The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport

Craig W. Emerson and Jonathan Grant
Department of Oceanography, Dalhousie University, Halifax, Nova Scotia B3H 4J1

Abstract

Bedload sediment transport, clam transport across the sediment surface, clam population density, and spat settlement were measured daily for 10 months to determine the magnitude and frequency of clam transport and its dependency on bedload transport and to evaluate the relative importance of this phenomenon to population growth of *Mya arenaria*. From July to April, the transport of juvenile clams was observed frequently on a sheltered and an exposed intertidal sandflat. The maximum rate of clam transport on the sheltered sandflat (790 ind. m⁻¹ d⁻¹) and on the exposed site (2,600 ind. m⁻¹ d⁻¹) coincided with peaks of bedload sediment transport (~35 kg m⁻¹ d⁻¹). At both sites, bedload transport was positively correlated with clam transport (r = 0.33 and 0.51; sheltered and exposed sites, P < 0.001); on the sheltered site, clam transport was negatively correlated with clam density (r = -0.47, P < 0.001). Cross-spectral analysis showed that bedload and clam transport time series were significantly coherent with zero lag at periods of <10 d. Clam transport on the high-energy sandflat accounted for an order-of-magnitude increase in clam density in early September, a precipitous decline 2 months later, and the complete removal of recently settled spat. A net population increase on this sandflat was most likely a result of clam import during bedload events.

Persistent indications that the demography of coastal benthos is regulated by sediment transport have failed to incite a quantitative evaluation of bedload transport as a regulator of population dynamics in soft sediments. Movement of the bed frequently has been linked to settlement success (Rhoads and Young 1970), mortality (Kranz 1973), food supply (Miller and Sternberg 1988), somatic tissue growth (Emerson 1990), and intertidal zonation (Matthiessen 1960). Most attempts to explain the density and distribution of infauna continue, however, to examine variation in larval settlement and postsettlement survivorship without knowledge of local sediment dynamics. If bedload transport, population density, and spat settlement are measured simultaneously, it may be possible to account for unexplained variation in the distribution and growth of infaunal populations.

Although biological processes such as predation and competition can limit the abundance of free-swimming and settled recruits, hydrodynamic forcing during the planktonic larval or postlarval period is often a more important factor controlling adult densities (Eckman 1979; Johnson and Hester 1989). The extent to which hydrodynamics control benthic recruitment, however, will not be limited to the regulation of planktonic larval distributions and settler densities. When bottom currents exceed the critical shear stress of the sediment, it is possible that movement of the bed will affect recruitment rates by importing or exporting individuals that become exposed to dispersive currents or become trapped in migrating bedforms (Palmer 1988). Infaunal transport is often associated with sediment erosion during large storms, and even tidally forced bedform migration can be sufficient to redistribute organisms living near the sediment surface (Grant 1981). It is possible, therefore, that the magnitude and frequency of bedload transport caused by winds and tides controls the population density and distribution of relatively sedentary infauna.

*Mya arenaria*, the soft-shelled clam, is an
ideal species with which to test the hypotheses that bedload transport, through the removal and transport of established clams, is responsible for changes in the density of infaunal bivalves and that the import of clams from neighboring populations can be more important to population recruitment than local spat settlement. High numbers of juvenile clams live in the upper few centimeters of sediment where the effects of bedload transport would be greatest, where they can rapidly reburrow after becoming exposed, and where they are highly resistant to damage from abrasion and burial (Emerson et al. 1990). Matthiessen (1960) speculated that intertidal zonation of M. arenaria results from clam transport, but the passive movement of clams across the sediment surface has never been measured directly. If clam transport occurs with high frequency and can be linked to an increase in population density, the common assumption that relatively sedentary infauna rely exclusively on local spat settlement for recruits must be rejected.

Materials and methods

Study sites—The effect of bedload transport on M. arenaria recruitment was determined on two intertidal sandflats separated by a small sand and grass peninsula at Eastern Passage, Nova Scotia (Fig. 1). Study sites were confined to 300 m² of the midintertidal at each sandflat, where the maximal water depth was 1.6 m and the average air exposure was 8 h d⁻¹. Mya arenaria, Macoma balthica, Nereis diversicolor, and Spio setosa are dominant macrofauna on both sandflats. Gemma gemma, Hydrobia sp., and Arenicola marina are unique to the sheltered sandflat, whereas the surf clam Spisula sp. is found only on the exposed sandflat. Both sandflats are subject to recreational fish-bait (M. arenaria, A. marina) digging from April to October.

The proximity of the two sandflats ensured that each was exposed to the same precipitation, solar radiation, air temperature, and water mass, while providing a temporal contrast in wind-wave forcing. The exposed sandflat, facing the Atlantic Ocean, is subjected to relatively large waves (~1 m high) throughout the year, whereas several islands and a restricted harbor fetch (~<10 km) usually protect the sheltered sandflat. Large waves approach the sheltered sandflat only during strong northwest winds. Despite the apparent difference in exposure to hydrodynamic forcing, each sandflat has a similar grain size distribution (median grain size, 250 μm; silt-clay content, <1% by wt) and a surface slope of ~1°. Sediment ripples 1 cm high and 2–3 cm in wavelength are often observed on the exposed sandflat, but are less common on the sheltered one. Semidiurnal tidal currents are ~<10 cm s⁻¹ over the sandflats and are insufficient to generate bedload transport (Emerson 1991).

Sampling protocol—Sampling was conducted from 1 July 1988 to 30 April 1989 to ensure that a wide range of bedload transport would be encountered and to adequately monitor the period of M. arenaria spat settlement (late summer to early fall; Broussseau 1987). Because wind-wave forcing is responsible for most of the bedload transport on the sandflats (Emerson 1991), and because most of the energy in the local wind field is contained between 2- and 10-d pe-
periods, a sampling interval of 1 d was required. Accordingly, samples were collected at alternate low tides; each “day” lasted ~25 h (1 tidal cycle = 12.5 h). On average, the study areas were sampled 22 d each month (min, 20 d; max, 30 d) with no more than two consecutive days separating sample collection. The only exceptions to this schedule were in early September and early November, when seven and four consecutive days could not be sampled, respectively. During these periods, bedload transport was estimated indirectly from a numerical bedload model (Emerson 1991).

Sediment temperature (5-cm depth) and water temperature were monitored daily with a mercury thermometer (±0.2°C). Hourly windspeed and direction, air temperature, and precipitation were obtained from the Atmospheric Environment Service, Bedford, Nova Scotia, which operates a meteorological station within 4 km of the study sites. Wind was partitioned into U and V vector components after adjusting the reference axis so that north was aligned with 310° (Fig. 1). As a result, true northwest winds (+U component) impinged directly on the sheltered sandflat, whereas the exposed site was subjected to southeast winds (−U component). The V component was not considered because alongshore winds do not generate significant waves. Hourly sea-level data measured by tide gauges in Halifax Harbor were obtained from the Marine Environmental Data Service, Ottawa.

Sediment and faunal transport—Direct measurements of gross bedload and faunal transport were obtained with subsediment bedload traps consisting of acrylic cylinders (60 cm long, 3-cm i.d.), each surrounded by a PVC shoring pipe (Fig. 2). By remaining in the sediment, the pipes permitted frequent replacement of the bedload trap without disturbing the surrounding sediment. The tops of both the trap and pipe were flush with the sediment surface, and a rubber gasket prevented particles from collecting between them. From an assessment of the collection and retention efficiency of the trap (Emerson 1991), we concluded that the traps were better for the measurement of daily and seasonal variation in gross bedload and faunal transport than of absolute rate of transport. We also found that traps with an aspect ratio of 20 and a length of 60 cm may underestimate intertidal bedload transport in excess of 35 kg m⁻¹ d⁻¹.

Initially, 10 replicate traps were deployed at each site with a minimum of 5 m between traps. Because the variation between trap collections on 1 d (~20%) did not decrease with more than two traps, two replicate traps were used after August. Macrofauna were picked out of bedload samples and preserved in 10% Formalin. After the remaining material was dried to constant weight (70°C), kelp and seagrass detritus were separated from the sand grains by sieving with a 500-μm mesh. Although some small fragments of biogenic material could not be separated from the sand in this manner, ashing (500°C for 2 h) and weighing indicated that at least 96% of the sediment dry weight was composed of sand grains. Bedload transport was expressed as sediment dry weight per
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meter (extrapolated from the trap diameter) per day ($\sim 25$ h, two tidal cycles). Transport of clams was expressed as number of individuals per meter per day. Material collected by traps that had become partially clogged was not analyzed. Subsamples of both the trapped sediment and the surface sediment (0–2 cm depth) within 5 m of the traps were retained for grain-size analysis.

Net sediment transport—the balance between erosion and deposition—was determined from the daily change in sediment height above two 900-cm$^2$ acrylic plates initially buried at a depth of 20 cm. Sediment disturbed during the initial deployment was allowed to equilibrate for 2 weeks before the first height measurement. Sediment height was measured by inserting a thin graduated rod vertically into the sediment to the plate depth. If ripples were present, the rod was inserted into the trough. Sampling precision (range of six duplicate measurements) was $\sim 6$ mm. Results were illustrated as deviations from the 10-month average height of sediment above the two plates.

Clam density—The population density of *M. arenaria* was determined from five sediment cores (300 cm$^2 \times 10$ cm deep) collected daily at each site. Cores were not taken within 2 m of either a bedload trap or a buried plate, and the same area was not resampled later. After the core samples were sieved (1.5-mm mesh), clams were measured (max shell length) and preserved in 10% Formalin. Clams longer than 3 cm were not included in density estimates because a sampling depth of 10 cm is not adequate to estimate their density. Bimonthly, three box-core samples (0.1 m$^2 \times 25$ cm deep) were collected randomly within the study area, though not within 2 m of previous sample sites, traps, or buried plates. These samples indicated that clams in the top 10 cm of sediment constituted 34–76% of the total population density.

The density of clam spat (metamorphosed larvae 250–1,000 $\mu$m long) was estimated from 10 sediment cores (3 cm$^2 \times 1$ cm deep) collected daily at each site. The entire sediment core was stained with Rose Bengal and preserved in 10% Formalin. Spat were separated from much of the sediment by wet sieving (125-µm mesh) to facilitate enumeration with a binocular microscope. No attempt was made to distinguish newly settled clam spat from that already established.

Spectral analysis—Power spectral analysis was used to examine the relationship between time series of bedload sediment transport, clam transport and clam density at each sandflat. With this procedure, the variance of the time series is partitioned into contributions at frequencies that are harmonics of the length of the data set (Denman 1975); frequencies where most of the variance of the signal is concentrated can be identified easily. Long-period trends were removed from each series by the variance-difference method because the mean and variance of the series should depend only on the series length and not on the absolute time. Any missing data were reconstructed by linear interpolation of adjacent points.

Density spectra were smoothed with a Parzen spectral window of width $M = 30$ ($\sim 10$% of the series length). The bandwidth associated with this window type is $(3.72 \pi)/M$, and $\nu$, the degrees of freedom, equals $(3.71N)/M$, where $N$ is series length. The chosen sampling frequency and duration allowed the practical resolution of spectral peaks at periods of 2–155 d. Critical values of squared coherence at the 95% C.L. were calculated following Jenkins and Watts (1968). Phase spectra revealed the amount of shift (lag) between the first and second signal.

Results

Sheltered site—Seasonal bedload transport at Eastern Passage was consistent with the observation that the most intense oceanic response to wind stress occurs in fall due to a sharp transition from minimal summer winds to strong winter storms (Smith et al. 1978). During the summer calm ($|U| \leq 4$ m s$^{-1}$, Fig. 3A), bedload transport was usually $<1$ kg m$^{-1}$ d$^{-1}$ at the sheltered site (Fig. 4A)—a magnitude similar to that observed by Commito et al. (in prep.; 1.5 kg m$^{-1}$ d$^{-1}$) on an intertidal sandflat on Assateague Island, Virginia. After the shift to strong northwest winds in mid-November, bedload rates at our study site often reached
Fig. 3. Time series of the daily average of the U component of wind velocity, maximal daily range in sea level, daily percentage of ice or snow cover on the sheltered sandflat and days on which ice armoring was observed at the study sites, and daily range in air temperature and mean water temperature. (Ice or snow cover was not observed on the exposed site.)

> 10 kg m\(^{-1}\) d\(^{-1}\), with maximal transport (\(\sim 36 \text{ kg m}^{-1}\text{ d}^{-1}\)) on 21 November. After January, bedload transport rarely exceeded 5 kg m\(^{-1}\) d\(^{-1}\). As with the local wind field, nearly all the energy in the bedload time series was contained between the 2- and 10-d periods, with a peak centered at \(\sim 2.5\) d (Fig. 5A).

Without high winds, spring tidal currents were insufficient to produce high rates of bedload transport on the sheltered site (e.g. late-July, Figs. 3B, 4A). Even with high winds, minimal bedload transport was occasionally observed when 100% of the sandflat was covered by 40 cm of snow and ice (e.g. mid-February, Figs. 3C, 4A); direct observation of the sediment surface near the traps revealed little ice scouring at these times. Ice-armoring of the sediment occurred when air temperature was very low

Fig. 4. Time series of the daily bedload transport and sediment height above buried plates (expressed as deviations from the 10-month average), daily clam transport measured from trap collections, and daily clam density (\(\pm 1\) SD) in the upper 10 cm of sediment on the sheltered site. (Clam spat were not observed on the sheltered site.)
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(Fig. 3C, D), but the freezing of interstitial water in the top 1.5 cm of sediment had little potential to stabilize the sediment surface because the sediment remained frozen for only 15 min after submergence by the rising tide. At warmer temperatures, surface runoff from rain or melting ice created erosion channels in the sediment surface, but not within the study area.

The high rates of sediment transport, indicated from trap deployments between November and January, were not apparent in the sediment height profile (Fig. 4A). The low-amplitude, high-frequency variation that was observed in sediment height (±1 cm) was likely a result of sampling error or the presence of sediment ripples (avg ht, 0.8 cm). A significant correlation between sediment height and time \( (r = 0.45, P < 0.001, n = 250) \) suggested that there was a net sediment deposition of 2 cm by the end of the 10-month sampling period. There was no evidence of significant episodes of deposition or erosion at this site (cf. exposed site, see below).

Transport of *M. arenaria* across the sediment surface at the sheltered site was observed throughout the sampling period (Fig. 4B). Although rates were usually low (avg 24 ind. m\(^{-1}\) d\(^{-1}\)), the maximum exceeded 750 ind. m\(^{-1}\) d\(^{-1}\). As with the bedload time series, almost all the variation in spectral density of the clam transport time series was contained within the 2- and 10-d periods, with peaks at periods of 2 and 3 d (Fig. 5B). Clams with shells 4 cm long were occasionally found in the traps, but 80-95% of those collected during the early winter period of high clam transport were only 8-15 mm long. Mean shell length of the clams in the top 10 cm of sediment was 22 mm (min, 4 mm; max, 28 mm). Clams caught in the traps could reburrow if placed on the sediment surface.

A visual comparison indicated that the seasonal pattern of clam transport was linked to that of bedload transport (Fig. 4A, B). In mid-November there was an abrupt transition from a summer period of low clam transport to high transport in winter, followed by moderate transport throughout the remaining sampling period. Clam transport maxima coincided with bedload peaks on 20 November and 28 December. From a simple linear regression, we determined that bedload transport accounted for 26% of the variation in passive clam transport \( (r = 0.51, P < 0.001, n = 250) \). This analysis, however, suffers from the assumption that these time-series samples are independent. Cross-spectral analysis of bedload and clam transport time series revealed significant coherence \( (\text{max. } -0.85) \) between these series at periods > 2.5 d (Fig. 6A) and no lag between the signals of the series. Neither daily sediment height above the buried plates nor the daily change in sediment height was significantly correlated with clam transport \( (P < 0.05) \).

The link between bedload and clam transport did not extend to changes in population density on the sheltered sandflat. With the exception of an obvious density peak in late July (423 ind. m\(^{-2}\), Fig. 4C), high sampling variation (C.V. = 67%) inhibited detection...
of smaller peaks and seasonal trends in population density. It was clear, however, that during the period of maximal clam transport, clam density in the top 10 cm of sediment remained relatively constant. A negative linear correlation existed between clam transport and clam density for the entire sampling period ($r = -0.47$, $P < 0.001$, $n = 236$) because of long-term trends in both, but cross-spectral analysis showed that the level of coherence between the power spectra of clam density (Fig. 5C) and both bedload and clam transport (Fig. 5A,B) were not significant. Neither sediment height nor the daily change in sediment height was correlated with clam density ($P > 0.05$).

No clam spat were observed in the top 1.0 cm of sediment even though *M. arenaria* usually spawn in early fall on the eastern shore of Nova Scotia. Clam larvae in the water were not sampled during the study.

**Exposed site**—The low bedload transport in summer observed at the sheltered site was also evident at the exposed site (Fig. 7A), but the fall transition to a period of predominantly high bedload ($10-20$ kg m$^{-1}$ d$^{-1}$) occurred earlier (mid-October) and was preceded by two bedload peaks followed by at least 2 weeks of negligible transport. Another disparity was that bedload transport remained relatively high from January to April. Despite these seasonal differences, most of the variation in the spectral density of bedload transport on the exposed sandflat was still contained between the 2- and 10-d periods, with peaks centered at 2.5 and $=4$ d (Fig. 5D).

Average bedload transport on the exposed sandflat was six times greater than that observed on the low-energy site, but the maximal rate of transport at the exposed site ($34$ kg m$^{-1}$ d$^{-1}$, 3 November) was similar to that on the sheltered site. During bedload maxima at both sites, the level of trapped sediment rose to within 10 cm of the trap opening, decreasing the effective trap aspect ratio to below 5. As a result, traps may have underestimated bedload transport at these times. Nonetheless, median grain size of the trapped sediment (258 $\mu$m) was not significantly different from that of the surrounding sediment ($t$-test, $P > 0.05$, $n = 5$).

Two periods of rapid deposition followed by gradual erosion were the only perturbations in the otherwise gradual rise of the exposed-site sediment surface during the sampling period (Fig. 7A). After storms on 5 September and 3 November had deposited at least 5–8 cm of sediment onto the exposed site, the sediment surface was eroded to predeposition levels within 2 months. A positive correlation between sediment height above the buried plates and time ($r = 0.71$, $P < 0.001$, $n = 250$) suggested a net deposition of $\sim 6$ cm during the 10-month study period. Several periods of high sediment transport detected with the bedload traps were not revealed by daily measurements of sediment height (e.g. mid-April).

Despite a separation of $<300$ m, the population dynamics of *M. arenaria* at the exposed site were markedly different from those at the sheltered site. In addition to...
higher peaks of both clam transport and density, high numbers of clam spat were observed in the surface sediment (max, 23,000 ind. m⁻²; Fig. 7B). Spat were not observed below a sediment depth of 3 mm. Average transport of clams (shells >1 mm long) was still relatively low (79 ind. m⁻¹ d⁻¹; Fig. 7C), although it was >2,100 ind. m⁻¹ d⁻¹ on 3 d in September. These three peaks and a prolonged period of high clam transport in mid-October (400-1,000 ind. m⁻¹ d⁻¹) corresponded to periods of high bedload transport. Over the entire sampling period, bedload transport was positively correlated with clam transport (r = 0.33, P < 0.001, n = 250). Again, we stress that these time-series samples are not independent. Cross-spectral analysis showed significant coherence between the two time series at zero lag between bedload and clam transport (Fig. 6B).

The density of clams in the top 10 cm of sediment rapidly increased from 200 to 2,000 ind. m⁻² immediately following high levels of bedload and clam transport in early September (Fig. 7D). A subsequent rise to >5,000 ind. m⁻² in mid-October also corresponded with a period of high bedload and clam transport. The size distribution of clams within the prolonged fall density peak (mean, 9 mm; range, 6–28 mm) was similar to that of clams that had been transported during the three peaks in September (mean, 9 mm; range, 6–15 mm), but clam transport and population density were poorly correlated (r = 0.21, P = 0.004, n = 236). Cross-spectral analysis showed that coherence between the power spectra of clam transport (Fig. 5E) and population density (Fig. 5F) was not significant, but coherence between bedload transport and clam density was significant at a period of ~3 d (Fig. 6C). A negative phase spectrum indicated a lagged response of clam density to bedload transport.

Removal of clams on 3, 5, and 15 November reduced the clam population to 4% of peak density levels, but surprisingly few clams were collected in the bedload traps at these times. Excavation of ambient sediment below a depth of 10 cm indicated that the decrease in clam density was not a sampling artifact associated with net deposition of sediment because there were no clams with shells <3 cm long below the depth of sampling. Clam density remained relatively
Fig. 8. Relationships between clam density and height of sediment above the buried plates on the exposed site. Two density-dependent simple linear regressions were calculated; the upper regression used data within the fall peak of clam density (10 September–3 November), and the lower regression was calculated with the remaining data.

low until the end of April, except for a few minor peaks in February and March consisting of clams 10–15 mm long (~1,500 ind. m⁻²). The population density from December to April was about twice that of the preceding summer.

Net sediment transport, indicated by changes in sediment height, explained up to 52% of the variation in clam density on the exposed site, but the correlation was highly density-dependent (Fig. 8). When the entire data set was used, no significant correlation was found between clam density and sediment height above the buried plates. Inspection of the scatterplot of these variables, however, revealed two distinct data clusters. Linear regressions calculated for each cluster suggested that clam density was negatively correlated with sediment height from 10 September to 3 November and positively correlated at other times. Levels of significance could not be assessed, however, due to lack of independence.

Discussion

Bedload and clam transport — Evidence of passive transport of infaunal bivalves has been restricted to qualitative anecdotes (Baptist 1955) or incidental observation (Savidge and Taghon 1988); as a result, juvenile immigration has often been assumed to be negligible in studies of population dynamics (Brousseau 1978). At Eastern Passage, however, the transport of clams across the sediment surface was responsible for rapid and large fluctuations in clam density and net population growth on an exposed intertidal sandflat. Local spat settlement could not contribute to this net growth because all the spat that had settled in August had been removed by early October. Clearly, the growth capacity of an infaunal population cannot be appreciated fully if local spat settlement is assumed to be the only significant source of recruits.

The transport of clams across the sediment surface will not always be coupled to changes in population density because import may balance export or the clams may not become established. On the sheltered sandflat, high numbers of clams were collected in the sediment traps yet the population density remained relatively constant. In contrast to the exposed site, a prolonged period of negligible bedload transport immediately following peaks of clam transport was absent. Without this period of minimal sediment disturbance, establishment of clams transported into the area may have been inhibited. Bedload transport was not responsible, however, for the absence of spat in late summer.

In view of several reports of M. arenaria spawning without subsequent spat settlement (e.g. Pfitzemeier 1962), the absence of spat on the sheltered site was unusual only in comparison to the high numbers of spat that settled on the nearby exposed site. High turbulence intensity, which could have limited settlement, was more likely to exist at the exposed site than at the sheltered site, and dense algal mats that prevent settling larvae from attaching to the substrate (Olafsson 1988) were not observed in the study area. The differential settlement of M. arenaria may reflect the high density of G. gemma on the sheltered site (>30,000 ind. m⁻²) and its absence on the exposed site. It has been suggested that an inverse relationship exists between G. gemma and M. arenaria abundance because recently settled M. arenaria larvae cannot survive where resource competition and predation are high (Sanders et al. 1962). Thus, a biological rather than a physical limitation may ac-
Table 1. Parameters of the von Bertalanffy growth equation, \( L_t = L_{\infty} \left( 1 - \exp\left[ -k(t - t_0) \right] \right) \), where \( L_t \) is shell length (mm) at time \( t \), \( L_{\infty} \) is length at zero growth, \( k \) is growth rate to \( L_{\infty} \), \( t \) is age (yr) at given length, and \( t_0 \) is the age at which length is zero. The average of each variable was used to calculate the time required for a newly settled clam (\( \sim 500 \mu m \) long) to grow to 6 mm. Clam populations from Nova Scotia unless otherwise indicated.

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<th>( L_{\infty} )</th>
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<th>( t_0 )</th>
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<td>-0.164</td>
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Despite a cumulative spat settlement of \( >400,000 \) ind. \( m^{-2} \), the net effect of spat settlement on population growth at the exposed site was not different from that at the sheltered site. The absence of the 1988 settlers after the mid-October transition to high bedload transport suggests physical control of clam density, but this hypothesis is not consistent with observation that spat had decreased steadily until mid-October, even during periods of negligible transport. With only circumstantial evidence, predation is often invoked to explain declines in the 0-age group of *M. arenaria*; when detailed data are obtained (e.g. Möller and Rosenberg 1983), this assumption is often supported. A link between predation and the removal of the 0-age group on the exposed sandflat cannot be discounted, but the evidence from the bedload trap collections is clear; bedload sediment transport cannot be ignored as a potential mechanism controlling the density of organisms living near the sediment-water interface.

**Bedload and passive clam transport**—The significant coherence between bedload and clam transport time series at both study sites and the observation that clam transport was observed only during periods of bedload transport suggest that clams were dispersed by bottom currents after becoming eroded from the sediment surrounding the site or from neighboring sandflats. Active emergence and migration of small clams over a few meters has been reported (Dow and Wallace 1961), but it is unlikely that active migration of *M. arenaria* can account for the transport of \( >2,000 \) ind. \( m^{-1} \) \( d^{-1} \) into the study area in early September when there were \(<200 \) ind. \( m^{-2} \) in the sandflat. Moreover, Belding (1930) demonstrated that clams of the sizes frequently found in the traps (\( >12 \) mm) remain in their burrows.

Smith (1955) claimed that clam recolonization of azoic intertidal sediment in Massachusetts resulted from active migration, but his observations can be explained equally well by the passive import of clams during sediment transport. Indeed, he observed the highest recolonization rates in fall, when high bedload transport would be expected. Thus, although it is unlikely that small clams never leave their burrows, the presence of clams in the bedload traps at Eastern Passage is indicative of passive transport rather than active migration.

The slow growth rate of *M. arenaria* at temperate latitudes negates the possibility that the growth of spat was responsible for the large peak in population density in September and October on the exposed sandflat. By using published parameters of the von Bertalanffy growth equation derived for nearby clam populations (Table 1) and assuming a 2-week planktonic period (Witherspoon 1982), we estimated that the mean time required for a 500-\( \mu m \) spat to grow to 6 mm (i.e. the smallest clam within the density peak) would be \( \sim 170 \) d (Fig. 7B). Further, the stepwise increase in cumulative clam transport (Fig. 7C) closely resembled the increase in clam density at that time (Fig. 7D), and the size structure of trapped clams was identical to that of the clam pop-
ulation during the fall density peak. We suggest, therefore, that transport of juvenile clams during bedload events was responsible for the September increase in clam density. The mechanism for the rapid removal of most of these clams in early November was less apparent.

Although there is little doubt that predation can reduce clam populations severely (e.g. 99.8% density decrease after 5 months: Möller and Rosenberg 1983), biological factors were unlikely to be responsible for the removal of 2,000–4,000 clams m⁻² in 24 h in early November. Major clam predators such as gulls (Larus argentatus), green crabs (Carcinus maenas), nemertean worms (Cerebratulus lacteus), and gastropods (Lunatia heros) were rare on the exposed sandflat, and feeding pits associated with flatfish predation were not observed in the study area. The absence of damaged shells in both the sediment and the bedload traps also indicates a low predation rate. Lastly, in a small area of low sediment transport adjacent to the exposed site, clam density remained high (~2,000 ind. m⁻²) until April. Although this estimate was derived from a collection of 10 cores on 1 d (22 April; asterisk in Fig. 7D), the observation of numerous siphon holes in this area from September to April indicated that clam predation on the exposed sandflat was relatively low.

It follows that bedload sediment transport was probably responsible for the rapid export of thousands of clams from the study area. The fate of these clams remains unknown, but a cursory sampling survey throughout the remaining sandflat indicated that clams were removed from, rather than redistributed within, the exposed sandflat.

Net sediment transport — The deployment of bedload traps identified both the mechanism and the potential magnitude of fluctuations in population density but not the net result of this change. Estimates of net sediment transport with the buried plates were expected to fill this data gap; erosion would indicate export of clams and deposition would be associated with import. Unfortunately, the daily change in sediment level at both sites could not be correlated with clam density because of an inappropriate sampling interval. For example, a storm on 3 November deposited at least 3 cm of sediment on the exposed site, but instead of net immigration, a precipitous density decrease was observed. The possibility that clams were removed during a period of erosion within the storm could not be substantiated from the measurement of sediment height on the following day; only the net effect of the storm could be determined.

If clams were removed during the peak bedload event, why were there so few clams in the traps? In contrast to the clams present before the fall peak, clams making up the density peak were small (shell length, 6–15 mm), lived closer to the sediment surface, and were very susceptible to removal during the bedload maximum on 3 November. Unfortunately, the 20-cm-deep traps were likely inadequate to monitor accurately the clam transport associated with sediment erosion because the effective aspect ratio of the traps had decreased under abnormally high accumulation of bedload. As a result, the ability of the traps to collect and retain small clams and other light particles was reduced.

Although changes in the sediment surface from day to day could not be related to clam density, a significant relationship between density on the exposed sandflat and sediment height was found at longer time scales (Fig. 8). Because both the sediment surface and the clam population increased with time, a significant direct proportionality between sediment height and clam density was expected, but the inverse correlation during the fall clam density peak was surprising because it implied that sediment erosion was coupled with an increase in clam density. This incongruity can be explained if we assume that the degree of erosion was insufficient for clam removal and did not prevent the establishment of clams transported into the study area. Because the rate of erosion was only ~1.3 mm d⁻¹, and because Emerson et al. (1990) showed that M. arenaria can adjust their vertical position in response to a changing sediment surface, the first assumption appears reasonable. It is more dif-
ficult to validate the second, but the potential for clam import was present since clam transport was frequently observed during this period.

Implications of clam transport—Because of occasional reports of clam washout during storms (Baptist 1955), a link between bedload transport, clam transport, and clam density was not surprising. Intense, long-term sampling on low- and high-energy sandflats, however, showed that clam transport is not limited to large storms and that its significance is probably not restricted to M. arenaria recruitment; many infauna living near the sediment–water interface will be susceptible to the movement of their substrate. Polychaetes, nematodes, gastropods, and other bivalves were frequent constituents of the trapped material at our study site. The results also provided vivid evidence of the risk in estimating annual secondary production from biomass samples that are obtained infrequently. This problem would be particularly acute on temperate sandflats, where bedload transport may control the age structure of a population.

If average annual water temperature is low, clam maturation will be delayed and spawning and settlement will occur immediately before the fall transition to high bedload transport. When the period between settlement and high bedload transport is short, the ability to become established will be limited and the possibility of removal will be high. As a result, the age structure of clam populations in moderate- or high-energy areas may comprise a few cohorts that recruited to the population in a year of anomalously low bedload transport (or high water temperature).

Another consequence of the passive transport of M. arenaria across the sediment surface is its potential to reduce the effects of overfishing on commercial clambeds. Depressions in the bed, as areas of reduced shear stress, are sites where organic matter accumulates (Nowell and Ju-mars 1984) and fauna collect (Savidge and Taghon 1988). It is possible, therefore, that the numerous pits created by intense clam digging could entrain clams that otherwise would pass across the sediment surface and thereby enhance recovery of the clam population.

References


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