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## Chapter 11

# The Effects of Sediment Transport and Deposition on Infauna: Results Obtained in a Specially Designed Flume

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## Introduction

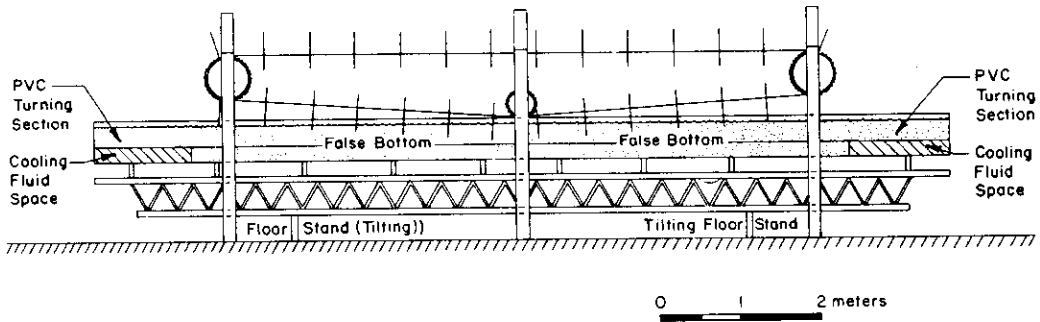
Surprisingly little is known about the effects of steady sediment transport or of natural rates of deposition on the process of deposit feeding. This situation persists despite the theoretical reasons for believing that sediment supply by physical processes in many environments is important or dominant in controlling food supply to individual deposit feeders (Miller et al. 1984), despite newly collected field evidence suggesting that sediment transport rate overwhelms processing rates by deposit feeders in environments of

(Saila and Pratt 1972) to more subtle "sediment-mediated" (Wilson 1981; Thayer 1983) effects of organisms on each other. Given the ubiquity of ripples and the importance of burial in applied and basic research, consideration of the fact that organisms in some environments go through repeated burial and erosion cycles is curiously rare in this literature. There have been no systematic field or laboratory treatments on the effects of ripple migration on infauna where geophysical as well as biological measures have been made. (See Goldring (1962), however, for an interesting discussion in a philological context.)

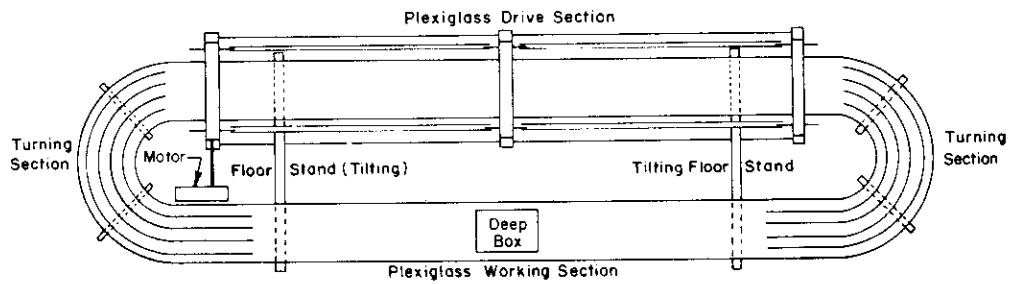
The apparent reasons for the paucity of information on the biological consequences of ripple migration in particular and sediment transport in general are that the relevant observations are difficult to make in the field, and that continuous, relatively natural sediment transport is difficult to produce in a laboratory system capable of supporting marine organisms. Most laboratory flow tanks or flumes heretofore used (e.g., Rhoads and Yingst 1978; Nowell et al. 1981; Vogel and LaBarbara 1978) have not been designed to allow continuous transport of sediments. Sediments once eroded either went down the drain or deposited in the return section. Flumes that have been designed to allow continuous sediment transport either have had inherent 3-dimensional flow due to their geometries or Froude number and wall effects due to their small sizes (e.g., Taghon et al. 1984; Jumars and Nowell 1984; Miller 1984) that made them unsuitable for production of ripples having natural geometries and dimensions. Conversely, the flumes in use by sediment dynamicists for the study of ripple migration generally either have been remote from sites of ecological expertise and sources of organisms for experimentation or unsuitable for use with corrosive salt water.

There was thus arguable need for a facility capable of maintaining continuous sediment transport in general and ripple migration in particular at a site convenient not only to ecologists and biological oceanographers but also to fluid dynamicists. We have built such a facility at the Friday Harbor Laboratories of the University of Washington, San Juan Island, Washington, U.S.A. We describe here the properties of the flume, together with initial observations of responses of several intertidal organisms to ripple migration. The ubiquity and diversity of responses by these common species underscores the importance of an appreciation of sediment transport phenomena in understanding organisms' interactions with their environments and with each other.

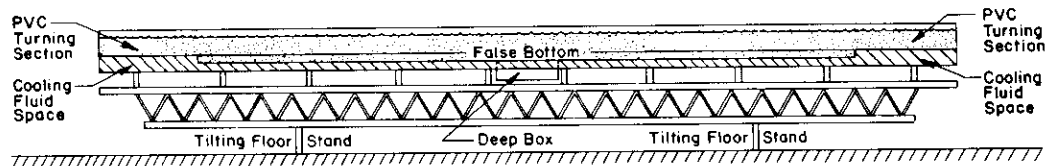
## SIDE VIEW OF DRIVE SECTION



## TOP VIEW



## SIDE VIEW OF WORKING SECTION



## Dimensions

Total length ~ 10m	Total width ~ 2 m
Total working section length ~ 8m	Working section width 0.75 m
Total height ~ 3m	Working depth 0 - 20cm

Figure 11.1: Side and elevation views of the flume and its working section. Because the flow can be driven in either direction, all aspects of the flume are symmetrical. The 2-channel laser-Doppler system can be traversed along the entire working section.

## Materials and Methods

### Flume design, construction and testing

The goal is to produce a one-dimensional flow and sediment-transport regime resembling that in nature. Ideally, flow velocity and sediment transport would vary only vertically, not in the along-stream or cross-stream direction. General considerations of flume design for bottom boundary-layer and sediment-transport simulation in biologically oriented experiments are discussed elsewhere (Middleton and Southard, 1984; Jumars and Nowell 1984; Nowell and Jumars 1986).

We ruled out impeller-driven pumps (e.g., Miller 1984) and propeller-driven flows for several reasons. They pulse inherently at low rates of the drive mechanisms, producing complex, unsteady 3-dimensional flows. Propellers and impellers also produce strong local shears, affecting the structure and dynamics of particle aggregates and increasing the likelihood that bacteria will be detached from suspended particles. These same shears and the close tolerance of moving parts damage larger organisms that emerge from sediments and circulate with the fluid. In 1979, we designed a circular, paddlewheel drive for a racetrack-shaped channel in an attempt to circumvent these difficulties and started construction in 1981. Boyer and Rhoads (1982) adopted our tentative design and retained the circular paddlewheel drive but allowed the blades to feather, thus reducing undesirable secondary circulation.

Our design effort included estimates of power required for high sediment transport rates. A paddlewheel of reasonable size could be used to impart substantial fluid momentum, but only if it turned rapidly or had a small clearance with respect to the flume bottom and sides. In either case, regions of unnaturally high shear would be produced. For this reason, we elected to distribute the drive mechanism, resembling the tread of a tracked vehicle, over one entire straight stretch of the racetrack (Fig. 11.1); comparatively mild shears are produced by distributing force over an area equivalent to the test section. The drive is built to feather, with 28 paddles of 67.3 by 47.7 cm of clear, 0.64-cm thick acrylic. The paddles reach an adjustable, nearest proximity to the bed at the center point of the return channel. Symmetry of the drive arrangement allows reversibility of paddle direction and thus the flow for simulation of tidal currents. The channel is uniformly 69.8 cm wide (inside diameter) and walled with clear acrylic of 1.91 cm thickness. A false bottom of acrylic, when in place, allows maximal flow depths of 30.5

cm. The working channel (straight section opposite the drive section) accommodates 7 additional cm of sediment throughout when the false bottom is removed, and a central (in the working channel) acrylic box of 76.2 by 50.8 cm accommodates an additional 20.3 cm of sediments for use of natural cores or for work with large or deeply burrowing organisms. The (inside) radius of curvature of the outer edge of each polyvinyl chloride (wall thickness of 0.64 cm) turning section is 122.2 cm. The bottoms of the working section and turning sections are lined with heat exchangers for temperature control. The false bottom of the drive side was designed to accommodate a conveyor belt occupying the full width and length of the return section, for potential use when transporting very delicate clay floccules and particle aggregates. Having the bottom (conveyor belt) and the paddles move in the same direction could reduce the shear across the intervening water column to zero.

For the present experiments all false bottoms indicated in Fig. 11.1 were in place, save that covering the deep box of the working section. Drive blades in the return section were set to be 1.3 cm from the false bottom at their closest approach. Before sediments were emplaced, we checked to see whether the simulated bottom boundary-layer structure was indeed primarily one dimensional. We filled the flume to 14 cm water depth. We then profiled mean velocity vertically and across the channel with a TSI (9100-8) two-axis, laser-Doppler velocimeter.

Approximately 500 liters of sediments were then dug from the uppermost, rippled sediments 1.3 m above MLLW in False Bay, San Juan Island, Washington. The physical and geological environment at this tidal height is described in detail by Miller (1985). Sediments were lain by adding approximately 10 liters at a time to the turning section just upstream of the drive section to fresh water at a paddle velocity capable of maintaining bedload transport (approximately 25 cm/s). The filling took three days of collection (at low tide) and transport of sediments back to our facility. Water and suspended material were siphoned off twice a day during filling and replaced with additional fresh water until dead and injured macrofauna were no longer in evidence and the suspension was dilute enough that the center of the filled working section could be viewed easily (roughly six exchanges of water). This procedure was found in pre-tests to be more efficient than sieving for the removal of undesired macrofauna and very fine silts that would obscure observation. The flume was then thrice drained entirely of water, refilled with seawater, and run under conditions of weak bedload transport to bring it back up to seawater salinity (28.7 to 28.8 ppt during the course

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of our experiments) and establish a rippled bed. The median grain size of the resultant deposit was 130  $\mu\text{m}$ . Water depth was 14 cm over a 7-cm layer of sediments. Dissolved oxygen was monitored with a polarographic electrode, and never fell below 75% of the saturation value, even when the paddles were still. The flume has a large surface area for gas exchange, and the bulk of labile organic matter was intentionally removed by the rinsing process. Temperature was allowed to rise to that of the room (16° C) before observations began. Temperatures this high are experienced daily at this season by species inhabiting the intertidal zone of False Bay.

Initial observations of bedform geometry as the bed was being lain showed that turning vanes would be necessary for precise quantification of ripple migration. We therefore constructed a makeshift turning "vane" and ran the flume for roughly 4 h at a paddle velocity of 20 cm/s to allow the bed to equilibrate with this new entrance condition.

### Experimental organisms and procedures

We chose infaunal surface-deposit and suspension feeders from a range of False Bay environments because their feeding modes oblige them to maintain or repeatedly make connection with the sediment-water interface. The environments and community structure are reviewed thoroughly in Pamatmat (1966) and Brenchley (1981). We chose *Pseudopolydora kempj japonica*, a spionid polychaete (c. 1.5 cm long), and *Macoma nasuta*, a tellinid bivalve (3-5 cm maximal shell length) from the same tidal level at which sediments were gathered. These animals were selected specifically because they are the only conspicuous macro-infauna in the tidal channels that drain False Bay, though our collections were from outside these channels. Ripple migration occurs routinely on outgoing tides in the channels, so we suspected that *M. nasuta* and *P. kempj japonica* would be adapted to the process. Both are surface deposit feeders with functional capability for suspension feeding.

We chose several species from the outer bay because of the high-energy nature of this environment. Ripples apparent there at low tide appear to be produced by surface waves (symmetric oscillatory or cat's back ripples as opposed to asymmetric current ripples). While the surface grain layer on such ripples moves back and forth with the wave period, the ripples may migrate at very slow rates set by the mean or steady component of water motion. Thus it was not clear whether organisms from this environment would have easily characterized responses to the comparatively rapid migration of current-produced ripples. The species chosen were the suspension-feeding bi-

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valves *Transenella tantilla* (c. 5 mm maximal shell length) and *Clinocardium nuttali* (of 5-8 cm maximal shell dimension) and the functionally deposit and suspension-feeding polychaete *Owenia fusiformis* (tube lengths 8-12 cm).

We chose one species specifically because we believed it might be poorly adapted to ripple migration. *Eupolyornia heterobranchiata* is a terebellid polychaete (individuals 7-12 cm long, not including tentacles), which we suspected to be a surface deposit feeder. Terebellids in our previous experiments (Jumars et al. 1982) had shown limited ability to feed under flowing water. *E. heterobranchiata* inhabits about the same tidal level as *Owenia* (near MLLW), but occurs under large patches of nearly complete *Ulva* coverage, which it helps to maintain by cementing pieces of the alga to its tube. This *Ulva* layer effectively armors the bed from fluid forces (Jumars and Nowell 1984) and precludes sediment erosion or ripple migration except in severe storms.

The experimental organisms were introduced to the flume at zero flow velocity, and allowed to burrow and acclimate in the absence of flow for 24 h before experiments with ripple migration. Animals were segregated by species and distributed over the test section from 3 m downstream of the turning section to the end of the straight test section, in the region of strongly two-dimensional ripples. The smallest numbers of individuals observed were for *C. nuttali* (6), *E. heterobranchiata* (7) and *M. nasuta* (15). *M. nasuta* and *C. nuttali* were placed in the deep box to accommodate their potentially deep burrowing and large body sizes, respectively.

We experimented with simulation of tidal periodicity in the strength of sediment transport, starting with no flow, increasing first to weak bedload transport, then to strong, and then slowing the flow again to zero, with the full cycle taking a tidal period. This level of apparent sophistication was discontinued subsequently as premature, given the number of novel qualitative behaviors observed (Results). Each of the resulting behaviors we describe was elicited no matter what the immediately preceding flow and sediment transport history. For purposes of describing behaviors, we examined only two broad stages of sediment transport in addition to observations under still water. Visual observations at the smallest scales were aided by use of a dissecting microscope (Wild) and a long-range microscope (QM-1, Questar Corporation) through the flume wall.

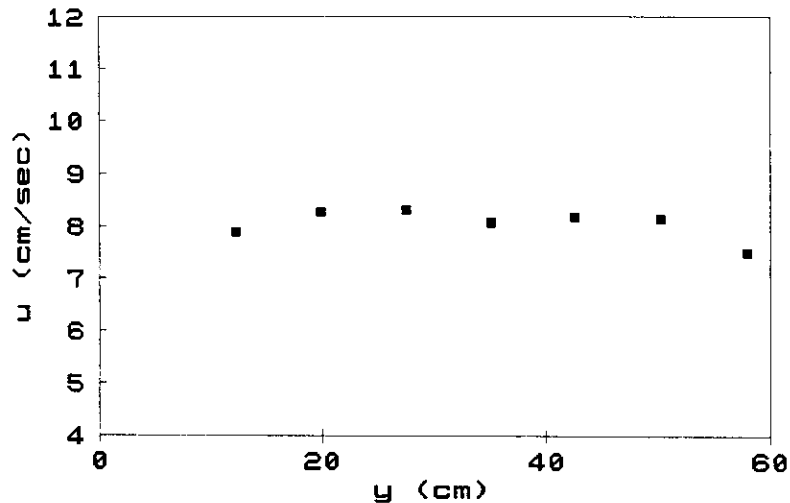


Figure 11.2: Cross section of velocities at a fixed height above the bed in order to demonstrate the nearly one-dimensional nature of the flow field. The Y direction is across the flume.

## Results

### Flume performance

Laser-Doppler velocimetry validated the presence of mainly one-dimensional flow structure over most of the test section. Some decreases in flow velocity and consequent bed shear stress was measured toward the inner edge of the test section, but this was only of order 10 percent (Fig. 11.2). When sediments were added, they deposited preferentially, as expected, under the comparatively slowly moving fluid at the inner edge of the turning sections (analogous to point bar deposition in meandering channels).

A simple turning device in the upstream turning section ensured that the 3-dimensional structure of ripples exiting the bend disappeared within 3 m, and no depositional bar was present in the turning section. This turning device ensured that the flow around the bend was sufficient to scour the bottom of the turning section clear of sediments. The resulting deceleration of fluid downstream of the flow blockage caused downstream variation (decrease) in ripple wavelength, of about 20%. In this configuration, as a further test of potential performance of a flume of this design, we increased paddle velocity to 35 cm/s (about 20% of maximum achievable). This test

was carried out after experiments with animals were finished to demonstrate that the flume can replicate the spectrum of sediment transport observed in the field. Ripples were rapidly "washed out" as abundant material, including sand, went into suspended transport and was maintained in suspended load transport until the paddle velocity was reduced.

### Animal responses

The spionid polychaete, *P. kempji japonica*, displayed a highly consistent response to ripple migration over its tube. At slow ripple migration rates it was observed to feed and produce fecal pellets at all phases of the ripple migration. Palps were held in the helical coils characteristic of suspension feeding (Taghon et al. 1980) except between the top and bottom of the lee side of the ripple, when they were appressed to the sediments in the deposit-feeding posture. Deposit feeding resumed immediately upon cessation of flow, no matter what their positions in a ripple. While suspension feeding, the palps were held in the local downstream direction. In the recirculation region in the lee of a ripple crest (Fig. 11.3, discussed in more detail by Nowell and Jumars 1984), the palps thus pointed upstream relative to the primary flow direction of the flume. Downstream orientation of the palps appeared to be effected passively: they oscillated with a period of roughly 1 Hz when the position of the reattachment point of the flow oscillated with that frequency over the animal, the palps seemingly "weathervaning," with the coiled distal portions carried downstream by fluid drag. Feeding was observed at all phases of ripple migration and was substantiated by the appearance of two types of fecal pellets. Flocculent material that traveled in suspension was brownish in color, and some pellets were of the same hue. Others, resulting from material ingested during the deposit-feeding phase, were gray and more granular in appearance.

Active tube building occupied part of the animal's time as the lee side of a ripple marched over it. Material could be seen being transported along the palps to the mouth nearly continuously, with the mouth appearing episodically in tube building, especially immediately after an avalanching episode. Avalanching is not continuous at low rates of ripple migration. As the ripple crest went by, the tube was gradually exposed. At slow ripple migration rates, however, no more than 4 mm of exposed tube was seen, despite greater ripple amplitudes. Closer observation revealed active tube cutting whenever exposed tube length exceeded 2-4 mm. We thought that the stimulus might be the observed strumming by vortex shedding of long, exposed tubes (like

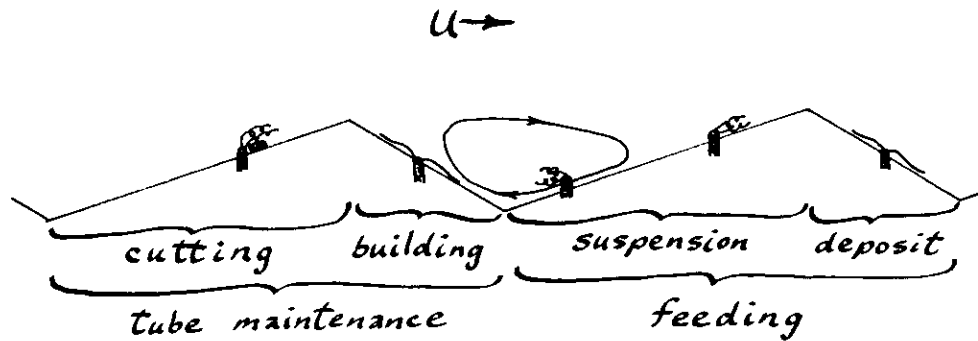


Figure 11.3: Differing palp orientations and positioning of *Pseudopolydora kempji japonica* at selected positions along a sand ripple. Different feeding strategies are identified in the different regions of a ripple.

that heard near telephone lines), but we also observed tube cutting when the flow had been turned off. Cutting apparently is effected by extension of the modified fifth-setiger setae characteristic of the genus. Although details of the process could not be resolved in the natural setting, the animal was extended precisely this far (to the fifth setiger) as the cut section fell, and flashing of reflected light from these large, extended setae could be seen. Drag from the flow on the cut section often aided the final cutting and removal. Even under weak transport, the cut section rolled away and suspension feeding resumed.

Under strong sediment transport conditions, neither feeding nor pellet release was continuous. Individuals were buried soon after the top of the lee side of the ripple passed, though they could be seen building tubes actively until they disappeared from view. Individuals reappeared somewhere along the stoss side by the combination of erosion and tube building and went into suspension-feeding postures, despite strong, turbulent buffeting by the flow. More than 4 mm of tube often was exposed by comparatively rapid rates of erosion on the stoss side at the higher transport rates.

The tellinid bivalve, *M. nasuta*, had the most complex repertoire of behaviors. This species typically maintains its exhalant siphon below the sediment surface, so that the frequency of defecation is not easily monitored. At zero flow velocity, it produced the asterisk-shaped feeding traces characteristic of deposit-feeding tellinids (e.g., Schafer 1972), and individuals moved often. Pseudofecal ejections were frequent. At weak transport levels, movement to new locations was rare, and asterisk-shaped feeding traces

were not observed. Movements of siphons that produced asterisk-shaped traces under zero flow conditions occasionally were observed at weak transport, but the resultant depressions were filled by bedload transport. More frequently, inhalant siphons were not extended at all but were used to maintain a small, funnel-shaped depression from which the animal fed. As the lee side of a ripple migrated over, the siphon maintained contact with the surface, the conical depression reappearing at the crest. The animal feeds from the depression, apparently specializing on particles passively collected by deposition into the pit, although we cannot exclude the possibility of suspension feeding as a supplement. Volumetric output per ejection as well as frequency of pseudofecal ejections is reduced from the no-flow case. Under strong transport, most individuals still maintained contact with the sediment surface. They held their inhalant siphons flush with the sediment surface acting like a bedload trap.

The bivalve, *T. tantilla*, which makes abundant surface crawling traces under still water (e.g., Nowell et al. 1981), burrowed in and was rarely observed to move from its position whenever sediment transported. Under zero flow, when not moving, it held both siphons equally and fully extended. Under weak transport, it held the exhalant siphon fully extended, but the inhalant only partially extended. The higher the transport rate, the fewer individuals were evident at the sediment surface. The siphonal tentacles of the bivalve, *C. nuttali*, provided some structural protection of the inhalant stream from coarse grains. As transport rate increased, the inhalant opening was constricted, rotating additional siphonal tentacles into a position where they would intercept transporting grains. When the siphonal tentacle array became sufficiently filled with transporting sand grains that the latter would begin to fall into the inhalant opening, the animal violently "sneezed". This expulsion of fluid from the inhalant opening cleared the tentacle array of sand grains. The frequency of such sneezing increased both as the lee side of a ripple approached upon the inhalant opening and when bedload transport was increased. The cockles used both burrowing and sneezing to keep at the sediment surface.

The polychaete, *O. fusiformis*, under still water formed a moat-like, circular depression about its tube (Eckman et al., 1981, Fig. 11.1). It nodded the protruding section of its tube back and forth at roughly 0.3 Hz, with individuals nodding in different directions. The tentacular crown touched the bed rarely, so that most time it appeared to be suspension feeding. Under weak transport, the nodding stopped, and tubes trailed uniformly downstream. The tubes were arched so that the tentacular crown touched the

bed, and came close enough to the bed so that vortex shedding increased the local instantaneous shear. This same posture was maintained under strong transport.

*O. fusiformis* did not appear to respond to the same recirculation that reversed orientation in *P. kempji japonica*. The top of the arch projected high enough to be affected and oriented by the stronger, primary flow. The most notable behavior, evident at both transport stages but more frequent at the higher, was "unburrowing" as the lee side of a ripple buried the projecting tube. The animal threw the flexible tube into two right angle bends, the first parallel with the sediment surfaces and the second pointing upstream. It would then rotate 90 degrees about its vertical axis, using its "arm" to move sediment. No correspondingly dramatic burying behavior was seen, because the tube is much more easily pulled under by the animal in the direction of imbrication of the grains.

As expected, the terebellid polychaete, *E. heterobranchiata*, showed no apparent active response to ripple migration. Unexpectedly, individuals spent most of their time subsurface either in the presence or absence of sediment movement. The tube was constructed more or less continuously and horizontally about 2 cm below the sediment surface, but a connection to the surface was maintained, facilitating the burrowing mechanism and allowing defecation on the sediment surface. The position of the head could be seen as the animal proceeded forward, characterized by pits indicating subsurface deposit feeding, and new posterior openings appeared when the old ones were far removed from the present position of the head. Head and tail openings sometimes were exchanged. The head could be localized by the emission of a fluid-particle stream. The animal fluidized the bed via antiperistalsis in its tube; fluid could be seen (by virtue of the particles it contained) entering the rear opening of the tube, and a fluid-particle mixture could be seen escaping at the head. Tentacles sometimes emerged on the sediment surface with this excavation stream and engaged temporarily in surface deposit feeding. In the presence of either weak or strong sediment transport, emerging tentacles streamed in the local (including recirculation) downstream direction.

## Discussion and Conclusions

### Flume performance

Flume design proved entirely sound from the standpoint of power, with complete sediment transport conditions being produced up to and including sands in suspension. The drive mechanism achieved its design objective of producing primarily one-dimensional flow (Fig. 11.4) in the downstream portion of the working section in the absence of sediments. The existence of the logarithmic profile was checked along the test section; fully developed one-dimensional flow (gradients in only the z-direction) was found in the downstream 50% of the test section. The turning vane allowed uniform ripple morphology to develop within 3 flow widths of the turning section.

We had expected some secondary circulation in the racetrack flume. Its extent is in fact predictable from fluid dynamic models (Nelson and Smith, unpublished). The major cause of secondary circulation in a racetrack-shaped flume is the fact that fluid must move faster around the outside of the turn than around the inside in maintaining the average flow velocity of the straight channel. This lowered flow velocity and consequently lower bottom shear stresses allow greater deposition of material at the inside edge, as we observed in the absence of any turning device. The simple turning device, which divided the flume in two in the turning section, reduced problems from cross-stream flow heterogeneity. But to produce steady rates of ripple migration and equilibrium bed configurations, allowing more precise quantification and warranting extensive flow and sediment transport measurements, has required a change from our initial design. Thin turning vanes (5 across the flume's width in the turning section) have now been installed. While fluid flow equilibrium is very rapidly established, long running times will be needed to bring the bed to equilibrium configuration before a given paddle velocity will result in a constant bedload transport rate. Only then can a constant, well-defined set of stimuli be provided for more quantitative (interval or ratio level of measurement) treatment of organism response.

### Organismal responses to ripple migration

On a species-by-species basis, the observations of animal response add small increments to an understanding of natural history and raise additional questions. In *P. kempji japonica*, it is apparent that the animal cycles between suspension and deposit feeding at slow ripple migration rates, putting some earlier laboratory observations of switching between feeding modes into an-

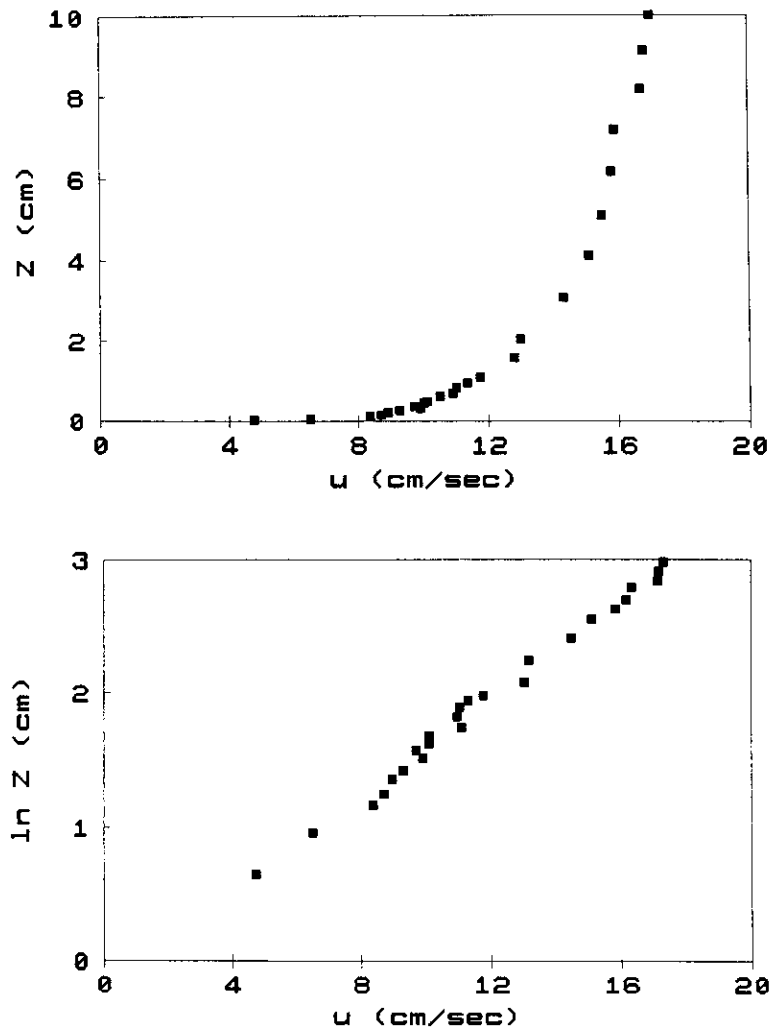


Figure 11.4: Velocity profile over a flat bed of fine sand, plotted in arithmetic and semi-logarithmic form. The former shows the growth of the boundary layer to the free surface, while the semi-log plot shows the existence of the log layer and the viscous sublayer in the region below 0.1 cm.

other environmental context. Tube cutting in polychaetes has been noted before among chaetopterids (MacGinitie and MacGinitie 1968) and terebellids (Aller and Yingst 1978), but only as an activity related to the need for a larger tube as individuals grow. Hence, those previous reports are of an infrequent, lengthwise slitting. The stimulus for *P. kempji japonica*'s tube cutting is less clear, but it may involve the elastic yield of the above-sediment portion of the tube as the animal poles along it with setae. The net results are that the tube opening is kept in a position that allows suspension and deposit feeding and that the bulk of the animal's body remains below "ground" level, presumably safer from both erosion and predation. The energetic costs of building and cutting the tubes must be high; it would appear to be worthwhile because in the field ripple migration rates are quite slow (Middleton and Southard 1984).

In *O. fusiformis*, a longer segment of tube is kept exposed. Its tube is more flexible because only oblate grains are chosen (Fager 1963), and they are glued in imbricated fashion to the flexible tube matrix by only one (the anatomically posterior) edge. Field-collected animals do not appear to add to the tube unless it has been damaged. In the laboratory, and presumably in the field, they carry the tube along as they move. Again the length of tube that is left exposed appears to provide the option for either suspension or deposit feeding. When a shorter tube length is temporarily exposed and the animal occupies it, flexibility appears insufficient for the animal's short tentacular crown to reach the sediment surface for deposit feeding.

*E. heterobranchia*'s mode of movement via continuous or repeated extensions of its tube has been noted before (Fauchald and Jumars 1979), but its proclivity to feed below the surface has not. Our previous observations (Fauchald and Jumars 1979) were made in poorly sorted sediments (including gravel) where the hydraulic tunneling mechanism seen in the present, comparatively well sorted sand presumably would not work well. A common feature of the bivalve behaviors was a lack of horizontal movement during periods of sediment transport, but the apparent reasons for these behaviors are disparate. In *M. nasuta*, the sediment transport prevents both local depletion of deposited resources and accrual of fecal mounds (e.g., Fig. 1 of Jumars and Nowell 1984), two likely stimuli to move horizontally. With its long, extensible siphons, *M. nasuta* appears to have little difficulty maintaining contact with the interface. Adult *C. nuttali*, by virtue of their large sizes and comparatively minor adjustments of siphon length, also appear to require little vertical burrowing in maintaining access to their suspended food, although some upward burrowing was observed as ripples migrated

over. Their use of papillae as a "snow fence" to exclude bedload material from the inhalant siphon, with "sneezing" to clear it, appears not to have been noted previously. Because of its small body size and short siphonal lengths, however, *T. tantilla* must burrow frequently to adjust its vertical position when ripples migrate. Also (like the cockle) a suspension feeder on fine particles, it appears to avoid gravitational slumping into the exhalant siphon by holding it above the level of the sediment-water interface and to avoid saltating grains by virtue of the siphon's small size.

The diversity and ubiquity of these animal responses to ripple migration leave little doubt as to the importance of this sediment transport phenomenon in the evolutionary histories of intertidal organisms from False Bay. What remains obscure is the frequency of such events in natural populations and its importance at the individual and population levels from one day to the next. Miller (1985 and in preparation) has suggested that bedload transport of sediments occurs on most days in False Bay. His measurements were carried out at one location, so the degree to which they can be extrapolated to the whole of the bay is unknown. Certainly there are locations, such as in the tidal channels, where ripple migration occurs for a substantial fraction of each day (during outgoing tides). False Bay certainly is not unique among intertidal and shallow subtidal environments in showing frequent ripple migration (e.g., Grant, 1983). The responses we saw thus motivate further study because analogous responses probably occur in many species and locations.

Our previous modeling and measurement effort (Miller et al. 1984; Jumars and Self 1986; Miller and Jumars 1986) has stressed the potential energetic benefits of an enhanced food supply from sediment transport processes, but the present observations also suggest obvious costs of maintaining a connection with the sediment-water interface (Ed. note: The actual costs associated with deposit feeding are not obvious; see chapters by Taghon and Forbes, this volume). At high ripple migration rates, for example, *P. kempfi japonica* is unable to maintain contact with the sediment surface while a ripple crest goes by and presumably is unable to feed. "Sneezing" in *C. nuttali* under comparable migration rates is so frequent and convulsive that net energetic gain may well be negative. Resolution of these issues requires two things: feeding and growth rates must be measured under precisely controlled sediment transport conditions that are of much longer periods than we report here, and field ripple migration rates must be better known at sites of ecological interest. The former we hope to accomplish, and the latter is readily achievable by time-course observation or time-lapse photography

(e.g., Smith et al. 1986). Similarly, our observations raise questions at the population and community levels about the relative and absolute importance of amensal interactions among trophic (Wilson 1981) or motility (Brenchley 1981) groups. We would not expect, for example, amensalism mediated by defecation to have significant influence on population dynamics in an environment where individuals were routinely buried and exposed by migrating ripples. Potentially sediment-mediated, amensal interactions, whether evaluated in the laboratory or the field, need to be set in the contexts of sedimentary dynamic environments (e.g., Grant 1983). Horizontal mobility has been stressed as an escape from amensal effects (Jumars and Fauchald 1977; Brenchley 1981; Wilson 1981), but the behaviors observed here suggest that vertical mobility deserves substantial attention. We studied only adult specimens here. Before population or community response could be predicted, it would be essential to know whether smaller life stages showed either lesser ability or alternative behaviors. Again, laboratory simulation and precise control of sediment transport conditions and better characterization of field transport regimes are essential. There is a need to progress from empirical correlations between sediment composition and community structure, to a mechanistic understanding of the reasons for them and a consequent need to set biological interactions in the contexts of their physical environments.

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