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Dispersal of meiofauna in a turbulent tidal creek

by M. A. Palmer[1] and G. Gust[2]

ABSTRACT

Traditionally meiofauna have been viewed as strictly infaunal organisms adapted for life between sediment grains. Recent evidence has shown that marine meiofauna also occur in the water column. A set of field experiments investigated processes controlling the abundance of meiofauna in the water column. The transport of meiofauna in a tidal creek was identified to be primarily a passive process resulting from mechanical removal due to current scour. Drifting meiofauna included interstitial, burrowing, and epibenthic species. Copepods, foraminiferans, and juvenile bivalves were suspended in greatest numbers relative to their sediment abundances. Suspension of meiofauna was greatest for species residing in the upper sediment layers and/or occasionally crawling about on the sediment surface. Suspended meiofauna and sediment were well-mixed within the water column, suggesting that behavioral control over water column dispersal was limited once the animals were in the water. Suspension of meiofauna was not a function of winds, time of day, lunar cycle (neap vs. spring tides), or the abundance of meiofauna in the sediment. The abundance of meiofauna in the water was determined primarily by the magnitude of the friction velocity (u_*). The emerging concept is that in habitats where water currents are strong enough to lead to sediment scour, meiofauna dispersal is a two-step process with erosion rather than active water column entry (modified by behavior patterns for some species) and subsequent mixing and transport as passive particles.

1. Introduction

Unlike many marine benthos, meiofauna typically lack pelagic larval stages. This led Sterrer (1973) to suggest that meiofauna may be one of the most sedentary fauna with a very low rate of dispersal. Dispersal is presumably important for the invasion of new habitats and for maintaining gene flow (Burton and Feldman, 1982). Gerlach (1977) proposed several mechanisms by which meiofauna may be dispersed. These mechanisms included rafting on drifting material and dispersal in the water column. The studies of Bell and Sherman (1980), Hagerman and Rieger (1981) and Sibert (1981) support the latter as the most plausible mechanism of meiofauna dispersal. Abandoning the traditional view that meiofauna do not occur in the water column invites benthic ecologists to reassess various concepts which embrace meiofauna

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population dynamics. Firstly, the well-known small-scale patchiness of meiofauna distributions (Findlay, 1981) may vary temporally depending on the frequency and extent of meiofauna drift. Secondly, water column transport (drift) could explain the rapid meiofaunal recolonization into denuded or disturbed areas (e.g., Scheibel, 1974; Sherman and Coull, 1980; Thistle, 1980). Thirdly, epibenthic and pelagic predators are known to feed on drifting macrobenthos (Keenleyside, 1962; Nelson, 1979), thus the availability of meiofauna as prey may be related to their water column transport.

The transport of meiofauna in the water may result from active migration into the water or from erosion of animals from sediment. Both views are expressed in the literature for sand-dwelling meiofauna. Hagerman and Rieger (1981) concluded that wave effects controlled the abundance of meiofauna in the water of a shallow lagoon, while Sibert (1981) concluded that the occurrence of meiofauna in the water column resulted from the upward migration of animals from intertidal sands. Neither study attempted to sample the benthic community at the time water samples were collected nor to investigate the role of behavior in the transport of meiofauna. Based on experiments performed in a muddy-bottom tidal creek, Palmer and Brandt (1981) hypothesized that benthic copepods were suspended into the water via tidal scour. In a series of laboratory experiments, Palmer (1984) showed that the occurrence of meiobenthos in the water was not behaviorally controlled. Although a small fraction of the meiofauna crawled on the sediment surface when flow was absent, rarely did individuals swim up into the water.

Here we report on a set of field experiments designed to investigate four questions dealing with the erosion of mud-dwelling meiofauna. The specific null hypotheses that were tested follow each general question:

a. Is suspension of meiofauna important?
   H_0: The percent of sediment meiofauna suspended in the water column is not significantly different from zero.

b. Are differences in percent suspension of various taxa (phylum level and for copepods, species level) related to behavioral differences?
   H_0: There is no relationship between the percent of benthic individuals in suspension and the swimming ability/propensity for surface activity of the taxa.

c. Does suspension of meiofauna follow a pattern similar to suspension of sediments?
   H_0: There is no correlation between the concentration of suspended sediments and the abundance of meiofauna in the water.

d. Can the abundance of meiofauna in the water be related to specific environmental parameters?

H_0: The abundance of meiofauna in the water is not statistically related to sediment meiofauna abundance, water flow (bottom stress), light (day vs. night), and lunar phase (spring vs. neap tides).

2. Methods

a. General

The study area, North Inlet Estuary, Georgetown, South Carolina, USA (33° 22′ N, 79° 10′ W), is a high-salinity, well-mixed estuary with semidiurnal tides (mean tidal range 1.37 m), wide expanses of *Spartina alterniflora* Loisel marsh, and meandering tidal creeks. The sample site was an unvegetated intertidal mudflat composed of cohesive sediments (flocs of 40 μm median diameter). A map of the region and a cross-section of the tidal channel adjacent to the mudflat are shown in Miller and Gardner (1981).

Two sampling sets were completed in the field: one during neap tides (June 24, 25, 26, 1981) and one during spring tides (June 30, July 1, 2, 1981). For each sampling set the following measurements were made simultaneously at 23 times over a 48 hr period: (1) Meiofaunal abundance—in the sediment, at the sediment/water interface, and at 17, 37, and 57 cm height in the water column; (2) Suspended sediment—at 17, 37, and 57 cm height in the water column; (3) Meteorological, hydrographic and hydrodynamic measurements—water level, wind, temperature, salinity, bottom stress, and mean flow at 27 cm above the bottom. The sampling rate was not pre-set; sampling was attempted at certain water levels during the flood, slack, and ebb tides of each set. Heights in the water column are from the mudflat surface ($z = 0$). See figures for the water level and time at which each sample was collected. The right-handed coordinate system (with associated velocity components) will be used throughout with x (u) pointing downstream, y (v) in the transverse, and z (w) in the vertical direction.

b. Water column

Water sampling. Water samples for meiofauna and suspended sediment were collected using marine bilge diaphragm pumps (Par 37202) which delivered approximately 15 $l \cdot \text{min}^{-1}$, were powered by 12 V batteries, and did not damage animals. For both meiofauna and suspended sediment, two replicate water samples were collected at each of 3 levels: 17 cm, 37 cm, and 57 cm above the bottom. Intakes at these 3 levels were positioned into the flow on each of two pump stands (as in Schiemer and Schubel, 1970). Six pumps simultaneously drew water from the intakes (1.9 cm dia) and transported the water via tubing for sample collection. Studies conducted *in situ* by injecting Rhodamine dye near the intakes showed that during slack water the pumps drew from an area below the intakes approximated by a flattened sphere (7 cm, x direction; 5 cm, z direction). At flows above 8–10 cm $\cdot$ sec^{-1} the pumps drew from an area approximated by a flat ellipse (6 cm, x direction; 1 cm, z direction). Data were examined to be certain that samples collected from intakes at the same level on the two different stands were not significantly different. For all taxa and suspended sediment there was no stand effect ($p \geq 0.05$).

Water-column meiofauna. Meiofauna were collected from the water column by directing the six pump outflows through 63 μm sieves. Average volume pumped per sample was 75 *l*. The exact volume pumped for each of the 6 samples was calculated based on flow calibrations just prior to each sampling and known pumping times. Animals were gently rinsed from sieves into labeled jars and fixed in a 10% Rose Bengal-formalin solution for later enumeration and identification.

For a constant meiofauna abundance, concentrations would be diluted at high tide and concentrated at low tide levels due to differences in water volume in the creek. Meiofauna concentrations were corrected for changes in volume of water over the mudflat by using the tidal storage curve of Miller and Gardner (1981, Fig. 4), which estimates the volume of water in the sampling area vs. tide height. Thus, abundance of meiofauna in the water column as numbers $\cdot$ m^{-3} collected by pumping was multiplied by a correction factor (appropriate for tide level at time sample was pumped) to adjust abundances for water volume when tide height was 67 cm (mean tide level).

Total abundance of meiofauna in the water (from the bottom up to the surface of the water) was determined by integrating abundance over depth. Thus the data in Figures 2 and 3 are given as number $\cdot$ m^{-2} (e.g., for one stratum: number $\cdot$ m^{-3} × distance to next pump intake in m = number $\cdot$ m^{-2}). Abundance of meiofauna at the bottom pump intake (17 cm) was assumed representative down to the sediment surface. Since large interface values were not used (see discussion of potential problems below), our calculations of total meiofauna abundance in the water are very conservative.

Suspended sediment. Suspended sediment samples were collected by filling six 500 ml Nalgene bottles directly from the pump outflows. Samples were stored on ice for immediate transport to the laboratory where they were filtered through preweighed glass microfiber filters (0.70 μm retention, 4.25 cm dia., Whatman GF/F). Total suspended solids (mg $\cdot$ l^{-1}) were determined by drying the filters at 50°C for 8 hrs., cooling them in a desiccator and reweighing the filters on a Mettler HC1AR balance (McCave, 1979). Replicate samples and filter blanks indicated that the weight was accurate to within 0.1 – 0.2 mg. The flocs were probably broken in the sampling process therefore we could not identify the suspended sediment to size classes.

c. Sediment-water interface

Meiofauna. Meiofauna were collected simultaneously at the sediment/water interface and in the sediment using a specially designed coring device that separated a sediment core (2.5 cm dia.) from the core water overlying it. A 3 m stainless steel rod was used to lower the coring tube (10 cm length) from the boat to the sediment surface. A sleeve was built into the coring tube 5 cm up from the tube bottom. This sleeve formed a lip around the outside of the core tube and contained a 4 mm thick stainless steel plate that could be manipulated remotely using a wire pulley attached to the stainless rod. The plate was disengaged before lowering the core tube from the boat to the bottom and the tube was placed into the sediment to the sleeve depth. The plate was inserted across the core tube (engaged) using the pulley and thus the core was partitioned into the sediment component and the water overlying the plate.

Four replicate cores were taken haphazardly at each sampling time. The interface samples (water from the sediment surface to 5 cm height above the bottom; 25 cm^3 water) and sediment samples (1.5 cm deep; 7.36 cm^3 sediment) were transferred to separate labeled containers and fixed with Rose Bengal-formalin for later enumeration and identification.

Bottom sediment and microtopography. Bottom sediments in South Carolina saltmarshes consist of silt and clay sediments, with the latter being mostly kaolinite and illite (Ward, 1981). The sediment surface was unvegetated and free of visible worm tubes or other biogenic structures protruding up from the sediment surface. *Uca pugilator* burrows (~1.5 cm dia.) were present, with roughly 40 burrows $\cdot$ m^{-2}. These burrows were flush with the sediment surface, with no mounds or "lips" protruding up around their edges. Aside from these burrows, the sediment surface was relatively flat and featureless (e.g., neither bedforms, ripples, fecal mounds, nor steep surface slopes). Roughness elements did include fecal pellets and tracks by meiofauna, both protruding up from the sediment surface less than 0.5 mm. From the associated microtopography, a hydrodynamically transitional (roughness Reynolds number $Re_k = u_* k_s/\nu < 70$) flow was expected. During slack water, a thin fluff layer of nonconsolidated flocs accumulated on the sediment surface.

Cohesiveness of the sediments was most certainly enhanced by the presence of bacteria and algae. Although we did not quantify bacterial or algal populations, samples were collected at the same time on a nearby subtidal mud flat (grain size ~32 μm) by Montagna *et al.* (1983). They found diatom abundances of $\sim 3 \times 10^7$ cells $\cdot$ $(10\ cm)^{-2}$ and bacterial abundances of $\sim 150 \times 10^9$ cells $\cdot$ $(10\ cm)^{-2}$. Bacterial abundances did not change significantly throughout the summer and fall. Diatom abundances began to decrease in late August through September.

d. Hydrodynamic, hydrographic, and meteorological measurements

Hydrodynamic considerations. To evaluate the distribution of meiofauna in the water column and test the hypothesis of active entry versus passive erosion, the hydrodynamics of the boundary layer of the tidal creek need to be considered. Generally, benthic boundary-layer flows close to the bottom show logarithmic mean velocity profiles, obeying the universal 'law of the wall'

$$U^+ = 1/k \ln z^+ + C - \Delta U^+, \tag{1}$$

also expressible as

$$U^+ = 1/k \ln (z/z_o) \text{ (Wimbush and Munk, 1970; Bowden, 1978).} \tag{2}$$

Here $U^+ = \overline{u}/u_*$ is dimensionless velocity, $\overline{u}$ = mean local velocity, $u_* = (\tau/\rho)^{1/2}$ is friction velocity, τ = bottom stress, ρ = fluid density, k = von Karman's constant, $z^+ = zu_*/\nu$ is dimensionless wall distance, z = wall distance with $z = z_o$ at bottom, ν = kinematic velocity, C = integration constant, ΔU^+ = dimensionless roughness shift of velocity profile (see Clauser, 1956) and z_o = roughness length. Eqs. 1 and 2 hold for smooth-wall flows with $C \sim 5.5$ and $\Delta U^+ = 0$ in Eq. 1 and $z_o = 0.1\, \nu/u_*$ in Eq. 2. Eqs. 1 and 2 also hold for rough-wall turbulent flows (see, e.g. Hinze, 1975) as long as the flows exhibit a single logarithmic layer for $z_o < z < \delta$ (with δ being logarithmic layer thickness). The universal law of the wall also entails the presence of a constant-stress layer and allows the determination of the bottom stress (here and later in the text expressed interchangeably by the friction velocity, $u_* = (\tau/\rho)^{1/2}$) from a mean vertical velocity profile via Eqs. 1, 2, and also from

$$\overline{u}_*^2 = \rho\, C_{Dz} u_z^2 \tag{3}$$

where $C_{Dz} = (u_*/\overline{u}_z)^2$ is the drag coefficient for the specific flow at height z.

The universality of Eqs. 1 and 2 is presently debated within the benthic boundary layer community with claims of its existence presented e.g., by Nowell (1983), Gross and Nowell (1983), and Grant *et al.* (1984). Chriss and Caldwell (1982), Gust and Southard (1983), and Gust (1984) present data from experiments which suggest that the 'universal law of the wall' is limited for field flows due to a variety of site-specific fluid dynamical processes and geometric boundary conditions. In cases where Eqs. 1, 2 or 3 do not yield the correct skin friction, mean local velocity $\overline{u}$ and friction velocity u_* should be treated as independent variables.

In the creek flow studied here, tidal (accelerative) effects, turbulent-drag reduction due to the suspended cohesive sediments (Gust, 1976) and effects of microtopography (Chriss and Caldwell, 1982) could contribute to u_* values modified from Eqs. 1 and 2. To measure mean flow from one or several selected heights in a logarithmic layer for bottom stress estimates is then insufficient unless the validity of Eqs. 1 and 2 is proven. Ambiguity in the skin friction data was avoided in our study by measuring the skin friction (bottom stress) directly by flush-mounted hot-film sensors developed and utilized in earlier deep-sea and laboratory studies (Gust and Southard, 1983; Paola, 1983; Gust and Weatherly, 1984).

Velocity and skin friction sensors. The experimental plan was originally designed to identify mean velocity profiles, turbulence, Reynolds stress and skin friction over two spring and two neap tidal cycles by deploying a sensor array consisting of five flow probes (one e.m. current meter, 2 metal-clad single hot wires, 2 metal-clad crossed hot wires). The field deployment of the sensors was only partially successful since the hot wires and hot films were not run in temperature-compensating electronics circuitry but at a pre-set (fixed) overheat ratio based on an assumed *in-situ* temperature. This pre-set overheat ratio proved to be too low for the actual, higher *in-situ* temperatures and resulted in the loss of data from the three hot-wire probes, and a partial loss from the skin-friction sensor. The problem arose since the hot-wire and hot-film sensors were set to an overheat ratio of 1.05 at 25°C in the laboratory before shipment to the field site. With temperatures approximately 30°C encountered in the field, the overheat ratio dropped to ~1.01 which brought the sensors to their detection thresholds. We were thus left with ~40% of the skin friction data (direct measurements of u_*) and measurements of mean flow ($\bar{u}$) at 27 cm height from the electromagnetic current meter (Marsh McBirney 201, 2.5 cm diameter head). Using simultaneously measured u_* and $\bar{u}$ data we were able to establish an averaged drag coefficient C_{D27} (see Eq. 3) which was then used to obtain u_* for those runs where direct skin-friction measurements were not available.

The specifics of the skin friction sensors and data collection/reduction have been described in more detail in Gust and Weatherly (1984). Among other fluid dynamicists, Bellhouse and Schultz (1966), Brown (1967) and most recently Kalamuck (1983) have discussed the theory and application of heated-film sensors for measurement of skin friction and showed that the heat loss from the sensing element is proportional to the one-third power of the bottom stress. The use of such probes has been extended to seawater applications (Gust and Weatherly, 1984) by utilizing epoxy-coated, flush-mounted nickel grids with 50 ohms resistance at 24°C. The probes were used in connection with standard hot-wire electronics at an overheat ratio of 1.05 which generates a temperature difference of 9°C between sensor and ambient fluid. The skin friction sensor is a nickel grid with a surface of 0.09 cm^2. The sensors were calibrated in a recirculating, hydrodynamically smooth, open-channel flow with known velocity and bottom-stress characteristics. It had been determined earlier (Gust and Southard, 1983) that these probes could be calibrated to 3–5% accuracy in controlled flume environments, and their calibration curves (ibid, Fig. 3a) apply to fresh water as well as salt water flows.

In the field, all probes were mounted in a cage arrangement which was rotated 180° when the direction of the tide changed so they would be oriented into the flow and measure velocities and friction velocity upstream of the sensor mount. Prior to each data sampling, the skin friction probe, which was mounted in the center of a 1.5 mm thick, bevelled fiberglass plate of 10 cm diameter, was cleaned remotely using a jet of compressed air which flowed from a scuba tank via tubing to a nozzle positioned above (and not interfering with) the probe. Flume tests showed that the jet was sufficiently narrow that it impinged only on the sensor surface and did not stir up sediment. The signals from the probes were recorded for 8.5 min intervals (at each sampling) at a scan rate of 16 Hz per channel using a microprocessor-controlled digital underwater recorder (Sea Data 655). Data tapes were translated on a Sea Data 12A reader interfaced to a PDP 11/03 computer with two 9 track tape drives. The output voltages were converted into velocity time series with the aid of a calibration curve generated in a recirculating flume for the skin friction sensor at the exact overheat ratios given by the *in-situ* water temperatures. Subsequent time series analysis generated statistical moments and one-dimensional spectra of the friction velocity.

The critical friction velocity. One of the characteristics of flows of tidal creeks and flats is their ability to transport passive contaminants over long distances. Correlation between peak magnitude of tidal flow and maximum concentration of suspended sediments and/or meiofauna at a chosen measuring site in the creek then does not necessarily provide evidence of local erosion. The design of an experiment to test for local scour of meiofauna requires as input parameters critical friction velocities and settling velocities of the bottom sediment as well as of the meiofauna. In case $u_{*\mathrm{crit}}$ (meiofauna) $<$ $u_{*\mathrm{crit}}$ (sediment) and meiofauna do not actively enter the water column, meiofauna erosion is controlled by $u_{*\mathrm{crit}}$ (sediment) since the animals can hide in the sediment. In case $u_{*\mathrm{crit}}$ (meiofauna) $>$ $u_{*\mathrm{crit}}$ (sediment), sediment parameters are insufficient to be used as an indicator of meiofauna erosion and $u_{*\mathrm{crit}}$ (meiofauna) needs to be determined. The critical friction velocity of meiofauna has not been determined yet. Treating meiofauna as purely passive, cohesionless particles, and extrapolation of the Shields diagram (see, e.g. Graf, 1971, Fig. 6.7) suggests a $u_{*\mathrm{crit}}$ of < 0.1 cm · sec^{-1} for particles with 1.06 g · cm^{-3} and 200 μm diameter. This indicates that the sediment properties may control meiofauna erosion. Consequently, we decided to measure $u_{*\mathrm{crit}}$ of the site-specific bottom sediment.

An open laboratory channel (114 cm long, 8 cm wide, 9 cm deep) was constructed with a removable section (5 cm wide, 9 cm wide) located 64 cm from the channel entrance which could hold a box core sample. During September 1982, four such box cores were taken from the mudflat during low tide, transported back to the laboratory, and held in aquaria for erosion tests later that day. The box cores were inserted into the flume channel so that the sediment surface was flush with the channel. Seawater at field temperature (the September value was 20°C) was supplied by a head tank and flow rate of water through the open channel was controlled by simultaneously operating gate valves at the upstream and downstream sides of the channel. Water was recirculated from the tail tank to the head tank after passing it through 5 μm retention filters. A skin friction probe was mounted flush with the sediment surface in the box core to measure $u_{*\mathrm{crit}}$. The length of the flume was insufficient to obtain a fully developed logarithmic velocity profile, which would be required if Eqs. 1 or 2 were used to determine the bottom stress. Since the skin friction sensors (surface area 0.09 cm^2) measured u_{*crit} directly, no such constraints were placed on the velocity profile.

Flow was increased at an acceleration of 0.20 cm · sec^{-2} from zero, while an observer watched sediment particles through a stereomicroscope (12×) until their rolling velocity was reached. At this point, a particle population of 10 or more was in the field of view rolling in contact with the bed (after Rhoads *et al.*, 1978). Mean u_{*crit} values are based on measurements from four cores. An additional measurement, designated mass-erosion, was made on each core. Flow was increased beyond u_{*crit} until large sediment aggregates were 'ripped' off the bed.

Other. Wind speed and direction were measured with an Airguide Windial (Model 919) at each time a sample was collected. Water temperature and salinity were measured at surface and mid-depth with a Beckman RS-5 Induction Salinometer. Water level over the mudflat was recorded every 10 min. All depths (including probe locations) refer to vertical distance up from the bottom.

e. *Statistical analyses*

Parametric statistical tests were used after the data were examined to determine that appropriate assumptions were valid. Analysis of variance (ANOVA) was performed using the General Linear Model techniques (Helwig and Council, 1979) and multiple comparisons were performed when significant main effects were present. Analysis of covariance (ANCOVA) was used to determine which factors control suspension of meiofauna, since the same experiment was conducted during both spring and neap tides. See Kirk (1982) for a discussion of ANCOVA with more than one covariate. This technique clarified the relationship between the various independent variables or covariates (e.g., flow) and the dependent variable, number of meiofauna in suspension, by removing, and simultaneously testing for any spring vs. neap effect. The latter were the class variables in the ANCOVA. Covariates included mean current velocity ($\overline{u}$), friction velocity (u_*), wind, water depth, abundance of meiofauna in the sediment (meiosed), and concentration of suspended sediment (suspended). We are not suggesting any causation between meiofauna in suspension and suspended sediment. This term was included in the model for correlative purposes in testing hypothesis c as outlined in the Introduction.

The analysis was performed in the three steps. First, a linear model depicting the relationship between the dependent variable and the set of independent variables was chosen using forward and backward elimination stepwise regression procedures (Sokal and Rohlf, 1981; p. 662). Second, the regressions were tested for parallel surfaces. Third, if the surfaces were parallel, the regression lines were tested for differences in elevation; i.e., which line had the higher or greatest least mean square (LSM). This analysis was performed on total meiofauna and total benthic copepods (the 3 dominant mudflat species) to determine if information at the species level reduced the unexplained sum of squares. This analysis was not performed on nematodes because at the present time we do not have information at the species level.

3. Results

a. Meiofauna and sediment in the water column

Meiofauna data. Throughout this paper detailed data will only be presented on nematodes, benthic copepods, bivalves and foraminiferans. These were chosen as the target organisms to investigate the suspension effect. Other taxa were low in abundance and/or seldom seen in the water column (polychaetes usually exceeded 500 μm and were not considered meiofauna). Benthic copepods refer to the three species, *Stenhelia (Delvalia) bifidia, Enhydrosoma propinquum, and Nannopus palustris,* that comprised 99% of the copepod fauna from the mudflat sediment. Advected copepods refer to any other species of benthic copepods found in samples but known to exist primarily in other areas (e.g., sand-dwellers or species from the high marsh). The distinction between benthic and advected copepods was made to allow us to estimate the fraction of total copepods in suspension which could have been eroded locally vs. the fraction known to be advected in from other areas. Nevertheless, some of the benthic copepods we found in the water and assumed were locally eroded may have been advected (no way to distinguish without tagging), therefore percent meiofauna suspended should be considered maximal estimates while percent advected are minimal estimates. Benthic foraminiferans consisted almost entirely of *Ammonia beccarii,* thus only this species was considered in water samples. Bivalves were primarily juvenile *Tellina* sp. and *Mulinia* sp. To avoid inclusion of presettlement bivalves in the water column data, all bivalves were measured, but only those >250 μm were considered (settlement size is usually 150–200 μm; Chanley and Andrews, 1971).

Abundance of meiofauna at the three levels in the water column (Fig. 1), were significantly different only during the spring sampling ($p \leq 0.05$). Spring abundances at the bottom intake were significantly greater than abundances at the middle and top intakes ($p = 0.003$). Since vertical stratification was not the rule, throughout the remainder of the paper meiofauna abundance in the water refers to total abundance (depth integrated—see methods). Abundance of meiofauna in the water (Figs. 2, 3) was quantifiable and varied significantly over the tidal cycle ($p \leq 0.001$). The dominant meiofauna in the water were nematodes, followed by advected copepods, formaminiferans, and benthic copepods (Table 1). Less than 1% of the targeted sediment meiofauna were in suspension at any one sampling time (Table 2) but the mean differed from zero and varied with the tide (ANOVA, $p \leq 0.001$). The estimates of percent suspension do not include interface data (see below) and therefore represent conservative estimates. Thus we were able to reject the null hypothesis of no suspension (Introduction, question a).

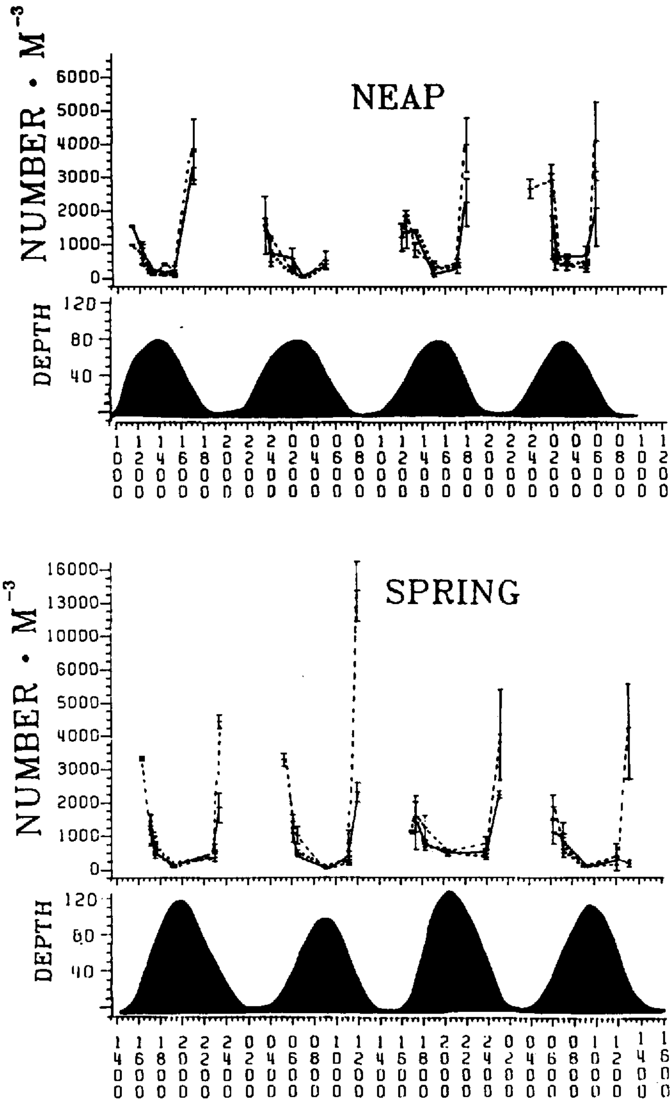

Figure 1. Abundance of total meiofauna (number • m^{-3} water) at three levels in the water column: 17 cm (dashed line), 37 cm (solid line) and 57 cm (dotted line) above the bottom. Data are for two neap and two spring tidal cycles; stage of the tide is shown as water depth (cm) over the mudflat; 95% confidence intervals are shown.

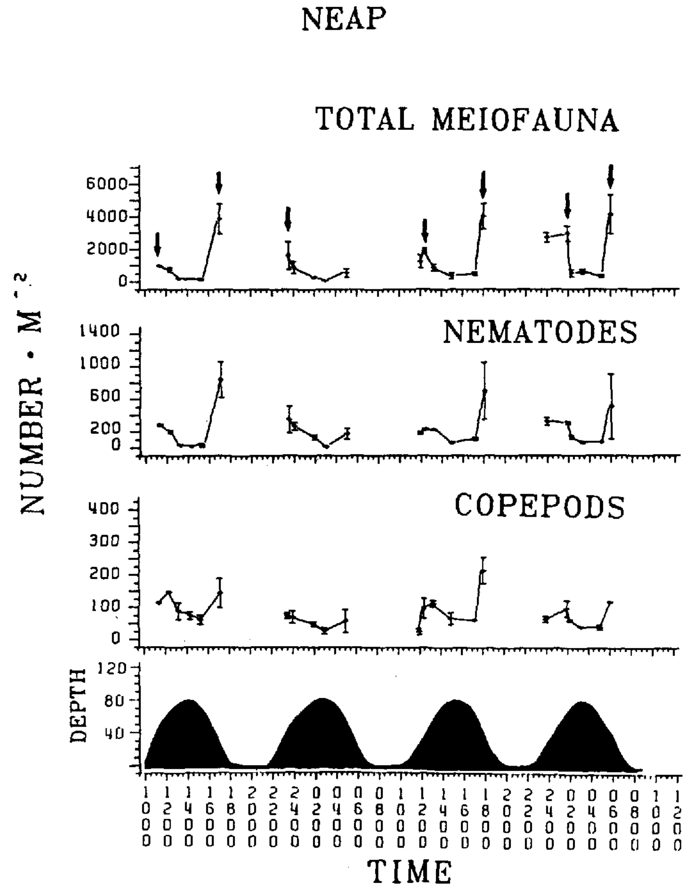

Figure 2. Abundance of total meiofauna, nematodes, and copepods in the water over two neap tidal cycles. Abundances were integrated over depth (excluding interface data—see text); values represent total number of animals from the sediment up to the surface of the water, thus number · m^{-2}; 95% confidence intervals are shown. For all figures, stage of tide is shown in bottom diagram as shaded area, with water depth (cm) over the mudflat as ordinate and abscissa represents time. Arrows indicate sampling times during which mean u_* measured on the mudflat exceeded the u_{*crit} measured in the laboratory (0.58 cm · sec^{-1}).

Calculations of meiofauna abundance at the sediment/water interface (Table 3) were problematic, because the interface volume sampled was small and had low numbers of meiofauna (e.g., 1–4 animals · 25 cm^{-3}). Extrapolation of such abundances to number · m^{-2}, (which would facilitate direct comparison with other water column data) was considered inappropriate, particularly since the sampling error associated with the interface data was large compared to that from the water column data (coefficient of variation: interface = 44.5%, water = 17.8%). Thus, while

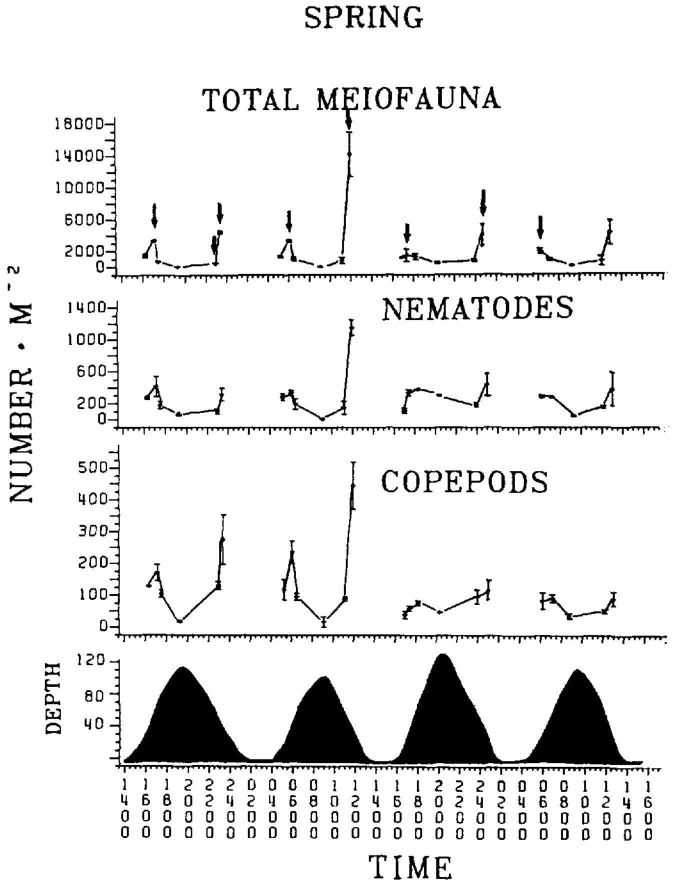

Figure 3. Abundance of total meiofauna, nematodes, and copepods in the water over two spring tidal cycles. For explanation see legend of Figure 1.

suggesting large abundances of meiofauna just above the sediment, the interface data were of limited use and were not incorporated into calculations of percent suspension.

Taxon and species effects. Copepods, foraminiferans, and bivalves were more abundant in the water, relative to their abundance in the sediment, than were nematodes (2 way ANOVA: effect of set and taxa on percent suspended, taxa significant $p < 0.001$; Duncan's multiple range test, % nematodes significantly lower, exptwise error rate = 0.05). Nematodes comprised approximately 60% of the sediment meiofauna and copepods comprised approximately 25% (Table 4). Meiofauna abundance in the sediment fluctuated widely with tidal state (Figs. 4, 5). There was a significant taxon ($p \leq 0.05$), tide ($p \leq 0.05$), and taxon × tide interaction affect ($p \leq 0.05$) on the abundance of total meiofauna in the sediment.

Table 1. Composition of suspended meiofauna; values for each taxon are the percent dominance (of total meiofauna) found in the water column. All samples from all levels combined. N = 138 samples for each set (neap and spring). S.E. = standard error.

	Neap		Spring	
	%	S.E.	%	S.E.
Nematoda	26.6	1.2	32.0	1.2
Copepoda	16.6	1.2	13.3	0.7
Nauplii	5.5	0.4	13.6	1.4
Advected Copepoda	20.2	1.1	17.7	1.3
Bivalvia	9.1	1.2	5.7	0.4
Foraminifera	17.6	1.3	16.1	1.1
Turbellaria	3.0	0.4	1.4	0.3
Kinorhyncha	0.3	0.1	0.2	0.1

Table 2. Mean percent of sediment meiofauna suspended in the water during a sampling time. Values for each taxon are a mean of the fraction: mean number meiofauna in the water/mean number in the sediment for each sampling time; the interface data were not included in these calculations, thus number meiofauna in the water are minimal estimates. Standard Errors are shown.

	Flood		Slack		Ebb	
Neap	%	S.E.	%	S.E.	%	S.E.
Copepoda	0.065	0.006	0.032	0.005	0.069	0.013
Nematoda	0.031	0.005	0.004	0.001	0.046	0.013
Bivalvia	0.078	0.022	0.012	0.006	0.099	0.031
Foraminifera	0.142	0.004	0.031	0.014	0.160	0.061
Total	0.114	0.015	0.023	0.005	0.092	0.054
Spring						
Copepoda	0.104	0.009	0.018	0.003	0.166	0.031
Nematoda	0.054	0.005	0.017	0.008	0.092	0.023
Bivalvia	0.203	0.082	0.036	0.012	0.312	0.102
Foraminifera	0.189	0.034	0.041	0.008	0.285	0.046
Total	0.229	0.027	0.020	0.008	0.706	0.222

Table 3. Abundance of meiofauna (all taxa combined) at the sediment/water interface. Values are mean number · liter^{-1} and thus are not directly comparable to Figures 2 and 3 (see text for explanation); Standard errors are in parentheses.

	Flood	Slack	Ebb
Neap	330.4 (53.1)	214.0 (57.0)	260.2 (54.8)
Spring	449.1 (90.7)	368.2 (123.5)	440.6 (87.33)

Table 4. Composition of sediment meiofauna as percent of total for each taxon found in the sediment. All samples combined. N = 92 cores for each set (neap and spring); S.E. = standard error.

Taxon	Neap %	Neap S.E.	Spring %	Spring S.E.
Nematoda	64.9	1.0	60.1	0.7
Copepoda	12.5	0.5	13.4	0.4
Nauplii	10.9	0.4	12.2	0.5
Advected Copepoda	0.2	0.1	0.4	0.1
Bivalvia	0.4	0.1	1.5	0.1
Foraminifera	6.1	0.4	5.6	0.4
Turbellaria	0.9	0.1	1.2	0.1
Kinorhyncha	1.9	0.2	2.6	0.2
Ostracoda	0.1	0.1	0.2	0.1
Others	2.1	0.2	2.8	0.2

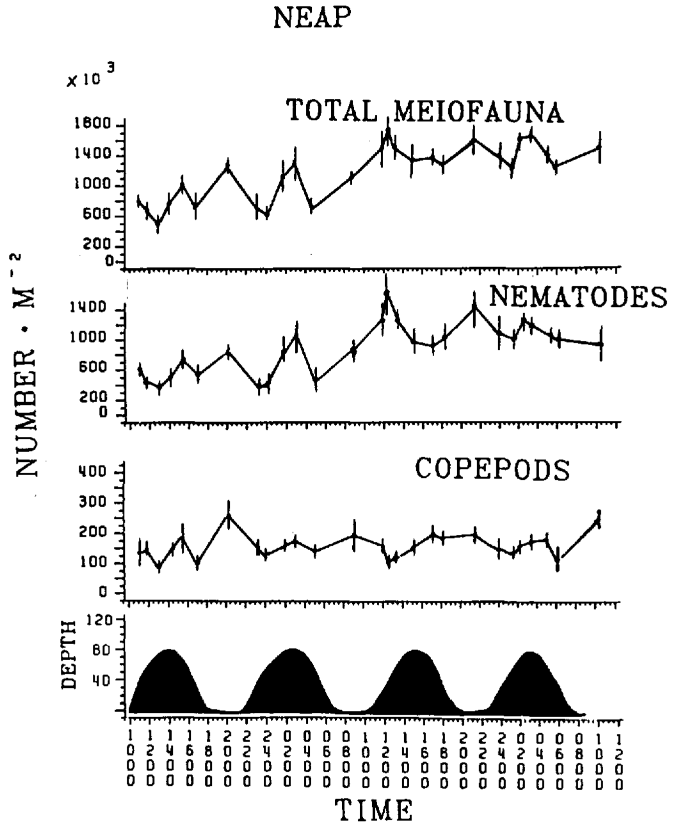

Figure 4. Abundance of total meiofauna, nematodes, and copepods in the sediment over two neap tidal cycles. Values ($\times 10^3$) are mean number · m^{-2} sediment; 95% confidence intervals are shown.

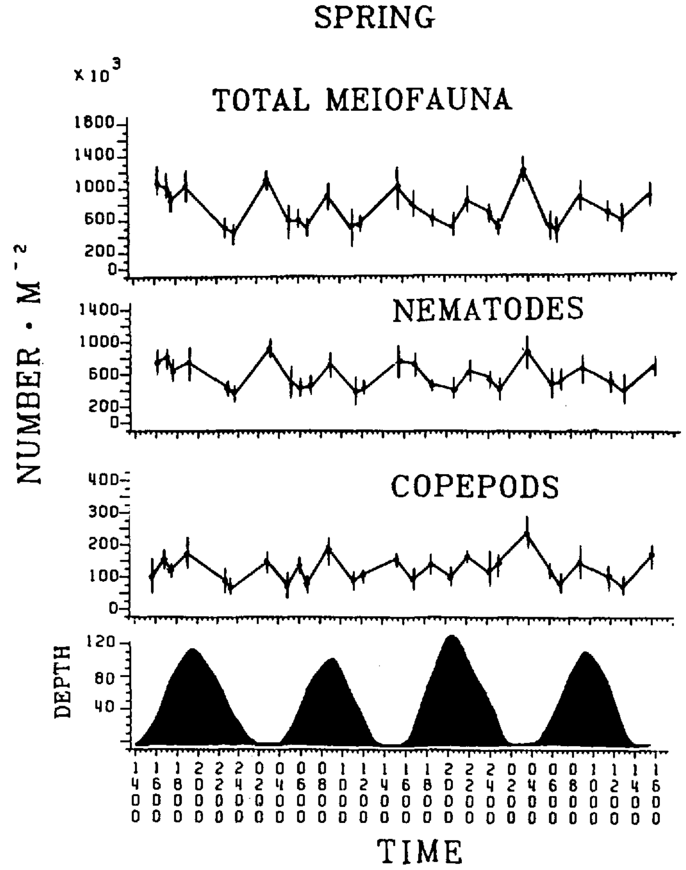

Figure 5. Abundance of total meiofauna, nematodes, and copepods in the sediment over two spring tidal cycles. Values ($\times 10^3$) are mean number · m^{-2} sediment; 95% confidence intervals are shown.

Identification of the copepods to species (Table 5) indicated that at least 50% of the suspended copepods were advected (brought in from other areas). This estimate is minimal since some of the suspended individuals belonging to the three benthic species may have actually been advected. Species richness of benthic copepods was much greater in the water than in the sediment.

To test for the affect of species and sexual stage on suspension of copepods, an analysis of variance was performed. Set and sample were considered block effects and thus were not included in the interaction terms nor hypothesis testing (Sokal and Rohlf, 1981; p. 350). A significant site (water, sediment) × sexual stage interaction ($p < 0.001$) reflected that, averaged over all species, gravid females occurred in the water in very low numbers (relative to sediment densities) compared to the other sexual stages considered. A significant site × species interaction ($p < 0.001$) demonstrated

Table 5. Mean abundances are given for those species of copepods that occurred in densities greater than 1 · m^{-3} in the water and 0.5 · cm^{-3} in the sediment. Data based on all spring samples. *indicates rarely occurred; — absent; S.E. in parentheses.

Taxon	Water (# · m^{-3})	Sediment (×10^3 = # · m^{-3})
Ameriidae		
Nitocra lacustris (Schmankevitsch)	*	*
Nitocra typica (Boeck)	*	—
Canthocamptidae		
Mesochra pygmaea (Claus)	*	*
Canuellidae		
Scottolana canadensis (Wiley)	*	—
Cletodidae		
Cletocamptus helobius Fleeger	*	*
Enhydrosoma propinquum (Brady)	52.9(4.8)	275.1(18.1)
Heteropsyllus nunni Coull	*	—
Nannopus palustris (Sars)	1.0(0.3)	815.0(38.2)
Cylindropsyllidae		
Paraleptastacus sp.	*	*
Leptastacus macronyx (Scott)	*	*
D'Arcythompsoniidae		
Leptocaris brevicornis (Douwe)	*	—
Diosaccidae		
Protopsammotopa wilsoni Wells	*	—
Robertsonia propinqua (T. Scott)	*	—
Schizopera knabeni Lang	2.6(2.2)	*
Stenhelia (D.) bifidia (Coull)	48.6(5.5)	7705.3(228.1)
Ectinosomidae		
Ectinosoma sp.	*	—
Halectinosoma winonae Coull	9.6(3.2)	*
Hastigerella leptoderma (Klie)	*	—
Pseudobrayda pulchella (Sars)	*	—
Harpacticidae		
Zausodes arenicolous (Wilson)	*	—
Laophontidae		
Heterolaophonte stromi (Baird)	3.0(0.8)	—
Paronychocamptus wilsoni (Coull)	5.4(3.5)	*
Paralaophonte sp.	3.6(3.5)	*
Normanella sp.	4.0(3.1)	—
Tachididae		
Microarthridion littorale (Poppe)	20.2(14.1)	51.4(17.6)
Tegastidae		
Parategestes sp.	*	—
Thalestridae		
Diarthrodes aegideus (Brady)	*	*
Tisbidae		
Tisbe holothuriae (Humes)	*	—

that all species were not suspended equally (relative to their sediment abundances). *E. propinquum* occurred in the water in greatest numbers relative to sediment densities, although, this result may be misleading if *E. propinquum* was eroded from other areas in the marsh while sediment abundances for percent suspension were based on mudflat data. However, a large abundance of *E. propinquum* in the water would be predicted based on the finding of Palmer (1984) that this species spends more time on the sediment surface than *N. palustris* or *S. (D.) bifidia,* which should increase its susceptibility to erosion. Transport may, however, be avoided by rapid burrowing as flow increases.

At the phylum level, the percent nematodes in suspension was low (see above) which is consistent with the observation that nematodes are rarely active at the surface of the sediment and are poor swimmers (Palmer, 1984). Turbellarians and ostracods were rarely found in the water column in the present study which is consistent with the finding of Palmer (1984) that these taxa may be active at the sediment-water interface but burrow or "cling" to the sediment surface so that very few are transported in the water. Therefore, based on the above comparisons between meiofauna in suspension from the present study and behavioral information from earlier studies, the null hypothesis of no relationship between taxon behavior patterns and percent suspension (Introduction, question b) was rejected.

Suspended sediment. Suspended sediment concentrations varied from 20 to 110 mg $\cdot$ l^{-1} (Fig. 6). Data were analyzed to determine the affect of set (neap, spring), tide (flood, ebb, slack high) and water level (top, middle, bottom) on the concentration of suspended sediment. There was no difference in the amount of suspended sediment at spring vs. neap. There was a significant tide effect ($p \leq 0.001$); sediment concentrations at slack high were lower than concentrations during ebbing or flooding tide ($p = 0.05$). Sediment concentrations at the three water levels were different only during the spring sampling when concentrations were greater at the bottom intake than at the middle or top ($p = 0.004$).

b. Factors controlling transport: erosion and entrainment

Throughout the study, depth profiles of temperature and salinity showed no vertical water stratification. Neap salinities were decreased and temperatures increased relative to spring values ($\bar{x}$: neap = 33.5‰, 29.1° C; spring = 34.8‰, 25.3° C) due to the passage of a rainstorm at the onset of neap sampling. Winds were light and variable (neap: ~3.5 m $\cdot$ sec^{-1}, predominately out of SSW; spring: ~2.5 m $\cdot$ sec^{-1}, out of SSW for first tidal cycle, then ~3.5 m $\cdot$ sec^{-1}, out of SSE).

Critical friction velocities, u_{*crit}, for onset of sediment erosion (and potentially, of the meiofauna buried in the sediment) determined in the laboratory flume, ranged from 0.48 to 0.70 cm $\cdot$ sec^{-1} for the 4 box cores from the field site. The mean u_{*crit} was 0.58 ± 0.09 cm $\cdot$ sec^{-1}. The mean critical friction velocity necessary for mass-erosion (large sediment aggregates ripped off the bed) was 0.87 cm $\cdot$ sec^{-1}.

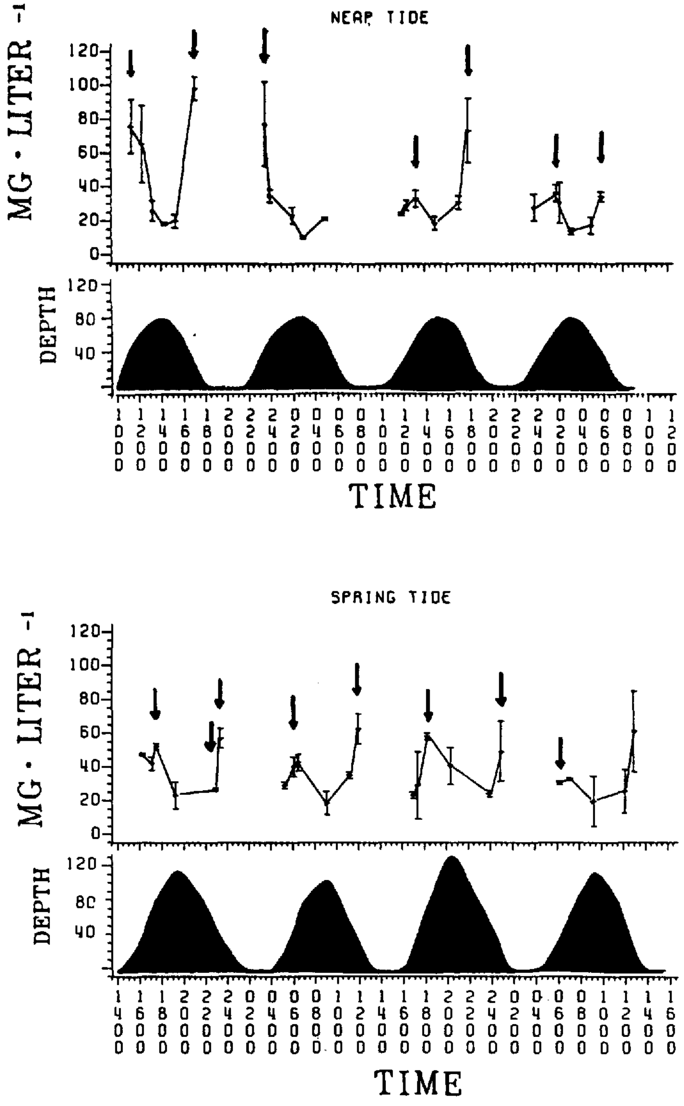

Figure 6. Concentration of suspended sediment (mg · l^{-1}) in the water over two neap and two spring tidal cycles. Concentration was integrated over depth thus values represent the total concentration from the sediment to the surface of the water; 95% confidence intervals are shown. Arrows indicate sampling times during which mean u_* measured on the mudflat exceeded the u_{*crit} measured in the laboratory (0.58 cm · sec^{-1}).

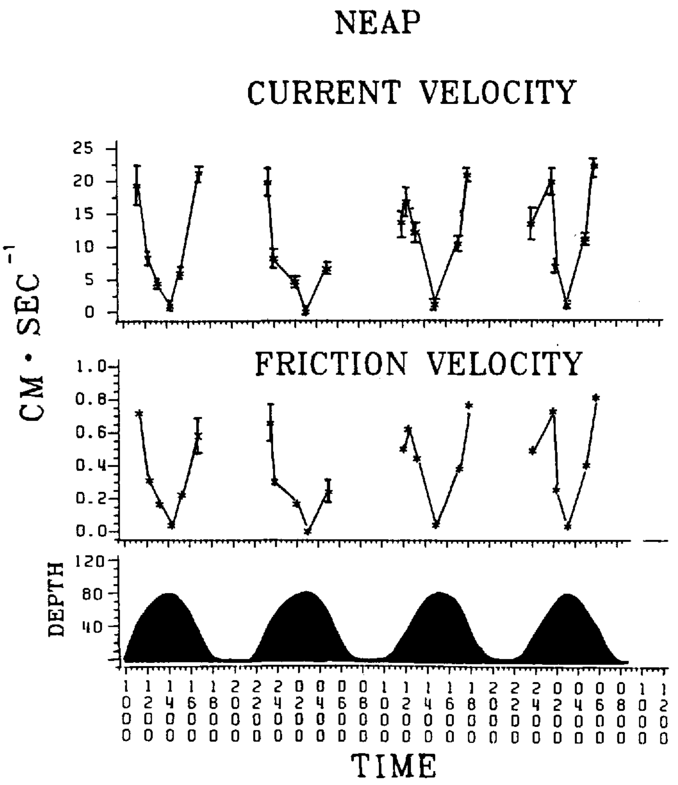

Figure 7. Mean flow ($\overline{u}$) measured 27 cm off the bottom and friction velocity, $u_* = (\tau/\rho)^{1/2}$, at the sediment/water interface over the two neap tidal cycles. Direct measurements of u_* were made for those samples with 95% confidence bars shown; the remaining u_* values were estimated via the drag coefficient C_{D27} (see text).

The *in situ* friction velocities are direct measurements for those values presented with 95% confidence bands in Figures 7 and 8 and estimated values (via Eq. 3 and see below) for the remainder of the samples. Measured values of u_* deviated most from estimated u_* values for the first samples prior to and just after slack water, explainable by nonsteady flow, effects of microtopography and/or turbulent drag reduction. The ensemble of the directly measured u_* values and those estimated from the drag coefficient, C_D, were not significantly different (Paired t-test; $p \leq 0.05$).

From the samples where both the skin friction and the velocity at 27 cm height were measured, an average ratio $\overline{u}/u_*$ of 27 was determined, with a resulting drag coefficient C_{D27} of 1.4×10^{-3}. For comparison, the ratio $\overline{u}/u_*$ and the drag coefficient for smooth-wall flume flow at comparable u_*, taken from Gust and Southard (1983) and extrapolated to $z = 27$ cm were 25 and 1.6×10^{-3}, respectively. The error estimates for u and u_* were $\leq 5\%$ each in that study, while for our field site the instrument errors are augmented by uncertainty in exact sensor position and the total

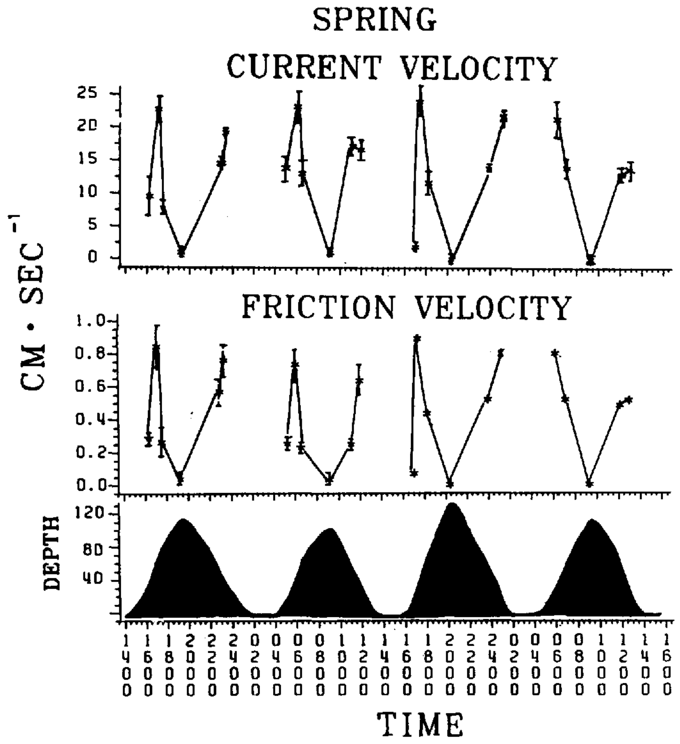

Figure 8. Mean flow ($\bar{u}$) measured 27 cm off the bottom and friction velocity, $u_* = (\tau/\rho)^{1/2}$, at the sediment/water interface over the two spring tidal cycles. Direct measurements of u_* were made for those samples with 95% confidence bars shown; the remaining u_* values were estimated via the drag coefficient C_{D27} (text).

error might be as large as 10% for u_*. In Figure 9, a skin friction spectrum from the field site (spring set, sample number 5) is compared to a smooth-wall spectrum collected in laboratory open channel flow. It reveals that the spectral shapes are similar in their frequency distribution and magnitude. The frequency response of the skin friction sensors exceeds 20 Hz and did not affect the spectral shape.

When the measured velocities and skin friction data are inserted into Eq. 1, it becomes evident that the flow was not hydrodynamically transitional as suggested originally from a visual appearance of the crab-burrowed sediment surface. The velocity shift (ΔU^+) is positive and not negative, which is compatible with dynamic processes indicating the presence of turbulent-drag reduction, or of a logarithmic layer thickness <27 cm followed by a wake (see, e.g. Tennekes and Lumley, 1972), and may also be the result of measuring uncertainties. No differentiation is possible between these options due to lack of complete mean flow profiles.

The most important result for answering the biological questions raised is the observation that the friction velocity, u_*, ranged between 0 and 0.90 cm · sec^{-1} and did

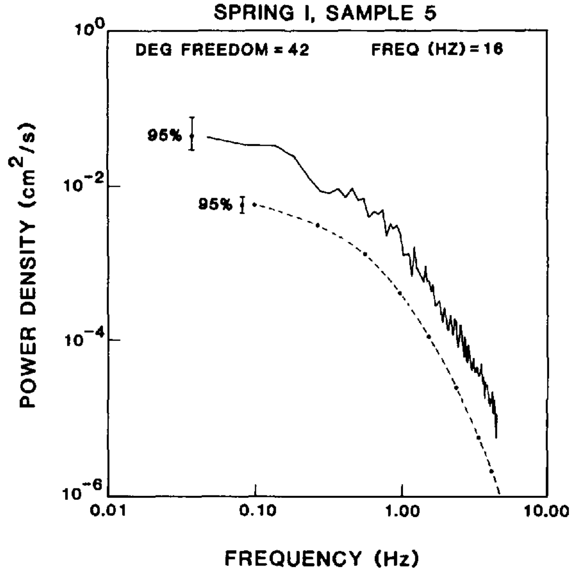

Figure 9. Comparison of a smooth-wall skin friction spectrum collected in open channel-flow at $u_* = 0.46$ cm · sec^{-1} (dashed line) with one obtained at the field site of $u_* = 0.56$ cm · sec^{-1} (solid line); significance levels of 95% are based on 210 degrees of freedom (*df*) for the open channel data and 42 *df* for the field data.

periodically exceed the critical friction velocity, $u_{*\text{crit}}$, required to erode the bottom sediment, thus justifying the search for a direct correlation between local erosion and meiofauna concentration in the water column.

c. *Meiofauna suspension: statistical analyses*

The best model for predicting meiofaunal (total or any taxon) suspension, determined by stepwise regression, included the following independent variables: friction velocity (u_*); mean flow ($\bar{u}$); water depth; abundance of meiofauna in the sediment (meiosed); concentration of suspended sediment (suspsed); and the interaction terms, $\bar{u}$ × depth, u_* × depth, $u_* \times \bar{u}$, and $\bar{u} \times u_*$ × depth. Light (night, day) and wind were not significant effects and thus were not considered further. Because u_* and $\bar{u}$ were colinear (u_* is physically related to $\bar{u}$ and for many samples was calculated from $\bar{u}$), the slopes estimated in the statistical model would not have been reliable if both were included (Helwig and Council, 1979). A comparison of the above model with a model excluding $\bar{u}$ and all interaction terms involving $\bar{u}$ showed that the error sum of squares was not significantly reduced by including the $\bar{u}$ terms in the former model ($p \geq 0.05$; *SS*-drop test; Ott, 1977, p. 472). Thus the following reduced model was used to investigate abundance of meiofauna in the water:

$$\text{abundance} = f(\text{set}, u_*, \text{depth}, \text{meiosed}, \text{suspsed}, u_* \times \text{depth})$$

Table 6. Analysis of covariance for the effect of the class variable set (spring, neap) and the covariates erosional velocity (u_*), depth, suspended sediment (suspsed), sediment density of total meiofauna (meiosed), and $u_* \times$ depth on the abundance of total meiofauna in the water column. Entire data set used.

Source	*df*	*SS*	*F*
Set	1	14998101.26	5.35
u_*	1	116534047.94	41.57***
Depth	1	30277453.78	10.80**
Suspsed	1	27681420.61	9.88**
Meiosed	1	532932.34	0.19
$u_* \times$ Depth	1	56287795.15	20.18**
Error	85	238268949.12	
Total	91	484580700.22	

** = significant, $p \leq 0.01$; *** = significant, $p \leq 0.001$

The ANCOVA (Table 6) showed that set (neap vs spring tides) and abundance of meiofauna in the sediment did not have a significant effect on abundance of meiofauna in the water. However, meiofauna abundance in the water was significantly related to friction velocity, depth, $u_* \times$ depth, and suspended sediment. Thus, the null hypothesis of no correlation between the concentration of suspended sediment and the abundance of meiofauna in the water (Introduction, question c) can be rejected. The relative importance of each term in explaining the variability in abundance of meiofauna in the water was determined by comparing the magnitude of the slopes which relate each term to abundance of meiofauna drifting. The abundances were first standardized to mean = 0 and variance = 1 to remove scale effects. The effect of each term, in order of decreasing importance and with direction of effect in parentheses (−, +), was: $u_* \times$ depth interaction (−), u_* (+), suspended sediment concentration (+), and depth (−).

Similar analyses performed on only the benthic copepods, instead of total meiofauna, produced the same conclusions and did not reduce the unexplained error. Since for a subset of the data, direct measurements of u_* were made (i.e., not calculated from $\overline{u}$), it was possible to compare the value of u_* and $\overline{u}$ in investigating suspension of meiofauna. Therefore, with this subset of data, an analysis utilizing the following model was compared to an analysis using the prior model (in which u_* and not $\overline{u}$ was used):

$$\text{abundance} = f(\text{set}, \overline{u}, \text{depth}, \text{meiosed}, \text{suspsed}, \overline{u} \times \text{depth})$$

The unexplained error was significantly reduced by using u_* instead of $\overline{u}$ (*SS*-drop test, Ott, 1977, p. 472; for total meiofauna, $p \leq 0.10$; for benthic copepods, $p \leq 0.001$), indicating that the abundance of meiofauna in suspension was more closely related to friction velocity than mean flow. Thus the null hypothesis of no relationship between the environmental parameters measured and the abundance of meiofauna in the water (Introduction, question d) can be rejected.

4. Discussion

a. The magnitude of meiofauna transport

Less than 1% of the total meiofauna community was in suspension at a fixed point in time (our sampling times); however, if one assumes that new individuals are suspended by the next sampling time and integrates abundance with respect to time, then over the course of a tidal cycle 1.6 to 5.7% of the meiofauna were suspended. These values corresponded to a complete neap tidal cycle and a complete spring tidal cycle, respectively. Furthermore, our suspension estimates should be conservative, since we did not include the interface data (with suggested abundances near the sediment >100× greater than at 17 cm intake) in our calculations. Thus, transport in the water likely represents a significant dispersal mechanism for meiofauna populations. Over half of the benthic copepods in suspension were eroded and advected from other areas and the center of distribution for some of these species could be traced to sand flats or high marsh areas at least 200 m away. Thus some meiofauna were transported considerable distances. The copepod species advected from other areas included typical interstitial species (e.g., *Leptastacus macronyx*) and species common in other mud and muddy/sandy areas (e.g., *Schizopera knabeni,* high-marsh vegetated areas). Thus drift of meiofauna was not limited to mud-dwelling and/or surface-dwelling copepods and the species richness of drift fauna was much higher than the richness of fauna in the sediment.

The fact that the fraction of sediment nematodes in suspension was lower than for other taxa was not surprising because nematodes are poor swimmers (Hopper and Meyers, 1966) and are rarely active on the sediment surface (Palmer, 1984). The higher percent of sediment copepods in suspension, compared to nematodes, may be related to behavior patterns which made them very susceptible to erosion by currents. They typically reside in the uppermost sediment layers (Fleeger, 1980), some frequent the sediment surface (Palmer, 1984), and some are capable swimmers (Hauspie and Polk, 1973). Rarely were juvenile copepod stages found in the water. Although it is not possible to state that all juvenile stages were absent in the water (we probably lost many of the naupliar 1–3 stages through the 63 μm collecting mesh), later naupliar stages and all copepodite stages were suspended infrequently relative to adults. Additionally, fewer gravid female copepods were in suspension than other females or males. Egg-bearing individuals may avoid suspension by burrowing deeper when flow increases, as do other meiofauna (Rhoads *et al.,* 1977; Palmer, 1984) or gravid females may be less frequently suspended because of their increased weight due to egg cases. Perhaps this is advantageous if gravid females are more susceptible to predation than other stages.

b. Sediment-meiofauna suspension intercomparison

This study assumed that the hydrodynamic processes controlling erosion of meiofauna are the same as those controlling sediment erosion. This, of course, is a simplification because meiofauna can respond to flow by moving. The suspension in the creek can be viewed as a mixture of cohesive sediments (flocs ≤ 60 μm, densities $1.06 < \rho < 1.2$ g $\cdot$ cm^{-3}) and meiofauna (size ≤ 250 μm, densities $1.02 < \rho < 1.06$). The concentration was ≤ 100 mg $\cdot$ l^{-1}. Settling velocities of cohesive sediments for these concentrations and observed salinities have been reported by Owen (1970) to be <0.01 cm $\cdot$ sec^{-1}, while Palmer (1984) measured a median settling velocity of ~ 0.15 cm $\cdot$ sec^{-1} for the meiofauna. These values suggest that (to first order) meiofauna are similar in their settling behavior to quartz grains of ~ 40 μm diameter, for which the settling velocity is ~ 0.17 cm $\cdot$ sec^{-1}, based on Stokes Law (at 20°C). Despite the differences in settling velocities, meiofauna and suspended sediment concentrations followed similar tidal patterns and were depth stratified at the same sampling times. The ANCOVA showed a significant correlation between abundance of meiofauna in the water and suspended sediment concentrations. However, meiofauna suspension was more highly correlated with u_* than was sediment suspension. The fact that suspended sediment concentration explained significantly less of the variability in meiofauna drift than did u_* suggests that differences exist in the entrainment and deposition dynamics of sediment and meiofauna in the creek due to the different settling velocities and perhaps behavior.

c. Factors controlling transport of meiofauna

For the sediment (and meiofauna) to be eroded locally, the condition $u_* > u_{*\text{crit}}$ (sediment) had to be met for flow in the vicinity of the measuring site. We measured $u_{*\text{crit}}$ of sediment cores from the field site in September, some time after the experiment had been done, and it is shown below that these values can reasonably be used to discuss the u_* measured in the field in June/July.

Two effects need to be addressed, one is the temperature of the sediment/fluid systems and the second is bioturbation. The temperature increase between flume runs (20°C) and field experiments (25–29°C) was less than 10°C, and Kelly and Gularte (1981) have shown that erosion rates then increase by $<30\%$. This indicates a decrease in $u_{*\text{crit}}$ with increasing temperatures, and we can consider the $u_{*\text{crit}}$ of 0.58 cm $\cdot$ sec^{-1} measured at 20°C as an upper limit for the June/July experiment. In addition this value of $u_{*\text{crit}}$ compares to $u_{*\text{crit}}$ of 0.7 cm $\cdot$ sec^{-1} measured for a similar mud bottom by Gust (1976) at ~ 30°C. Differences in algal and/or bacterial coatings near our sample site based on data from Montagna *et al.* (1983) suggest that the only change may have been higher algal densities in July, with increased sediment binding and $u_{*\text{crit}}$. However, this should have been offset by increases in macrofaunal activities (e.g., Rhoads, *et al.* 1978; Grant *et al.*, 1982) which tend to decrease $u_{*\text{crit}}$. Grant *et al.* (1982, Fig. 5) showed that no seasonal effect was discernable for the period

June–September on $u_{*\text{crit}}$; values did increase in October. The evidence in the literature thus suggests it is permissible to use the $u_{*\text{crit}}$ of 0.58 cm · sec^{-1} measured in September also for the June/July experiment. For benthic meiofauna with lower specific densities than sediments (1.04 g · cm^{-3}; unpub. data), the $u_{*\text{crit}}$ is so low that they are also likely eroded when the fluff layer is resuspended after slack.

$u_{*\text{crit}}$ was repeatedly exceeded during both ebb and flood flow (see Figs. 7 and 8). The values shown are mean u_* averaged over 8.5 min, with no reference to higher instantaneous u_* values which may have occurred within a sampling time. For example, examination of instantaneous u_* values during the spring sample 5 indicates that even though the mean u_* was 0.57 cm · sec^{-1}, instantaneous values exceeded $u_{*\text{crit}}$ more than 40% of the time.

Our measured field data of u_* and also $u_{*\text{crit}}$ exceed values reported by Migniot (1968) who showed that $u_{*\text{crit}}$ for cohesive sediments with a high water content can be as low as 0.26 cm · sec^{-1}. In our study, a nonconsolidated fluff layer of sediment was deposited on the mudflat during slack water. This layer, with a high water content probably had a lower $u_{*\text{crit}}$ than 0.58 cm · sec^{-1}, compared to the underlying, more consolidated cohesive sediment as suggested by Migniot's study. If meiofauna reside in this fluff (as our interface data imply), then resuspension had occurred at very low u_* values. Future studies need to document (1) the dynamics and presence of meiofauna in such fluff layers and (2) $u_{*\text{crit}}$ for the meiofauna themselves. These are difficult tasks because a fluff layer is hard to maintain in a laboratory flume, yet realistically (1) and (2) can only be approached in a lab setting where one can make pertinent observations while controlling flow. Jumars and Nowell (1984) have also recently argued for the need for direct observations of benthic recruitment under controlled flow conditions.

In the present study, the correspondence between changes in u_* measured on the mudflat and changes in meiofauna abundances in the water over the mudflat (compare Figs. 2, 3 with 7, 8) coupled with the knowledge that u_* exceeded $u_{*\text{crit}}$, argues for local erosion. On the other hand, the lack of correspondence between abundance of meiofauna in the sediment and abundance in the water column (Table 6, meiosed insignificant) implies that a fraction of the suspended meiofauna were not eroded locally. One cannot possibly sample all of the benthic communities in the marsh that potentially contribute to the pool of suspended meiofauna; thus, using abundance of animals in the sediment to study suspension problems is apparently fruitless—a discouraging result. Nevertheless, the fact that we found a significant relationship between flow over the mudflat and meiofauna suspension for both local and advected animals argues for a passive mechanism (flow/erosion) throughout the marsh. Flow parameters and meiofaunal response in other marsh areas must have followed a pattern similar to that we found on the mudflat. Behavioral differences between those meiofauna on the mudflat and meiofauna elsewhere in the marsh are possible, which may have contributed to the difficult problem of linking dynamics of water column meiofauna to sediment meiofauna dynamics.

Another indicator of local passive erosion of the meiofauna can be found in the vertical abundance distribution in the ebb current at times when $u_* > u_{*\text{crit}}$. Following the derivation of Monin and Yaglom (1971, Eq. 10.149 and 10.149′) on vertical turbulent diffusion of material eroded from the bottom, the mean and variance of the particle height can be expressed as a function of time and friction velocity as

$$z = 0.77\, k u_* t$$

and

$$z'_{\text{rms}} = (0.32\, k^2 u_*^2 t^2)^{1/2}.$$

From these equations a time interval can be determined, within which meiofauna are completely mixed in the water column, or reach a specific water level; e.g., the sampling port at 17 cm height. Based on these equations with water depth of 60 cm and a mean u_* of 0.6 cm · sec^{-1} (individual values vary per tide), eroded meiofauna should be homogeneously dispersed in the water column and consequently be sampled in comparable abundances at the three sampling ports after travelling a downstream distance of ≥50 m for a mean transport velocity of 15 cm · sec^{-1} in the creek. The statistically significant stratification in the meiofauna distribution of Figure 1 for certain samples when u_* was ≥0.6 cm · sec^{-1} indicates for the animals a mean diffusion time of 92 sec. to reach the sampling port at 17 cm. For the observed transport velocity, the source of the meiofauna for these samples could then only be erosion in a localized area within ≤15 m upstream of the sampling port but not advection.

These observations on nonhomogenous vertical meiofauna distributions at specific tidal phases, the relationship of abundance of meiofauna in the water with measured friction velocities when it exceeded critical friction velocities of the bottom sediment and the lack of behavioral swimming emergence (Palmer, 1984), make the direct pathway of meiofauna entering the water column through passive erosion very plausible if not certain.

The fact that meiofauna abundance in the creek water was most strongly related to flow, and did not vary diurnally or with a lunar cycle, also points toward meiofaunal drift as a passive erosional process and not an active behavioral process. This reinforces the conclusions of Palmer (1984). Thus, meiofauna in the water column were not from hyperbenthic populations (cf. Sibert, 1981) that migrate up into the water column with diurnal, tidal or lunar frequency, as do some beach Crustacea (e.g., Jones and Naylor, 1970), freshwater stream benthos (e.g., Waters, 1972), or marine demersal zooplankton (e.g., Alldredge and King, 1980). There is not a clear distinction as to what the latter category includes and some epibenthic harpacticoid copepods, previously considered meiofauna, should probably be considered demersal zooplankton (e.g., see Arndt *et al.,* 1982). Although we have no evidence of sunrise/sunset changes in meiofauna suspension (insufficient replication at these times to statistically test for such an effect) it is possible that our lumping all the night time vs. daytime hours diluted or missed a sunrise/sunset effect. If present, such an effect must have been highly ephemeral because these changes were not visible in the few samples we took immediately after sunrise or sunset.

The overall fit of the statistical model (Table 6) was low ($R^2 = 0.50$; significant $p \leq 0.05$) for several possible reasons. First, Lesht (1979) pointed out that using mean shear stress (or mean u_*) makes predicting transport difficult. Shear stress has an inherently high sampling variability in tidal systems because of the intermittent nature of intense shearing near the bottom (Heathershaw and Simpson, 1978). Knowledge of short periods of very high shear or 'bursting phenomenon', which most commonly occur during the accelerating and the decelerating phases of tidal flow, may be very important in predicting erosion (Grass, 1970; Soulsby, 1983). Second, direct measures of u_* throughout the present study were needed. Use of the drag coefficient for calculating u_* from $\bar{u}$ is problematic, and wake effects as well as drag reduction may have been present. Third, there was no inclusion of a measure of biological activity that may have affected erodibility of sediments. Others (Rhoads *et al.*, 1978; Nowell *et al.*, 1981; Grant *et al.*, 1982) have emphasized the importance of sediment reworking and/or disturbance by fauna on resuspension. A flounder foraging on the flat for a short time period or a fiddler crab unplugging its burrow, may have caused a brief increase in local erosion which added to the variability in the data set.

While it can be expected that refined future studies will improve on the overall fit of the statistical model, we do not expect they will change the pathway of the meiofauna from the sediment into the water column as determined in this study. Our goal was to determine which parameters were related to the entrainment process and we found this to be passive erosion, both locally and in other areas.

d. Emerging concept of meiofauna dispersal

Even though meiofauna lack pelagic larval stages they are dispersed via the water column. This may allow them to rapidly colonize new and/or disturbed areas (e.g., Scheibel, 1974; Bell and Coen, 1982; Chandler and Fleeger, 1983). This dispersal mechanism may alter patchiness of meiofauna which are commonly suspended, e.g., copepods. Meiofauna population abundances have inherently high variability. In this study, within a sampling time, the average coefficient of variation for abundance of meiofauna in the water was 18% of the mean. However, between sampling times (tide effect) the abundance fluctuated by more than 30% (sometimes by 100%; Figs. 2 and 3). Thus, despite the high inherent variability, tidal variations in suspension are measurable. So that in a habitat where erosion occurs, the time one chooses to sample meiofauna may affect both abundance estimates and perhaps spatial scales of patchiness. Our data suggest that these small benthic organisms are subject to the same erosion/suspension processes that act on sediments.

The present study presents evidence for dispersal of meiofauna in a tidal creek being primarily a passive process. Behavior merely modifies the effect by determining which fauna are most susceptible to erosion and suspension. Dispersal of meiofauna is probably not a purely passive process and might vary from habitat to habitat. The results we found should be common to other areas with swift flow and high bottom shear. In systems that are more benign hydrodynamically, meiofauna dispersal mechanisms may be quite different. There are some data which demonstrate that meiofauna do emerge from the sediments in such habitats (e.g., Arndt *et al.*, 1982; Walters, pers. comm.). Evidence is accruing that in some cases the distinction between epibenthic meiofauna and demersal zooplankton is unclear. Clearly, meiofauna are not the sediment-bound organisms we have assumed, whether their dispersal is via active, passive, or both mechanisms.

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