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Fluid flow and suspended particulates as determinants of polychaete feeding behavior

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ABSTRACT

We examined the interactive effects of fluid flow, bed characteristics and suspended load on the feeding behavior of four species of marine polychaetes. Two species of obligate deposit feeders (*Marenzelleria viridis* and *Ampharete parvidentata*) and two species of palp-coiling facultative suspension feeders (*Spiochaetopterus oculatus* and *Spio setosa*) were exposed to flow and sediment-bed treatments that served to decouple fluid flow and particle flux. We employed low (no particle transport), medium (transport of flocs only) and high (transport of sand) flow speeds in factorial treatments of natural sediment, winnowed bed (flocs removed), armored bed (no sand transport at high flows), and armored bed plus fines (flocs added). For each species, worms were exposed to an increasing (low, medium and high) and then decreasing (high, medium and low) flow leg for each bed treatment. We recorded visual observations of animal behavior of the four polychaete species.

We found little systematic response to flow and bed differences in the two obligate deposit feeders. When fine material was present, one of the two species exhibited higher variability in time spent deposit feeding, possibly responding to small-scale depositional pockets enriched with fine particles and organic matter. For both facultative suspension feeders, there was an increase in time spent suspension feeding with increasing flow and suspended particle concentrations. Percent suspension feeding was also greater on the decreasing flow legs in treatments with fine material available for suspension. Exploratory analyses of the data reveal a direct relationship between time spent suspension feeding and the flux of suspended high quality organic matter. For both species, compositional parameters of particulate nitrogen and enzymatically available amino acid concentrations were the best correlates of suspension feeding behavior.

1. Introduction

Studies in both unidirectional flow (e.g., Nowell *et al.,* 1989 and Levinton, 1991) and oscillatory flow (e.g., Miller *et al.,* 1992) show three major behavioral patterns among surface-feeding polychaetes and deposit-feeding bivalves. As flow speed increases (1) organisms with many thin feeding appendages cannot feed at the sediment surface, (2) organisms with strong feeding appendages continue to feed at the sediment surface, and (3) organisms with long, thin feeding appendages coil

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them and feed in the near-bottom flux (Taghon *et al.,* 1980). To date, more than twenty species have been studied under flow, including all the macrofaunal members of one sand flat community (Cape Henlopen, DE, as reported in Miller *et al.,* 1992). The conclusions enumerated above should be broadly applicable and indicate the range of feeding responses to be expected. Miller *et al.* (1992) thus assert that general predictions of behavioral options can be based on morphology alone. Even so, such empirical studies cannot provide a cause and effect understanding of how fluid flow and particle flux influence feeding behavior.

It has been long recognized that under flow, suspended particles induce suspension feeding behavior in many marine polychaetes (Taghon *et al.,* 1980; Dauer *et al.,* 1991), primarily as a response to particulate flux (the rate at which suspended particles are transported through the feeding volume) rather than flow speed alone. However, the independent roles of fluid flow and suspended particulates are largely unknown since particle transport and fluid flow are as coupled in nature as they are in most laboratory experiments. In particular, the influence of particle concentration and particle nutritional value are unresolved in previous experiments on passive suspension feeders. Particle characteristics which are cues for deposit feeding include particle size, texture, specific gravity and food concentration (e.g., Cammen, 1980; Jumars *et al.,* 1982; Taghon, 1982; Self and Jumars, 1988; Taghon and Greene, 1990; Karrh and Miller, 1994). Since suspension feeders also consume particulate organic matter, it is likely that one or more of these particle parameters will influence suspension-feeding behavior and rate.

In a laboratory study, Miller *et al.* (1992) found that at equal flow velocities, the feeding response of two polychaete species on the increasing flow leg was different from the response on the decreasing flow leg. Thus, there was some hysteresis in the feeding response, with more suspension feeding on the decreasing leg and the largest differences in feeding behavior occurring at low flows. These differences in behavior are not explained by bulk flow and sediment flux rates, even among comparable flow-flux experimental treatments (Miller *et al.,* 1992). This variability may be attributable to flow and flux parameters that are poorly controlled or unmeasured in previous studies. These results suggest that flow history is an important additional factor to be considered. Given the normal interdependence of particle and flow parameters, we intended to manipulate flow, sediment flux and particle characteristics in the experiments described below.

We have devised competing hypotheses concerning feeding behavior in benthic marine polychaetes which are listed in Table 1. The hypotheses are based on the work cited above, and certain hypotheses are, in general, favored by published results. The results of Miller *et al.* (1992) suggest that time spent deposit feeding is adversely affected by fluid flow and bedload transport, supporting D1 and D2. The hysteresis in deposit feeding found in Miller *et al.* (1992) suggest that deposit feeding is enhanced when particles are deposited, supporting D3. The results of Miller *et al.*

Table 1. Hypotheses of feeding behavior under flow based on previous work. All of these hypotheses refer to the time spent engaged in a particular feeding behavior and not necessarily the feeding rate. The results column shows our interpretation of the validity of each hypothesis based on the results presented in this paper. EDA stands for exploratory data analysis.

	Hypothesis	Results
(D1)	Surface deposit feeding is independent of flow speed	Unresolved for *M. viridis*
(D2)	Surface deposit feeding is only possible in the absence of bedload transport	Reject
(D3)	Surface deposit feeding is a response to the deposition of high quality particles	Unresolved
(S1)	Suspension feeding will increase with fluid flow alone	Unresolved
(S2)	Suspension feeding will increase with particle flux	Accept, followed by EDA
(S3)	Suspension feeding will increase with suspended particle concentration	Accept, followed by EDA
(S4)	Suspension feeding will increase with particle food concentration	Accept, most consistent with EDA
(M1)	Feeding mode is determined by flow speed alone	Reject
(M2)	Feeding mode is determine by the transport of particles of the highest food value	Reject
(M3)	Deposit feeding is compensatory to suspension feeding	Accept

(1984), Luckenbach *et al.* (1988) and Bock and Miller (1995) also show the importance of deposition to deposit feeding. A large body of research on feeding behavior under flow has implicated the roles of fluid flow, particle flux, particle concentration and particle food value on suspension feeding and feeding mode choice which support hypotheses S1–S4 and M1–M2 (e.g., Taghon *et al.,* 1980; Dauer *et al.,* 1981; Muschenheim, 1987; Nowell *et al.,* 1989; Levinton, 1991; Miller *et al.,* 1992 and Bock and Miller, 1994). Turner and Miller (1991b) used the independent adjustment of wave period and orbital amplitude and observed *Spiochaetopterus oculatus* feeding. The authors concluded that bed stress was the best predictor of deposit feeding frequency, which ceased before the onset of sediment movement, in support of hypothesis D2. However, it is well established that sediment food quality (as variously defined) plays a predictable role in deposit-feeding rate (Cammen 1989; Taghon and Green 1990; Karrh and Miller 1994) and selectivity (Taghon 1982). Flow-alone hypotheses S1 and M1 are doubtful in light of Miller *et al.* (1992) hysteresis results which implicate the importance of suspended particulates. The results column in Table 1 shows the interpretation of these hypotheses based on the results of the present study.

These hypotheses also bear on the premises of optimal foraging and digestion theories (Penry and Jumars 1987; Dade *et al.,* 1990) as applied at the functional group level (*sensu* Fauchald and Jumars, 1979). We presume that worms act to maximize their rate of encounter with nutritious, easily digested particles, subject to anatomical and hydrodynamic constraints. Reflecting the current state of the art, we use several operational measures of food value. In the interest of generality, we have chosen members of the functional groups of interest: two oblique deposit feeders and two facultative suspension feeders.

In this paper we present the results of a series of experiments designed to test these hypotheses. We subjected four species of polychaetes individually to a series of bed and flow treatments in a laboratory oscillatory flow facility. By using beds differing in thresholds for suspended load transport and bedload transport, we were able to decouple, in part, fluid flow and particle transport. While these hypotheses are neither independent nor mutually exclusive, crossed manipulations of bed properties and flow conditions will allow some to be provisionally accepted and some to be rejected (Table 1, right hand column).

2. Target species

Four marine polychaete species were used in this study. Three species are members of the intertidal sandflat community at Breakwater Harbor Delaware, USA (38°46′N and 75°06′W). *Spiochaetopterus oculatus* is a chaetopterid polychaete, which builds a thin-walled transparent tube which extends from 2 to 20 mm above the sediment surface. It feeds in the water column as a facultative passive-suspension feeder or on the sediment surface using its two tentacles. *Spio setosa* is a spionid polychaete that builds a sediment tube which extends up to 5 mm above the sediment surface, and it can feed in the water column or on the sediment surface using its two tentacles (Muschenheim, 1987). *Marenzelleria viridis* (formally *Marenzelleria jonesi* in Miller *et al.,* 1992) is a surface deposit-feeding spionid polychaete which builds a mucus-lined burrow which does not extend above the sediment surface. *Ampharete parvidentata,* an ampharetid, is found at the LEO-15 site off Tuckerton, New Jersey, USA (39°29′N and 74°13′W). It builds a sediment tube which extends from 10 to 40 mm above the sediment surface. The tube recurves toward the sediment, forming an arc which ends about 5 mm above the sediment surface, where it feeds using a crown of 20 to 30 thin tentacles about 10 mm in length. These species were selected for study based on their feeding guilds, as determined by Miller *et al.* (1992). *Marenzelleria viridis* and *Ampharete parvidentata* are both tentaculate, obligate deposit feeders (Table 1 in Miller *et al.,* 1992 and Bock, unpublished observations). Dauer *et al.* (1981) examined two populations of *Marenzelleria viridis* (formally *Scolecolepides viridis*) and found that one population exclusively deposit feeds and one can be induced to suspension feed. Our population keeps its feeding appendages in contact with the sediment surface under flow, but it does lash at the sediment and arch its appendages (e.g., Dauer *et al.,* 1981), and so we classify them as obligate deposit feeders (Bock, 1992 and observations during these experiments). *Spiochaetopterus oculatus* and *Spio setosa* are palp-coiling suspension feeders and facultative deposit feeders (Muschenheim, 1987; Turner and Miller, 1991b; Dauer *et al.,* 1981; Table

Table 2. Water tunnel settings used to impose flow treatments. Fluid excursions and peak flow speeds were calculated as described in Miller *et al.* (1992). The second section shows the grain size data for the various bed treatments.

Flow treatment	Stroke, cm	Period, s	Fluid excursion, cm	Peak flow speed, cm s^{-1}
Low	7	21.6	17.2	5
Medium	12	18.5	29.4	10
High	12	9.2	29.4	20

Bed	Median grain size, μm	phi standard deviation	% silt-clay
Natural	221	0.61	0.84
Winnowed	222	0.60	0.08
Armored	360	0.38	0.00
Armored + Fines	363	0.37	0.02

1, Miller *et al.,* 1992). All polychaetes were housed individually in 50-ml centrifuge tubes containing 1-mm sieved macrofauna-free sediment from the sandflat in Breakwater Harbor. Organisms were maintained in a seawater table at 17°C until used in the water tunnel experiments.

3. Materials and methods

a. Water Tunnel experiments. The Lofquist Oscillatory Water Tunnel is a U-shaped device with pistons located in two sets of vertical cylinders which drive water through a horizontal working section. The working section (255 cm long × 21 cm wide × 30 cm deep) is composed of clear acrylic. Velocities in the working section can be controlled by adjusting the stroke and period of the pistons. For a more complete characterization of flow in the water tunnel see Turner and Miller (1991a,b) or Miller *et al.* (1992). A 20-cm deep sediment bed underlies the working section. The bottom 10 cm was pea gravel, and the top 10 cm was 1-mm sieved, macrofauna-free sediment from Breakwater Harbor.

The four target species were sequentially exposed to experimental conditions consisting of a series of flow treatments nested within a series of bed treatments. The four bed treatments included: (1) natural, 1 mm-sieved surficial sediment from the sandflat at Breakwater Harbor, (2) winnowed sediment which is produced by repeatedly resuspending a natural bed and flushing the sediment-laden water, (3) armored bed, consisting of a 3-cm layer of sand from the beach at Cape Henlopen over the winnowed bed, and (4) armored plus fines, in which fine material (derived from a suspension of Breakwater Harbor sediment) is added to an armored bed. The grain size parameters for these bed treatements are given in Table 2. For each bed

Table 3. Observations of sediment transport under the crossed bed and flow treatments used in the water tunnel experiments.

Bed treatment	Low flow	Medium flow	High flow
Natural	none	suspended load only	both
Winnowed	none	none	bedload only
Armored	none	none	none
Armored + Fines	none	suspended load only	suspended load only

treatment, six flow treatments of 75 min each were applied in the following order: low, medium, high, followed by high, medium and low, resulting in an increasing and then decreasing flow leg. Table 2 presents the drive period and piston strokes used to impose the experimental flow conditions. We made visual observation of the bed and sediment transport (if any) to confirm our intended treatments. In low flow, we observed no movement of bedload or flocs in natural sediment. In medium flow, we observed movement of flocs in natural sediment. At high flow, bedload transport at ripple crests occurred in natural sediment. In the winnowed bed, there was no flocculent material suspended at any flow speed due to the absence of very fine-grained material. In the armored bed there was no bedload transport or suspended flocs at any flow speed used. In the armored plus fines there was no bedload transport, but flocs were suspended at medium and high flow speeds due to the addition of very fine-grained material. The relationship between the bed treatments, flow velocities and particle transport are summarized in Table 3. It is important to note that although our bed manipulations allowed use to control the availability of particles for transport, it did not allow us to control the food concentration in the sediment bed.

Complete bed and flow treatments were performed on each species using the following procedure. At least two days before each bed treatment, 20 individuals from the species of interest were placed in the water tunnel for acclimation. Individuals were transferred in their centrifuge tubes and placed flush with the sediment surface. The water temperature was held at 20°C (±2°) at all times. By the end of the acclimation period the tube height of the species which build tubes had stabilized to the heights mentioned previously for 'old' tubes (pers. obs.). On the day before a bed treatment, the water tunnel was set to the first flow treatment (low) and allowed to run overnight. For each subsequent flow treatment, the worms were given 45 minutes to acclimate before observations were begun. A two-minute scan sampling rule (Martin and Bateson, 1986) was used to collect behavioral observations over 30 minutes, resulting in 15 observations per flow treatment per worm. Every two minutes the behavior was observed and scored in one of these categories: suspension feeding, deposit feeding, defecating and not visible. Concurrently, water samples for suspended solids concentration and food value were collected through the sampling ports located one and five cm above the bed (see below). Between bed treatments, the water tunnel was drained and the sediment bed was sampled randomly for food concentration. Drained water was reserved in a holding tank and pumped back into the water tunnel prior to the next flow treatment.

All six flow treatments for any one species and bed combination were conducted in a single day, and we term this set of treatments a single "run" of flow levels. We required a week between runs for setup, takedown and sample processing. For all species, the order of bed treatments was that which minimized disturbance: Natural Bed, Winnowed Bed, Armored Bed and Armored Bed plus Fines. These experiments were performed during the summer of 1993: *Marenzelleria viridus,* from 18 May to 8 June; *Spiochaetopterus oculatus,* 29 June to 14 July, and *Spio setosa,* 27 July to 25 August. For these species, new individuals were used for each run. For the *Ampharete parvidentata* experiments, we had a limited number of worms because the LEO-15 collection site was accessible to us only once and by submersible. We used the same 20 individuals in all four *A. parvidentata* bed treatments, conducted in a two week period from 7–21 September.

b. Analytical methods. Several techniques were used to assess the food quality of the sediments and the suspended material from these experiments. Analyses included chlorophyll, enzymatically hydrolyzable amino acids (EHAA), particulate organic matter (POM), particulate organic carbon (POC) and particulate nitrogen (PN).

Suspended particulate samples were obtained through a sampling port with glass tubes at 1 cm and 5 cm above the bed of the water tunnel (diameter of tube opening, 1.7 mm). Samples for POC and PN were filtered through GF/F glass fiber filters (0.7 μm nominal pore size). All of the other water column samples were filtered through GF/C filters (1.2 μm nominal pore size). Two replicate samples were taken at each height for each parameter, with 100 ml being filtered for POC and PN, 300 ml for suspended solids and POM, 300 ml for chlorophyll, and 600 ml for enzymatically hydrolyzable amino acids. Three sediment samples were taken for each parameter at each flow and bed combination. The 95 × 20-cm subsection of the sediment bed occupied by the organisms was randomly sampled using a 1.5-cm diameter corer, with the top 5 mm being retained for analysis. All samples were placed immediately on ice and frozen and stored at −20°C within 6 hours.

Chlorophyll was measured as chlorophyll *a* using the spectrophotometric methods of Lorenzen (1967). Samples were extracted at −20°C for 18–24 hours in 90% acetone (by volume) with one drop of $MgCO_3$ suspension added to prevent the loss of the Mg ion from chlorophylls. Samples were centrifuged and analyzed for chlorophyll *a* and phaeopigments. Enzymatically hydrolyzable amino acids were measured using the one-point freeze-dried method of Mayer *et al.* (1995). This method measures enzymatically digestible proteins, oligopeptides and free amino acids. Particuate organic matter was measured as the mass loss on ignition at 450°C for 24 hr (Williams, 1985). Particulate organic carbon (POC) and particulate nitrogen (PN) were measured following vapor-phase acidification on a Carlo Erba 1108 Elemental Analyzer using the methods described in Cutter and Radford-Knoery (1991).

4. Data analysis

For all statistical tests, we used the conventional critical level of $p \leq 0.05$ to indicate significant differences. The feeding behavior counts obtained during scan sampling were analyzed using repeated-measures ANOVA for each species and bed treatment, with behavior as the repeated factor being tested among the flow and leg treatments (Kirby, 1993). In univariate repeated measures ANOVA, an assumption is made that population covariances are equal among treatment levels for within subject tests with two or more degrees of freedom in the numerator (i.e., the sphericity assumption). Because we cannot support this often violated assumption, we report conservative probabilities using the Greenhouse-Geisser (or G-G, see Kirby, 1993) adjustment to the p-values. Specifically, this conservative adjustment to the within-subject tests is applicable to the flow and flow × leg tests. Although the leg contrast is also within-subject in our design, there are two levels (hence, one degree of freedom), and thus the G-G correction to the p-values is not applicable. Posthoc comparisons of the means were performed using the C-matrix method (Kirby, 1993) to examine flow and leg effects. This method insures that tests are independent and truly distributed as an F statistic with the appropriate degrees of freedom (Kirby, 1993). Here, a Bonferroni adjustment was made to the p-values within each bed treatment by multiplying by the number of tests done, six in our case. Exploratory analyses using multiple regression and correlation were also done to further examine the relationship between flow, food quality of the seston and the sediment, and feeding behavior.

5. Results

Sediment and seston sampling show that experimental treatments varied in particle and food quality as predicted. As an example, Table 4 presents the food quality measurements of the surficial sediments from all experiments averaged for each day or run. For all food quality proxies, there is a fairly consistent ordering of values among the bed treatments: Natural bed > Winnowed > Armored + Fines ≫ Armored. There are differences among species' which probably reflect temporal variability of the source material from Breakwater Harbor and the beach at Cape Henlopen. Our statistical comparisons are made only within a species, so this source of variability is not a complicating factor. Additional detail is presented in Figure 1, showing selected food quality measurements for flow treatments within runs for the *M. viridis* experiments, the first set to be conducted. Note that there is no consistent variation related to flow speed, and the rank order of values among the

Table 4. Food quality measurements for bed samples from all experiments. Tabulated values represent averages for each run of flow treatments on the indicated bed.

Species	Bed Type	POM mg g^{-1}	Chl $\mu g\ g^{-1}$	EHAA mg g^{-1}	Carbon mg g^{-1}	Nitrogen mg g^{-1}
M. viridis	Natural	3.41	3.57	0.10	0.53	0.043
	Winnowed	2.67	4.64	0.08	0.49	0.052
	Armored	0.43	1.48	0.01	0.12	0.008
	Fines Added	1.54	3.35	0.02	0.27	0.023
A. parvidentata	Natural	4.41	15.74	0.62	1.25	0.176
	Winnowed	3.98	15.22	0.43	1.07	0.138
	Armored	0.66	0.88	0.04	0.04	0.001
	Fines Added	2.17	2.56	0.08	0.14	0.010
S. oculatus	Natural	3.41	11.36	0.40	1.07	0.115
	Winnowed	3.23	8.40	0.27	0.75	0.070
	Armored	0.84	1.03	0.04	0.09	0.003
	Fines Added	2.53	4.95	0.15	0.33	0.034
S. setosa	Natural	4.27	17.52	0.24	1.32	0.164
	Winnowed	3.84	8.01	0.14	0.94	0.110
	Armored	0.93	0.44	0.02	0.05	0.003
	Fines Added	1.86	2.76	0.04	0.19	0.012

bed treatments is identical whether looking at mean values or individual flow treatments. Examination of all the bed data shows that these results are representative of those with other species' runs and treatments (Table 4).

In contrast, seston values varied appreciably with flow and bed treatments. Figure 2 shows the seston and food concentration measurements for *S. oculatus* experiments, the first to be conducted with a mode-switching species. For the natural bed treatments (top row of plots), total seston, carbon and EHAA are generally higher in higher flows and closer to the bed. Winnowed and armored bed treatments showed, as expected, considerably reduced concentrations and little flow dependence (middle two rows). Recall that the intent here was to reduce seston flux and uncouple it from flow speed. Seston values were higher when fines were added (Fig. 2, bottom rows of plots), falling between the natural bed and winnowed and armored values. Again, these results were representative of those with other species (data not shown but available in Bock, 1995).

Deposit-feeding responses differed between the two obligate species studied. Figure 3 depicts the percentage of time spent deposit feeding for *M. viridis* and *A. parvidentata* for the four bed treatments (rows) and six flow treatments (symbols within a plot). Except in the winnowed and armored bed treatments, *M. viridis* deposit-feeding behavior varied with flow treatment and leg (Table 5) as indicated by significant main effects or interaction for the natural bed run. When no material was transported as either bedload or suspended load (i.e., on the armored bed), percentage feeding was relatively low (about 40%) and less variable than in other

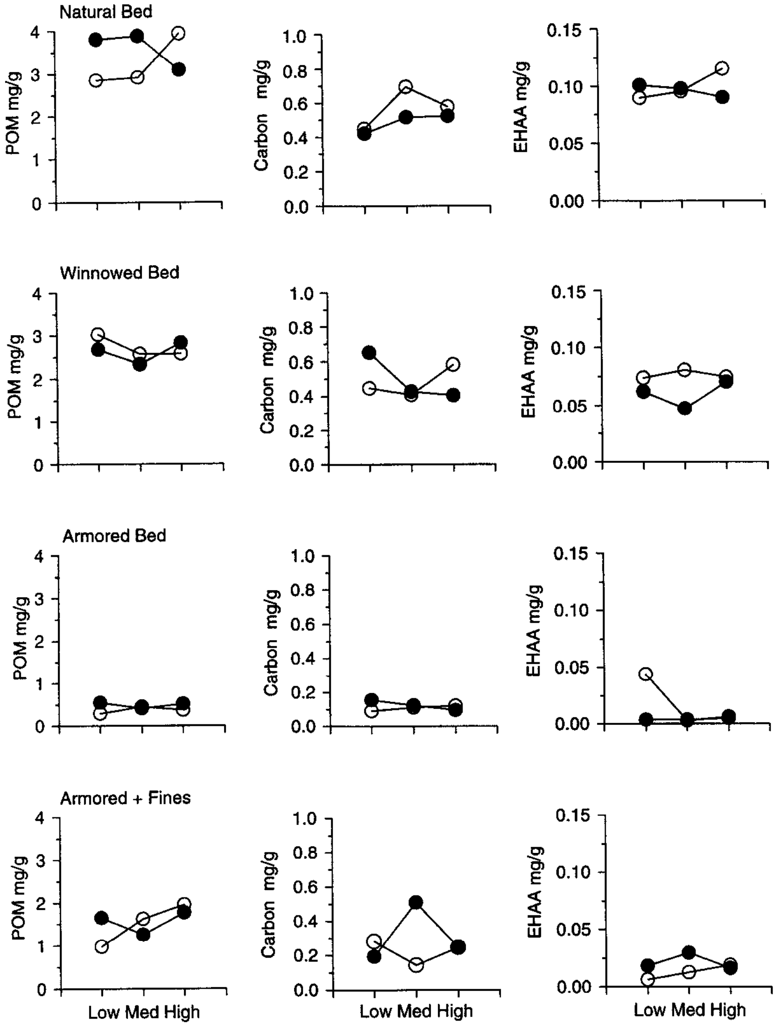


Figure 1. Food quality of the surficial sediments in the *Marenzelleria viridis* experiments. Observations associated with the increasing flow leg are plotted with open symbols and observations associated with the decreasing leg are plotted with filled symbols.

runs. There were no significant differences in any of the *A. parvidentata* comparisons (Table 4, third column, Fig. 3, right side). Under all four bed conditions, these worms spent > 80% of the time deposit feeding, regardless of flow and sediment flux. Both deposit-feeding species continued deposit feeding at high fluid velocities and sediment fluxes (Fig. 3).

Suspension-feeding behavior showed strong responses to flow and bed treatments for both mode-switching species. The results for *S. oculatus* are shown in Figure 4 and the results for *S. setosa* are shown in Figure 5. For both species, a statistical

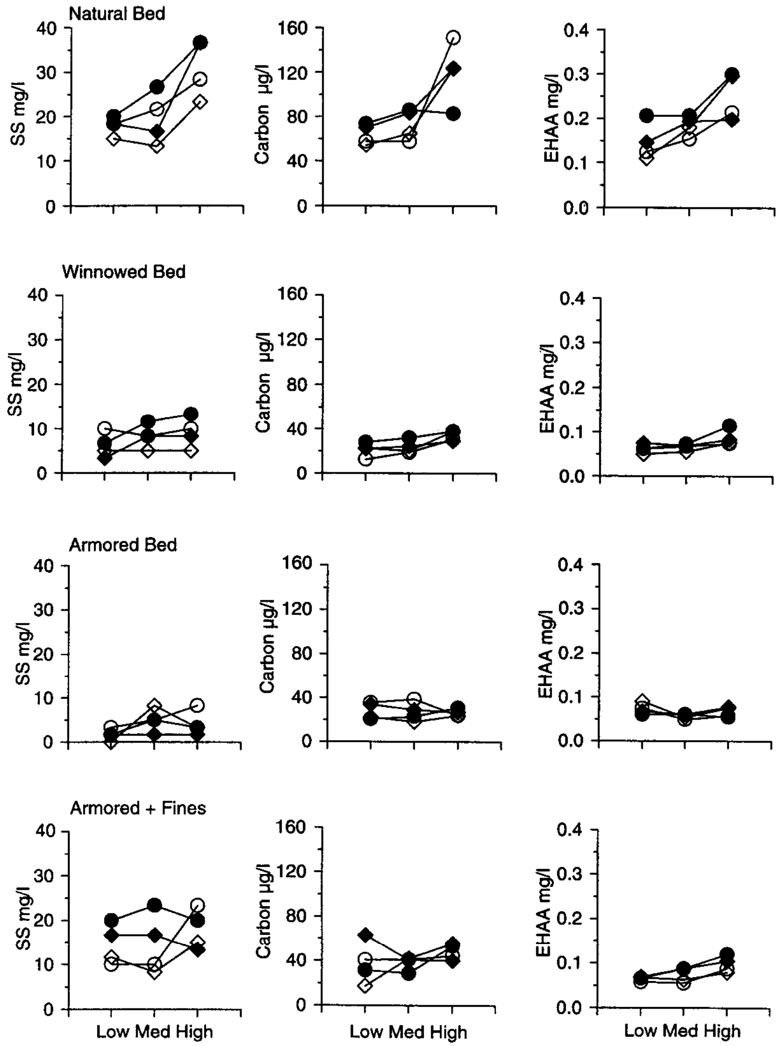


Figure 2. Suspended-particle food measurements obtained during the *Spiochaetopterus oculatus* experiments. Open symbols are used to denote observations associated with the increasing flow leg and filled symbols denote observations associated with the decreasing flow leg. Circles denote data collected at 1 cm above the sediment bed and diamonds denote data collected at 5 cm height.

summary of differences is again presented in Table 5. It is apparent that there was an increase in suspension feeding and a decrease in deposit feeding with increasing flow. For both species there was a significant flow effect in all bed treatments. For *S. setosa* there was a significant leg effect and a significant flow × leg interaction in experiments in which fine material is available for suspension (natural bed and

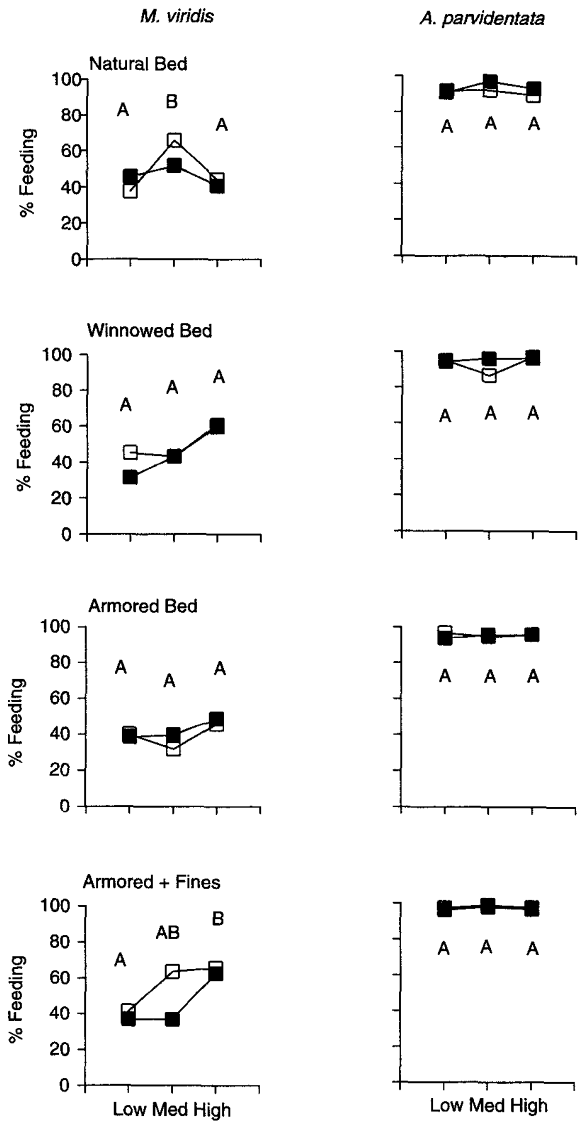


Figure 3. Percent deposit feeding for the *Marenzelleria viridis* and *Ampharete parvidentata* experiments. Open symbols denote the increasing flow leg and closed symbols denote the decreasing flow leg. For each panel, flow speeds denoted with the same letter are not significantly different from each other. Asterisks are used to denote significant differences between legs at the same flow speed ($p \leq 0.05$ = *; $p < 0.01$ = **; $p < 0.001$ = ***)

Table 5. Summary of significance tests from repeated-measures ANOVAs: $p \leq 0.05$ = *; $p \leq 0.01$ = **; $p \leq 0.001$ = ***. Significance levels for the flow and flow × leg factors represent conservative, G-G adjusted values. No adjustment is necessary for the leg factor since it has only a single degree of freedom.

		M. viridis	*A. parvidentata*	*S. oculatus*		*S. setosa*	
Bed	Treatment	Deposit	Deposit	Deposit	Suspension	Deposit	Suspension
Natural	Flow	***	ns	***	***	***	***
	Leg	ns	ns	***	***	ns	*
	Flow × Leg	*	ns	***	***	*	***
Winnowed	Flow	**	ns	***	***	**	**
	Leg	ns	ns	ns	ns	ns	ns
	Flow × Leg	ns	ns	ns	ns	ns	ns
Armored	Flow	ns	ns	**	***	**	**
	Leg	ns	ns	ns	ns	ns	*
	Flow × Leg	ns	ns	ns	ns	ns	ns
Armored + Fines	Flow	**	ns	***	***	***	***
	Leg	ns	ns	**	***	ns	ns
	Flow × Leg	ns	ns	ns	**	ns	**

armored plus fines) but not in the other treatments (winnowed bed and armored bed). For *S. setosa,* leg effects and flow × leg interactions only appear in the suspension feeding contrasts. There was a significant leg effect and flow × leg interaction in the natural bed and only a significant flow × leg interaction in the armored plus fines bed. There was also a significant leg effect in the armored bed. For both species, in cases in which there was a significant leg effect, there was more suspension feeding and less deposit feeding on the decreasing flow leg (Figs. 4 and 5). Detailed, significant differences as determined by multiple comparison tests are indicated by letters in these figures. Overall, the important patterns in the ANOVA tests are first, that flow affects deposit and suspension feeding in all cases, and second, that leg differences are apparent only when fine sediment is available for transport and not in the winnowed and armored bed runs.

For all of the bed and flow treatments the organisms were actively ingesting particles, as evidenced by our observations of defecation (data not shown). Unfortunately, the frequency of defecation was not sufficient to allow an estimate of relative feeding rates among the flow and bed treatments. The importance of the time spent not visible is unclear. It is obvious from the data that the organisms varied the division of time between feeding and other activities (Fig. 3, 4 and 5). In addition, the response to fluid flow and particle transport in the mode switching species (*S. oculatus* and *S. setosa*) was both a change in the time spent feeding and not visible, and the division of feeding time between deposit feeding and suspension feeding (Fig. 4 and 5). During the time spent not visible the organisms could have been engaged in tube maintenance or other, unknown activities.

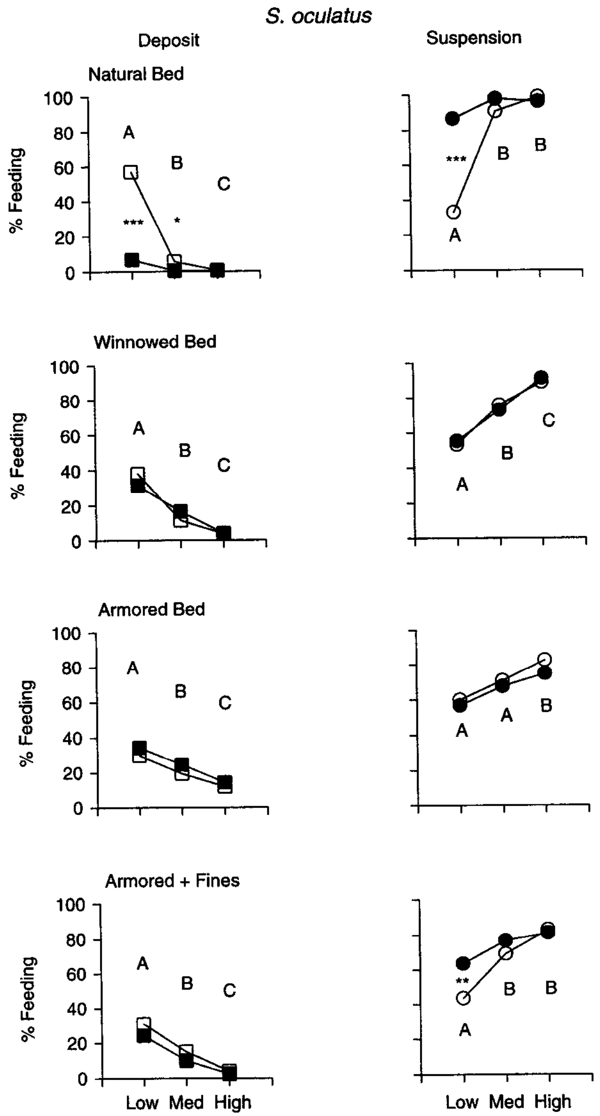


Figure 4. Percent suspension feeding and deposit feeding for the *Spiochaetopterus oculatus* experiments. Squares denote deposit feeding and circles denote suspension feeding. Open symbols show the increasing flow leg and closed symbols show the decreasing flow leg. For each panel, flow speeds denoted with the same letter are not significantly different from each other. Asterisk are used to mark significant differences between legs at the same flow speed ($p \leq 0.05$ = *; $p < 0.01$ = **; $p < 0.001$ = ***).

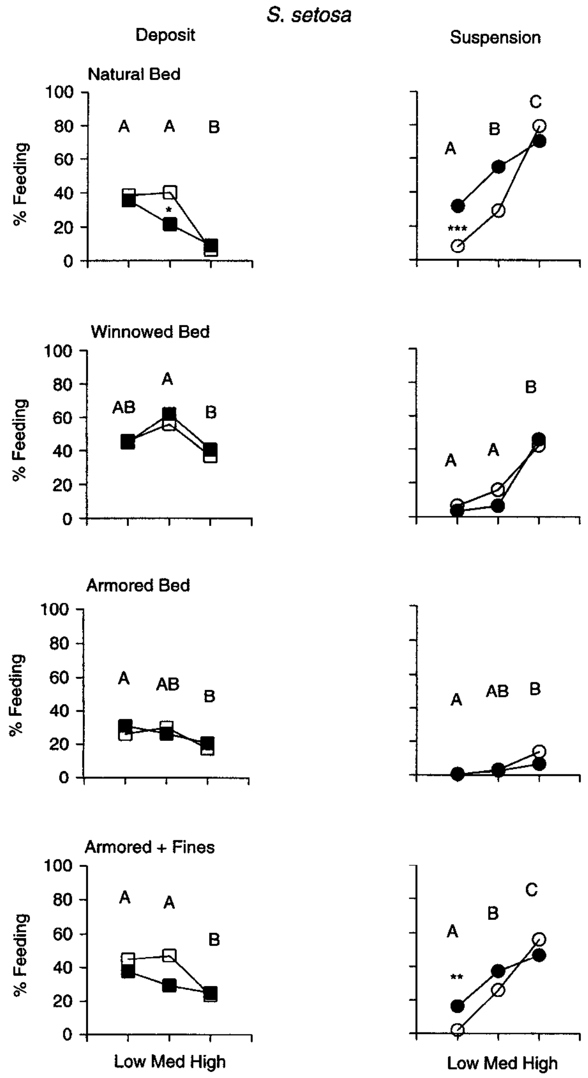


Figure 5. Percent suspension feeding and deposit feeding for the *Spio setosa* experiments. Squares denote deposit feeding and circles denote suspension feeding. Open symbols show the increasing flow leg and closed symbols show the decreasing flow leg. For each panel, flow speeds denoted with the same letter are not significantly different from each other. Asterisk are used to mark significant differences between legs at the same flow speed ($p \leq 0.05$ = *; $p < 0.01$ = **; $p < 0.001$ = ***).

6. Discussion

The hypotheses put forth above can be accepted, rejected or modified based on the results of the ANOVAs. Additionally, we employed exploratory analysis of the data to untangle the roles of fluid flow and particle related parameters as determinants of behavior.

a. Hypotheses revisited. The obligate surface deposit feeders showed little response to flow and bed treatments with no consistent flow or particle transport related patterns. Deposit feeding occurred in all bed and flow treatments, even during periods of bedload transport, meaning we can safely reject hypotheses D2 (deposit feeding is only possible in the absence of bedload transport, Table 1). Although there was no systematic response to flow in the obligate deposit feeders (Fig. 3) we cannot reject D1 (deposit feeding is independent of flow speed) due to the finding of significant flow effects for *M. viridis* in Table 5. If deposit feeding is a response to the deposition of high quality particles (D3), we would expect an increase in deposit feeding on the decreasing flow legs of bed treatments with material available for transport (i.e., natural bed, winnowed bed and armored plus fines) although this was not observed. Since there was high quality material which was suspended (Fig. 2) and subsequently deposited, we have no evidence to support hypothesis D3 (Table 4). However, our random sampling protocol revealed no demonstrable increase in the food quality of the surficial sediments on decreasing flow legs (e.g., Fig. 1), and deposition could have created food patches that were not necessarily near the observed worms (Yager *et al.,* 1993). Thus, it would be unwise to dismiss conclusively the role of the deposition of high quality material on deposit feeding at this time especially considering that the time spend feeding (as reported here) is not equivalent to the volumetric feeding rate. The results do show that deposit feeding is more variable among flow treatments in the presence of fine material (natural bed and armored plus fines) for *M. viridis.* If deposit feeding is affected by particulate food value in the way determined in still-water experiments (e.g., Cammen, 1980; Taghon and Greene, 1990; Karrh and Miller, 1994), particle transport and patchy deposition could serve to modulate local food value and feeding rate. Previous results have shown that at low transport rates the food value within a deposit feeder's feeding area can be reduced in the field (Bock and Miller, 1995) but the role of local food value could not be resolved using our random sampling protocol. In order to detect local food value, samples must be taken from within the feeding areas (e.g., Bock and Miller 1995).

In summary, it is still viable to put forth a hypothesis concerning deposit feeding based on small scale patterns: (D4) Deposit feeding is a function of local food value, the scale of which is determined by the diameter of the feeding area. The feeding area diameter is determined by the length of the feeding appendages and the propensity of the organism to extend its anterior out of the safety of its burrow (Woodin, 1982). If *M. viridis* and *A. parvidentata* do not extend their anterior ends out of their burrows to feed, the diameters of the feeding areas for these species should be about 10 mm based on the observed length of the feeding appendages. As Bock and Miller (1995) discuss, local variations in food concentration would not be adequately sampled by a random sampling design, although it has been detected using the syringe sampling and analytical methods employed in the present study.

Food quality control on feeding rate has been demonstrated in several deposit feeding species (Taghon and Jumars, 1984; Cammen, 1989; Taghon and Greene, 1990; Karrh and Miller, 1994; Bock 1995).

Previous work has shown a reduction in deposit feeding at high fluid velocities (e.g., Miller *et al.,* 1992), but this effect was not found in the present experiments. Miller *et al.* (1992) found leg differences in experiments with another obligate deposit feeder from the continental shelf, *Terebella rubra* (Miller *et al.,* 1992, Fig. 4), though no strong hysteresis was found here for *M. viridis* and *A. parvidentata* (based on the finding of no significant differences by the multiple comparisons tests in Fig. 3) Since these obligate deposit feeding species have exhibited different responses in three similar but independent experiments, the common mechanisms cannot be resolved. However, it seems reasonable to conclude that obligate deposit-feeding behavior is not systematically affected by flow and sediment flux, at least within the moderate range of conditions used here.

Based on the results we cannot conclusively accept a unique hypothesis concerning suspension feeding. Time spent suspension feeding increased with flow speed, supporting S1 (suspension feeding is a response to fluid flow alone). Although we had low suspended particle concentrations in the winnowed and armored bed treatments, some particles were present and so we had no flow only treatments to test rigorously S1. As a result we cannot safely reject or accept S1. Since suspension feeding was highest in experiments in which fine material was available for suspension, obviously suspended particles play a role, supporting hypotheses S2–S4 (suspension feeding is a response to: (S2) particle flux, (S3) particle concentration, and (S4) food concentration). As explained below, the most likely determinant of feeding behavior is the capture rate of nutritious particles, a complex function of the flow rate and the particle concentration/composition, supporting a modified version of S2 and S4. Of the feeding mode hypotheses (M1–M3) we can reject M1 (feeding mode is determined by flow speed alone). Since suspension feeding is higher in the presence of suspended particles, flow speed alone cannot account for the results. Since at no time did the food quality of the suspended particles (per gram) fall below that of the surficial sediments, we can also reject M2 (feeding mode is determined by the transport of particles of the highest food value). The lowest EHAA concentration of the suspended particles was 3.3 mg g^{-1} (obtained by dividing the food concentration by the suspended solids concentration), yet in many cases deposit feeding predominated over suspension feeding (Fig. 4 and 5). The results support M3, and are consistent with deposit feeding being compensatory to suspension feeding as discussed below.

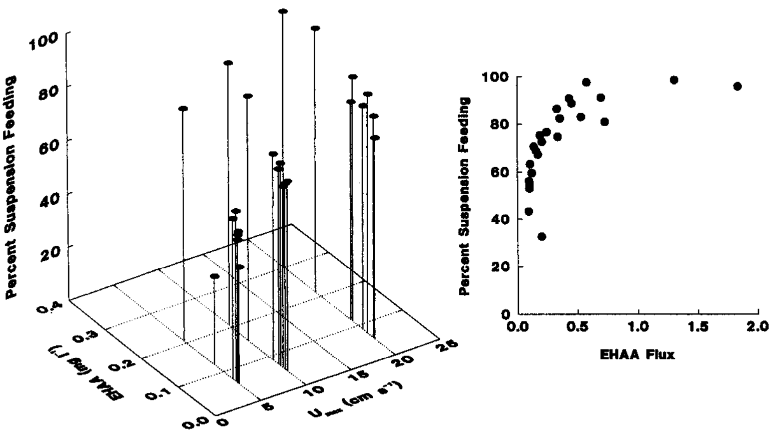
If deposit feeding is compensatory to suspension feeding, it is more appropriate to say that deposit feeding is induced by the lack of fluid flow and suspended particulates, rather than suggesting that suspension feeding is induced by these factors. The results suggest that suspended material is preferentially ingested if present in sufficient quantities. Fine, low-density suspended material will have a high food quality per particle, and if ingested, per unit gut volume. Considering that the mechanical cost of feeding is believed to be negligible (Taghon, 1988) organisms should attempt to maximize the assimilation of material per unit time. Based on optimal foraging/digestion theory, if given a choice, organisms will ingest suspended material in preference to surficial sediment. However, suspended material may not be present in high enough quantities to meet the energetic demands of the organism, i.e., they compensate for the reduced intake of suspended organic matter by deposit feeding. In this case, the worm should ingest surficial sediment to supplement suspended material. The results of Taghon and Greene (1992) are consistent with this scenario. They found that in *Pseudopolydora kempi japonica* which were restricted to suspension feeding, growth is reduced. However, *Bocardia pugettensis* grew as well or better when suspension feeding. The differences in growth between the various treatments and species can be explained if *B. pugettensis* is either more efficient at suspension feeding, has lower energetic requirements or has a higher assimilation efficiency than *P. kempi japonica.* Alternatively, deposit feeding may not be compensatory to suspension feeding but rather the organisms simply ingest whatever is available in sufficient quantities to meet their needs.

The possible differences between *P. kempi japonica* and *B. pugettensis* described above could also apply to these experiments. *S. oculatus* consistently spent more time suspension feeding than *S. oculatus* at similar bed and flow treatments and comparable EHAA fluxes (Fig. 6). Previous experiments on suspension feeding have revealed species differences in thresholds for suspension feeding (e.g., Miller *et al.,* 1992) and it may well be that these reflect differences in feeding efficiency and/or digestion.

b. Suspended matter and feeding. It is possible to further examine the role of suspended particles in determining feeding behavior through exploratory analysis of the data. By performing an ANOVA on the mean time spent suspension feeding for each bed/flow treatment versus flow (low, medium, high) it is possible to control or remove the influence of flow speed, without presuming the form of the relationship between flow and behavior. The residuals of this ANOVA can be compared to the water column data (suspended solids, POM, etc.) to explore the role of suspended matter in determining behavior while statistically controlling for flow effects.

The Pearson's correlation analyses of residuals of the ANOVAs described above were performed versus suspended solids, POM, chlorophyll, POC, PN and EHAA. For *S. oculatus,* only PN and EHAA were significantly correlated ($p \leq 0.05$) following a Bonferroni adjustment. For *S. setosa,* suspended solids, POM, PN and EHAA were significantly correlated to the residuals. The presence of significant correlations between the water column parameters and the residuals confirms the relationship between feeding mode and suspended particles. For both species, both

Spiochaetopterus oculatus



Spio setosa

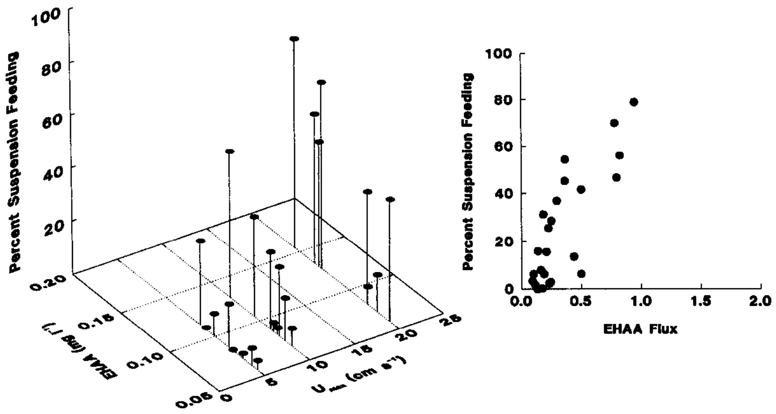


Figure 6. Exploratory, three-dimensional plots. The panels above show the percent suspension feeding versus flow velocity (U_{max}) and the concentration of enzymatically hydrolyzable amino acids for both *Spichaetopterus oculatus* and *Spio setosa*. To the right are plots of the percent suspension feeding versus the EHAA flux (mg cm^2 sec^{-1}).

PN and enzymatically hydrolyzable amino acids (EHAA) were significantly correlated to the residuals. Figure 6 shows the relationship between percent suspension feeding, flow speed and suspended EHAA, as well as the relationship between suspension feeding and the EHAA flux (water flux times the EHAA concentration). The results suggests that nitrogenous compounds could be an important cue for suspension feeding, supporting hypothesis S4, but that relationship differs between species.

Table 6. Exploratory ANCOVA models of suspension feeding behavior. Velocity Class is a categorical variable and all other variables are range variables. Variables separated with an '×' indicated a test of the interaction between those two variables. All models incorporated a "constant" intercept parameter in addition to those listed. Values with a (1) indicate suspended particle measurements from 1 cm above the bed.

Model	*Spiochaetopterus oculatus* R^2	*Spio setosa* R^2
Velocity	0.46	0.42
Velocity + EHAA(1)	0.62	0.72
Velocity × EHAA(1)	0.45	0.67
Velocity Class	0.57	0.42
Velocity Class + EHAA(1)	0.76	0.72
flux	0.42	0.41
flux + EHAA(1)	0.43	0.71
EHAA(1) flux	0.45	0.66
Velocity + flux × EHAA(1)	0.56	0.68
Velocity Class + EHAA(1) flux	0.68	0.69

c. Statistical models of suspension feeding behavior. We fit various models to our data to explore which factors or measured parameters are most closely linked to suspension feeding. By utilizing multiple general linear hypothesis testing (i.e., ANCOVA) it is possible to examine the ability of various parameters to predict feeding behavior. Using these methods we evaluated the importance of flow, particle or food concentration and particle or food flux to feeding behavior. We modeled suspension feeding using flow and particle parameters with the MGLH module of SYSTAT (Wilkinson, 1990) and compared R^2 values to assess the fit of the various models. Table 6 shows the results of these analyses for suspension feeding in *S. oculatus* and *S. setosa.* The flux is the volume of water (cm^3) passing through one cm^2 per unit time and so for example the chlorophyll flux is the chlorophyll concentration × water flux. Models which include flow and particle concentration generally have a better fit than those which consider flow alone or flux (Table 6).

Although the absolute responses of the two species differed (Fig. 4, 5 and 6), for both species the best predictor of suspension feeding is a model including both fluid velocity and the concentration of a food-related parameter (in this case we used enzymatically hydrolyzable amino acids). The fit is improved when flow is expressed as a categorical (nominal) variable, indicating that the flow response in not necessarily linear. It is surprising that the food flux (EHAA flux in Table 6 and the right-hand column of Fig. 6) did not provide a better fit, as the food flux presumably best describes the amount of material available to the organisms. However, particle capture is not totally dependent on the flux, possibly explaining the high degree of scatter in Figure 6. There is a complex relationship between flow velocity, turbulence and particle contact in suspension feeders (Shimeta and Jumars, 1991). The situation is further complicated by the roles of particle retention. As a first order approximation, particle ingestion is a function of particle contact and particle retention, with particle contact increasing with flow and particle retention decreasing as a function of flow velocity (or shear stress). Because of the interaction between flow, particle contact and particle retention, an increase in flow could either increase or decrease the particle capture rate (Shimeta and Jumars, 1991). However, an increase in particle concentration will yield an increase in particle capture, up to some maximum value. Considering the interaction between flow, particle concentration, particle contact and particle capture, the capture rate of high quality material may be a better predictor of feeding mode than the flux.

d. Proposed determinants of feeding behavior. Our results suggest a number of new experiments. Our conclusion that the deposition of high quality material had no effect on deposit feeding should be more rigorously tested (Table 5, Fig. 3). The role of local bed characteristics as determinants of feeding behavior has been implicated in other work (Karrh and Miller, 1996). Additionally, centimeter-scale variations in food quality have been documented in the field (Bock and Miller, 1995). Experiments which measure an individual worms feeding rate and local food concentration could be used to test this hypothesis. The local food concentration could be manipulated by allowing the organisms to remove material by feeding, with the application of fresh material simulating sediment transport.

These experiments complement the results of Taghon *et al.* (1980), showing a relationship between suspension feeding and suspended particles. These results go beyond previous work in that they explore the particle related parameters that may be responsible for the change in feeding behavior. Our results show that both fluid flow and the concentration of high quality material are linked to suspension feeding. For both species, nitrogenous compounds seem to be cues for suspension feeding. Future experiments should examine the roles of the various classes of organic matter on feeding. Artificial particle coatings could be used to compare the response to nitrogen rich (i.e., protein) versus nitrogen poor (i.e., carbohydrates) particles at similar total organic matter concentrations. The rapid response described here and in other studies (Dauer *et al.,* 1981; Turner and Miller, 1991b; Miller *et al.,* 1992) suggests that polychaetes can detect organic matter either on the feeding appendages or in the foregut, in contrast to the slow response of a hemichordate to a change in diet and the resulting hindgut-feedback hypothesis (Miller, 1992). This hypothesis can be further tested by examination of the feeding appendages for sensory apparatus or by examining the temporal response to a change in diet (Miller, 1992).

Based on the results of these experiments, we can begin to discuss the processes controlling feeding behavior in surface deposit-feeding and suspension-feeding polychaetes. It appears as though flow and sediment transport have little systematic affect on deposit feeding behavior, at least over the range of conditions used here.

Other studies have shown that deposit feeding is linked to food concentration (Cammen, 1980; Taghon and Greene, 1990; Karrh and Miller, 1994). Local food quality can be controlled or influenced by particle transport (Miller *et al.,* 1984; Bock and Miller, 1995) and and this effect has been implicated as an important process controlling feeding rate (Karrh and Miller, 1996). Our results implicate the role of local food concentration and its control by particle transport on feeding behavior. Deposit feeding was more variable in *M. viridis* bed treatments in which material was available for transport (Fig. 3). This fine material would be deposited according to local bed topography (Yager *et al.,* 1993), leading to spatial heterogeneity in sedimentary food resources. This heterogeneity in food resources could lead to the observed patterns in feeding behavior.

The food concentration of the suspended organic matter was a strong correlate of feeding behavior. The results suggest that polychaetes can detect nitrogenous compounds (e.g., proteins and amino acids) although this conclusion is based on exploratory analysis of the data and must be tested experimentally. If the organisms are nitrogen limited (e.g., Carey and Mayer, 1990), being able to detect and respond to high quality nitrogenous material would be advantageous.

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