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The dynamics of near-bed seston flux and suspension-feeding benthos

by D. K. Muschenheim^{1,2}

ABSTRACT

Benthic suspension feeders depend on the fluid medium for their supply of edible particles. The horizontal flux of organic seston is a function of the interaction of particles of varying densities with the near-bed velocity field. Analytical and numerical models of this process predict that the shape of the flux profile varies with flow rate, bottom roughness and particle settling velocity. Bulk horizontal particle flux may either decrease or increase with height above the bed. Flume experiments with natural sediments from Eastern Passage, Nova Scotia confirmed the trends predicted by the model. In a complex suspension, denser, inorganic particles have flux maxima closer to the bed than lighter, organic seston, so suspension feeders must reach several centimeters above bed level to maximize the organic composition of their ration. The feeding ecology and diet of a passive suspension feeder, the polychaete, *Spio setosa*, were examined in light of the modelled seston dynamics and suggested that *S. setosa* is adapted to feed at 4 to 5 centimeters above the bed and specializes on suspended macrophyte detritus and flocculated organic-mineral aggregates. The influx of this organic seston at Eastern Passage is periodic and coincident with the local seiche period, showing that the hydrodynamic control of seston transport is an important factor in benthic trophic interactions.

1. Introduction

Few subtidal benthic marine environments attain rates of *in situ* primary production sufficient to fuel the observed community metabolism. Benthic detritivores are generally forced to rely on advective sources for their food supply (LaBarbera, 1984; Miller *et al.*, 1984) and thus are dependent on the fluid medium for transport of this material. Benthic suspension-feeders are especially adapted to the forces of drag and shear encountered in the benthic boundary layer (c.f. Koehl, 1977). Although these fluid forces disperse particles and create local gradients in velocity and concentration, prior considerations (summarized in LaBarbera, 1984) of suspension-feeding have made the tacit assumption that the organisms take their ration from an essentially homogeneous medium. This idea may stem from the extensive study of pelagic filter-feeders which feed in an environment where, at local scales, the concentration of

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food particles is considered to be uniform. Another legacy of the attitudes developed from plankton research is the assumption that there is little or no differential transport of the predator and prey items—that they are both suspended in, and subject to, the same fluid forces. The last point illustrates a fundamental difference in the physical nature of the benthic and pelagic environments. Suspension-feeding organisms anchored in the bottom may take advantage of vertically settling material but primarily feed on seston flowing horizontally past them. Warner (1977) has shown how the shapes of their feeding structures are often adapted to local current conditions.

Recent attention to the ecological significance of the benthic boundary layer (McCave, 1974; Vogel, 1981; Jumars and Gallagher, 1982; Carey, 1983; Nowell and Jumars, 1984) has pointed out that the near-bed region is one of strong vertical gradients of flow velocity and particle concentration. The significance of this physical regime has been examined in light of the reciprocal effects of organisms, sediments and fluid acting to determine the grain characteristics of the bed (Rhoads, 1974; Rhoads *et al.*, 1978; Young and Southard, 1978; Nowell *et al.*, 1981; Eckman *et al.*, 1981; Eckman and Nowell, 1984; Grant, 1985; Grant *et al.*, 1987). The consequences for deposit-feeding benthos have been examined in terms of substrate stability (Eckman *et al.*, 1981; Jumars *et al.*, 1981; Rhoads and Boyer, 1982), but also in terms of the lateral transport of food particles to an essentially sedentary fauna (Carey, 1983; Jumars and Nowell, 1984; Miller *et al.*, 1984). Study of the horizontal transport of organic detritus augments well established patterns of vertical supply of organic materials to the benthos (e.g., Rowe and Smith, 1977; Honjo *et al.*, 1982). The processes that laterally distribute and sort the material falling out of the water column are as important as vertical settling in determining the availability of this material as food.

This paper describes and analyzes the horizontal flux of organic and inorganic particles in the near-bed (0–10 cm) region, and its significance to suspension-feeding benthos. An analytical approach to the hydrodynamics of particle flux is used and applied to flume experiments using natural sediments. Finally, the feeding ecology of a tube-dwelling polychaete, *Spio setosa*, is examined in light of the predicted flux profiles.

Suspension-feeding benthos. Only those organisms classed as “passive suspension feeders” (*sensu* Warner, 1977; LaBarbera, 1984), are considered here but the general approach is relevant to all benthic suspension-feeding organisms. Many organisms, previously considered as uniquely deposit-feeding, are now known to take at least some portion of their ration from suspension. The common tellinid bivalve, *Macoma balthica*, takes over 50% of its food by suspension feeding (Hummel, 1985). Spionid polychaetes (Taghon *et al.*, 1980; Dauer *et al.*, 1981; Dauer, 1984), terebellid polychaetes (Carey, 1983), dendrochirote holothurians and ophiuroids (LaBarbera, 1984) have been observed using their appendages to intercept suspended particles traveling past them, although the behavioral demarcation between suspension- and

deposit-feeding may be problematic, as in some Amphipoda (Mills, 1967). Nevertheless, there is mounting evidence that many macrobenthic species may at some time take part of their ration from suspension.

In their theoretical analysis of mechanisms of particle capture, Rubenstein and Koehl (1977) concluded that direct interception and inertial impaction were the two most important mechanisms used by marine seston feeders. LaBarbera (1984) supports this contention and Taghon (1984) has used scaled models to look at particle interception by spionid polychaetes as a function of palp orientation and the Reynolds number of the flow. He concluded that the feeding responses of spionids are adaptive and are the most efficient possible under given flow conditions. Again, these analyses assume a uniform suspension of particles. While direct interception is solely dependent on the relative diameters of the particle and filter element, inertial impaction also relies on there being a difference in the densities of the particle and the fluid medium. The density difference between seawater and most organic particles in suspension is so small that the particles essentially follow streamlines and tend to be diverted with the flow around a single filter element. The greater mass and inertia of the inorganic fraction means that they are less likely to be diverted, serving to increase their effective capture. Thus the hydrodynamics of filtering may work against optimal capture of organic particles in a complex suspension. Any behavioral adaptation that may minimize this effect should confer an advantage.

Experimental studies of the food supply to suspension-feeding benthos have looked both at the mass transport of seston (Wildish and Kristmanson, 1979, 1984) and at changes in particle trajectory (Carey, 1983) caused by turbulence near the seabed. Carey's work showed that local conditions of scour around polychaete tubes could enhance particle availability to seston feeders. Wildish and Kristmanson (1979) considered the vertical flux of material, augmented by near-bottom turbulence, but their concern was with large-scale effects acting on populations. They did not consider the vertical structure of the velocity or particle concentration fields, or their effects on differential horizontal transport of seston.

Vertical structure is important because it is the product of the velocity and particle concentration fields together that determine the flux of material past an organism suspension feeding at the sediment-water interface (Taghon *et al.*, 1980; Jumars and Gallagher, 1982; Jumars and Nowell, 1984). The shape of the flux profile determines whether the greatest flux of edible particles occurs close to the bed or somewhere above it. Consideration of concentration alone can be misleading; it must be recognized that the interaction with the near-bed current regime determines the availability of these particles to benthic organisms. Particles that settle at different rates will also behave differently in a given flow. If it is possible that hydrodynamic sorting results in the horizontal flux of suspended sand grains being greater slightly closer to the bed than the flux of suspended organic detritus, a suspension feeder able to reach an extra centimeter or two into the water column would thus increase the quality of its ration.

To investigate the specific form of the flux profile over a range of flow conditions, I developed a model based on the theoretical equations for two-dimensional velocity and particle concentration profiles.

2. Model development

a. Analytical. Dimensionally, the horizontal flux of suspended particulate matter is defined as Mass per unit Time per unit Area, with area in coordinates normal to the axis of flow. Thus flux is equivalent to the product of velocity and concentration. As we are concerned only with advective, and not diffusive processes, appropriate time-averaged measures of the velocity and concentration profiles can be used to calculate the average flux profile. Theoretical formulations exist to predict both of these quantities as a function of the flow, bed roughness and particle fall velocity. This allows us to derive an analytical model of how the horizontal flux profile should vary under changing conditions.

b. Velocity. The Karman-Prandtl formulation of a logarithmic velocity profile predicts the mean downstream velocity (u_z) at any height, z , in the boundary layer:

$$u_z = \frac{u_*}{\kappa} \ln \frac{z}{z_o} \quad (1)$$

where κ is von Karman's constant and z_o , called the roughness length, is the z -intercept of the profile. The slope of the velocity profile, and the shear-generated turbulence in the boundary layer, are expressed by the shear velocity, u_* . This parameter has units of velocity (cm s^{-1}) and is equal to $(\tau_o/\rho)^{1/2}$, where τ_o is the fluid shear stress at the bed and ρ is the fluid density. The derivation of Eq. (1) and explanation of its terms are presented by various authors (e.g. Landau and Lifschitz, 1959; Tritton, 1977; Middleton and Southard, 1984; Nowell and Jumars, 1984; Muschenheim *et al.*, 1986). For the sake of analytical tractability, the existence of a viscous sublayer very close to the bed will be ignored. If present, it is generally less than 1 cm thick so that its effect on this analysis is minimal. Similarly, only the non depth-limited form of Eq. (1) is used and is sufficient for the current purpose.

c. Concentration. Rouse (1937) first formulated a theory for the vertical distribution of sediment in suspension. Detailed explanations may be found in Vanoni (1946, 1975), Raudkivi (1976) and Middleton and Southard (1984). It expresses the sediment concentration, C_z , at a height z above the bed in terms of the ratio of the fall velocity of the sediment, \bar{w}_s , to the friction velocity, u_* :

$$C_z = C_a \left(\frac{a}{z} \right)^p \quad (2)$$

where C_a is a reference concentration at a height, a , above the bed and the exponent p , referred to as the 'Rouse Number,' reflects the ratio of \bar{w}_s to u_* :

$$p = \bar{w}_s / \kappa u_*.$$

The use of the Rouse equation imposes certain limitations on the model. Rouse (1937) assumed that the flow has developed over sufficient length and time to produce a seston concentration profile which is in equilibrium and is fully contained within the benthic boundary layer. This means that both the mean velocity and concentration profiles do not change with distance downstream. Although these may be reasonable conditions to expect in many shelf, slope and abyssal environments, they are untenable assumptions in shallow coastal situations, where varying bottom topography, wave-induced resuspension and bioturbation are significant effects. Nevertheless, the simplified velocity (1) and seston concentration (2) equations are analytically useful for examining the trend of flux profile behavior under varying conditions.

d. Flux. The flux profile may be expressed as a function of height above the bed by:

$$F_z = u_z \cdot c_z. \quad (3)$$

Substituting Eqs. (1) and (2) for u_z and c_z we obtain:

$$F_z = C_a \left[\left(\frac{a}{z} \right)^p \cdot \left(\frac{u_*}{\kappa} \ln \frac{z}{z_o} \right) \right]. \quad (4)$$

Taking the derivative and setting it to zero yields an expression for the height of the flux maximum for a given sediment in a steady, uniform flow:

$$\frac{\partial F}{\partial z} = \frac{1}{z} \left(\frac{a}{z} \right)^p - \frac{pa}{z^2} \ln \frac{z}{z_o} \left(\frac{a}{z} \right)^{p-1} = 0 \quad (5)$$

which reduces to:

$$z_{\max} = z_o t \exp \left[\frac{1}{p} \right]. \quad (6)$$

Particles with different settling velocities, when exposed to the same flow, will be subject to hydrodynamic sorting. Eq. (6) predicts that, in a seston mixture composed of mineral grains, organic-mineral aggregates (OMA's), plankton and resuspended benthic microalgae, denser particles will exhibit flux maxima closer to the bottom than the less dense fractions. This also represents a sorting of potential food particles of differing quality. Under these conditions, a benthic suspension-feeder will gain an energy advantage by increasing the height above bottom at which it feeds. If a suspension-feeder increases the organic portion of its ration by reaching another

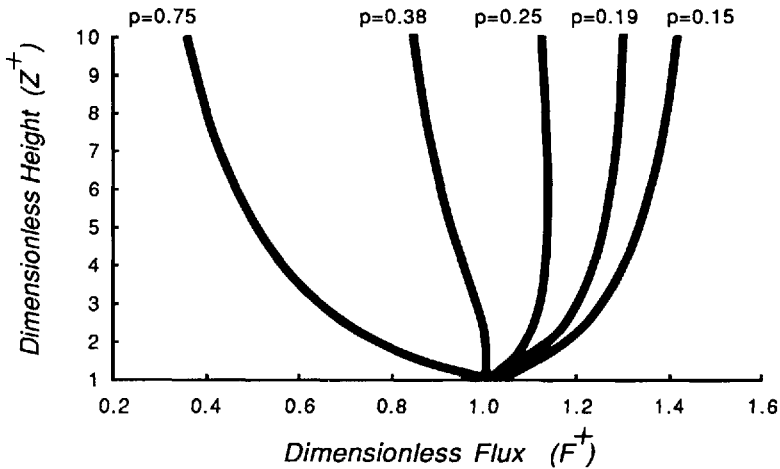


Figure 1. Model profiles of the vertical gradient of horizontal seston flux. The dimensionless flux (F_z/F_a) is plotted as a function of dimensionless height (z/a) above the bed, for five values of the Rouse number, p , ranging from 0.15 to 0.75. The parameter values used are: $z_o = 0.1$ cm, $u_* = 0.25$ cm s $^{-1}$, and $\kappa = 0.41$; therefore \bar{w}_s varies from 0.02 to 0.08 cm s $^{-1}$. The reference height, a , is 1 cm.

centimeter or two into the water column, the energetic cost of building and maintaining a tube may well be repaid.

e. Numerical. A second approach involves taking the derived expression for the flux profile (Eq. 4) and examining it for a range of values of p ($p = 0.15$ to 0.75, Figure 1) under constant flow conditions (u_* , $z_o = \text{const.}$). The different curves then reflect only an increase in particle settling velocity as p increases. The five curves plotted show a progression in the shape of the flux profile. At high values of p , the horizontal flux decreases with height above the bed, is essentially uniform at intermediate p -values and increases with height at low p -values.

To determine the conditions under which the flux profile (a) increases toward the bed, (b) increases away from the bed, or (c) is relatively uniform within the near-bed region, the skewness (γ_1) was calculated for each profile modelled. Profiles where the flux decreases with distance from the bed (“bottom heavy”) exhibit a $\gamma_1 > 0$, those with the flux increasing with distance from the bed (“top heavy”) are characterized by a $\gamma_1 < 0$. Figure 2 shows the results of this analysis plotted in parameter space. The curve describes the combinations of u_* , \bar{w}_s , and z_o for which $\gamma_1 = 0$, i.e. where the flux profile is uniform. The range of the Rouse Number examined here is well below the critical value of 2.5, which defines the theoretical change from suspended to bedload transport (Middleton and Southard, 1984). Thus we are considering only sediment in suspension. The result shows that, over the range of $p = 0.2$ to 0.9 and $z_o = 0.01$ to 0.75 cm there is a transition from “bottom-heavy” to “top-heavy” flux profiles. At

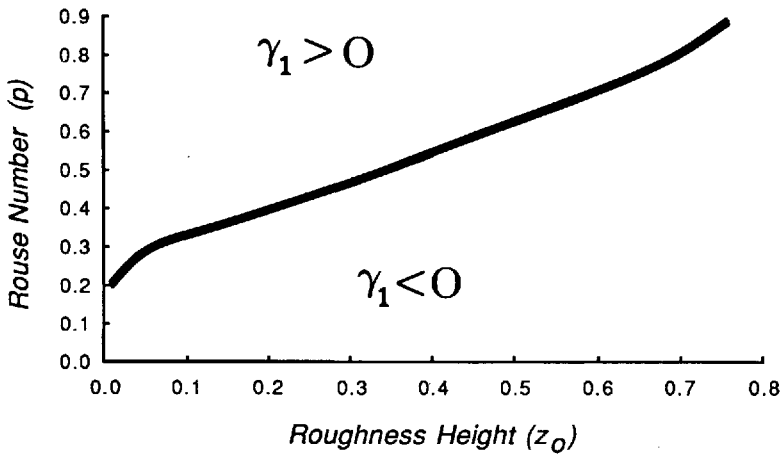


Figure 2. Parameter space plot of zero skewness isopleth. Skewness describes flux profiles calculated from Eq. (4) and indicates whether the flux decreases ($\gamma_1 < 0$) or increases ($\gamma_1 > 0$) with distance from the bed.

lower values of p the flux maximum is well above the bottom. This is in fact generally true for cases where $\bar{w}_s < 10u_*$; i.e., for particles of relatively low specific density. The effect of increasing the roughness of the bottom is to increase the value of p at which the flux maximum moves away from the bed.

The specific shape of the flux profile is dependent on the vertical range modelled. Indeed, the flux will always ultimately decrease with height as seston concentration decreases outside of the boundary layer and the velocity profile becomes uniform. I am concerned here only with the near-bed region, somewhat arbitrarily defined as the ten centimeters immediately overlying the bed, which is the region of greatest relevance to the feeding of most benthic suspension feeders.

3. Methods

a. Laboratory experiments. The experiments were run in the Dalhousie seawater flume, described in Muschenheim *et al.* (1986). Filtered seawater from the Dalhousie Aquatron was mixed with concentrated suspensions of seston (described below) pumped into the flume manifold. Flow velocities were determined in two ways. At low velocities ($< 10 \text{ cm s}^{-1}$) dye pulses at discrete heights above the bottom were timed along a 10 cm path. A Thermometrics FP-14 thermistor in a bi-polar voltage divider provided fine-scale velocity resolution while a separate thermistor circuit measured the water temperature. Thermistors were temperature calibrated using the fitting scheme of Steinhart and Hart (1968). Velocity calibrations used a pipe flow method, suggested by Vogel (1981), in the apparatus described in Muschenheim *et al.* (1986). An Octagon Systems SYS-2A microcontroller and an Osborne-1B microcomputer pro-

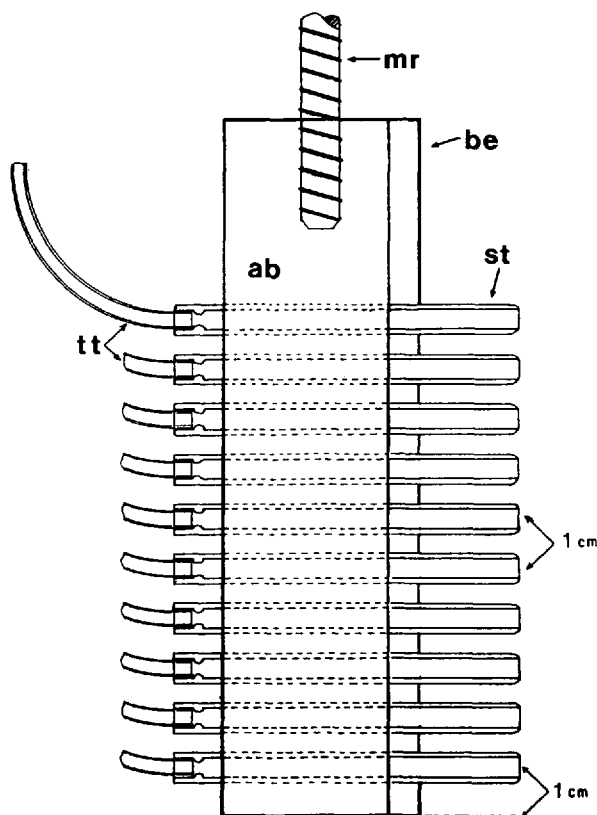


Figure 3. Seston sampling apparatus used in flume experiments. The tube array is suspended by a machined rod (mr) attached to an instrument platform spanning the flume. The acrylic block (ab) with a leading beveled edge (be) supports glass sampling tubes (st), centered 1 cm apart. Clear PVC transfer tubing (tt) runs from the sampling tubes to the collection jars (not shown).

vided A/D conversion and data logging. Only experiments where the boundary layer was fully developed were used for analysis. One criterion for full development was taken as a value of u_* (calculated from the measured velocity profile) less than or equal to 0.05 times the free-stream velocity. This value is typical of observed natural boundary layers (Bradshaw, 1975; Tritton, 1977). A second measure of boundary-layer development was the comparison of the measured flume boundary-layer thickness with the boundary-layer thickness predicted for the particular conditions of channel length and flow velocity (from Schlichting, 1967). By these two criteria, all experimental flows used in this analysis were fully developed.

Seston concentrations were sampled at six heights (1–5, 7 cm) using the apparatus shown in Figure 3. The design complies with suggestions put forward by the

Inter-Agency Committee on Water Resources (1941). Glass sampling tubes of 0.55 cm diameter were mounted in an acrylic block. The leading edge of the block was beveled and the block was suspended in the flume by a machined rod attached to one of the instrument platforms spanning the flume. To ensure isokinetic sampling, velocities at the inlet of each sampling tube were adjusted, by a Hoffman clamp on the PVC tubing, to match the flow at that height above the bed. In practice, the sampling velocity was set to 25% above ambient to minimize settling in the PVC tubing that carried the sampled water to the six collection jars. A constriction at the rear of each glass tube further accelerated the flow into the smaller diameter PVC tubing. These measures worked well to minimize settling in the lines, the contents of which were always rinsed into separate jars at the end of a flume run, and treated as all other samples (see below). Only the slowest flume flow rates (free-stream velocity $<1.0 \text{ cm s}^{-1}$) resulted in settling that required correction, and then only for the 1 and 2 cm samples.

Samples were filtered through pre-combusted Gelman AE glass fibre filters ($1 \mu\text{m}$ nominal pore diameter), rinsed with filtered seawater and dried at 60°C for 48 hours before weighing. Filtered seawater blanks were used to correct for salt retention. Samples were also ashed at 500°C for 12 hours for bulk organic matter determinations.

b. Natural sediments. To determine the concentration and flux profiles of a natural seston, sediment was scraped from the top 3 mm of a fine sand flat at Eastern Passage, N.S. and returned to the laboratory. The flat receives high organic loading from Halifax Harbour and is also characterized by a dense infauna, the most conspicuous members being *Mya arenaria* and *Spio setosa*. Gentle resuspension in filtered seawater and decanting through a $250 \mu\text{m}$ sieve provided a concentrated suspension. During an experiment stirring kept the suspension even and prevented time-dependent changes in concentration in the flume flow. This was tested by placing an Optical Backscatterance Sensor (OBS, see Downing *et al.*, 1981) at a fixed height in the flow. OBS output remained constant over an hour-long experiment, indicating a concentration of 61.3 mg l^{-1} (calibration $r^2 = 0.98$). Although it may be an oversimplification to characterize a poorly sorted sediment by a single fall velocity, the concept of "effective fall velocity" has been applied to estuarine sediments by Krone (cited in McCave, 1979). An effective fall velocity of 0.14 cm s^{-1} was established for the Eastern Passage surficial sediment after settling trials in a 20 cm column in a cold room at 6°C (to match flume conditions) and agreed well with the value of 0.15 cm s^{-1} , determined by Krone's method (see Muschenheim, 1987).

Due to length limitations of the flume, flow rates had to be kept low. This was done both to ensure a fully-developed boundary layer and to allow enough residence time for the seston distribution to reflect the hydrodynamic conditions. With an estimated effective settling velocity of 0.14 cm s^{-1} , 50 s residence time would be required for the

Table 1. Ratios of organic to inorganic particles from ambient surficial sediment and gut contents of *Spio setosa* sampled at Eastern Passage, Nova Scotia. The particle types considered are Organic-Mineral Aggregates (OMA), Benthic Diatoms, Quartz grains and Macro-Algal Fragments (Algae). Differences in median tested by Wilcoxon rank-sum test.

Particle types	Ratios			
	Ambient sed.	Spio gut	<i>N</i>	<i>p</i>
OMA/Quartz grains	0.73	1.69	18	.001
Algae/Quartz grains	0.04	0.58	18	.001
Diatoms/Quartz grains	0.50	0.04	18	.001
Diatoms/OMA	0.66	0.02	18	.001

sediment to "clear" from a 7 cm water depth. With 250 cm of channel length available, the maximum flow rate that allows this much residence time is 5 cm s^{-1} . Thus four experiments were run at u_* 's ranging from 0.1 to 0.24 cm s^{-1} . To fully adhere to the "equilibrium" seston distribution of the Rouse equation, a channel length of 15 to 20 m would be required. These experiments approximate the short-term response of the sediment-water system to upstream resuspension. Given the dynamic environment characteristic of shallow estuarine environments (distributed roughness, bioturbation), the experimental conditions may be more representative of natural conditions than an idealized "equilibrium."

An additional experiment was run at $u_* = 0.22 \text{ cm s}^{-1}$ to collect samples for SEM analysis. Sampling tubes were run directly into a filter manifold and filtered onto Nuclepore 1 micron polycarbonate filters, fixed and carbon coated and viewed on a Cambridge Autoscan Scanning Electron Microscope at the Bedford Institute of Oceanography.

c. Field studies. *Spio setosa*, obtained from Eastern Passage, were dissected to obtain gut samples of recently ingested material. The animals were removed from their tubes as the tide went out, narcotized in 6% MgCl_2 and returned to the lab within one hour. The foregut region (approximately 60 setigers after the pharynx) was dissected and the contents perfused with filtered ($0.45 \mu\text{m}$ pore size) seawater. Samples were stored in 1% formaldehyde at 4°C until analysis.

Samples were filtered onto Nuclepore polyester filters ($1 \mu\text{m}$ pore diameter), cleared with glycerol and examined at 200X under a Zeiss light microscope with phase contrast. 30 fields were counted for the particles in the categories listed in Table 1. Only samples that yielded >100 particles in 30 fields were used for analysis. Some samples were treated with Hertzberg's Iodine stain after a brief acid hydrolysis. The polychromatic stain is specific for chitin, cellulose and carbohydrate, allowing differential recognition of OMA's and gut lining sloughed off during the perfusion.

In addition to *S. setosa* gut contents, samples of the ambient surficial sediment were taken from Eastern Passage. A modified 1 cc syringe was used to core the top 3 mm of sediment. Samples were placed in plastic scintillation vials and preserved with 1%

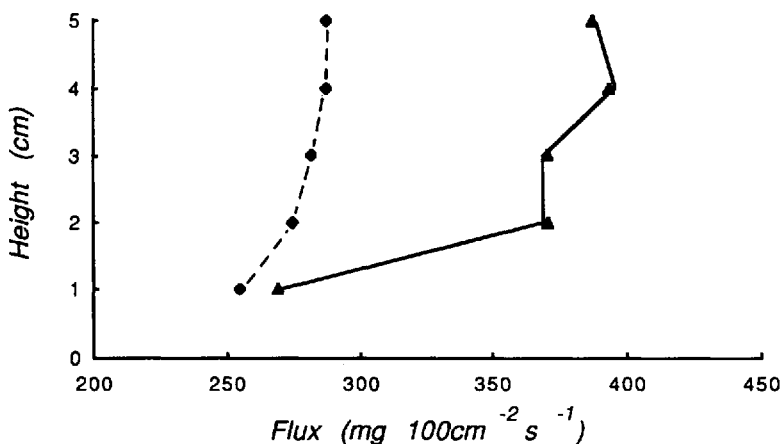


Figure 4. Model (dashed line) and experimental (solid line) flux profiles for Eastern Passage sediment ($\bar{w}_s = 0.14 \text{ cm s}^{-1}$) in a flow with $u_* = 0.24 \text{ cm s}^{-1}$ and $z_o = 0.01 \text{ cm}$.

formaldehyde at 4°C. Prior to filtration the samples were briefly shaken, allowed 10 seconds to settle and decanted. Due to the amount of material present, only 15 $\frac{1}{4}$ -fields were counted from each sample. Other details of analysis were the same as for the *S. setosa* gut samples.

An *in situ* record of suspended particle concentration and *S. setosa*'s feeding response was obtained during a single tidal cycle, using a Benthos Instruments plankton silhouette camera. The instrument consists of a 35 mm camera and data chamber in line with a collimated strobe, separated by a 4 cm-wide aperture. The aperture is flooded with ambient water and particles. The camera is usually suspended in the water column and triggered on a preprogrammed schedule. For this work, the camera was equipped with a remote triggering control allowing a variety of sampling schedules as well as single shot control. The camera was placed in the sediment, with several *S. setosa* tubes centered in the aperture and aligned with the predominant longshore current flow to minimize interference. The camera was left in place from slightly before tidal coverage of the *S. setosa* patch, until all wave action had ceased after tidal ebb. The shooting sequence was set at 3 shots, 8 seconds apart, cycling every two minutes for an eight minute period. This pattern was repeated every 16 minutes. In addition, manually triggered series of three shots were taken at approximately 15-minute intervals, resulting in an 8 $\frac{1}{2}$ -hour tidal record of over 500 shots.

4. Results

a. Flume flux experiments. Figure 4 compares the model and flume results with Eastern Passage sediment exposed to a flow at $u_* = 0.24 \text{ cm s}^{-1}$. The model and flume results agree in general trend within the boundary layer. Exact numerical agreement is not expected for two reasons: (1) for analytical tractability, only the ideal, non

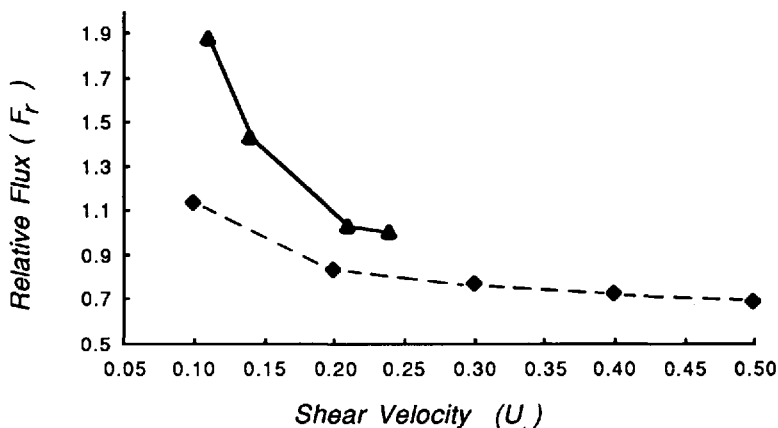


Figure 5. Model (dashed line) and experimental (solid line) determinations of relative flux, covering a u_* range of 0.11 to 0.24 cm s^{-1} . Relative flux is taken as the flux at 1 cm divided by the flux at 7 cm.

depth-limited forms of the velocity and concentration equations were used, and (2) the physical assumptions behind the Rouse equation (viscous forces unimportant; no inter-particle collisions) fail to hold very close to the bed. How close “very close” may be, and how it relates to the reference height, a , is not specified by sedimentologists. Presumably, it is the region where suspended merges with bedload transport, within the first centimeter above the bed, but is often operationally defined as the height closest to the bed from which samples were taken (c.f. Sternberg *et al.*, 1986). In the development of his suspended sediment equation Rouse (1937) made the stated assumption that the boundary layer extends for the full depth of the water column. As the flux model is based in part on this equation, it cannot be expected to yield reasonable results beyond the boundary layer. Nevertheless, the qualitative agreement between theory and observation supports our basic understanding of the boundary-layer physics controlling particle availability to benthic suspension-feeders. Through the range of experimental u_* values (0.11 to 0.24 cm s^{-1}) with Eastern Passage sediment, the flux profile went progressively from “bottom heavy” to “top heavy,” supporting the contention that sediment of a given fall velocity (\bar{w}_s) exhibits flux maxima higher off the bed as flow rate increases. A measure of the “relative flux” was taken as the flux at 1 cm relative to that outside the boundary layer. The results of four experiments ranging from $u_* = 0.11$ to 0.24 cm s^{-1} are compared with modelling results in Figure 5. Again the general shapes of the curves agree, showing that, for sediment of a given effective settling velocity, increasing the flow rate moves the flux maximum further from the bed.

Eq. (6) not only predicts the height of maximal seston flux; it also suggests that particles with different fall velocities (and, presumably, of differing organic content) will have flux maxima at different heights above the bed. Such hydrodynamic sorting

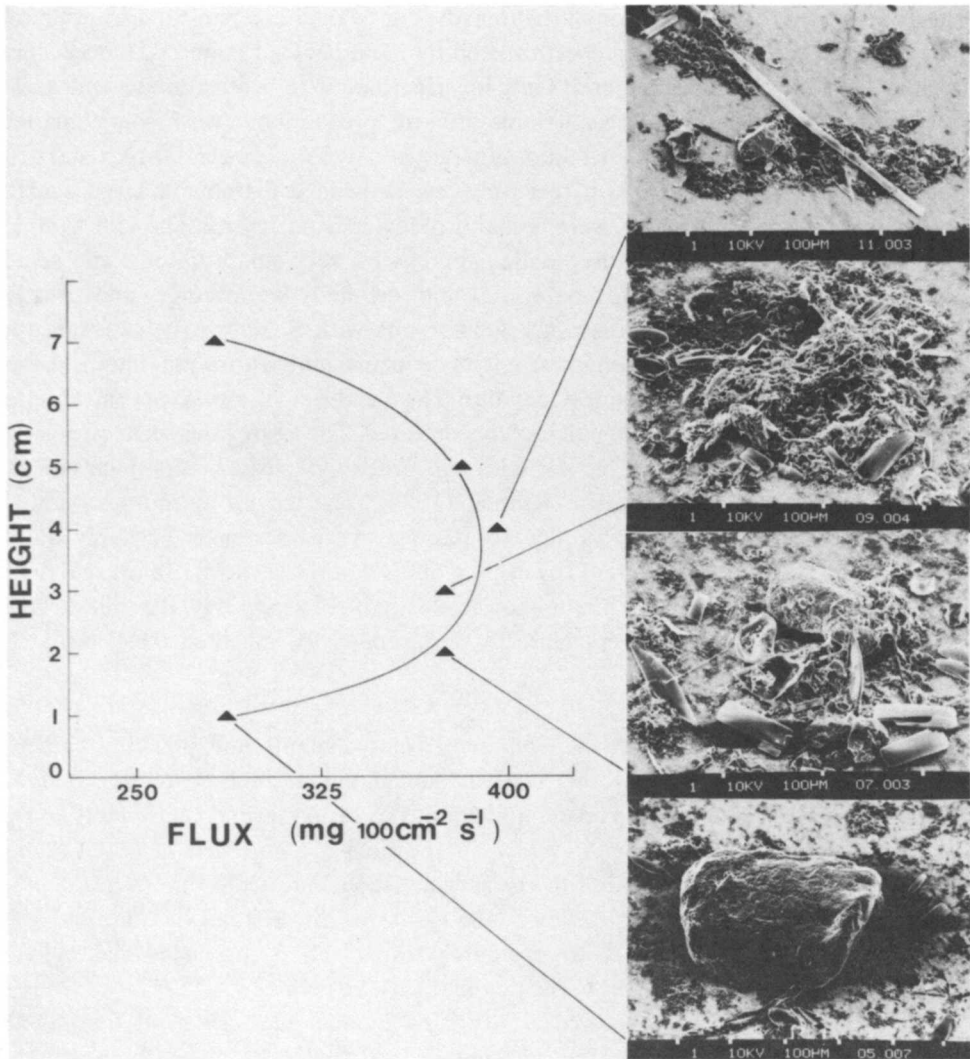


Figure 6. Scanning electron micrographs of seston samples taken in a flow with $u_* = 0.22$ cm s⁻¹. Micrographs are related to their positions in an experimental flux profile taken in a flow with similar shear velocity ($u_* = 0.24$).

may produce compound flux profiles, which are simultaneously “top heavy” for the lighter fraction (organic detritus and OMA’s) and “bottom heavy” for heavier (inorganic) sediment. Figure 6 shows the SEM photographs of the types of material predominating at different heights in the flow at $u_* = 0.22$ cm s⁻¹. It is superimposed on the flux profile for a similar flow ($u_* = 0.24$ cm s⁻¹). The 1 cm sample contained large quartz grains, some clean, some coated, as well as larger diatoms. Very few

aggregates were observed, although that may be due to their mechanical disruption by flow shear or abrasion by contact with the bottom and bedload material. Indeed, this sample probably combines material truly in suspension with bedload material traveling in saltation. At 2 cm large diatoms are still predominant, with some smaller mineral grains, sometimes bound into aggregates. At 3 cm larger OMA's start to appear. These seemed to contain relatively few embedded diatoms or large quartz grains and, in spite of their size, were probably of low specific density. The 4 cm sample is less concentrated and contains smaller aggregates, very small diatoms and some plant debris. Although the latter material would seemingly be refractory and of little nutritional value to benthic organisms, field results with *S. setosa* (below) indicate otherwise. Thus the flux maximum seems to be coincident with a maximum in the organic content or quality of the seston in flux. The 5 and 7 cm samples (not shown) are similar to the 4 cm sample, although less concentrated. The aggregates seem especially free of large embedded inorganic particles and probably consist of silt to clay-sized grains held in an organic matrix. Kranck (1984) reported an optimum organic/inorganic ratio of 2:1 to 3:1 for floc formation, so this seston is probably quite organic-rich. Bulk organic content (by ashing, 500°C) of the surficial (3mm) sediment at Eastern Passage was 30%. Although it was not analyzed separately, the thin surface layer (300 μm) is probably very close to the proportions indicated for flocculated aggregates.

b. Field experiments. Analysis of *Spio setosa* gut contents and plankton camera photographs from the field site at Eastern Passage support the contention that *S. setosa* is primarily a suspension feeder and obtains its ration several centimeters above the bed. Particles ingested by *S. setosa* in the field are enriched in OMA's and macro-algal fragments, compared to the surficial sediment, while time-series photographs show that these particles are abundant in the seston. In addition, the photographic record shows that larger aggregates as well as suspended macrophyte detritus show a variation related to the dominant seiche period.

Preliminary gut analyses showed a surprising number of large plant fragments. Locally abundant tufts of *Enteromorpha* supplied suspended strands to the nearby *S. setosa* patches and they showed up in the guts of the worms. Initial analysis indicated that they were absorbed very quickly in the *S. setosa* gut, usually within 2–3 hours. In contrast, small twigs or *Spartina* root fragments were often found projecting from the hindgut when the animal was broken during sampling. Occasionally tri-radiate calcareous spicules (Porifera:Calcarea) would be found, probably after a storm had dislodged sponges and other epifauna from the deeper channels.

c. Ingested Particles. Strong evidence that *Spio setosa* is primarily a suspension-feeder is given by the feeding ratios in Table 1, which compares gut material from *S. setosa* with material in the top 3 mm of Eastern Passage sediment. Significant

differences ($p < .001$, Wilcoxon Rank Sum test) between the gut and ambient samples occur in four categories of organic/inorganic ratios. In these instances the *S. setosa*'s foregut samples were always enriched in organic particles when compared to the ambient sediments. The abundance of diatoms in the sediment samples and their virtual absence from the *S. setosa* gut samples show that *S. setosa* must feed above the sediment-water interface. Significant post-capture particle selection by *S. setosa* may be ruled out because they are decidedly nonselective when observed feeding under the microscope. Feeding experiments, using *S. setosa* exposed to controlled flux conditions in the flume (Muschenheim, 1987), showed that they readily ingest diatoms when these are present in suspension. In light of *Spio*'s observed nonselectivity, the absence of diatoms in their guts in the field must be due to *Spio*'s feeding higher off the bottom than where the maximum flux of diatoms occurs. Grant *et al.* (1986) showed significant sediment binding due to diatom films. This may keep the diatoms themselves out of suspension. Even if the diatoms are bound to the sediment, it is likely that they could be dislodged by a deposit-feeding *S. setosa*'s strong palps.

These data, combined with Dauer *et al.*'s (1981) finding that *S. setosa* built tubes tall enough to prevent its palps from reaching the sediment surface, indicate that the Eastern Passage population was feeding mainly from suspension or on material adhering to the tops and sides of the tubes. In either case the observations show that *S. setosa* takes its ration primarily from suspension and not by deposit feeding. This conclusion is supported by the greater occurrence of macroalgal and terrestrial plant fragments in *S. setosa*'s guts than in the sediments. As was expected from preliminary observations, plant fragments were more common in the *S. setosa* gut than in ambient sediment samples. Unfortunately, the suspended sediment supply in the flume experiments was taken from those surficial sediments, so there was little macrophyte detritus in the experimental seston. The role of this component of the seston in *S. setosa*'s feeding ecology was further elucidated by the plankton camera data.

d. Plankton camera. The plankton silhouette camera, illustrated in Eisma *et al.* (1983), has been used previously to photograph large, nonliving particles in suspension (Eisma *et al.*, 1983; Kranck, 1984). Typical silhouette photos from the Eastern Passage series are presented in Figure 7. Due to the size of the camera it was expected that there may be distortion of flow streamlines through the aperture. Whether there was acceleration or deceleration of the flow is not known. Occasional resuspension was observed and there was sedimentation within the aperture during the time series. The sedimentation was due mostly to bedload transport at the beginning of the flood cycle and was eroded away late in the ebb cycle. Even if the *in situ* concentration profiles are distorted, the long-period effects discussed below are unaffected, as was *S. setosa*'s feeding response to the material in suspension.

Analysis of the 8-hr tidal series of plankton camera photographs revealed evidence of *S. setosa* engaged in suspension feeding *in situ* (Fig. 7). Secondly, there is a periodic

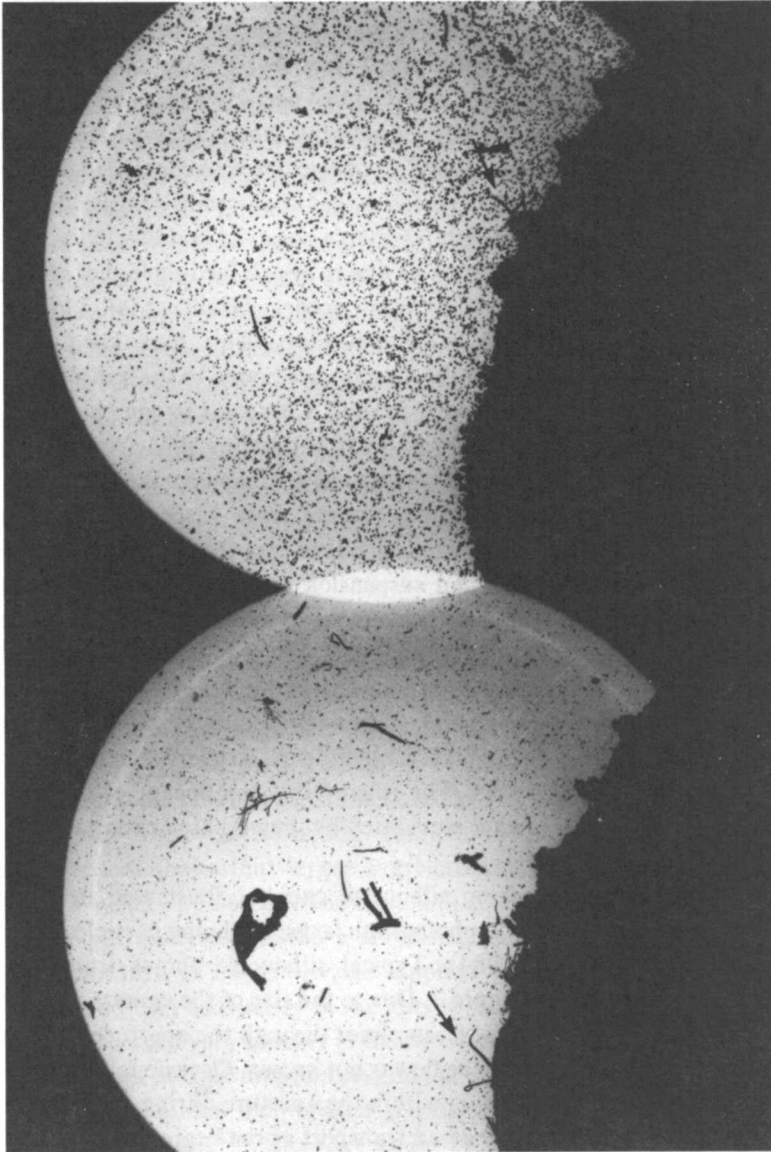


Figure 7. Plankton silhouette camera photographs, taken 15 min. apart during tidal series. At left *S. setosa* is visible in suspension-feeding mode, while seston concentration is low. At right, suspension feeding in high seston concentrations.

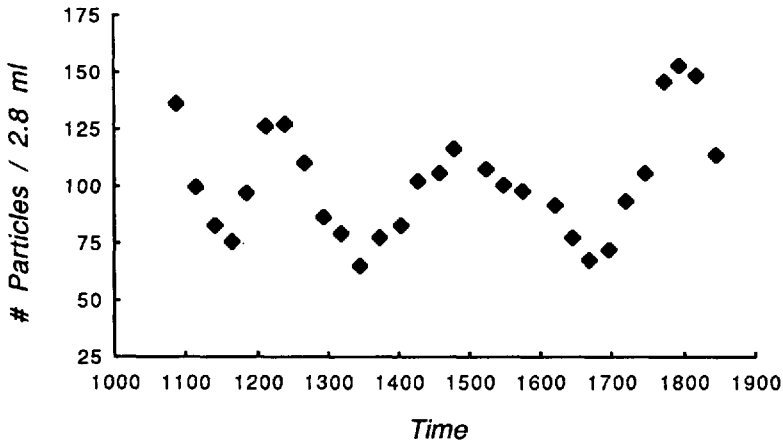


Figure 8. Tidal cycle time series of seston concentration, measured from plankton camera photographs. All particles greater than $90\ \mu\text{m}$ are represented. Three-point running means were used to smooth the data.

influx of large particles of macrophyte detritus in suspension (Fig. 7, left), material that is not found in surficial sediment samples. *S. setosa* can be seen actively feeding on this and other suspended materials, as is borne out by the gut analyses. Visual counts of suspended particles at three heights (0–1, 2–3, and 4–5 cm) in the photographs showed that particles larger than $90\ \mu\text{m}$ are almost uniformly distributed above the bottom if averaged over the tidal cycle, although the instantaneous profile is variable. Assuming a local u_* of $0.25\text{--}0.50\ \text{cm s}^{-1}$ (estimated from timed dye marker measurement of the free-stream velocity) in the longshore direction, the flux of this uniformly distributed material would “track” the velocity profile and exhibit a maximum flux several centimeters above the bottom. The influx of macrophyte detritus has a period of around two and a half hours.

The results of the depth-integrated particle concentrations are presented in Figure 8 for all particles larger than $90\ \mu\text{m}$, and in Figure 9 for particles larger than $300\ \mu\text{m}$. They are presented as three-point running means to smooth the data. The distinct periodicity in both the greater than $300\ \mu\text{m}$ fraction and the greater than $90\ \mu\text{m}$ fraction comes close to matching the 2.2-hour dominant seiche period characteristic of outer Halifax Harbour (McGonigal *et al.*, 1974). The analysis of the photographic record has been limited to 15-minute intervals and is too coarse to resolve any short-period variation, which may well occur, but it is appropriate to the longer-period oscillation shown.

5. Discussion

Two fundamental consequences of the analytical and numerical models are that (1) the flux profile is variable and may increase or decrease with distance from the bed

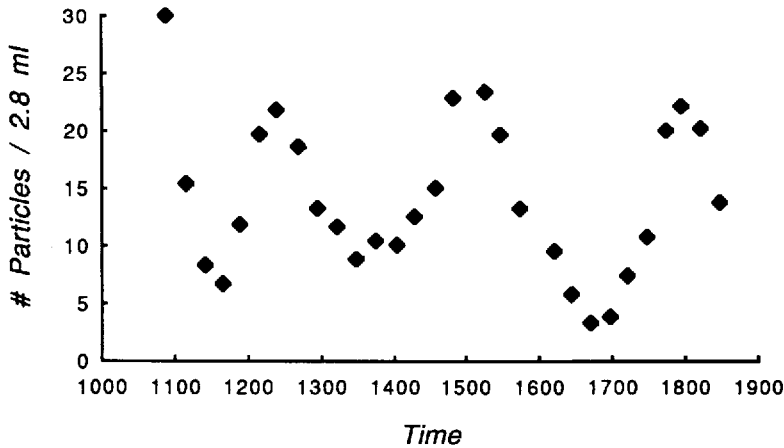


Figure 9. Tidal time series of seston concentration, measured from plankton camera photographs. All particles greater than $300\ \mu\text{m}$ are represented. Three-point running means were used to smooth the data.

(Figs. 1 and 2), and (2) in a given flow, hydrodynamic sorting results in the maximum flux of denser (inorganic) particles occurring closer to the bed than that of lighter (organic and OMA) material (Eq. 6). The flume experiments have shown that the flux profile changes from “bottom heavy” to “top heavy” with increasing values of u_* (Fig. 5), and that there is a qualitative change in particle type with height above the bed.

The smooth-bed conditions of the flume experiments do not reflect the field site's conditions of distributed roughness, nor were they intended to. Sand ripples and even *Spio setosa*'s tubes create local conditions of elevated bed shear stress and scour (Eckman *et al.*, 1981; Carey, 1983) and affect the total drag that the bottom exerts on the flow. The flume experiments tested whether or not the predictions of the analytical model could be seen under simplified conditions, and were potentially important to benthic seston feeders.

The use of resuspended surficial sediment in the flume experiments introduced two artifacts. The first is the absence of macrophyte fragments in the experimental flow. Although this component of the seston is periodically abundant in the tidal time series photographs, it is uncommon in the surficial sediment at Eastern Passage. Secondly, diatoms were abundant in the flume seston but, except for major resuspension events (wind-wave induced), are probably too strongly bound to the sediment to be transported (Grant *et al.*, 1986). Once in suspension, most benthic diatoms behave hydrodynamically like small quartz grains (Muschenheim, 1987). The presence of OMA's in suspension most likely reflects flocculation of small inorganic and colloidal organic particles resuspended from the sediment.

The application of dynamic similarity in comparing the lab and field situations demands that one recognize the boundary layer developed in the flume as a scaled model of the naturally-occurring one in the field. In natural boundary layers the

logarithmic portion is generally limited to the lower 15% (Grant and Madsen, 1986). The laboratory boundary layer was fully logarithmic to 5 cm in 10 cm of water. The *S. setosa* population at Eastern Passage probably never receives more than 1 to 1½ m of water coverage and is exposed to a longshore current of between 2 and 10 cm s⁻¹ (estimated by dye stream) when fully covered. Allowing for a 1 m thick depth-limited boundary layer means that the bulk flux maxima would occur 2 to 3 times higher off the bed in the field than in the laboratory. Even if *S. setosa* is incapable of reaching fully to the maximal flux height, an increase in feeding height should result in exposure to increased flux and organic particle content.

The $u_* = 0.22 \text{ cm s}^{-1}$ experiment incorporating SEM particle analysis (Fig. 6) indicated that the effects of hydrodynamic sorting proposed by Eq. (6) do indeed occur. Although not quantifiable on the SEM stubs, visual inspection of the sample series (1–5, 7 cm) showed a progression from large, inorganic particles to smaller and more organic material with increasing distance from the bed. In a separate series of feeding experiments (Muschenheim, 1987), the gut contents of *S. setosa* feeding at different heights above the bed reflected a similar gradient in particle quality. Aggregates sampled from the flume appeared much the same (after SEM preparation) as do the large flocculated aggregates reported by Eisma *et al.* (1983) from the Ems estuary.

The plankton camera data suggest that the supply of high-quality organic seston is periodic and, in this case, related to the dominant seiche period of Halifax Harbour. The relationship between seiches and seston variability has been discussed by Kranck (1980), who noticed a similar phenomenon in Petpeswick Inlet, Nova Scotia. Her investigation of short-period (45 minute) seston variations concluded that they were seiche-related, through associated changes in turbulence levels and continual floc formation and breakup due to these changes. She also cited evidence of seston response to seiche periods of 15–20 minutes in St. Margaret's Bay, Nova Scotia.

An important question arises concerning the physical strength of these macro-aggregates. Large flocs are fragile and notoriously hard to sample without breaking (Kranck and Milligan, 1980; Eisma *et al.*, 1983; Honjo *et al.*, 1984). They may also break up while settling out of the water column into the shear field of the benthic boundary layer. Kranck (1984) has shown that these large flocs disaggregate into smaller, more stable units. Although larger flocs tend to settle rapidly (Chase, 1979; Kranck, 1984), their disaggregation may make them more easily resuspended (Kranck and Milligan, 1985) so that, except at periods of slack water, this material never really reaches the bed.

My observations in the flume indicate that large OMA's are a preferred food item for *S. setosa*. A unique feeding behavior has been observed in *S. setosa* which intercept a large floc. If such a particle is trapped while the palps are in coiled position, the palp which trapped the particle is lowered to the bed and the other palp ceases feeding to lower and cross over the first one. This allows both food grooves to contact the floc and rapidly transport it to the mouth. At lower flow speeds, both palps come together in the water column to guide the particle to the mouth. Such behavior suggests the

importance of suspended OMA's as a food source for *S. setosa*. This agrees with Bowen's (1984) contention that morphous and amorphous OMA's are assimilated with efficiencies approaching 85% and may be an important food source for many seston feeders. With an adult palp length of 2–3 cm and tubes up to 4 cm high, *S. setosa* seems well adapted to maximize its chances of intercepting OMA's while avoiding bedload and suspended particles with low organic/inorganic ratios.

Of special note is the active feeding response of *S. setosa* in high concentrations of macro-algal detritus; they often intercept large suspended fragments. The direct nutritional value of this material is probably low (Tenore, 1983), but it may be the bacterial epiflora found on suspended detritus that is most important. During the summer months there are also numerous fragments of labile chlorophyte species in suspension, which also appear in the worms' guts.

Most importantly, these organic detrital particles of low specific density (but high concentration) are in almost uniform suspension. If their uniform concentration profile is combined with a fully logarithmic velocity profile (typical of well-mixed estuaries, Anwar, 1983), the resulting flux profile will "track" the velocity profile and increase continually with height above the bed. Thus the higher a suspension feeder such as *S. setosa* can reach into the water column the greater is the flux past its appendages. The benefit is twofold, for in reaching into the region of greater organic flux *S. setosa* places itself above the region of maximum flux of inorganic components.

It appears that the conspicuous sand tubes of *Spio setosa* are adaptive in at least two ways. They protect the worm in a dynamic sedimentary environment, where mechanical abrasion from bedload transport would make it difficult to feed during periods of strong current flow and maximum material flux. The tubes also elevate *S. setosa* out of the region in which inorganic components of the sediment predominate, both as bedload and suspended load, into a region where the flux of material more useful as food is increasing with height above the bed.

The *Spio setosa* population at Eastern Passage is conspicuous, but patchy, with densities of up to 750 individuals per square meter. Tubes often coalesce into small mounds in the densest patches. The animals have two generations per year, as reported by Simon (1967) for populations in New Hampshire. Tube destruction is common and greatest during storms, primarily due to beach scouring by storm-tossed macroalgae. If broken at the surface, the tube is generally rebuilt to its original height in 24–48 hours. *S. setosa* starts feeding immediately after the tube is covered by the incoming tide, often holding its palps coiled in the wave swash. The same behavior is observed on the falling tide.

S. setosa were seen suspension feeding throughout the 8½ hours of tidal coverage (Fig. 6). No obvious periodicity related to long-period seston concentration was observed; they seemed to feed more or less continuously. This observation of spionids suspension feeding throughout a tidal cycle illustrates the importance of this mode of feeding to the group. Their ability to suspension feed may make it possible for them to occur in the densities observed at Eastern Passage. A 10 cm worm, with about 8 cm of

gut following the mouth, pharynx and esophagus and a gut internal diameter of 0.3 mm, has a gut volume of 2.26 ml. Laboratory feeding experiments with organic-coated glass beads (300 μm median grain size) indicate that *S. setosa* can fill its gut in 45 to 75 minutes. If it feeds continuously, it would replace its gut volume a minimum of 6.8 times in the 8½ hours of tidal coverage. If we assume that by deposit feeding *S. setosa* would have access to the top 3 mm of the sediment column it would require a radial palp length of just over 4 cm to cover enough sediment surface (assuming no replenishment) to meet its needs. In dense assemblages, this amount of surface area is not available to individual *S. setosa* and their ration must come directly from suspension. An example of food limitation in deposit-feeding spionids was given by Miller and Jumars (1984), who reported that spionids deposit feeding in dense assemblages decrease their feeding rates as fecal material accumulates.

Quite apart from the areal requirements, the quality of material ingested by deposit versus suspension feeding will be drastically different. Gut contents of *S. setosa* forced to suspension feed in flow in the lab appear different from those that are allowed to deposit feed in quiescent conditions (Muschenheim, 1987). The gut contents of suspension feeders have a much more "fluffy" texture and contain fewer and smaller mineral grains, probably representing more labile material than the deposit feeders are able to take in. The energetic costs of constantly scanning the sediment surface versus holding the palps erect or coiled in a flow are not known but are worth investigating. Any rigorous optimization argument (c.f. Hughes, 1980) would have to account for this metabolic cost.

6. Summary

The incidence of suspension feeding among soft-bottom marine benthos appears to be of greater importance than previously appreciated. This realization has prompted a closer look at the fluid and sedimentary phenomena that affect the distribution and availability of organic seston to suspension-feeding benthos. Analytical and numerical models of the near-bed flux profile, predict that there are (i) sharp vertical gradients in the horizontal flux of material, and (ii) hydrodynamic sorting of particles of differing food value. The ecological implications of these findings are that organisms which can obtain their ration from several centimeters above the bed may benefit in terms of increased population and greater overall production.

Field studies have shown the importance of low-density organic seston in the diet of one suspension feeder, *Spio setosa*, and that the periodic availability of such organic seston may be controlled by tidal factors, such as seiches. A greater appreciation of the small-scale hydrodynamic forces acting in the near-bed region will help our understanding of the transport of organic matter in all benthic habitats.

Acknowledgments. This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada (E. L. Mills, principal investigator). The author was supported by a Dalhousie Graduate Fellowship. D. A. Huntley gave advice on the analytical model and other aspects of particle flux. K. Kranck and T. Milligan provided the Benthos

Instruments Plankton Camera, as well as facilities for OBS calibration. U. V. Bathmann took the SEM photographs. The author was assisted in the field by U. V. Bathmann, J. Grant, C. Hopper and M. Snyder. The manuscript was substantially improved by the constructive criticism of J. Grant, B. T. Hargrave, D. A. Huntley, K. Kranck, M. Lewis and E. L. Mills. Detailed comments from D. A. Carey and P. A. Jumars contributed to a more coherent and balanced presentation.

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