. 1976, Armonies 1994, Cummings et al. 1995, Lundquist et al. 2004). The dispersal of these bivalves may not be strongly related to sediment transport (e.g. Armonies 1996, Turner et al. 1997). Although *Mya arenaria* and *Gemma gemma* have been found in the water column in some studies (*M. arenaria*, Möller 1986; *G. gemma*, Sellmer 1967), our data and other studies (Emerson & Grant 1991, Commito et al. 1995a, Hunt & Mullineaux 2002) suggest that if sediment transport at a site can be predicted, the likelihood of transport of juvenile *M. arenaria*, and other bivalves whose dispersal is generally linked to sediment transport, also can be predicted. It is likely that some dispersal of juvenile *M. arenaria* and *G. gemma* does occur at low flow speeds when individuals do not burrow into the sediment. Such behaviour will be particularly important at sites where flow speeds do not exceed the critical erosion velocity of the sediment. Dispersal at these flow speeds was not addressed in this study.

Predictions of transport in the field

In this laboratory experiment, sediments from the 4 sites were exposed to a range of flow speeds to separate the effects of flow speed and sediment erodability on rates of erosion of sediment and clams. However, the 4 sites do not experience the same flow regime in the field. Shear velocities recorded at site 4 reach a maximum of approximately 1.5 cm s⁻¹ (Fugate & Chant 2005), equal to the lowest shear velocity used in this experiment. As a consequence, only a small amount of sediment and bivalves are likely to be transported in the field at this site. At Site 2, flow speeds are also low (Table 1), probably because of the site's position in a side channel in the estuary. Little erosion of sediment and clams occurred at any of the flow speeds to which they were exposed in the laboratory, including shear velocities considerably higher than those recorded at this site. This is most likely due to a combination of the coarser sediment than at Site 4 and 'armouring' by amphipod mats. As a result, little erosion of sediment and clams is expected to occur at this site in the field. In contrast, Sites 1 and 3 regularly experience shear velocities at which sediment and bivalves were eroded in the flume experiment (Tables 1 & 4). At Site 1, erosion of sediment is likely to be

particularly high as shear velocities are estimated to exceed 1.7 cm s⁻¹, the speed at which much erosion occurred in the lab, on virtually every flood tide and to reach shear velocities of 3 cm s⁻¹ (Fugate & Chant 2005). The patterns of bivalve dispersal recorded in the Navesink in June 2002 and 2003 (H. L. Hunt et al. unpubl. data) agree with these predictions: rates of dispersal were considerably higher at Sites 1 and 3 than the other 2 sites. However, some dispersal of juvenile bivalves did occur at the sites with lower shear velocities. The results of this flume study indicate that differences among sites in the erodability of the sediment and the flow regime contribute to patterns of variability in rates of bivalve dispersal in this estuary. In the field, ambient density of bivalves available to be transported will also be important. In the Navesink, juvenile bivalves were most abundant at the 2 sites at which rates of sediment transport also were highest. The lower numbers of bivalves at Sites 2 and 4 may be due to the unsuitability of a habitat with a dense tube mat, which reduces flow velocity at the bed and makes it more difficult for clams to burrow into the sediment.

CONCLUSION

For *Mya arenaria* in sediment from the Navesink River estuary, bivalve and sediment transport appear to be tightly linked at high shear velocities. At the

Table 4. Mean velocity at 9 cm above the bottom (U_9) and shear velocity (u_*) measured with a laser doppler velocimeter. Most profiles were run after the experiment using leftover sediment rather than undisturbed cores (undisturbed cores are marked with an asterisk). Averages for each flow treatment were calculated without the data for the undisturbed cores with amphipod mats for Sites 2 and 4. Amphipod mats created increased shear above the core, and likely decreased flow closer to the bed, below the height at which flow was measured

Flow treatment	Site	Free stream velocity (U_9)	Shear velocity (u_* , cm s ⁻¹)	Mean flow speed (cm s ⁻¹)
1	1	34.4	1.37	34, $u_* = 1.4$
	2	34.8	1.45	
	3	34.3	1.27	
	4	33.8	1.36	
	4*	35.1	1.53	
2	1	38.7	1.55	38, $u_* = 1.6$
	2	38.8	1.57	
	4	37.6	1.56	
	4*	39.0	1.70	
3	1	42.9	1.8	43, $u_* = 1.7$
	2	42.8	1.59	
	2*	43.1	2.27	
	4	41.8	1.74	
	4*	42.9	2.53	
4	1	46.7	1.9	47, $u_* = 1.9$
	2	46.8	1.88	
	2*	48.0	2.31	

shear velocities used in this experiment, juvenile *M. arenaria* and *Gemma gemma* did not appear to actively promote their own dispersal or to be able to avoid transport once sediment erosion occurred. Some dispersal did occur when sediment transport was low due to clams that did not burrow into the sediment. This study reinforces previous work showing that sediment transport can be a useful indicator of the probability of transport of these juvenile bivalves. It also indicates that in order to use shear velocities measured in the field to predict the probability of transport of juvenile bivalves and sediment, it is necessary to have information about sediment erodability at a given flow speed, the biogenic features that may modify erosion, and the behaviour of the species being studied. Models predicting the onset of sediment erosion can be modified to take into account factors affecting sediment stability (e.g. sediment phaeopigment content, Lelieveld et al. 2003).

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