

## EFFECTS OF BIOLOGICAL ACTIVITY ON THE ENTRAINMENT OF MARINE SEDIMENTS

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### ABSTRACT

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The effects of animal tracks and fecal pellet production on the critical entrainment velocity of marine sediments were examined experimentally. Laboratory measurements in a free-surface, seawater flume were made using three sediment sizes. Effects of three species of polychaetes and two species of bivalves were tested. Boundary shear velocity was calculated from the mean velocity profile in the logarithmic region of the boundary layer. Measurements were made with a hot film anemometer. Tracking doubled the boundary roughness and decreased the critical entrainment velocity by 20%. Ambient or "free" sediments were more easily entrained than fecal mounds, which were restrained from movement by mucous adhesion between the fecal coils. Isolated pellets, such as those egested by *Amphicteis scaphobranchiata*, transported readily as bedload over a cohesive sediment surface.

### INTRODUCTION

The entrainment of sediment in the ocean operates within the triptych of flow—animal—sediment interaction. The effects of biota on surficial sediments have been investigated experimentally (cf. Rhoads, 1974, for summary), but the influence of flow on organism—sediment interaction has been largely ignored. Such an influence is biologically important, for the advection of sediment past suspension feeders and the rate of deposition of sediment utilized by surface deposit feeders will influence the relative abundances of these two feeding guilds (e.g., Jumars and Fauchald, 1977; Wildish and Kristmanson, 1979).

Benthic organisms play a significant role in modifying the conditions for sediment entrainment by: (1) altering the individual particle characteristics, their vertical and horizontal distribution and, hence, their availability for entrainment; (2) changing the bulk characteristics of the sediment, such as its permeability; and (3) varying the boundary properties of the flow by

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altering the surface roughness of the bed. As both the sediment properties and the variability and magnitude of the imposed fluid stress are influenced by biota, it is necessary to evaluate the boundary characteristics incorporating these biogenous effects.

The empirical study of animal—sediment interaction has resulted in the bicameral classification (bioturbation versus biostratification) of biogenous sedimentary structures (Frey, 1973) and, consequently, a dichotomous taxonomy of biotic effects on sediment transport. Biological activity in marine sediment is classified as either binding (e.g., mucous coatings) or destabilizing (e.g., destruction of sediment cohesion by burrowing) (Yingst and Rhoads, 1978). However, such categorical statements about the effects of particular biological activities are difficult to make. Biological effects are variable and depend, for instance, on organism density, sediment composition and the activities of co-inhabitants. For example, isolated polychaete tubes that emerge above the bed will entrain higher-velocity fluid down to the sediment surface causing local scour. In contrast, field observations indicate that at very high densities tube mats may be associated with a local increase in the resistance to erosion (Fager, 1964; Woodin, 1976). A second example is provided by the tracks of organisms on the surface of the seabed. The tracks of small biota increase the small scale roughness of the boundary. Such a change increases  $z_0$  (the boundary roughness length scale) which may enhance entrainment of sediment. Some animal motion, however, may be associated with mucous production which results in adhesive binding between sediment grains; this will reduce the probability of particle entrainment. MacIlvaine and Ross (1979) have shown that benthic fauna may also reduce larger scale roughness and Cullen (1973) has even suggested that the tracks of epifauna may be smoothed by meiofauna.

A full understanding of animal—flow—sediment interactions can only be obtained by careful experimentation with isolated parts of the system. The entire matrix of interactions can be brought together with models, such as the Markov approach described by Jumars et al. (1981). However, the Markov models themselves do not make explicit the processes that control the transition probabilities. There are two divergent ways to estimate the transition probabilities of the Markov model described by Jumars et al. One is to introduce tracer particles and to monitor their transfer from one compartment to another. The other is to identify and quantify the processes affecting the individual transitions and, from the resulting mechanistic understanding, to predict the magnitudes of the respective transition probabilities. The former approach does not allow generalization from one environment to another. Consequently, the latter has been adopted, leaving the empirical method as a later test of the model's predictive capacity.

Experiments have been carried out in the laboratory to examine the influence of biogenous processes on marine sediment transport and to identify the responses of soft-bottom benthos to different flow environments. The feeding strategies of some macrobenthos have been observed to change in response to particle flux (Taghon et al., 1980) and further details on

particle selectivity are reported in Self and Jumars (1978). The objective of the present paper is to describe recent experiments that aim to elucidate some of the biogenous processes that influence marine sediment transport—specifically entrainment of beds containing fecal pellets and of biologically roughened surficial sediments.

The various types of sediment transport models used in marine sedimentology are described by Smith (1977). He suggests that the Yalin bedload equation (based on a critical erosion velocity determined from the Shields diagram) and the Einstein bedload transport model (based on probabilistic parameters) are most suitable to predict bedload transport rates on the continental shelf. Neither model incorporates the effects of biota, despite the evident importance of organism activity on bed morphology and bulk properties. The Yalin model requires determination of whether the Shields diagram is applicable to marine sediment in which fecal pellets and ambient sediment may be mucus-coated. The Einstein model requires the evaluation of empirical parameters (such as the hiding factor). The effects of tracking and pelletizing the sediment are discussed here in light of these current models of sediment transport.

## BACKGROUND

### *Tracking by organisms*

With the exception of the surf zone, marine sediment transport is likely to be influenced by the presence and activities of both macrofauna and meiofauna. Exhalant and inhalant siphons and animal tubes may determine surface micro-relief while tracking may alter the surface roughness. Many authors working with slope sediments (e.g., Emery, 1960; MacIlvaine and Ross, 1979) have noted the importance of biota in determining surface roughness and sediment erodibility. Tracking by organisms has been well documented in deep-sea photos by Heezen and Hollister (1971), and a description of its effects on unconsolidated sediment on the continental slope is provided by MacIlvaine and Ross (1979). They noted that tracks increased the small-scale roughness and, in subsequent flume experiments on box cores, that mass erosion occurred preferentially at biologically produced surface irregularities. The observed decrease in critical entrainment velocity is consistent with the fact that increased roughness will alter the exposure of some particles. Some sediment grains (on the track ridges, for example) will be higher in the viscous sublayer (where they will be exposed to a higher stress). Fenton and Abbott (1977) have shown for coarse material (2.5 mm diameter) that with a relative protrusion of 0.5 (i.e., a particle is one-half diameter above the surrounding particles), the critical entrainment velocity is reduced by a factor of 1.7.

*Pelletized sediments: transport considerations*

The relative erodibility of pellets in comparison to the ambient sediment has important biological, stratigraphical, and sedimentological implications. Schafer (1972) suggested that organisms never reingest their own fecal pellets, because they lack nutritive benefit. The experiments of Lopez and Levinton (1978) with *Hydrobia ventrosa* showed that if fecal material is disaggregated and fed immediately to the snails, additional digestion is negligible. Similar results for fresh pellets have been obtained with *Amphicteis scaphobranchiata* (Taghon and Nowell, in prep.). There seems to be advantage in avoiding ingestion of recently produced feces, until they have been recolonized by microbes (Newell, 1965).

The transport of fecal pellets and their emplacement in the stratigraphic record has received little attention (cf. Ronan, 1977). Schafer (1972) suggested that cylindrical feces are rapidly destroyed by moving water and are rarely found in the stratigraphic record. However, Risk and Moffat (1977) observed that discoidal pellets (of *Macoma balthica*) are easily transported intact, and can form sedimentary deposits.

The ratio of settling velocity to entrainment velocity is used customarily to indicate that quartz particles finer than 100  $\mu\text{m}$  will move as suspended load (see Sternberg, 1972, after Sundborg, 1967). The pelletization of sediments may alter the nature of sediment movement by changing the particle-size distribution. The continued pelletization of the bed may alter dramatically not only the critical entrainment conditions but also change the mode of movement of the sediment from suspended load to bedload transport. McCall (1979) studied the effects of subsurface deposit feeders on particle size in Lake Erie and noted that tubificid oligochaetes produce pellets  $280 \times 70 \mu\text{m}$  in size in a region of lacustrine clay ( $D_{50} = 1.5 \mu\text{m}$ ). The bed surface, down to 1 cm, is comprised chiefly of such pellets which have a settling velocity of 1.03 cm/sec. The ambient "free" sediment has a settling velocity at least two orders of magnitude lower. This result is in close accord with the observations of Haven and Morales-Alamo (1966) on the settling velocity of fecal pellets of suspension-feeding oysters. It should be noted that the rate of physical abrasion of pellets and its effects on sediment flux rate has not yet been measured under realistic conditions of flow and sediment transport.

A common suggestion in the literature is that fecal pellets are eroded more easily than ambient "free" sediment. For example, Banner (1979, p.288) states: "heavily bioturbated muds will contain significant proportions of fecal pellets with settling velocities two orders of magnitude greater than that of the particles of untransformed mud (Haven and Morales-Alamo, 1966), just as the critical erosion velocity will be reduced to two orders of magnitude less (Rhoads and Young, 1970)". Based on observations at low tide in the Bay of Fundy, Risk and Moffat (1977) stated that for *M. balthica* "both feces and pseudo-feces are readily transported". They observed a lack of feces and pseudo-feces at low tide initially and subsequently increasing

numbers of pellets as the clams fed; pellets were found in "sand windows" and in the lee of large rocks. They inferred, therefore, that the pellets were easily transported.

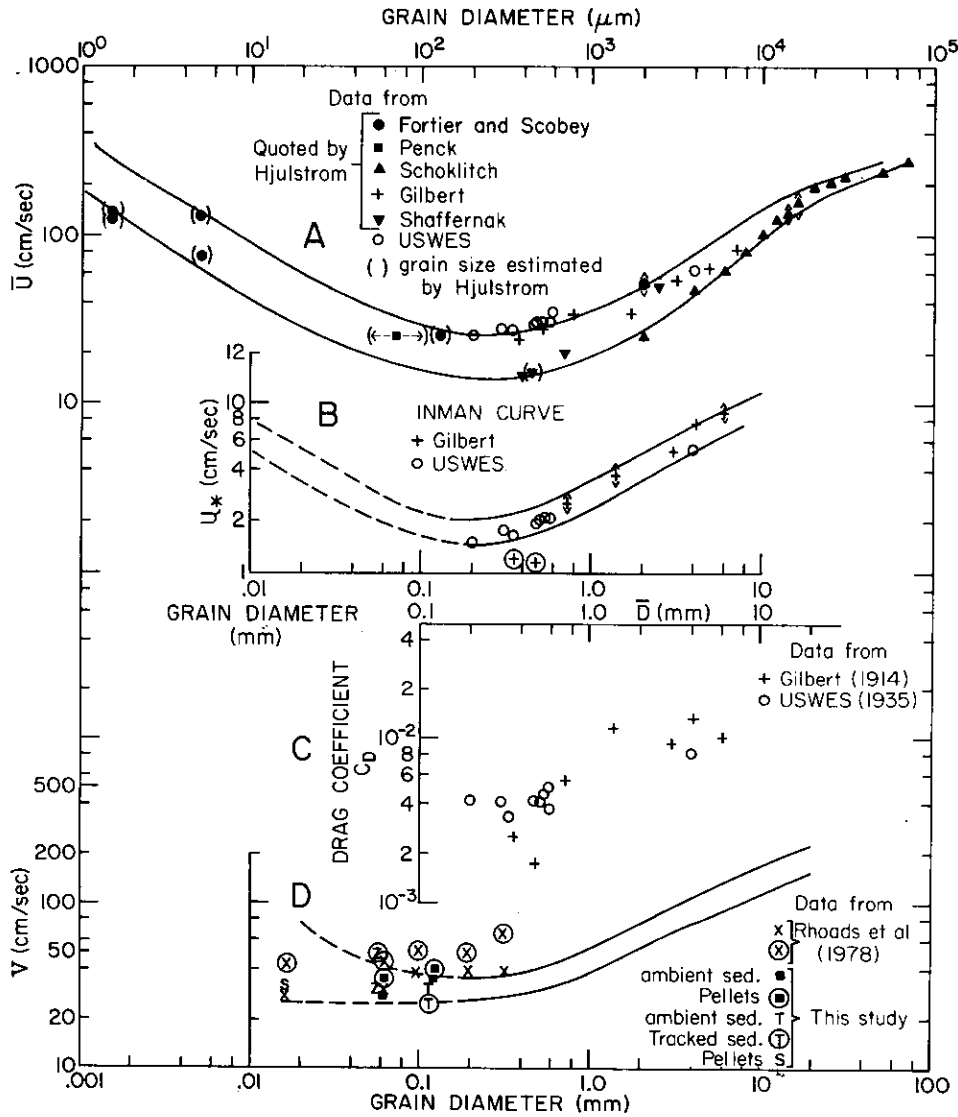
The original study of Rhoads and Young (1970), (upon which the notion of rapid fecal pellet transport seems to be based) compounded the effects of sediment burrowing (which increases pore water content), fecal pellet production, and microbial growth. Thus because they observed that biologically reworked sediment is entrained preferentially, it has been inferred subsequently that fecal pellets are more easily entrained. Rhoads and Young (1970), however, do not make this inference themselves. Specifically, they observed that in a transect across Buzzards Bay pore water content values of 30% in the upper 5 cm of sediment were found at stations dominated by suspension feeders and at two stations which were extensively burrowed by surface deposit feeders, the upper 5 cm had water content values of 70%. They concluded that burrowing increases the water content and that this results in a lower critical entrainment velocity (cf. Postma, 1967, fig.2b, p.159). Rhoads and Young (1970) undertook a laboratory experiment in a small, oscillatory, boundary-layer flow. They allowed surface deposit-feeding bivalves (*Nucula proxima*) to operate for 10 days on sediment finer than 62  $\mu\text{m}$ . The portion of the sediment that was inhabited by the bivalves was more easily eroded (water content 60%) than the uninhabited sediment (water content 50%). Postma's graph indicates that for this sediment size, an increase in water content from 50% to 60% is associated with a 25% decrease in the critical entrainment velocity. Subsequent experiments by Rhoads et al. (1978) have shown that after 10 days of microbial growth critical entrainment velocity is increased by 45% for material of 60- $\mu\text{m}$  diameter. The differences in erodibility documented by Rhoads and Young (1970) for sediments containing macrofauna versus *azoic* sediments thus may have resulted from a combination of differences in microbial binding, deposit-feeder pelletization, burrowing, and other deposit-feeder activities.

#### *Critical entrainment conditions*

In order to evaluate the variation in sediment entrainment conditions due to biological activity it is necessary to review the criteria used to estimate critical entrainment for abiotic sediments. Hjulsrom's (1935) plot of particle size (for  $\rho_s = 2.65 \text{ g/cm}^3$ ) versus water velocity is frequently used for a broad range of particle sizes and for sediment movements over rippled beds (cf. Sternberg, 1972; Rhoads et al., 1978). This curve (Fig.1A) is based on only five sets of data, and only three sets include measurements of both particle size and velocity; particle size was estimated for the other two sets (Middleton, 1966). None of the measured data used by Hjulsrom are for particle sizes smaller than 350  $\mu\text{m}$ ; the results quoted by Hjulsrom for small particles are based on a questionnaire sent to engineers who maintained irrigation canals. The velocities quoted represent average velocity; this velocity is defined for a channel as discharge divided by cross-sectional area, but is not readily measured in a marine boundary layer.

Inman (1949, p.56) plotted critical shear velocity versus particle diameter for quartz density material. Fig.1B shows this diagram and includes all the data on which he based his curve: no data were quoted for particles less than 100  $\mu\text{m}$  in diameter.

Drag coefficients are used to relate the mean velocity at some height above the seabed to the bed shear velocity. This method then permits the use of Inman's diagram to estimate the sediment threshold condition. A drag coefficient of  $1 \cdot 10^{-3}$  is commonly advocated. The studies on which Inman's curve is based (USWES, 1935; Gilbert, 1914) reported both  $u_*$  and the average velocity; from these the drag coefficient can be calculated. There is



considerable scatter (Fig.1C); the large variability in Gilbert's experiments is due to the presence of bedforms (cf. Gilbert, 1914; Rubey, 1938).

A plot used commonly to relate sediment entrainment to mean velocity 1 m above the bed was produced by Sundborg (1956, p.177). The curves shown in Fig.1D are based on Sundborg's (1967) review of sediment transport, and include data on both abiotic and microbially colonized glass beads (Rhoads et al., 1978).

Miller et al. (1977) analysed recent experiments on threshold velocity (for  $\rho_s = 2.65 \text{ g/cm}^3$ ) and produced a figure with the same axes as the Inman diagram (Fig.1B). In Fig.2 their diagram has been extended to include the recent experiments of Mantz (1977). Figs.1B and 2 demonstrate that little is known about  $u_{*cr}$  for particles of less than 100  $\mu\text{m}$  diameter. Many of the results below 100  $\mu\text{m}$  were obtained from experiments carried out in Newtonian oils; the relevance of these results to marine and fluvial sediments where microbial growth is ubiquitous, has yet to be demonstrated.

The dimensionless plot of critical boundary stress versus roughness Reynolds number ( $u_* d/\nu$ ) was produced by Shields (1936). Shields terminated his plot at  $u_* d/\nu = 1$  based on the smallest particle size used by Gilbert (1914) in his experiments. The trend of increasing dimensionless stress for decreasing roughness Reynolds number (below  $u_* d/\nu = 1$ ) has a slope of  $-1$  based only on dimensional arguments proposed by Shields. Fig.3 shows the extended Shields curve as suggested by Mantz (1978) which has a slope of  $-0.4$  for small particle sizes. Also shown on the figure is the Shields curve based on Inman's plot of critical entrainment velocity versus particle diameter.

For fine-grained materials, where the influence of soft-bottom benthos is most evident, a great deal of care has to be taken to demonstrate the significant differences between biologically altered and abiotic sediments. For sediments smaller than 100  $\mu\text{m}$ , there appears to be great uncertainty in predicting  $u_{*cr}$  even in azoic materials. Macrobenthos are restricted in size of particles ingested, and deposit-feeders are more abundant in finer sediments

Fig.1A. Plot of sediment diameter against mean velocity at which material will start to erode (after Hjulstrom, 1935). Mean velocity,  $\bar{u}$ , is not specified at any height, but is the discharge divided by channel cross-sectional area. To the data quoted by Hjulstrom has been added data from USWES (1935) study. Hjulstrom estimated grain size by transforming soil classifications (e.g., clayey loam, silty loam) to particle diameters.

B. Inman curve of critical entrainment velocity versus particle diameter. Inman used dashed lines to display relationship for median diameters below 100  $\mu\text{m}$ . Symbols as in A, with addition of  $\oplus$  from Gilbert (1914).

C. Drag coefficients for laboratory experiments used by Inman to construct B. The data from Gilbert (1914) show larger scatter because of loose classification of threshold of sediment motion.

D. Plot of critical velocity ( $v$ ) at a height of 100 cm from boundary versus particle diameter, from Sundborg (1967). He did not show data on which these curves were based. Data from present experiments are displayed; x and  $\otimes$ , from Rhoads et al. (1978), are for abiotic and microbially colonized glass beads, respectively.  $\odot$ ,  $\otimes$ , and  $s$  represent pellets of *H. florida* and *A. scaphobranchiata*; ambient sediment diameter is used for abscissa scale.

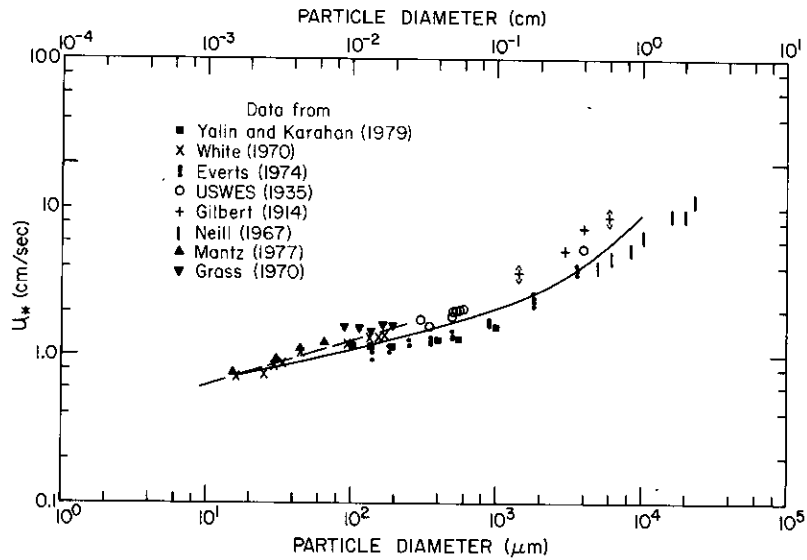


Fig. 2. Critical entrainment velocity plotted against particle diameter, modified after Miller et al. (1977). Solid line is empirical best fit to data suggested by Miller. Data from Mantz (1977) and Yalin and Karahan (1979) added. Dashed line is best fit suggested by Mantz (1977) for particles less than  $100 \mu\text{m}$  diameter.

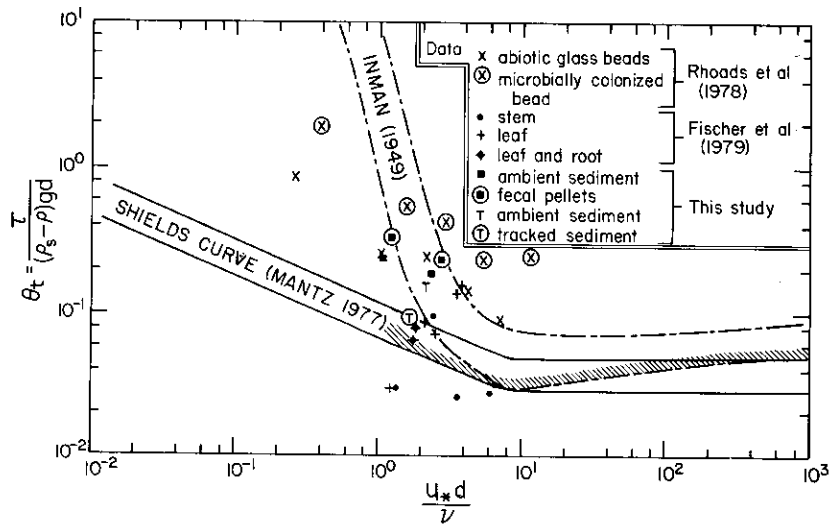


Fig. 3. Shields diagram with non-dimensional shear stress plotted against boundary Reynolds number. Hatched area is domain of curve suggested by Shields (1936). Mantz (1977) extended Shields curve (solid line); dashed line is calculation of dimensionless shear and Reynolds number for quartz-density material in water at  $20^\circ\text{C}$  based on Inman's curve (Fig. 1B). Data on biologically altered sediments (Rhoads et al., 1978), on biogenous material (Fischer et al., 1979), and from the present experiments are displayed. Particle diameter used by Fischer et al. is based on the equivalent quartz sphere settling velocity.

(Newell, 1970). For example, *Hydrobia minuta* with a shell size of approximately 3–5 mm has difficulty ingesting materials greater than 62  $\mu\text{m}$  (Lopez and Levinton, 1978). Taghon (in prep.) observed that *P. kempfi japonica* preferentially ingests material smaller than 150  $\mu\text{m}$ . In the sands of the continental shelf, particle selection and subsequent pelletization may thus (cf. Jumars et al., 1981) keep the fine material near the sediment surface where it may be subsequently eroded.

## EXPERIMENTAL METHODS

### *Seawater flume*

A series of experiments was performed in a recirculating seawater flume at the Friday Harbor Laboratories of the University of Washington, in order to investigate the effects of different flow and sediment transport regimes on the feeding behavior of macrobenthos and to parameterize the influence of such organisms on the initial entrainment of sediment. The plexiglass flume 2.5 m long and 50 cm wide has a bed with a removable section so that sediment cores 25 cm square and up to 20 cm deep may be placed coplanar with the surrounding bed of the flume. The leading edge of the sediment box is located 1.75 m from the entrance to the flume. Seawater, from approximately 10 m depth in Friday Harbor, is supplied to a 50-gallon, constant-head tank. This seawater enters the flume and is rectified through a 10 cm length of honeycomb (0.5 cm mesh size). The discharge is regulated by a butterfly valve on the output of the constant-head tank. A tail gate (comprised of vertical louvres) and an adjustable slope allows uniform flow to be established along the length of the flume. The water may be returned to the head tank using a small impeller pump coupled to a 10- $\mu\text{m}$  filter. The head tank may be supplied directly from the laboratory seawater system, or both direct supply and the pump may be used together. Throughout the duration of the experiments, some of which ran continuously for over 24 h, the seawater, which was recirculated through the pump and filter, remained constant to within 0.1°C of the starting temperature of 7°C.

### *Measurement of velocity*

Over the range of flow depths and velocities used in these experiments the boundary layer is fully developed within 1 m of the entrance to the flume. Boundary layer thickness increases as 4/5 power of distance and Schlichting (1968) notes that:

$$\frac{U_{\infty} \delta}{\nu} = 0.37 \left( \frac{U_{\infty} x}{\nu} \right)^{4/5}$$

where  $U_{\infty}$  is the free stream velocity,  $\delta$  the boundary layer thickness,  $x$  the downstream distance, and  $\nu$  the kinematic viscosity. Rearranging this yields:

$$\frac{x}{\delta} = 0.37 \left( \frac{U_{\infty} \delta}{\nu} \right)^{0.2}$$

Thus, for a free stream velocity of 30 cm/sec and a depth of 3 cm (the largest values of these variables in the experiments), the boundary layer intersects the free surface at a distance ( $x$ ) of 1 m; for lower velocities the distance is less.

The boundary shear velocity ( $u_*$ ) can be calculated from the water surface slope and flow depth. In this short flume considerable imprecision in estimating slope would be inevitable; moreover, as the boundary layer only reaches equilibrium after 1 m, determination of  $u_*$  by this method would yield an overestimate with respect to the local  $u_*$  over the sediment box (1.75 m from entrance). The boundary shear velocity was calculated from the slope of the logarithmic velocity profile:

$$U(z) = \frac{u_*}{\kappa} \ln \left( \frac{z}{z_0} \right)$$

where  $U(z)$  is the mean velocity at a height  $z$  above the bed and  $\kappa$  is Von Karman's constant. The roughness length  $z_0$  is related uniquely to particle size in the rough regime ( $z_0 = k_s/30$ , where  $k_s$  is the particle size and  $u_* k_s/\nu > 70$ ) and to the shear velocity and viscosity in the smooth regime ( $z_0 = \nu/9u_*$  for  $u_* k_s/\nu < 3$ ). In the transitional regime, and for distributed roughness (e.g., fecal pellet mounds, tracks) the relationship between  $z_0$  and particle size is poorly understood, and thus  $z_0$  is not known a priori. A minimum of ten points was used in each vertical profile and a least-squares fit to these points was performed using a Von Karman's constant of 0.4. Five velocity profiles taken at randomly selected coordinates over the box core were measured for each experimental run to determine the critical entrainment velocity. The five velocities, at each of the ten levels, were averaged together prior to the least-squares fitting.

The velocity was measured with Thermo Systems TSI 1231 W conical quartz film probes. The quartz-coated probes, operated with a TSI 1050 anemometer, were calibrated by first measuring the temperature-resistance relationship which was linear (correlation coefficient = 0.999); thus any arbitrary overheat could be selected. The mean-velocity-DC-voltage relationship was measured at an overheat of 19°C (corresponding to a resistance of 1.04 times the cold balance). The frequency response was checked in a low-turbulence water tunnel (cf. Nowell, 1974). Following the experiments the probes were recalibrated in a rotating water table. The probes were cleaned frequently using a super-saturated solution of potassium dichromate.

As the chief concern in the present experiments is for the mean velocity, the stability of the system rather than its frequency response is of greater importance. The mean velocities were calculated for 30-sec averages of the DC voltage-DC-voltage levels were constant over periods of 2-h continuous operation, the longest single period of measurement. The anemometer signal

was monitored at all times on an oscilloscope, and the output was low-pass filtered at 300 Hz with a Multimetrix variable-decade active filter. The RMS values of the AC signal corresponding to the turbulent fluctuations were obtained from a DISA 55D35 true RMS voltmeter using a 30-sec integration time constant. The AC signal was recorded on FM tape for subsequent statistical analysis of the fluctuating velocities.

The evaluation of the threshold of sediment motion has received considerable attention because of its inherently subjective definition. Shields (1936) defined critical entrainment as that velocity at which less than 0.1 pounds of sediment/ft. width of channel/h was moved. His criterion is based on studies (USWES, 1935) in which both sediment discharge rate and friction velocity were measured. Some authors have suggested extrapolating the sediment discharge curve plotted against imposed stress back to zero sediment discharge (cf. Johnston, 1943). In the present study such a method was not practical. A pelletized sediment is broken up by the return pump (thus changing the effective particle diameter of material in transport) and animal tracks are eradicated at high sediment transport rates (thus altering the effective roughness of the bed). Hence a non-steady state is imposed, where sediment discharge rate depends upon the production rate of fecal pellets, on the rate of animal tracking as well as upon  $u_*$ . Accordingly, a visual evaluation was used, equivalent to "weak" transport (sensu USWES, 1935).

#### *Entrainment of tracked sediments*

In order to measure the effect of tracking on the magnitude of the critical entrainment velocity an experiment was carried out using the small, motile bivalve *Transenella tantilla* (shell length approximately 4 mm). The flume bed was covered with sediment from Skagit Bay, Washington (median grain size 118  $\mu\text{m}$ , wet-sieved through 350  $\mu\text{m}$  to remove macrofauna and animal tubes, see Table I). A low-angled spot-light was used to enhance visually the topographic variability, and the bed was smoothed so that surface irregularities were less than 0.05 cm in relief. Discharge over the smoothed bed was increased until entrainment occurred. The discharge was then reduced to nearly zero and *T. tantilla* were dropped onto the bed and allowed to track for 15 h. The velocity was then increased until entrainment was observed through a stereo-microscope (magnification  $\times 10$ ). Several tracks were observed sequentially to insure that sediment entrainment was not just a local phenomenon.

#### *Entrainment of fecal pellets on non-cohesive sediments*

Few controlled laboratory experiments have been performed in which direct measurements have been obtained of the critical erosion velocity for biologically altered sediments. Hence, a study of the entrainment of fecal pellets was carried out using an ampharetid polychaete (*Hobsonia florida*), a spionid polychaete (*Pseudopolydora kempji japonica*), and a deposit-feeding

TABLE I

Sediment sizes used in critical entrainment velocity experiments\*

	Median diameter ( $\mu\text{m}$ )	$D_{16}$ ( $\mu\text{m}$ )	$D_{84}$ ( $\mu\text{m}$ )
Tracking by <i>T. tantilla</i>	118	32	174
Sandy silt— <i>H. florida</i>	64	16	104
Fine sand— <i>H. florida</i>	121	34	176
Sandy silt— <i>M. nasuta</i>	64	16	104
Fine silt**— <i>A. scaphobranchiata</i>	18.2	5	37

\*All sediments were wet-sieved at 350  $\mu\text{m}$ ; \*\*re-sieved at 61  $\mu\text{m}$ .

bivalve (*Macoma nasuta*). Polychaete tubes and the inhalent and exhalant siphons of the bivalves were allowed to surface from below the sediments, that were deposited and smoothed as described above. In all experiments, the animals were allowed to feed and defecate under low flow ( $U_{\infty} < 1$  cm/sec) conditions for at least eight hours.

The experiments with *H. florida* were carried out with two grain-size distributions. Natural sediment from two sites in Skagit Bay with median grain sizes of 64  $\mu\text{m}$  and 121  $\mu\text{m}$  was wet-sieved (see Table I). In each experiment after 8 h the discharge was increased until entrainment of the feces and the "free" sediments (sensu Jumars et al., 1981) was noted by an observer looking through a stereo-microscope.

Another tube-building polychaete, *P. kempi japonica*, on which extensive results on feeding rates and foraging strategies have been obtained (Taghon et al., 1980; Taghon, in prep.), was allowed to feed and defecate on a smoothed bed of glass beads (54–73  $\mu\text{m}$  diameter). This experiment was carried out using glass beads for two reasons: first, as a check on the ability to reproduce for narrowly graded, quartz-density material the critical entrainment velocity as determined from Shields diagram (as modified by Mantz, 1977). Second, the experiment was carried out in conjunction with a feeding experiment using the glass beads as food for *P. kempi japonica*. After 8 h the velocity was increased until entrainment of feces and "free" sediment was noted.

*M. nasuta* were allowed to burrow in the sediment box filled with silty sand (median size 64  $\mu\text{m}$ , see Table I). A layer of the same silt, from Skagit Bay, Washington, was then deposited over the whole flume bed and smoothed. The discharge was increased after 8 h until entrainment of feces and ambient sediment was observed through a stereo-microscope.

#### *Entrainment of pellets on cohesive sediments*

In order to extend the particle size range of the investigations, experiments were carried out using another ampharetid polychaete, *Amphicteis scaphobranchiata*. These surface deposit feeders were collected subtidally

from West Sound, Orcas Island, Washington, and placed in a flume box of wet-sieved, fine sediment (median diameter,  $18.2 \mu\text{m}$ , see Table I). A surface layer of the same sieved sediment was deposited from suspension over the whole flume to a depth of 1 cm. The animals were allowed to feed and defecate for 8 h. The discharge was then increased until the fecal pellets were observed to move.

## RESULTS

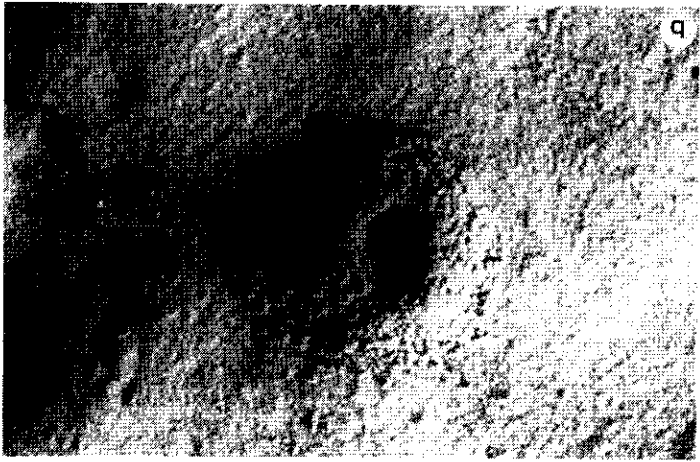
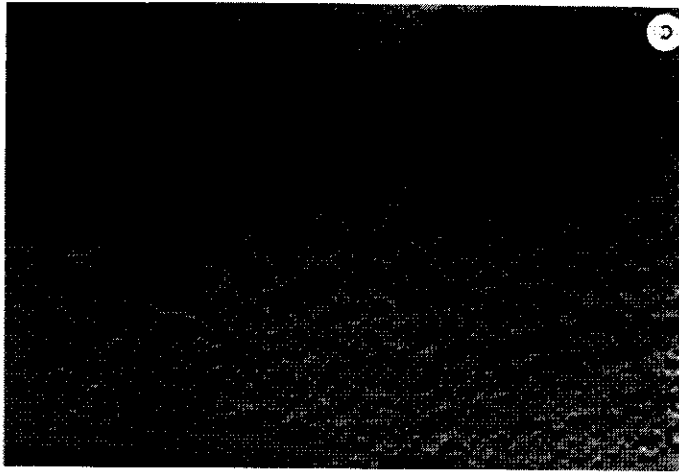
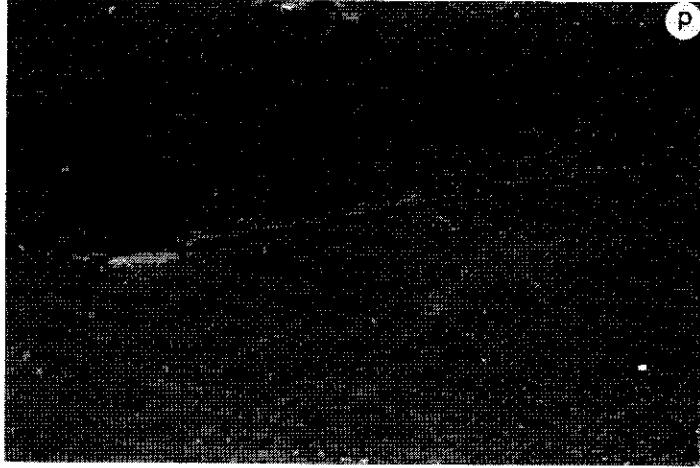
### *Surface tracking by *Transenella tantilla**

Previous to animal tracking the entrainment of the sediment occurred at a critical shear velocity of 1.74 cm/sec. Fifteen hours after the *T. tantilla* were introduced onto the sediment surface, the bed was covered with small "snow-plow" trails with steep banks and small levees of sediment approximately 10 grain diameters high (Fig. 4a). The sides of the tracks, some of which were 2 mm deep, were very steep, approximately at the natural angle of repose of the sediment. The tracks of the clams covered less than 10% of the total surface area of the bed. Sediment entrainment always occurred at the crest of the tracks at a shear velocity of 1.39 cm/sec. Individual grains from the crest of the trail rolled a considerable distance down the flume, if they were not trapped in the bottom of a trail. There was no visible difference in entrainment from tracks parallel to and those normal to the flow. After 30 min of flow at the critical entrainment velocity several of the tracks would be filled in with material advected from upstream. During this time the clams continued tracking over the sediment.

The velocity profiles (Fig. 5) obtained over the tracked bed showed that the critical entrainment velocity was reduced by 20% while the roughness length ( $z_0$ ) was doubled. The hydraulically smooth value for the azoic bed should be 0.0004 cm (based on  $z_0 = \nu/9 u_*$  and  $u_*$  derived from the Shields diagram); the measured value was  $0.0006 \text{ cm} \pm 0.0002$  at a  $u_*$  of 1.74 cm/sec. This yields a roughness Reynolds number of 2 which is approximately the upper limit for hydraulically smooth flow. After the bed had been tracked, the flow became transitional, with  $z_0$  of 0.0012 cm.

### *Transport of feces over non-cohesive sediments*

Because the flume discharge was reduced to nearly zero while the organisms were acclimating, the feces from the tube-building ampharetid (*H. florida*) were deposited at random locations around the tubes. The feces, which are coils of sediments, the interstices of which are filled with mucus, were deposited onto the surface in a distinct mound that was usually several tube diameters (about 5 mm) away from the ampharetid tube. With the polychaetes that have been studied so far in these experiments, the fecal materials were placed carefully in one sector in relation to the tubes, so that only occasionally were single, isolated coils observed. The fecal coils of *H. florida*



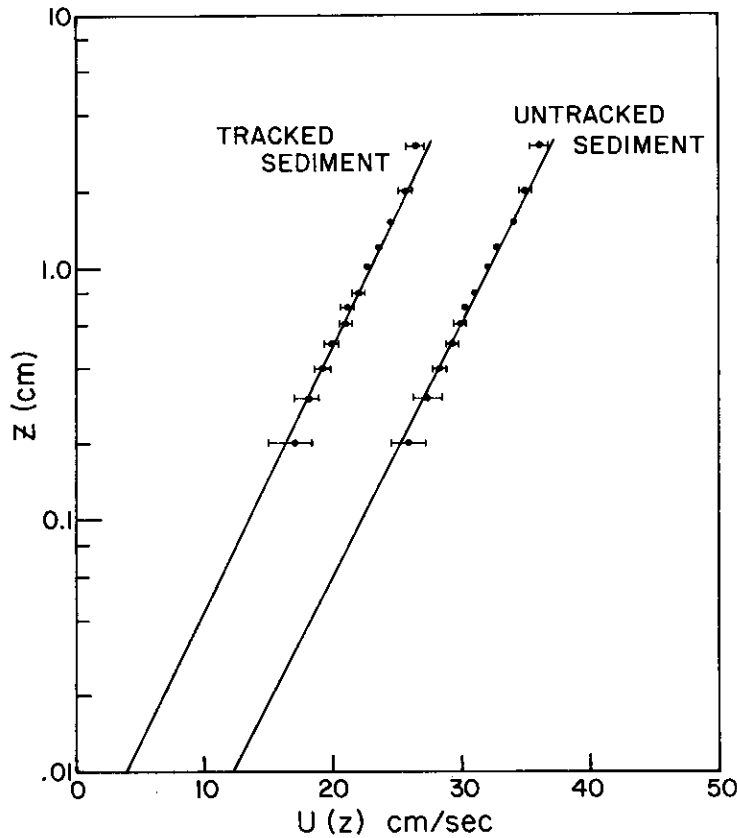


Fig. 5. Semi-logarithmic plot of mean velocity at critical entrainment condition for sediment before and after tracking by *Transenella tantilla*. Horizontal lines represent standard error from five vertical profiles. Where bars are not shown, standard error was less than size of point.

were about 200  $\mu\text{m}$  in diameter and were very adhesive, sticking readily to one another. Mounds of fecal coils in these experiments reached up to 1 mm high. This was sufficiently large to distort or even disrupt the continuous viscous sublayer.

Fig. 4A. Tracks made by bivalve *Transenella tantilla* on fine sand. Tracks are approximately 3 mm across; the levees are 1 mm high.

B. Fecal pellets of *Macoma nasuta* deposited in a mound 4 mm high around the exhalant siphon. Pellets adhere to one another by mucous contact.

C. Pellets of *Amphicteis scaphobranchiata* deposited in a weak flow ( $U_\infty < 1$  cm/sec). Pellets are ejected from the animal's feeding pit seen in the lower left of the photograph. The pellets, 9 mm long and 1 mm diameter are avoided by the feeding tentacles. Pock marking on the surface reflects feeding traces of polychaete.

D. Fecal pellet of *A. scaphobranchiata* and its landing trail at  $u_* = 1.5$  cm/sec. Pellet had travelled 15 cm after ejection by ampharetid. These trail marks were scoured preferentially.

As the shear velocity was increased, several of the coils were observed to vibrate in situ. This was not a continuous vibration but an intermittent shaking most noticeable on the upstream face of the mounds. However, there was no movement of the coils from the mounds because of the mucous adhesion between the coils. The shaking motion occurred prior to any motion of the ambient sediment. As the velocity was increased some of the coils on a mound began to shake more often and more rapidly. The frequency of the vibration of sediment prior to initiation of motion has been shown recently (M.A. Church, personal communication) to correlate with the turbulent macroscale. At this stage, some of the fecal coils began to lose their identifiable shape. The shaking apparently caused straining of the intra-coil adhesion and loss of some of the sediment grains from the coil. These grains would roll out of the coil into the lee side of the fecal mound. The whole bed was close to, but just below the critical entrainment velocity. This was a well-defined stage, the point when many particles readjusted their position (i.e., the particles rolled into more stable positions). The discharge was again increased, and particle entrainment of the "free" sediments occurred. The ambient sediment moved in a series of protracted rolls in contact with the bed, and was observed to be transported mostly in thin ribbons parallel to the flow. The fecal coils were still in place, although, occasionally, small portions of a coil would break off and these pieces would be transported rapidly as bedload. The fecal mounds were abraded as the upstream face of the mounds decayed from distinctive coils to an amorphous mass of mucus, from which the sediment grains had been removed. The lee side of the mounds remained distinct. A further increase in the velocity resulted in strong transport of all ambient sediment, and the mounds of fecal coils were removed rapidly, in part by attrition due to the transporting sediment. Quantitative results are summarized in Table II. Throughout this experiment, many of the *H. florida* were observed to feed, even though their tentacles were swept in a downstream direction.

Differences were noted between the experiments with the sandy silt (median diameter = 64  $\mu\text{m}$ ) and with the fine sand (median diameter = 121  $\mu\text{m}$ ). The coils from the silt bed could easily transport the length of the flume as bedload and still remain as recognizable cylinders, whereas those comprised of fine sand disaggregated during transport. In the coarser sediment, the coils also broke apart on the fecal mounds more easily. Ends of the coils would vibrate, break off from the mound, and then abrade rapidly as they rolled along the bed.

Similar results were obtained with the tube-building polychaete *P. kempji japonica*. The ambient sediment was entrained first ( $u_* = 1.19$  cm/sec) and rolled in parallel streams along the bed prior to entrainment of the fecal pellets. The individual coils were abraded in situ and tended to lose their identifiable form.

In the case of both *H. florida* and *P. kempji japonica* the fecal material exists as cylindrical coils of sediment rather than distinct pellets. The feces of *M. nasuta* (Fig.4b) are nearly discoidal and are deposited in a mound

TABLE II

Boundary shear velocities for experiments with *H. florida*

	Sandy silt (64 $\mu\text{m}$ )	Fine sand (121 $\mu\text{m}$ )
	$u_*$ (cm/sec)	$u_*$ (cm/sec)
Rocking of fecal mounds	1.20	1.52
Initiation of sediment motion	1.60	1.93
Removal of fecal mounds	1.87	2.18

near the exhalant siphon. The mound is held together with a netlike web of mucus formed at the pellet-to-pellet contacts. The mounds of discoidal pellets remained in situ after general bedload transport had occurred ( $u_* = 1.68$  cm/sec). Occasionally, individual *M. nasuta* pellets were broken off from the mound or vibrated free from the mucus. These pellets rolled easily and were transported as bedload material. However, the pellet mounds were not eroded until  $u_*$  reached 2.7 cm/sec.

Many deposit feeders sort material at their mouth, and reject considerable volumes of sediment. Among bivalves, the ejection of such pseudo-feces is dramatic. *M. nasuta* ejected into the water column a jet of material often reaching 3 cm above the bed (the free surface of the flow). This material was rapidly advected away from the organism, with many of the fines remaining in suspension, even at friction velocities well below that required for entrainment of sediment. The material, even in weak currents, was removed beyond the organism's feeding siphon and thus was not reingested. While its own fecal pellets are evidently recognizable to (and avoided by) *M. nasuta*, it seems less likely that it could recognize its voluminous and finely dispersed pseudo-feces. Hence ejecting such material into the overlying flow, with the resultant advection of this sediment downstream, is an effective strategy to avoid reingestion of such sediment.

#### *Transport of pellets on cohesive sediments*

The pellets egested by *Amphicteis scaphobranchiata* are thrown rearward (with the aid of two modified branchiae) several centimeters above the bed toward one section of the feeding circumference. The trajectory of the pellet is such that fluid motion can carry the pellets away from the feeding area of the polychaete. At a boundary shear velocity of 1 cm/sec, ejected pellets travelled downstream 10 cm before returning to the bed. With a  $u_*$  of 1.5 cm/sec pellets travelled 15 cm before impacting with the sediment. The critical entrainment velocity of the pellets was 1.8 cm/sec. If pellets land within the animal's feeding range, they are avoided by the probing tentacles (Fig. 4c). The pellets, 1 mm in diameter and up to 9 mm long, are approximately conical in shape and coated with mucus which appears to dissolve within one hour of ejection.

The pellets on the bed transported readily as bedload at a bed shear velocity of 1.8 cm/sec, whereas the critical erosion velocity ( $u_{*cr}$ ) for cohesive material with a grain size of 18.2  $\mu\text{m}$  is 6 cm/sec, based on Inman's version of the Hjulstrom diagram (see section "Background"). Because of the worm's method of pellet ejection, the pellets saltated for considerable distances at velocities near the critical shear stress necessary for pellet entrainment. As the pellets saltated, they created a series of small scour marks on the cohesive material (Fig.4d). These scour marks were enlarged as the bed material was eroded. The fecal pellets were transported the length of the flume without being destroyed.

The ratio of settling velocity ( $w_s$ ) to boundary shear velocity determines whether the sediment is moved as bedload (where  $w_s/\kappa u_* > 1$ ,  $\kappa$  being Von Karman's constant) or as suspended load ( $w_s/\kappa u_* < 1$ ) (Smith, 1977). A series of settling velocity experiments with pellets of *A. scaphobranchiata* yielded a mean settling velocity of 5.1 cm/sec. (range 4.2–6.0 cm/sec for 25 pellets from five individuals). This gives  $w_s/\kappa u_*$  equal to 7.1. However, the ambient sediment would yield a value of  $w_s/\kappa u_* = 0.01$  and thus would move only as suspended load.

#### CONCLUSIONS

The effects of two biological activities were investigated: tracking results in an increase in the boundary roughness and a decrease in the critical entrainment velocity. This decrease (20%) is less than might be anticipated, based on Fenton and Abbott's (1977) studies on the effect of relative protrusion in gravel beds on the critical entrainment velocity. The difference between the observed reduction and that predicted, reflects in part the influence of the viscous sublayer on particle entrainment. Fenton and Abbott worked with 25-mm gravel in their experiments; over such roughness there is no continuous viscous sublayer, and the velocity increases logarithmically from virtually the top of the sediment grains. In the present experiments the flow was smooth and transitional. Within the viscous sublayer the velocity increases linearly with distance from the bed and thus the actual kinetic energy exerted on a particle (for example, a particle one grain diameter above the surrounding bed) has increased much less than in the logarithmic portion of the boundary layer.

Laboratory observations with *H. florida* and with *P. kempji japonica* show that fecal mounds are not moved preferentially in comparison with the ambient sediment. Pelletization increases the roughness of the sediment surface, sometimes sufficiently to disrupt the viscous sublayer. Fecal coils were abraded in situ by the ambient sediment (from sediments greater than 60  $\mu\text{m}$  median diameter). The resistance to entrainment appears to be controlled by mucous adhesion between the fecal coils. A similar result was obtained with the discoidal pellets of *M. nasuta*. In fine-grained material, the pellets of *A. scaphobranchiata* transport readily as bedload. Thus pelletization may facilitate bedload transport in regions of fine, cohesive sediments,

resulting in the generation of periodic bedforms where they might otherwise be absent based on considerations of ambient sediment size (e.g., Hollister et al., 1976).

Critical entrainment velocity measurements from the present experiments and data are plotted in Fig.1D. The present results lie between the limits of entrainment estimated by Sundborg (1967), but at small sediment sizes these limits diverge widely (Fig.1D). When the results are replotted on a Shields diagram (Fig.3), the present data and that of Rhoads et al. (1978) cluster around the curve calculated from Inman's plot of critical shear velocity (Fig.1B). At the small sizes (below  $u_* d/\nu = 1$ ) the Inman curve and Shields curve (after Mantz, 1977) diverge; while the slope of the Shields curve below  $u_* d/\nu = 1$  was derived from dimensional considerations alone, the Inman curve in this figure has neither a theoretical nor dimensional basis. Moreover, as the Shields diagram is only in terms of particle diameter, density, fluid stress, and viscosity, but does not include any parameterization of interparticle adhesion, the divergence of results and model is to be expected. It will be necessary to include a direct measure of interparticle adhesion if a well-founded model of marine sediment transport is to be developed.

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11

12