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Deposit and suspension feeding in oscillatory flows and sediment fluxes

by Douglas C. Miller¹, Michael J. Bock¹ and Elizabeth J. Turner^{1,2}

ABSTRACT

We present a survey of feeding behavior of benthic organisms in oscillatory flow and sediment fluxes. These results are based on seventeen species from five phyla and several feeding guilds from an intertidal sandflat and the continental shelf of the Mid-Atlantic coast, U.S.A. General responses to oscillatory flows are: (1) nearly immediate change in feeding behavior or position of feeding appendage when flow is initiated, (2) decrease in feeding area for surface deposit feeders, often (3) alteration of feeding mode, and when anatomically permitted (4) rotation of feeding appendages to track flow direction. At high sediment fluxes, responses are functional group and morphology-specific. Organisms with one or two muscular feeding appendages continue to feed (e.g., *Spio setosa*, *Spiochaetopterus oculatus* and *Emerita talpoida*), while those with a crown of tentacles cannot (e.g., *Pista palmata*, *Serpula vermicularis granulosa*, and *Terebella rubra*). A continental shelf brittle star, *Amphipholis squamata*, ceases suspension feeding in high flows. Organisms with strong tentacles feed at the sediment surface in much restricted feeding area (*Marenzelleria jonesi* and *Saccoglossus kowalevskii*). Organisms with long, thin palps coil them helically and capture particles in near-bed flux (*Spiochaetopterus oculatus* and *Spio setosa*). Siphonate feeders maintain siphon tips near the sediment surface and continue pumping (*Ensis directus*, *Mercenaria mercenaria* and *Tagelus plebeius*). A sedentary omnivore (*Diopatra cuprea*) is able to capture food particles in low and moderate flow, but in high flows the tube opening is closed. Motile scavengers may either increase (*Pagurus longicarpus*) or decrease (*Echinarachnius parma* and *Ilyanassa obsoleta*) movement rate. Of all species studied, only the burrowing predatory starfish *Astropecten americanus* showed no change in behavior with respect to oscillatory flow.

In addition, we report detailed quantitative changes in feeding behavior by a facultative suspension-feeding spionid polychaete *Spio setosa* and an obligate deposit-feeding terebellid polychaete *Terebella rubra* which indicate hysteresis or time-dependence in the response to flow and sediment flux. We attempt a summary of responses by functional group and morphology and suggest that new descriptive terms combining low-flow feeding behavior and morphology are needed to characterize feeding modes adequately. Our analysis suggests that it is important to consider the possible presence of flow and flux micro-environments, an individual organism's variability, flow history and the various time scales of behavioral responses and other biological rate processes. There is a current need for dynamic feeding models that incorporate these factors as well as for experimental tests of the derived predictions.

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1. Introduction

a. Rationale. In shallow water, waves exert considerable influence on the sea floor. From the intertidal zone (e.g., Miller and Sternberg, 1988) to the continental shelf (e.g., Lyne *et al.*, 1990a,b), the near-bottom flow induced by surface gravity waves can be the dominant flow regime and the prime forcing function for sediment movement. The importance and relative rates of geophysical sediment movement have been evaluated in a number of recent studies: Grant (1983, 1985), Jumars and Self (1986), Miller and Jumars (1986) and Miller and Sternberg (1988). Benthic organisms which live and feed on the sea floor are in intimate contact with the overlying flows and resulting sediment fluxes. Those that can feed upon this particulate organic material, as deposited or in near-bottom flux, might well be expected to respond to the flow and sediment transport in feeding behavior and foraging strategy.

Though commonly used in laboratory experiments (e.g., Miller and Jumars, 1986), the typical seawater table is a poor simulation of the sea floor environment. Flow is often less than a few centimeters per second, and is rarely well characterized. Bulk sediment movement, resuspension and deposition do not occur in such flows. As a result, the structure of the sediment surface in these studies becomes completely dominated by biological processes. Initially the feeding and defecation of macrofauna create relief, and later (i.e., days) the activities of meiofauna (Cullen, 1973) and microflora (pers. obs.) affect surface relief and appearance. This is in contrast to what is seen on the sandflat at Cape Henlopen, Delaware, U.S.A., the collection site for most of the species used in the present study. Sediment ripples of 5–10 cm wavelength dominate, and the sandflat is relatively featureless on smaller scales except for localized worm tubes and fecal pellets and coils (pers. obs. and see Miller and Sternberg, 1988 for similar observations at False Bay, WA, U.S.A.). In the virtual absence of geophysical processes, the relative importance of certain biological (e.g., bioturbation) and chemical (solute transport via molecular diffusion) processes are likely to be severely overestimated. The result could well be a confusing, misleading picture of a benthic system composed of tightly coupled physical, chemical and biological processes.

Observations of feeding behavior in more realistic flows in laboratory flumes (e.g., Taghon *et al.*, 1980; Nowell *et al.*, 1989; Levinton, 1991) and oscillatory flow devices (e.g., Hunter, 1989; Trager *et al.*, 1990; Turner and Miller 1991a,b) add small increments to our understanding of the mechanics of feeding processes (Nowell *et al.*, 1989). Taken together, they serve as a necessary and preliminary step toward predicting changes in food resources and feeding rate responses via theoretical optimality and mass balance models. In this paper, we report observations of deposit- and suspension-feeding organisms made in oscillatory flow simulated in the laboratory. While the potential of unknown biases cannot be avoided, such laboratory flow devices permit the investigator to hold many factors constant and to vary flow and

sediment flux in a systematic fashion. We were thus able to observe and quantify responses of a number of shallow-water species to imposed flow and sediment transport conditions.

b. Preliminary theory. We summarize briefly the relevant fluid dynamics and foraging theory to provide the terminology and context for the observations which follow. The fluid-dynamical case of interest is that of flow near a sandy bottom varying sinusoidally in time (t):

$$U(t) = U_b \sin(\omega t) \text{ or } U(t) = (A_b \omega) \sin(\omega t), \text{ where } \omega = 2\pi/T. \quad (1)$$

For a general discussion of wave theory and boundary layer processes, see e.g., Mei (1983), Sleath (1984), Dean and Dalrymple (1984) or Denny (1988). Specifying any two of the three important parameters above, namely, the peak horizontal velocity U_b , the oscillation period T (or equivalently, specifying the wave frequency ω), or the near-bottom excursion semi-amplitude A_b , characterizes the near-bottom flow field. To a first approximation (e.g., as in linear wave theory), there is no net fluid motion. In the absence of turbulence, the fluid and suspended particles move back and forth in simple harmonic motion. Flows and boundary layers are, however, generally turbulent in field situations of interest (see Table 1).

In contrast to steady, unidirectional flows and their boundary layers, the characteristics of the wave boundary layer vary with time. This dependence leads to important features: rapid changes in fluid velocities lead to strong vertical gradients in velocity or shears and large, time-varying shear forces along the bottom. The thickness of the turbulent wave boundary layer is most frequently defined as:

$$\delta_w = 2\kappa u_* / \omega \quad (2)$$

where κ is von Karman's constant (about 0.4, and dimensionless) and u_* is the shear velocity with units of length per time. The corresponding relationship for a laminar boundary layer is $\delta_v = \sqrt{\nu/\omega}$ where ν is the kinematic viscosity of the fluid. For the cases of interest, turbulent boundary layers are thicker, for example, for $T \geq 3$ s and shear velocities $u_* \geq 1$ cm s⁻¹, δ_v is always less than one-fourth δ_w . The shear velocity u_* is related to the shear stress magnitude via $\tau_b = \rho u_*^2$, where ρ is the fluid density. Calculation of the bed stress (and shear velocity) is often made by the deceptively simple relationship:

$$\tau_b = \frac{1}{2} \rho f_w U_b^2 \quad (3)$$

where f_w is the friction coefficient and U_b is the maximum fluid velocity just above the wave boundary layer. The friction coefficient is a complex function of the flow Reynolds number $Re = U_b A_b / \nu$ and a roughness parameter A_b/k , where k is some characteristic measure of the bed roughness, usually a low multiple of the largest

Table 1. Sample calculations of comparable fluid dynamical parameters for field and laboratory situations of interest (see text). Symbols are defined in the text. The first four field parameters were calculated using linear wave theory (e.g., Dean and Dalrymple, 1984). Boundary layer parameters were calculated using equations in Mei (1983) and Sleath (1984), assuming a seawater medium of temperature 20°C and 30 psu salinity, density $\rho = 1.021 \text{ g cm}^{-3}$ and kinematic viscosity $\nu = 0.0104 \text{ cm}^2 \text{ s}^{-1}$. The bed was assumed to be a smooth, plane bed of medium, quartz sand grains of 250 μm diameter, 2.65 g cm^{-3} grain density and a Nikuradse roughness of twice the grain diameter. The friction coefficient was calculated using Jonsson's (1966) semiempirical formula. This bed has an estimated critical erosion velocity of 1.3 cm s^{-1} based on Shield's curve. Individual grains would settle at 2.6 cm s^{-1} based on an equation by Dietrich (1982).

	Wave period s	Wave height m	U_b cm s^{-1}	A_b cm	Re —	δ_w cm	u_* cm s^{-1}
Field:							
Shallow Intertidal, 2 m depth	3	0.3	23	11	2.5×10^4	0.79	2.1‡
Shelf, 10 m	10	1.0	43	68	28×10^4 †	3.7	2.9‡
Shelf, 30 m	10	1.0	17	27	4.4×10^4 †	1.7	1.3‡
Offshore, 100 m	15	2.0	13	31	4.0×10^4 †	1.9	0.99
			Piston				
	Drive period s	stroke cm	U_{LWT} cm s^{-1}	A_{LWT} cm			
Laboratory Water Tunnel:							
Case A or "Low Os- cillatory Flow"	20	12	9.2	29	2.6×10^4 †	1.8	0.70
Case B or "Bedload Transport"	10	12	18	29	5.2×10^4 †	1.8	1.4‡
Case C or "High Sus- pended Load"	5	12	37	29	10×10^4 †	1.8	2.8‡
Case D or "Low Os- cillatory Flow"	10	6	9.2	15	1.3×10^4 †	1.0	0.79

†Reynolds number and roughness criterion exceed that of Jonsson (1966) quoted in Mei (1983) for transition to turbulent wave boundary layers.

‡Equals or exceeds estimated critical erosion velocity for the bed.

grain size (Sleath, 1984). Flow Reynolds numbers larger than 1.26×10^4 usually indicate turbulent flows (Sleath, 1984).

The flow field specified by Eq. (1) is intended as an idealization of the flow induced by surface gravity waves outside the wave boundary layer. The characteristics of the near-bottom flow may be related to the surface manifestation of the wave by linear wave theory (e.g., Mei, 1983; Dean and Dalrymple, 1984; Denny, 1988). Sample calculations in Table 1 (top half) show that, for a range of wave periods and heights for storm conditions from the intertidal to the shelf, surface waves reach the bottom.

Wave boundary layers are turbulent (or nearly so), and peak velocities and shear stresses are often sufficient to transport material on sandy bottoms.

Unfortunately, the applicable geophysical theory is much further developed than that relevant to feeding behavior. The obvious candidates, optimal foraging theory (e.g., Stephens and Krebs, 1986) and optimal digestion theory (Penry and Jumars, 1987; Jumars and Penry, 1989; Dade *et al.*, 1990) are difficult to apply precisely because little is known about the feeding repertoire exhibited by macrofauna or the behavioral "decision space" (in mathematical terms) in which optimization can occur. Changes in feeding mode and food source have not been incorporated in current models and likely supersede the standard parameterizations of microphagous feeding such as bulk feeding rate (mass per time) and particle selectivity (some measure of the difference between available and consumed food items).

c. *Goals.* Our first goal is to describe and summarize feeding behavior by benthic organisms in oscillatory flow and sediment flux. We report observations of seventeen species in five phyla from an intertidal sandflat and the continental shelf of the Mid-Atlantic coast, U.S.A. Next, we report in detail quantitative changes in feeding behavior by a facultative suspension-feeding spionid polychaete *Spio setosa* and an obligate deposit-feeding terebellid polychaete *Terebella rubra*, focusing on response rapidity, persistence, consistency, repeatability and degree of memory or hysteresis. We will highlight the differences of these results from the conventional wisdom and suggest a revision in the current terminology of feeding behavior. Finally, we will discuss the implications for those wishing to experiment with, or construct models of, feeding in the benthic boundary layer.

2. Methods

a. *Collection and maintenance of organisms.* The well-studied (e.g., Kinner and Maurer, 1978; Maurer and Aprill, 1979; Brown, 1982; Bianchi, 1988) intertidal sandflat at Cape Henlopen, Delaware, USA (38° 47' N, 75° 06' W) was the source of most of our experimental organisms. Animals were collected by coring, sieving or hand-collection and immediately transferred to plastic containers filled with 1-mm sieved, macrofauna-free sand from Cape Henlopen. These animals were allowed to establish tubes and burrows in a seawater table (flow speeds $\leq 2 \text{ cm s}^{-1}$) to acclimate to laboratory conditions. Animals were transferred in their plastic containers and buried in the working section bed (see below) several days prior to observation in the water tunnel. *Marenzelleria jonesi* (6–8 cm body length), *Pista palmata* (10 cm), *Saccoglossus kowalevskii* (15 cm), *Spio setosa* (2 cm) and *Spiochaetopterus oculatus* (5 cm, see also Turner and Miller, 1991a) were collected and observed in March 1991. *Diopatra cuprea* (worm length, 6–8 cm) were collected and observed in October 1991.

Motile fauna were placed directly in the water tunnel on the working section bed.

Emerita talpoida (carapace length, 1–4 cm) were collected by sieving swash zone sand on the Atlantic Ocean beach at Cape Henlopen in June 1991. *Ilyanassa obsoleta* and *Pagurus longicarpus* (for both, shell heights 2 cm) were collected by hand from the sandflat at Cape Henlopen in August 1990. Year-old, 2.5–3.5 cm shell length, *Mercenaria mercenaria* were obtained from a local hatchery (Mercenaria Manufacturing, Millsboro, DE, see also Turner and Miller, 1991b) and were allowed to directly bury themselves in the working section bed. During work with *Mercenaria* in July–August 1989, clams were fed cultured algae supplied by a peristaltic pump (see Turner and Miller, 1991b for more details). Older, larger individuals of the hard clam, common on the Cape Henlopen sandflat, were also observed in this study. These hard clams and the razor clams *Ensis directus* and *Tagelus plebeius* were dug by hand or clam gun from the sandflat at Cape Henlopen in October 1991. Animals were allowed to acclimate in the water tunnel itself at least a day before observation.

The serpulid *Serpula vermicularis granulosa* and terebellid *Terebella rubra* were collected from the continental shelf off Delaware (38° 10' N, 74° 10' W, depth, 30 m) using a Smith-McIntyre grab in August 1990. Worm tubes (extending ≈ 1 cm above bed) were easily separated from surrounding material because of their attachment to an 8-cm, tube-encrusted shell of the Atlantic sea scallop, *Placopecten magellanicus*. Three species of echinoderms, the brittle star *Amphipholis squamata* (3–5 cm across arms), starfish *Astropecten americanus* (5–8 cm) and sand dollar *Echinarachnius parma* (3–5 cm in diameter), were collected from the same region of the shelf from depths of 30–108 m during cruises in August 1990 and February 1991. Shelf animals were kept with their natural sediment (a coarse sand) in a seawater table at 15°C prior to acclimatization and observation.

b. Simulation of oscillatory flow in the laboratory. The Lofquist Oscillatory Water Tunnel is U-shaped, with two pistons in vertical cylinders that drive water through a horizontal acrylic working section (255 cm long \times 21-cm wide \times 30-cm deep flow depth). The water tunnel is illustrated and described in more detail in Turner's dissertation (1990) and in Turner and Miller (1991a,b). A variable-speed motor and Scotch yoke drive the pistons and produce nearly sinusoidal flows in the working section. The piston amplitude can be adjusted up to 15 cm by manually resetting a pin. The period of oscillation is controlled by a variable speed motor and can range continuously from 3 to 30 seconds. The maximum freestream velocities and fluid excursions can be calculated from the drive period and piston stroke:

$$U_{LWT} = 15.4 \times (\text{Piston Stroke Amplitude, cm}) / (\text{Period, s}) \quad (4a)$$

$$A_{LWT} = U_{max} / \omega = 2.45 \times (\text{Piston Stroke Amplitude, cm}) \quad (4b)$$

The subscript "LWT" will be used with these variables to differentiate them from analogous quantities in the field (denoted with "b" subscripts). The combination of

adjustable stroke and oscillation period permit the simulation of the benthic environment generated by a wide range of wave conditions from short-period, shallow-water waves to storms on continental shelves. The lower half of Table 1 presents wave boundary layer calculations for typical laboratory runs in the water tunnel. A typical run varied flow by adjusting period and holding stroke constant at, for example, 12 cm as in Cases A to C in Table 1. The continuous adjustment of drive period by the motor speed is considerably faster and more convenient than the mechanical adjustment necessary to change stroke. Velocities U_{LWT} thus range from several cm s^{-1} to greater than 30 cm s^{-1} , while the fluid excursion amplitude A_{LWT} remains constant. As in the field, rough turbulent boundary layers develop and shear stress can easily exceed that needed to move sediment. As a result of fixing the fluid amplitude while varying the period, the calculated thickness of the rough turbulent wave boundary layer remains approximately constant (shown numerically in Table 1). Also as a consequence, the shear velocity u_* is inversely proportional to the drive period, and hence directly proportional to the wave frequency.

A 20-cm deep sediment bed underlies the working section. The bottom half is pea-sized gravel; the top 10 cm is 1-mm sieved, macrofauna-free, sand from the sandflat at Cape Henlopen, DE, U.S.A. This is a moderately sorted, medium sand of median grain size $240 \mu\text{m}$ and $<1\%$ silt-clay. Watertight hatches in the top of the working section provide access to add or remove animals. Water temperature in the tunnel remains near the ambient air temperature (typically 25°C , ranging from $20\text{--}32^\circ\text{C}$). For experiments with shelf species, a chiller system was used to maintain a water temperature of $14\text{--}15^\circ\text{C}$ in the water tunnel. In the greenhouse where it is located, there is sufficient light and primary production in the water tunnel to provide adequate dissolved oxygen and benthic diatom food for animals. We have operated the water tunnel as a "closed aquarium" for weeks at a time and held animals in it continuously for months in active and healthy condition (Turner, 1990; Turner and Miller, 1991a,b). All experiments were conducted in seawater of ≈ 30 psu salinity obtained from Indian River Inlet, DE, U.S.A.

c. Experimental procedures. We made observations of the deposit- and suspension feeders directly through the clear acrylic walls of the working section. Observations by the unaided eye were supplemented by those from a binocular microscope with long-focusing objective lens, photo- and video macrography. To obtain behavioral data, we began by observing organisms in the water tunnel before turning the drive mechanism on, denoted as the "no flow" condition. We then observed organisms with the drive mechanism operating at sequentially decreasing periods (i.e., increasing peak velocity and bed stress) to $> 30 \text{ cm s}^{-1}$ peak freestream velocity. Flow speeds were calculated from Eq. (4). We observed and visually classified any sediment movement into qualitatively different transport regimes. Generally, observations of several individuals were made in a single day, with individual flow

treatments lasting from 10 minutes to several hours preceded by acclimation periods of similar duration. We noticed no indication that the minimal noise and vibration of the drive mechanism affected behavior. The water tunnel stroke was fixed during any observational run, with increasing flow imposed by decreasing the period of oscillation. Specific details of flow treatments, temperature and other experimental parameters may be found in the table legends and figure captions. For several Cape Henlopen species, *Emerita talpoida* and *Spiochaetopterus oculus*, and *Mercenaria mercenaria* and the shelf echinoderms, observations have been excerpted from Turner (1990) and Turner and Miller (1991a,b), and Bock and Miller (in prep.), respectively.

In addition, we examined quantitative changes in feeding behavior by a facultative suspension-feeding spionid polychaete, *Spio setosa* (also known as an interface feeder, Dauer *et al.*, 1981; Muschenheim, 1987a,b), and an obligate deposit-feeding terebellid, *Terebella rubra* (for similar species, see Fauchald and Jumars, 1979). These data serve to examine certain characteristics of the response to oscillatory flow: its rapidity, persistence, consistency, repeatability and degree of memory or hysteresis. Behaviors were observed over 23 h to test a hypothesis of no difference over time under conditions of constant oscillatory flow. Behaviors were also observed under gradually increasing flow in 20-min intervals over 2 h, to test a hypothesis of no difference among flow conditions. In the third experiment, worms were observed under increasing then decreasing flows in stepwise changes between intervals of 20 min each (five increasing followed by five decreasing periods) to test a hypothesis of no difference between comparable flow speeds on increasing versus decreasing flow legs. There were numerous individuals of *Spio setosa* in the working section. Those we chose to observe were near the middle of the working section and conveniently placed for extended observation. Many were within a palp's length of one another, but this apparently had no effect on feeding behavior (see Dauer *et al.*, 1981). We recorded observations on all active *Terebella rubra* in the water tunnel. We collected data using a scan sampling rule (Martin and Bateson, 1986), observing each individual at 2 min intervals and recording its behavior at that instant. This instantaneous sampling procedure yields the proportion of sample points (i.e., time) on which a particular behavior was exhibited for the recording period. Sample points within a flow period are obviously not statistically independent observations and were not treated as such. Data for both species were obtained in a single series of experiments conducted in March 1991. The consistency experiment was conducted immediately following the persistence experiment; the hysteresis experiment was conducted the following day with the flow off in the intervening period. Water temperature was 14–16°C.

d. Data analysis. We tabulated observations of all the species by ordinal categories of flow and sediment transport regime which included no flow, low oscillatory flow, flow

sufficient to generate bedload transport on a rippled bed, combined bedload and suspended load, and high suspended load conditions. When quantitative behavioral data were available from this study or our previous efforts (Turner, 1990; Turner and Miller, 1991a,b; Bock and Miller, in prep.), we plotted a response (e.g., as percent suspension feeding or as crawling rate) against maximum oscillatory flow speed to gauge whether or not species responded similarly across flow speeds.

To test specific hypotheses (above) concerning the persistence, consistency and hysteresis of the response to oscillatory flow as illustrated by *Spio setosa* and *Terebella rubra*, we analyzed the data for differences in response among flow periods using a nonparametric analysis incorporating blocking by individual organism. These were Friedman's test for several flow treatments and Wilcoxon's signed ranks test for comparable flow speeds in the hysteresis experiment (Hollander and Wolfe, 1973; Zar, 1984). A block consisted of the observations (i.e., time proportions) of a single individual over the flow-period of interest; blocking was employed to increase the power of the experiment. We used the conventional significance level of $\alpha = 0.05$ in all analyses. When *a posteriori* multiple comparisons were made, we also used an overall α -level of 0.05. Data entry and machine computations were performed using Quattro Pro 3.0 (Borland International Inc., Scotts Valley, CA, USA) and SYSTAT 5.0 (SYSTAT Inc., Evanston, IL, USA). Multiple comparisons tests were conducted by hand using procedures from Zar (1984).

3. Results

a. Observation of response to oscillatory flow and sediment transport by intertidal sandflat macrofauna. Tables 2 and 3 are a summary of the behavioral repertoire of the twelve sandflat species. The flow and sediment transport conditions (based on our visual observations) are arranged in order of increasing flow strength and sediment flux from no fluid motion to highly energetic conditions (peak fluid velocities $\geq 30 \text{ cm s}^{-1}$), beyond which it was difficult to see the organisms in the working section because of high concentrations of suspended sediment. Although the sand from Cape Henlopen is relatively clean and well-sorted ($< 1\%$ silt-clay by weight), fine material in the erodible layers of the top few millimeters of the bed is easily resuspended and visibly clouds the water. Flocculent and detrital material begins to move in flows as low as $6\text{--}8 \text{ cm s}^{-1}$ maximum velocity. Initiation of bulk sediment motion occurred as bedload transport with ripple formation at $\approx 17 \text{ cm s}^{-1}$ freestream velocity. Suspension of sand grains from ripple crests began at $\approx 20 \text{ cm s}^{-1}$ freestream velocity. In high flows, erosion and suspension of the silt-clay fraction of even the top two millimeters can easily account for the suspended sediment concentrations (e.g., 100 mg l^{-1} vertical average) we have previously measured in the water tunnel (Fig. 2 in Turner and Miller, 1991b).

There is a remarkable disparity between behavior observed in still water and that observed in oscillatory flow (Tables 2 and 3). From still water to even gentle

Table 2. Response of Cape Henlopen worms to oscillatory flow and sediment transport. Codes for feeding activities based on literature reports cited in text are: Sc, scavenger; SDF, surface deposit feeder; SF, suspension feeder.

Species, common name, and further taxonomic distinction	Feeding mode(s)	Oscillatory flow and sediment transport conditions			
		No flow, still water	Low oscillatory flow	Bedload transport on rippled bed	Bedload and suspended load
Phylum Annelida, Class Polychaeta <i>Diopatra cuprea</i> , Plumed worm, Family Onuphidae	Sc	Worm at tube cap opening, flicking tentacles; captured food drawn into tube; maintenance of tube cap ornamentation	Can trap food particles and tube material as it moves by in flow	Worms hold detritus seeming to block tube cap opening. Worms occasionally extend 2–3 mm out of tube to sweep away sediment accumulating at base of tube cap	High suspended load
<i>Marenzelleria jonesi</i> , Red- gilled mud worm, Family Spionidae	SDF	SDF with palps held close to bed, occasional lashing	Palps flap back and forth on bed, with some apparent ability to control and pick up particles. No coiling or raising of palps above bed	Unable to SDF, tentacles (when not withdrawn) flap uncontrollably in oscillatory flow	Not visible
<i>Pista palmata</i> , Beard worm, Family Terebellidae	SDF	SDF with crown of tentacles, within 10 cm of base of tube	SF with helically coiled palps. At low flow or times of flow reversal, palps may be in contact with bed and pick up particles	Percent of time SF increases with bed stress, SF exclusively by initiation of bedload	palps on both halves of wave cycle
<i>Spio setosa</i> , Mud worm, Family Spionidae	SDF and SF	SDF by lashing bed			
<i>Spiochaetopterus oculatus</i> , Glassy tube worm, Family Chaetopteridae	SF, SDF	SDF with two palps near base of tube			
Phylum Hemichordata <i>Saccoglossus kowalevskii</i> , Acorn Worm, Class En- teropneusta	SDF	SDF with proboscis within cm's of burrow	Only tip of proboscis extended, burrow opening traps bedload material; feeds on small flocculent material after transport event		

Table 3. Response of Cape Henlopen arthropods and molluscs to oscillatory flow and sediment transport. Codes for feeding activities based on literature reports cited in text are: Sc, scavenger; SDF, surface deposit feeder; SF, suspension feeder.

Species, common name, and further taxonomic distinction	Feeding mode(s)	Oscillatory flow and sediment transport conditions		
		No flow, still water	Low oscillatory flow	Bedload transport on rippled bed suspended load High suspended load
Phylum Arthropoda, Class Crustacea				
<i>Emerita talpoida</i> , Mole crab, Order Decapoda	SF	Swimming and burrowing, little time feeding	SF with second antennae held upright in flow, posterior toward upstream flow direction at time of burial; crabs perpendicular to flow SF in both halves of the wave cycle by rotating second antennae	
<i>Pagurus longicarpus</i> , Hermit crab, Order Decapoda	Motile Sc and SDF	SDF with chelae, relatively little movement	Decreased SDF "scooping" rate with chelae, increased rate of movement, constant after initiation of bedload	
Phylum Mollusca				
<i>Ensis directus</i> , Razor clam, Class Bivalvia	SF	SF, siphons extended ≈ 3 mm above edge of shell	Continues to SF at all flows and fluxes, siphons ≈ 1 mm above bed and shell edge; siphonal tentacles close-in at high fluxes	
<i>Ilyanassa obsoleta</i> , Mud snail, Class Gastropoda	Motile Sc and SDF	Sc and SDF on sediment surface	Decreases rate of movement, eventually burrowing into bed with just siphon and tip of shell visible; little movement at high transport rates; subsurface particle feeding observed though changes in feeding rate unknown	
<i>Mercenaria mercena-</i> <i>ria</i> , Hard clam, Class Bivalvia	SF	SF, siphons extended above bed	Continues to SF even at high sediment fluxes with increased production of pseudofeces, siphons kept open near sediment surface, though not as widely in higher flows	
<i>Tagelus plebeius</i> , Stout razor clam, Class Bivalvia	SF	SF, siphons extended above bed	Continues to SF even at high fluxes, siphons kept open at sediment surface	

oscillatory flows, there is a noticeable, qualitative change in the feeding behavior or mode of all organisms. Close examination of the tables is necessary to fully assimilate the results of these experiments.

Among the Cape Henlopen polychaetes studied, *Marenzelleria jonesi* and *Pista palmata* are obligate deposit feeders (see Dauer *et al.*, 1981 and Maciolek, 1984, and for other terebellids, Fauchald and Jumars, 1979, respectively). Although differing greatly in size (e.g., <1 cm to >10 cm in tentacle reach, respectively), both had apparent difficulty in controlling palps and picking up particles in high flows. *Pista palmata* seemed entirely unable to feed in the highest flows. *Marenzelleria jonesi* may have had more success, but no coiling of palps or raising of them above the bed was observed (as seen for *Streblospio benedicti*, Dauer, 1984). Two suspension feeders, *Spio setosa* (see Dauer *et al.*, 1981 and Muschenheim, 1987a,b) and *Spiochaetopterus oculatus* (Turner and Miller, 1991a), have similar responses to flow despite belonging to different polychaete families. Both switched from surface deposit feeding to palp-coiling suspension feeding in low flows. This behavior was maintained even in the highest flow and sediment flux rates used.

The plumed worm *Diopatra cuprea* is an omnivorous scavenger (e.g., Fauchald and Jumars, 1979) and a well-studied member of east-coast benthic communities (Woodin, 1981; Bell, 1985; Luckenbach, 1986, 1987). Under low and moderate flow conditions (Table 2), worms were capable of catching food particles (here, commercial fish food pellets) and material for tube-cap ornamentation (e.g., bits of sea lettuce *Ulva lactuca*). In the highest flow, worms close the tube cap opening with pieces of detrital material and capture of such material was less frequently observed. Worms with tube cap openings near the bed occasionally emerged from their tube cap and swept away sediment accumulating near its base.

The acorn worm *Saccoglossus kowalevskii* is another obligate surface deposit feeder (Miller, 1992). In still water, the worm uses its proboscis to feed in a rayed feeding trace several centimeters in diameter (Table 2). In flows that transport flocculent or sand particles, the proboscis when exposed remains near the burrow opening. When the proboscis is fully withdrawn into the burrow at high flows, the opening traps particles in bedload transport, though we were unable to observe directly consumption of this material. However, we did note that feces produced following bedload transport were darker in color and apparently composed of finer material than feces produced in still water that were composed mostly of fine sand grains. Upon cessation of flow, the worm quickly (within minutes) returns to its still water mode, feeding on flocculent matter deposited on the bed near the burrow opening.

Emerita talpoida is the common mole crab inhabiting east coast U.S.A. ocean beaches. It normally lives in the highly energetic swash zone of the beach face as does its west-coast congener *Emerita analoga* (Efford, 1966; Siegel, 1984). Under the simpler flow regime in the water tunnel (Table 3), the mole crab readily burrows in

the bed and begins suspension feeding with its feathery second antennae. Mole crabs burrowed into the bed "abdomen-first" with their in abdomen in the upstream flow direction at instant of burrowing. Mole crabs that burrowed perpendicular to the flow axis (i.e., burrowed near slack flow) can feed in both halves of the wave cycle by rotation of the second antennae through 180°.

The other suspension feeders studied, *Ensis directus* (see Holland and Dean, 1977 and Shumway et al., 1985), *Mercenaria mercenaria* (see Turner and Miller, 1991b) and *Tagelus plebeius* (see Swennen et al., 1985 and Howe et al., 1988) had similar responses (Table 3): these species continued to feed as indicated by the production of feces and pseudofeces at high flows and sediment fluxes with siphons open, shielded by siphonal tentacles and held close to the level of the sediment surface, lower than in still water. More detailed results and discussion of the responses of *Mercenaria mercenaria* may be found in Turner and Miller (1991b).

Figure 1A and B depicts quantitative changes in behavior of two sandflat species *Ilyanassa obsoleta* and *Pagurus longicarpus*, both motile, epifaunal scavengers. As neither species makes fecal pellets, we have relied on proxy measurements of feeding behavior. The feeding biology of *Ilyanassa obsoleta* has been extensively studied (e.g., Curtis and Hurd, 1981; Bianchi and Levinton, 1981; Dimock, 1985; Levinton et al., 1985; Cranford, 1988). Low oscillatory flows stimulate crawling, and crawling is much reduced at flow speeds sufficient to erode and suspend sediment (Fig. 1A). In these conditions, snails burrow into the sediment leaving only the siphon and tip of the shell visible (Table 3) but are still able to deposit feed on subsurface grains (pers. obs.). The literature also contains much information on the hermit crab *Pagurus longicarpus*; see Auster and Crockett (1984) and Gibbons (1984). Crawling by *Pagurus longicarpus* exhibits a different response: crawling rate initially increases with flow speed, then remains constant (Fig. 1B). Scooping or pinching of the sediment surface with the chelae to collect particles (an indirect measure for deposit feeding rate) decreases in rate with increased flow speed. Crabs remain on the sediment surface in high transport conditions but are apparently unable to deposit feed.

b. Observation of response to oscillatory flow and sediment transport by continental shelf macrofauna. Table 4 is a summary of the behaviors observed with the five shelf species arranged in the same format as the previous table of Cape Henlopen species. The serpulid *Serpula vermicularis granulosa*'s crown of tentacle filaments (≈ 1 cm across and 1 cm above the bottom) remains deployed but depressed by drag forces in high flow, and it is unlikely that normal feeding is possible (e.g., Riisgård and Ivarsson, 1990). *Terebella rubra* was unable to deposit feed successfully at high flows with some or all of an individual's tentacles flailing (2–3 cm) in the oscillating flow. References to the feeding biology of species similar to these two may be found in Fauchald and Jumars (1979). The brittle star *Amphipholis squamata* appeared to suspension feed at low oscillatory flow, but was also unable to control feeding

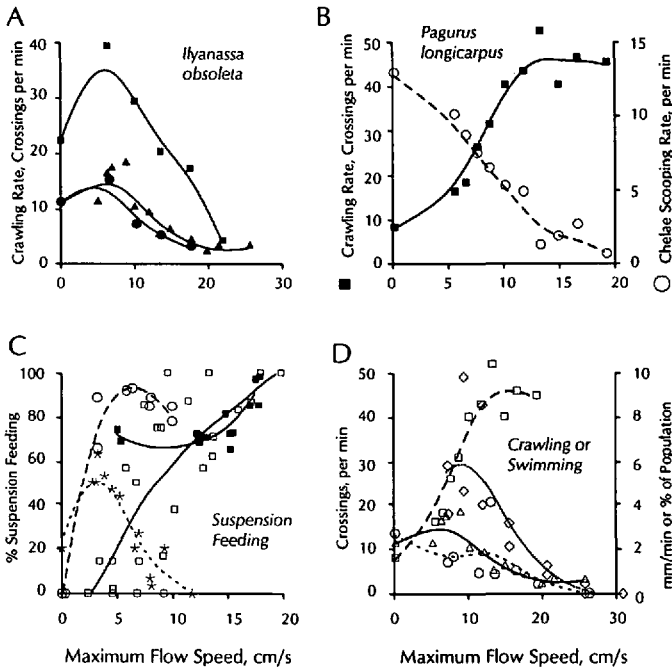


Figure 1. Crawling and feeding behavior versus maximum oscillatory flow speed in laboratory water tunnel. Note species' responses variously increase with flow speed, decrease or have a unimodal shape. Note also that behavior changes occur over a wide range of flow speeds. (A) Crawling rate of mud snail *Ilyanassa obsoleta* as number of snails per minute from a population of 40 crossing a imaginary line across the water tunnel. Data were obtained from runs on three days (various symbols) at temperatures of 25–29°C. Flow sequences used were both in increasing flow and random flow order and were preceded by a 10 min acclimation period. (B) Crawling rate of hermit crab *Pagurus longicarpus* for a population of 20 crabs, (squares, solid line) and chelae scooping rate per crab (circles, dashed line), a proxy measure of deposit feeding, as mean of five haphazardly chosen crabs. Temperature was 27°C and the flow sequence was random following a 15 min acclimation period for each flow-period. (C) Percent of time (open symbols) or percent of population (filled symbols) suspension feeding. Data are for: *Spiochaetopterus ocellatus*, squares and solid lines, Turner and Miller, 1991a, Figures 2 and 3; *Spiro setosa*, circles and dashed line, hysteresis experiment; and *Amphipholis squamata*, five-point stars and short dashed line, Bock and Miller (in prep). (D) For the left axis (crawling rate, crossings min^{-1}) data are: *Ilyanassa obsoleta*, triangles and solid line; *Pagurus longicarpus*, squares and dashed line. For the right axis: *Echinarachnius parma* crawling rate in mm min^{-1} from time-lapse images obtained by computer-controlled CCD camera at 12°C, circles and short dashed line, Bock and Miller, in prep., and *Emerita talpoida* percentage of population swimming, diamonds and dotted line, Turner (1990). In all panels, lines are distance-weighted least-squares fits to points (numbering 5–25) by SYSTAT using a tension parameter of 0.05. We visually judged this procedure to give an appropriate smoothed representation of the response in light of experimental scatter.

Table 4. Response of Mid-Atlantic Bight continental shelf macrofauna to oscillatory flow and sediment transport.

Codes for feeding activities based on literature reports cited in text are: P, predator; SDF, surface deposit feeder; SF, suspension feeder; SSDF, sub-surface deposit feeder.

Oscillatory flow and sediment transport conditions						
Species, common name, and further taxonomic distinction	Feeding mode(s)	No flow, still water	Low oscillatory flow	Bedload transport on rippled bed	Bedload and suspended load	High suspended load
Phylum annelida, Class Polychaeta						
<i>Serpula vermicularis</i> <i>granulosa</i> , Feather- cluster worm, Fam- ily Serpulidae	SF	SF with crown of tentacular filaments		Continues to SF, even when crown is severely deformed, depressed in one-half original width by flow		
<i>Terebella rubra</i> , Beard worm, Family Tere- bellidae	SDF	Tentacles rayed over sediment surface (within 1-2 cm of tube), particles move up or with tentacle into tube	Tentacles wave to and fro with oscillatory flow (without apparent ability to control); when tentacles contact bed pickup of particles is possible		Most worms retracted into tube, but visible tentacles flail in flow without contacting bed	
Phylum Echinodermata						
<i>Amphipholis squa-</i> <i>mata</i> , Brittle star, Subclass Ophiu- roidea	SDF and SF	Arms held on sediment surface	Arms held in flow, waving to and fro	Arms swept to and fro with current	No longer able to control movement of arms when swept by current	
<i>Astropecten america-</i> <i>nus</i> Starfish, Sub- class Asteroidea	P	No visible change in behavior under various flow and transport conditions				
<i>Echinarachnius</i> <i>parma</i> , Sand dollar, Class Echinoidea	SDF and SSDF	Bulldozing just below sediment surface	Bulldozing at reduced rate			Movement stops

appendages in higher flows. Suspension-feeding by other brittle star species has been relatively well studied, e.g., Warner and Woodley (1975) and LaBarbera (1978). The sand dollar *Echinarachnius parma* burrowed into the sediment but moved laterally with decreasing rates in flow transporting sediment (see also O'Neill, 1978; Telford, 1981; Ghiold, 1983; Ellers and Telford, 1984; Telford, 1990). With the notable exception of *Astropecten americanus* (for related species, see Schmid, 1981; Schmid and Schaerer, 1981; Penchaszadeh and Molinet, 1983; and Nojima, 1989), all species from both Cape Henlopen and the shelf alter behavior between no- (and low-flow) and the higher flow conditions.

c. Species responses versus oscillatory flow speed. In Figure 1C and D, we superimpose data from this and other studies (Turner, 1990; Turner and Miller, 1991a,b; Bock and Miller, in prep.), all plotted as a function of the maximum oscillatory flow speed. Although collected by different investigators at various times, these data were all obtained from organisms in our water tunnel and with a sand bed from Cape Henlopen. With increasing flow speed, all three species of suspension feeder depicted in Figure 1C (*Spiochaetopterus oculatus*, *Spio setosa*, and *Amphipholis squamata*) initially increase the percent suspension feeding. At higher flow speeds, the intertidal species (both polychaetes) continue to suspension feed. For *Spiochaetopterus oculatus* at low flows, the percent of the population suspension feeding (open squares, solid line) and the percent of an individual's time spent suspension feeding (filled squares, solid line) differ substantially (indicating heterogeneous behavior, see Levinton, 1991 and below), but in higher flows the difference is negligible. For *Spio setosa*, the hysteresis in suspension feeding is evident in the vertical displacement of circles about the dashed, smoothed curve in Figure 1C (see also Fig. 4 below). There is a definite unimodal character to the brittle star curve, with little suspension feeding exhibited in flows strong enough to move the bed. This may be generally related to the fact that *Amphipholis squamata* is a shelf species, or that its feeding appendages are ≈ 4 cm or $2-3\times$ longer, and thus subject to greater drag and difficulty of control than those of the smaller *Spio setosa* (2-3 cm) or even the somewhat larger *Spiochaetopterus oculatus* (3-4 cm).

Figure 1D shows the composite response in motility measured as crawling rate (*Echinarachnius parma*, *Ilyanassa obsoleta*, *Pagurus longicarpus*) and swimming (*Emerita talpoida*). With the exception of the hermit crab, there is a general decrease in movement with increasing flow. For both burrowing species, there is relatively little movement in still water or in flow capable of moving sediment (see also Fig. 1A).

d. Quantitative responses of Spio setosa and Terebella rubra. Figures 2 and 3 present the results of the persistence and consistency experiments. *Spio setosa* is a deposit feeder in still water and a facultative, palp-coiling suspension feeder in oscillatory flows (references cited above and Table 2). *Terebella rubra* is an obligate deposit

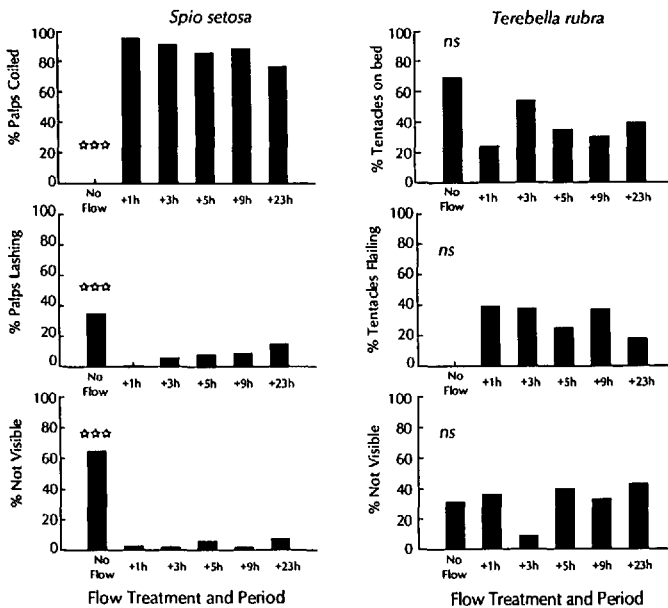


Figure 2. Results from persistence experiment illustrating temporal variability under constant oscillatory flow. Ordinate values are the mean percentage of time observed exhibiting each indicated behavior. Worms ($n = 19$ for *S. setosa*, 6 for *T. rubra*) were scan sampled (Martin and Bateson, 1986) every two minutes for 40 min, resulting in 20 observations per worm for each flow period. Symbols indicate the probability from a Friedman's test (Zar, 1984) of differences in response among flow periods: ns, $P > 0.05$; ***, $P \leq 0.001$. Flow and sediment transport during the flow periods were: No flow, maximum speed 0 cm s^{-1} ; +1 to +23h, Low oscillatory flow, no movement of bed material, maximum speed 6.8 cm s^{-1} .

feeder (Table 4). The persistence experiment was designed to determine if behaviors exhibited in short-term experiments (Tables 2 and 4) were maintained under constant flow conditions of nearly a day. For *S. setosa*, statistical tests reported some significant differences among flow conditions (Fig. 2), but further analysis with multiple comparisons tests show these are largely attributable to differences between no flow, and the low flow conditions, periods designated +1 h to +23 h, with behaviors similar among these low flow periods. Thus, changes in feeding behavior are not simply short-term, ephemeral responses to increased flow. The response and lack of change can be attributed to flow only: no sediment or flocculent material was observed moving at speeds used in this experiment. For *S. setosa*, multiple comparisons indicate a decrease in percent of palp coiling at +23 h and continuing to the following period (at same speed in the following experiment). This percentage increased rapidly when flow was then increased in the consistency experiment (see below).

The consistency experiment (Fig. 3) sought to determine if the response changes as flow and sediment flux is increased over relatively short (i.e., minutes) time scales.

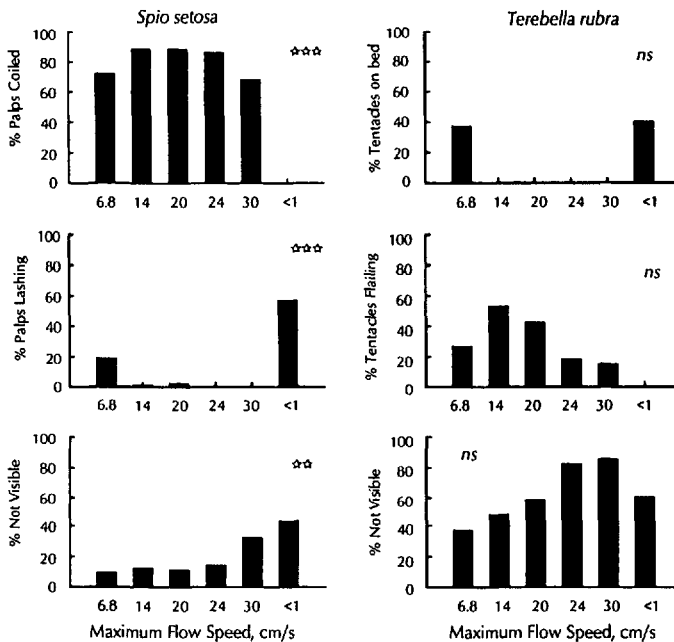


Figure 3. Results from consistency experiment illustrating behavioral variability under various oscillatory flow speeds. Ordinate values are the mean percentage of time observed exhibiting each indicated behavior. Worms ($n = 19$ for *S. setosa*, 6 for *T. rubra*) were scan sampled (Martin and Bateson, 1986) every two min, resulting in 10 observations per worm for each consecutive flow period, except that one scan was missed in the highest flow period because of difficulty in seeing organisms in high suspended sediment. Symbols indicate the probability from a Friedman's test (Zar, 1984) of differences in response among flow periods: ns, $P > 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$. These observation periods immediately followed those in the persistence experiment (Fig. 2). Flow and sediment transport during the flow periods were: maximum speed 6.8 cm s^{-1} , No movement of bed material; 14 cm s^{-1} , Flocs roll, detritus suspended; 20 cm s^{-1} , Feces and detritus in bedload; 24 cm s^{-1} , Widespread bedload transport; 30 cm s^{-1} , Sand suspended; $<1 \text{ cm s}^{-1}$, Flow stopped, suspended matter settling, little residual flow.

The flow speeds used (maximum speeds of 6.8 to 30 cm s^{-1}) include all the flow conditions listed in Tables 2, 3 and 4, but are described in more detail in the Figure 3 caption. Again for *Spio setosa*, significant results reflect primarily the difference between flow treatments and the no-flow ($<1 \text{ cm s}^{-1}$) period at the end of the experiment. Worm behavior, as percentage of time spent suspension feeding, is not substantially altered (range, 68–88%) under widely varying flow, suspended sediment concentrations and fluxes. Regardless of the high concentration of suspended matter above the bed (not measured, but typically $\approx 200 \text{ mg l}^{-1}$, Turner and Miller, 1991b) that now begins to settle (and will do so for the next hour), suspension feeding ceases (0% of time) and deposit feeding resumes (57%) immediately when flow is stopped (i.e., at $<1 \text{ cm s}^{-1}$, Fig. 3). For *Terebella rubra*, the results in Figures 2 and 3

are generally the same with largest differences between flow and no-flow periods. There is a trend to cease deposit feeding and withdraw into tubes in higher flow conditions. However, even the large differences in percentages among periods were not statistically significant. Closer examination of the data reveals that the lack of significant results is due to individual worms responding differently among the flow treatments. The percentages reported in Figures 2 and 3 are averages across individuals differing in behavior, thus adding a significant component of variance among individuals. This is interaction in statistical jargon, and it is well-known to reduce the statistical power of unreplicated blocked designs such as used here (Zar, 1984).

The results of the hysteresis experiment are presented in Figure 4. Statistical tests reported here compare virtually identical imposed flow conditions (though not flux or suspended sediment concentration) on the increasing and decreasing legs of varying flow conditions. For *Spio setosa*, the only significant differences are at low flows, with increased percentage of time suspension feeding on the decreasing flow leg at 6.4 cm s^{-1} and deposit feeding, $< 1 \text{ cm s}^{-1}$. For *Terebella rubra*, significant differences appear in deposit feeding at equal or higher flow speeds of $6.4\text{--}16 \text{ cm s}^{-1}$. For both species, these results indicate an increased feeding response in both suspension and deposit feeding on the decreasing flow leg of the experiment.

4. Discussion

a. Summary of general responses. As noted above, there is an obvious difference between behavior observed in still water and that observed in oscillatory flows and sediment fluxes. From still water to even low oscillatory flows, there is a conspicuous, qualitative change in the feeding behavior, position of feeding appendage, feeding mode or motility of most organisms (Tables 2, 3 and 4). Such a rapid response (see also Levinton's, 1991 observations of *Macoma* species) would be expected from organisms like surface deposit and suspension feeders which are both in intimate contact with the flow and ultimately dependent on it to supply food particles. Responses seem triggered by the flow itself (i.e., no movement of bed material, Figs. 2–4) and relatively low flux rates of particles (e.g., Taghon *et al.*, 1980). Large changes in bulk sediment transport rate and mode have comparatively less effect on observed behaviors (Tables 2 and 4, Fig. 3). Thus there is a modulation of behavior, but no qualitative change in response to movement of bedload particles or their resuspension at higher bed stresses. In fact, it is somewhat remarkable that most organisms continue to feed (or appear to attempt to feed) even at the high flow and sediment suspension rates that nearly obscure observations. Taken together, these results further confirm the widespread, across species and functional group, observation of a definitive behavioral response to flow and sediment flux (e.g., False Bay regions species, Nowell *et al.*, 1989; Levinton, 1991). With the data presented here, we have observed all surface-dwelling, macrofaunal members of a benthic community at

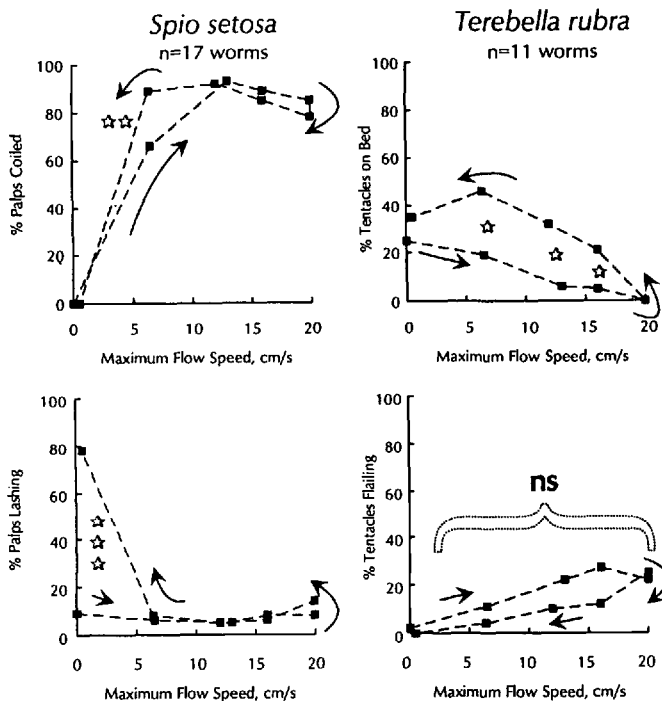


Figure 4. Hysteresis experiment results illustrating differences in behavior at comparable flow speeds. Ordinate values are the mean percentage of time observed exhibiting each listed behavior; abscissa is the maximum oscillatory flow speed. Worms ($n = 17$ for *S. setosa*, 11 for *T. rubra*) were scan sampled (Martin and Bateson, 1986) every two minutes for 20 min, resulting in 10 observations per worm for each consecutive flow period. Arrows and dashed lines indicate the temporal sequence of increasing and decreasing flow legs. Stars indicate significance of Wilcoxon's signed ranks test (Hollander and Wolfe, 1973) for comparable flow periods: ns, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$. For each flow period, flow and sediment transport conditions were: Increasing leg: maximum speed 0 cm s^{-1} , No flow, no movement of bed material; 6.5 cm s^{-1} , Flocs as bedload; 12 cm s^{-1} , Flocs suspended, feces in bedload; 16 cm s^{-1} , Bedload at ripple crests; 20 cm s^{-1} , Bedload over 80% of bed, tubes eroding, ripples forming. On the Decreasing leg: 16 cm s^{-1} , Bedload at ripple crests, much suspended matter; 12 cm s^{-1} , Ripple crests moving only at peak stress; 6.5 cm s^{-1} , No movement on bed; 0 cm s^{-1} , Fine particles still suspended, little residual flow.

Cape Henlopen. Statements regarding the widespread existence of a response to flow and its variety and relationship to functional morphology can be thus drawn convincingly from our data set.

Most of the organisms studied above live and feed entirely within the wave boundary layer (see values in Table 1), though feeding appendages of the largest suspension feeders, the mole crabs and brittle stars, extend well above the boundary layer into the outer flow. The thickness of the wave boundary layer in most of our experiments is constant ($< 2 \text{ cm}$ at its thickest point in time) because the friction

coefficient is here only a function of the roughness parameter, not the Reynolds number. This thickness and velocity gradients in the boundary layer apparently do not constrain feeding mechanics: palp-coiling *Spiochaetopterus oculatus* at 3 cm above the bed atop their glassy tubes experience the outer flow, while *Spio setosa*, using apparently the same particle capture structure and presumably mechanisms are well within the wave boundary layer (our population fed within 2 cm of the bed, see Muschenheim, 1987a,b). Based on their observation and previous studies (Taghon et al., 1980; Dauer et al., 1981; Muschenheim, 1987a,b), Turner and Miller (1991a) conclude that palp-coilings works effectively in both steady and oscillatory flows because particle capture is a relatively rapid process. In low steady flows, boundary layer and particle settling dynamics may create a near-bed gradient in particle concentration with regions in enhanced flux and particle food quality (Muschenheim, 1987a,b). For tentacle feeders generally, flow-induced drag on feeding appendages may be a important cue for mode-switching (e.g., in *Spiochaetopterus oculatus*, Turner and Miller, 1991a) or a factor limiting deposit feeding (e.g., *Pista palmata* and *Terebella rubra*, this study). Previous results (Taghon et al., 1980) and the spionid and terebellid results discussed below indicate that both flow and particle flux have roles to play in determining behavior. Our observation of relatively little animal movement in flow capable of moving sediment (Fig. 1A, B and D) is consistent with a widespread pattern of decreased motility in moderate and high flows; see similar results by Nowell et al. (1989) for the bivalves *Macoma nasuta* and *Tranzenella tantilla*.

b. Specific characteristics of response as illustrated by Spio setosa and Terebella rubra. Overall, these quantitative results (Fig. 2, 3 and 4) support the conclusions drawn from the analysis of Tables 2, 3 and 4. Though based on only two species, the results of these experiments suggests that the responses to oscillatory flow presented in the tables are not transient responses. The consistency of response under increasing flow also supports the conclusion that there is a distinct change in behavior from still water to low flow, but that at higher flow, responses are a modulation of feeding behavior, rather than a qualitative change. The changes in behavior or lack thereof in these experiments (Figs. 2–4) may reflect either a response to flow speed or particulate flux. For example, for *Spio setosa*, the moderate percent of palp coiling at +23 h (and continuing to the next experiment) increased rapidly when flow was increased in the consistency experiment (6.8 to 14 cm s⁻¹, Fig. 3). Both species rapidly resumed still water feeding modes when flow was stopped (Fig. 3 and 4) though substantial amount of particulate material remained in suspension (and settles as a vertical flux for up to an hour) throughout the observation interval. A similarly rapid response to flow speed and direction has been demonstrated by Trager et al. (1990) for the barnacle *Semibalanus balanoides*.

Both species show evidence for an asymmetrical response (Fig. 4) to increasing

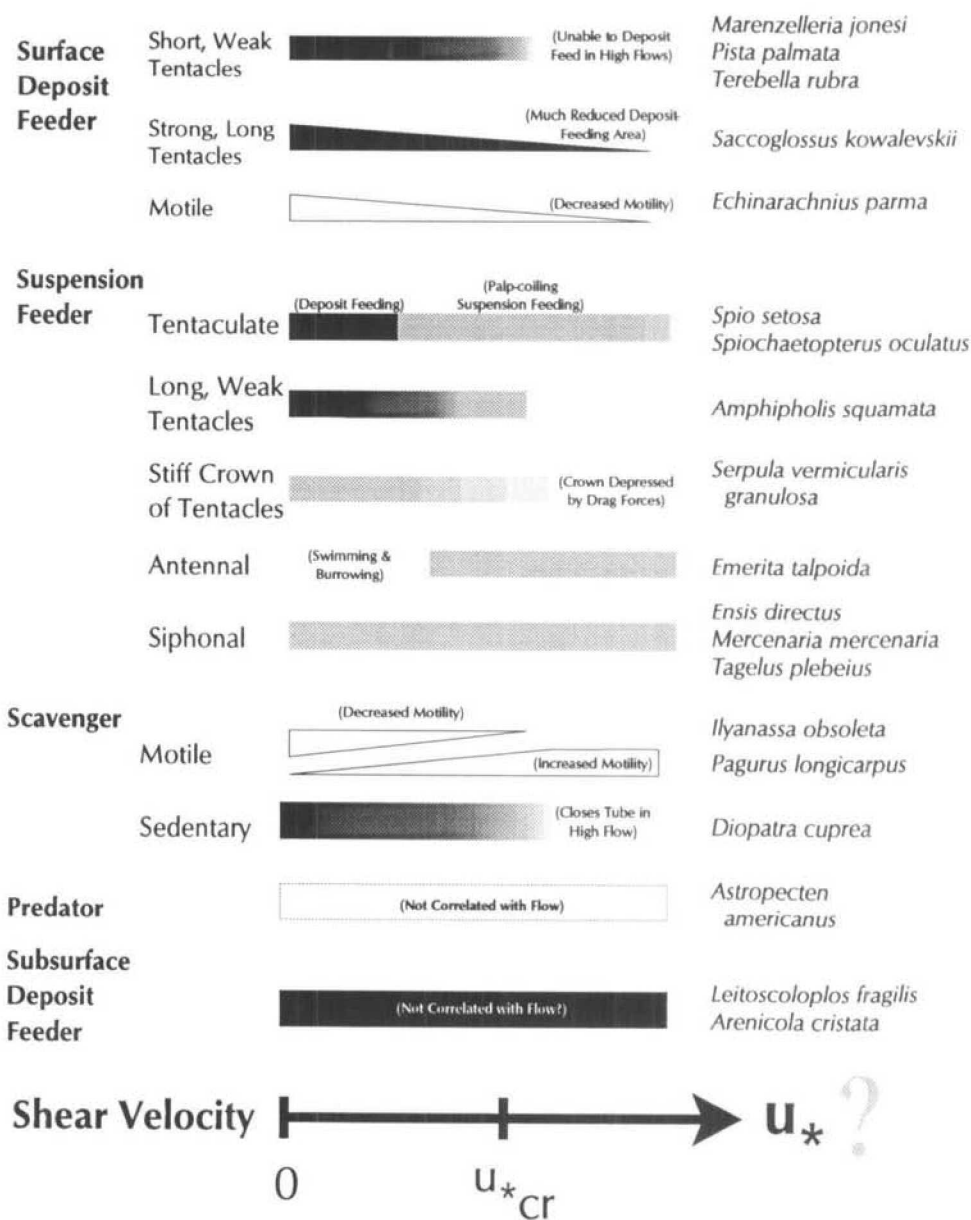


Figure 5. Graphical model of benthic microphages' response to flow shown against increasing bed stress, parameterized as u_* . See text for discussion of each group and species. Black indicates deposit feeding, gray, suspension or flux feeding, white, motility. Width or shading of bar indicates relative magnitude observed in our study. Note that most variability, in feeding mode within a species and among all species, is seen in the range of shear velocities below that needed to move bulk sediment (u_{*cr}). Though not the subject of any recent flow studies, subsurface deposit feeders (two species present at Cape Henlopen are identified, Bianchi, 1988) are thought to be relatively unaffected by flow and sediment transport (Miller *et al.*, 1984) except as it results in eventual burial or removal of sedimentary organic matter. The choice of bed stress as the horizontal axis is somewhat arbitrary since bed stress covaries with flow and sediment flux in the field, in our experiments and in most laboratory experiments to date. Results of experiments to uncouple flow and sediment flux (described in text) should reveal which parameter (e.g., flow speed, bed stress, bedload or suspended load flux) is most appropriate for the abscissa.

and decreasing flows, clearly indicating that flow and horizontal flux (not solely flow, concentration or vertical flux) are the determinants of behavior. A similar conclusion regarding the importance of particulate flux was reached by Taghon *et al.* (1980) for several spionid species, but their lowest particle concentrations were far below those typical of our water tunnel (see, Turner, 1990 for data). Turner and Miller (1991a) concluded that *Spiochaetopterus oculatus* exhibited no hysteresis, though the flow sequence used (in which both stroke and period were varied) may have obscured all but the most dramatic differences. Similarly, no hysteresis was observed by Levinton (1991) with *Macoma secta* over increasing and decreasing flow sequences. The question of which fluid-dynamical parameters determines behavior must apparently be examined experimentally for each species of interest.

c. Synthesis of response with respect to functional group and morphology. The modulation of feeding behavior is species and functional group specific (Tables 2, 3 and 4), and is generally seen as a change in position or rate of movement of the particle collecting appendages (Fig. 5). Organisms with one or two muscular feeding appendages continue to feed (e.g., *Emerita talpoida*, *Spio setosa* and *Spiochaetopterus oculatus*), while those with a crown of flaccid tentacles cannot (e.g., *Pista palmata* and *Terebella rubra*). Another terebellid polychaete, *Euploymnia heterobranchiata*, is similarly unable to deposit feed, and its tentacles stream in the local flow direction in steady flows (Nowell *et al.*, 1989). Even a stiff crown of tentacles, as in the *Serpula vermicularis granulosa*, may be so deformed by fluid drag forces that it is difficult to believe normal suspension feeding and particle capture is possible (Merz, 1984; Riisgård and Ivarsson, 1990). Organisms with large, strong tentacles feed at the sediment surface in a much restricted feeding area (*Saccoglossus kowalevskii*, but see also observations for *Macoma*, Levinton, 1991). Surface feeders with shorter palps (e.g., *Marenzelleria jonesi*) may have only limited success feeding at high flows. Organisms with long, thin palps coil them helically and capture particles in near-bed flux (*Spio setosa* and *Spiochaetopterus oculatus*, Turner and Miller, 1991a). For analysis and discussion of the diverse feeding responses of a number of spionid species including *Spio setosa*, see Taghon *et al.* (1980), Dauer *et al.* (1981), Dauer (1984), and Muschenheim (1987a,b). *Emerita talpoida* feed with their feathery second antennae in flows sufficient to transport sediment. *Spio setosa*, *Spiochaetopterus oculatus* and *Emerita talpoida* can rotate their feeding appendage to feed effectively in both halves of the wave cycle. Siphonate feeders maintain siphon tips (regardless of siphon length) just above the sediment surface and continue pumping (*Ensis directus*, *Mercenaria mercenaria*, Turner and Miller, 1991b, and *Tagelus plebeius*). Motile feeders may either increase (*Pagurus longicarpus*) or decrease (*Echinarachnius parma* and *Ilyanassa obsoleta*) movement rate. Although it is reasonable to expect surface deposit and suspension feeders to respond to changes in flow, it is less clear why there are only modest changes in behavior with dramatic changes in

sediment flux rate and transport mode (i.e., bedload to suspended load). Possible explanations include simple response to high fluid drag forces (e.g., burial in the bed by *Ilyanassa obsoleta*), or that transport rates so greatly exceed maximum consumption (e.g., Grant, 1983, 1985; Miller *et al.*, 1984; Miller and Sternberg, 1988) that any additional feeding response is impossible or non-advantageous. A sedentary omnivore (*Diopatra cuprea*) is able to capture food particles in low and moderate flow, but in high flows the tube opening is closed. *Astropecten americanus* is a predator with a propensity for burrowing beneath the sediment surface. Thus it is not surprising that this species showed no observable response to imposed flow treatments. The lack of response to near-bed flow by subsurface dwellers may be a general pattern, but this remains to be experimentally tested with, for example, species listed in Figure 5.

Response to flow is wide-spread and not unexpected from previous work (Taghon *et al.*, 1980; Nowell *et al.*, 1989; Hunter, 1989; Okamura, 1990; Trager *et al.*, 1990; Levinton, 1991; Taghon and Greene, 1992) concluding that hydrodynamic conditions are major determinants of behavior. However, its variability within conventional feeding guilds (i.e., deposit feeder, suspension feeder, scavenger, predator, e.g., Fauchald and Jumars, 1979) is surprising and clearly extends beyond the applicability of traditional terminology for certain groups (Fig. 5). Okamura (1990) noted such behavioral plasticity in suspension feeders and called for a revision of current paradigm regarding their feeding biology. In some cases, the still-water feeding mode must be considered largely a laboratory artifact (e.g., literature reports discussed in Turner and Miller, 1991a). Rather than creating new feeding modes or terms *de novo*, we suggest that using a label describing the feeding mode observed under some precise flow and transport regime, for example, at the initiation of movement of the sediment. This approach is straightforward and empirical and should be more appropriate than many present terms. Flows more energetic than that needed to move sediment do not seem to alter feeding mode, but only apparent success and time spent feeding (Figs. 2–4). Thus a term composed of this critical-flow feeding mode and a description of the form, position or function of the feeding appendage may be sufficiently accurate. For example, tentaculate deposit feeders observed in this study differ greatly in their response to flow. *Spio setosa* and *Spiochaetopterus oculatus* could be termed “palp-coiling suspension feeders” and “facultative deposit feeders” rather than simply “facultative suspension feeders.” *Pista palmata* and *Terebella rubra* could be distinguished from other tentaculate deposit feeders as “obligate splayed tentacle surface deposit feeders.” *Saccoglossus* exhibited a response to high flow and sediment transport similar to that seen for *Macoma* (Levinton, 1991). Though *Macoma* feeds with an (inhalant) siphon, its response to flow is much more similar to that of *Saccoglossus* (Table 2) than more typical siphonate suspension feeders (e.g., Table 3). Similarities in behavioral responses thus again seem much more closely related to feeding appendage morphology than *a priori* anatomical homology. *Echinarachnius parma*, *Ilyanassa obsoleta* and *Pagurus*

longicarpus are motile deposit feeders and scavengers but should be distinguished on the basis of their response to flow, for example, using compound terms such as "tardy rheokinesis" and "tachy rheokinesis." As discussed in Dauer *et al.* (1981), variation among populations or other intra- and inter-specific effects may continue to cause difficulty in assigning precise labels. For example, Dauer *et al.* (1981) observed a more varied response by the *Scolecopides viridis*, than we observed with *Marenzelleria jonesi*, a closely related species (see Maciolek, 1984). While based only on our observations (Tables 2, 3 and 4), this scheme holds considerable promise for more accurately categorizing species and for predicting responses of species similar to those studied to realistic flow conditions.

d. Implications for theory, experiment and modeling. Mechanistic theory of suspension feeding remains an active area of research. Shimeta and Jumars (1991) recently reviewed the literature and suggested new lines of inquiry. Because of the small length and short time scales involved in particle capture, much of the analysis conducted for steady flows will find application in oscillatory flows (Turner and Miller, 1991a). Hunter (1989) however shows a greater percentage of hydroid zooids feeding successfully in oscillatory than steady flows matched by mean flow speed and particulate flux. He hypothesizes that the difference may be attributable to reorientation of the colony in flow, fluid resampling, local depletion of particles or the reduced relative flow velocity experienced by the outer polyps as the colony flails in the oscillating flow. Turbulence effects, of which little is known at present, may be relatively more important in vertical fluxes across wave boundary layers. Holland *et al.* (1987) report that the suspension-feeding crinoid *Oligometra serripinna* did not reorient itself to flow reversals and that success in upstream versus downstream capture of particles differed by a factor of two. Temporal variation in flow and flux (and correlation between these variables) make it difficult to *a priori* predict which particle capture mechanism (Shimeta and Jumars, 1991) or combination thereof will maximize particle encounter rate. All of the initial published studies on microphagous feeding in oscillatory flow have dealt with suspension feeders (Holland *et al.*, 1987; Hunter, 1989; Trager *et al.*, 1990; Turner and Miller, 1991a,b). Although mechanistic theory for some deposit-feeding taxa (e.g., tentaculate deposit feeders, Jumars *et al.*, 1982; crustacean particle selection, Miller, 1984; sand dollars, Telford, 1990) has been published, experimental tests are rare (e.g., Self and Jumars, 1988). Theory integrating deposit-feeding mechanics with sediment dynamics, in particular, bedload transport (see Muschenheim, 1987a,b), has yet to be developed.

We find microphage optimal foraging theory wanting for several reasons. First, since it has been developed for a particular functional group (e.g., deposit feeder, Taghon *et al.*, 1978; Taghon, 1981; or the more general summary in Townsend and Hughes, 1981), it does not incorporate the changes in feeding mode, food source and particle type apparent from our observations. The general nature of published

models also precludes any specification of food capture mechanics or feeding appendage morphology now seen to be a necessary component. In conceptual terms, present models have a highly restricted, over-specified decision space for the forager that includes neither changes in feeding mode nor food source. Until these variables are included in models, we must be content to test models with organisms which have simple and highly predictable responses to flow, probably under constant, tightly controlled flow conditions in the laboratory. Even here, caution must be used when extrapolating from a single species or apparent functional group (Taghon and Greene, 1992). Note the range of flow responses exhibited by a single family of polychaetes (the Spionidae, Taghon *et al.*, 1980; Dauer *et al.*, 1981; Dauer, 1984; Muschenheim, 1987a,b). Current foraging theory predicts behavior in constant (Taghon, 1981) or steady-state (Brandon, 1991) conditions. This is inconsistent with the dynamic nature of the flow-sediment environment (Miller and Sternberg, 1988) and with the observation of rapid behavioral responses to that environment. New theoretical advances will have to be dynamic (as in Mangel and Clark, 1988) and permit a realistic behavioral repertoire.

There are several implications of these results for mass-balance (as opposed to optimality) modeling of benthic processes. First, to predict feeding behavior, one must allow for a change in particle type or bulk food composition as a function of flow. Current models include only a highly simplified, monolithic food type. Next, models of the forager-microbial resource dynamics have an unvarying feeding area (Miller *et al.*, 1984). Any realistic model must be dynamic, not static or steady state (e.g., Levinton and Lopez, 1977; Miller *et al.*, 1984) and include a wide range of time and space scales. The temporal evolution of the fluid and sediment dynamic environment as well as the rapid behavioral responses to it must be incorporated. Additional time scales of interest in the hours to days range include: response of the bedforms to flow, changes in egestion rate by deposit feeders (Miller, 1992) and change in food resource dynamics influenced by sediment microalgae and bacteria (Brandon, 1991). The smallest length scale of interest is probably that of an individual feeding area for deposit feeders (Miller *et al.*, 1984). The largest is determined by the ultimate upstream source of food particles, whether that be from within the same ripple as the feeding area or from meters away. This complexity suggests that considerable development of current modeling approaches will be required and that such refinement must be closely guided by experiment.

Major implications of this study for laboratory experimentation relate to individual organisms' variability and hysteresis in response to flow (see also Levinton, 1991). The differential response of *Terebella rubra* to flow treatments severely decreased the power of the nonparametric statistical analysis to the point where even large percentage changes were not judged significant (e.g., Figs. 2 and 3). Increasing sample size would obviously make the test more powerful, yet to completely account

for and remove the interactive effects would require a fully replicated design. It remains to be seen whether this is possible since experimental treatments must be imposed in some sequence (because there is only one water tunnel, or more generally one flow facility of a given design in any one laboratory) and observations must be taken at points in time within those treatments. The asymmetry or hysteresis exhibited by *Spio setosa* and *Terebella rubra* poses additional difficulties: results from one experimental series may not match those of presumably comparable runs with the same organisms and laboratory apparatus. Additional attention must be paid to the temporal sequence of an experiment and the flow history experienced by organisms in the laboratory (see also Jumars and Self, 1986). It is clearly possible to conduct experiments in simulated flow environments (e.g., Nowell *et al.*, 1989; Levinton, 1991; this study) in the laboratory, and it is probably necessary to do so to achieve the proper relative rates of major biological, geochemical and sedimentological processes (Nowell and Jumars, 1984).

In the field, as in the present experiments, flow and particle flux are highly correlated. In the water tunnel, the two can be uncoupled by armoring the bed and controlling the source and nature of suspended particles introduced, for example as done by Taghon *et al.* (1980) in their closed flume system. The method used by Turner and Miller (1991a), varying stroke and drive period independently should be combined with manipulation of the bed (e.g., armoring) and the composition of particles in suspension (e.g., filtering the return flow in a closed system, Taghon *et al.*, 1980) to better study the separate effects and interactions of fluid and sediment dynamical parameters. This experimental manipulation may yield results which help untangle flow from sediment flux effects. One possible explanation for individual differences and hysteresis is variability in flow and flux microenvironments. Nowell *et al.* (1989) observed the spionid *Pseudopolydora kempji japonica* to change feeding mode in response to changes in bed microtopography and flow microenvironments resulting from sediment ripple migration. Substantial spatial and temporal variation in flow on the organism's scale would be expected in our experiments, principally because of the evolution of bedforms in response to the flow, though this was not well characterized. The potential importance of flow and flux microenvironments clearly motivates development and application of new techniques that can quantify the flow and sedimentological microenvironment on centimeters and smaller length scales. This is a critical step toward understanding the role of bulk flow and flux and assessing the extent to which small-scale differences account for the individual and temporal variability noted in our experiments.

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