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# Potential flow artifacts associated with benthic experimental gear: Deep-sea mudbox examples

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#### ABSTRACT

In response to the growing recognition of the potential effects of near-bed hydrodynamics on various benthic processes, flume studies were conducted to document fine-scale flow patterns over several types of mudboxes that have been used to study colonization by deep-sea organisms. Mudboxes are typically filled with natural sediments or sediment treatments and placed in the field to observe how timing, larval supply and sediment composition may affect larval settlement. This study addresses potential hydrodynamic biases of mudbox structures as obstructions to the near-bed flow. Detailed velocity profiles were made over two types of "free vehicle" mudboxes that could be deployed and recovered from a surface vessel. One of these ("Old Free Vehicle") was not designed with regard for potential hydrodynamic biases whereas the other ("New Free Vehicle") was designed specifically to minimize flow disturbances and maintain a realistic boundary-layer flow over the mudbox sediments. Flume velocity profiles also were made over two smaller mudboxes designed to be deployed by a submersible, one ("Flush Sediment Tray") which was designed to be placed flush with the ocean bottom, thus minimizing flow disturbance, and another ("Raised Mudbox") which was not. Flume simulations indicated that the Old Free Vehicle and the Raised Mudbox cause considerable disturbance to the near-bed flow regime; flows over the mudbox sediment surface differed markedly from those predicted for the natural seabed and those observed over the flume bed in the absence of the mudboxes. Flow accelerations, growing secondary boundary layers and eddy formation were observed over these mudbox sediments, and vertical velocity profiles varied considerably in the along-channel direction. The alternative mudbox designs (New Free Vehicle and Flush Sediment Tray) were largely successful in reducing or eliminating these flow artifacts. Boundary-layer flows over both the New Free Vehicle and the Flush Sediment Tray were much more uniform, and velocity profiles over the sediment surfaces were very similar to those in the empty flume channel and those predicted for a natural deep-sea habitat. In addition, there was no evidence of eddy formation and other major flow disturbances. These flume studies underscore the benefit of considering potential hydrodynamic effects in designing benthic experimental sampling gear to reduce potential flow disturbances that may bias data collections and confound data interpretation.

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#### 1. Introduction

One of the major considerations in designing and deploying biological sampling gear in the marine environment is minimizing disturbances to the oncoming flow. Technically, any stationary object that is placed in moving fluid disturbs the flow both because the flow has to accelerate to go around the object, and because a boundary layer develops over the surface of the object. These flow artifacts may or may not affect sample collections depending on the kind and magnitude of the flow disturbances, and on the sensitivity of the organisms to such hydrodynamic effects. Organism responses to flow artifacts associated with sampling gear can affect collections both in the water column (e.g., Singarajah, 1969, 1975; Haury et al., 1980; Butman 1986b) and on the bottom (e.g. Dayton and Oliver, 1980; Hulberg and Oliver, 1980) and when hydrodynamic disturbances were sufficiently well-defined, they have been useful as experimental manipulations to test organism responses to specific flow effects (e.g., Eckman, 1979, 1983; Hannan, 1984; Butman, 1989; Mullineaux and Butman, 1990, 1991; Walters, 1992; Mullineaux and Garland, 1993; Snelgrove et al., 1993; Snelgrove, 1994). The focus of this study was on hydrodynamic artifacts associated with sampling gear placed on or in the seafloor, particularly in the deep sea, and on design criteria for minimizing flow biases that may be associated with benthic experimental structures.

Hydrodynamic processes may influence benthic biological processes in many different ways, including regulation of nutrient and oxygen flux; transport of detritus and other food sources for living organisms; biomechanical design of organisms with structures extending above the sea bed; sediment deposition, erosion, and sorting; and supply and redistribution of larvae and organisms in benthic habitats (e.g., reviews of Nowell and Jumars, 1984; Jumars and Nowell, 1984; Butman, 1987). Although this study was motivated by increasing evidence that near-bottom flows influence larval settlement (e.g., Butman, 1987; Snelgrove and Butman, 1994), documentation of flow bias around instruments has direct applications to many other biological and non-biological processes. This study is relevant, for example, to measurements of chemical fluxes across the sediment-water interface using benthic chambers (e.g., Smith, 1978), to measurements of various sediment-transport parameters using sea flumes (e.g., Young, 1977; Amos *et al.*, 1992), and to studies utilizing predator-exclusion cages (e.g., Woodin, 1974).

The near-bed flow field is now known to influence larval settlement. Many planktonic larvae are relatively poor swimmers, and under natural conditions they may encounter flows that exceed their swimming speeds at distances of only a few millimeters above the bottom (Butman, 1986a). Studies conducted in the field (e.g., Eckman, 1979, 1983; Butman, 1989; Emerson and Grant, 1991; Snelgrove, 1994) and under controlled flume conditions (e.g., Pawlik *et al.*, 1991; Jonsson *et al.*, 1991; Butman and Grassle, 1992; Pawlik and Butman, 1993; Snelgrove *et al.*, 1993) indicate

that even relatively subtle flow effects may influence planktonic larval distributions in near-bottom waters, and distributions of newly settled larvae and juveniles.

Accurate documentation, in the field, of larval settlement and recruitment is challenging; "snap-shot" sampling often does not yield meaningful results because the timing of larval settlement is notoriously unpredictable both spatially and temporally (e.g., Levin, 1990) and *in situ* structures that can integrate settlement are confounded by potential hydrodynamic biases. In shallow, subtidal habitats, the relatively high and variable flows over structures raised above the seabed generally result in trapping artifacts (e.g., Butman, 1986b, 1989), rendering data from suspended traps equivocal for accurate estimates of larval availability.

The problem of hydrodynamic bias in colonization studies has been circumvented in intertidal environments by placing defaunated sediments flush with the seafloor (e.g., Eckman, 1983; Gallagher *et al.*, 1983). A similar approach has been used in the deep sea, where submersibles have been used to bury small colonization trays flush with the ocean bottom (e.g., Snelgrove *et al.*, 1992, 1994). These trays were designed in response to criticism of previous deep-sea colonization studies (e.g., Smith, 1985), where boxes filled with defaunated sediment ("mudboxes") were placed directly on the seabed (e.g., Grassle, 1977; Desbruyères *et al.*, 1980, 1985; Levin and Smith, 1984; Grassle and Morse-Porteous, 1987). Unfortunately, submersibles are not always a feasible approach to deep-water studies, necessitating the use of "free vehicle" arrays (e.g., Smith *et al.*, 1979; Desbruyères *et al.*, 1980, 1985; Levin and Smith, 1984; Maciolek *et al.*, 1987). Free vehicles are designed to be deployed and recovered by a ship; they free-fall to the bottom and, upon release, float to the water surface. Free vehicles can thus be deployed in virtually any oceanographic environment at a relatively low cost.

Mudboxes can be an excellent experimental tool for understanding basic ecological processes that occur in the deep sea. Mudbox sediments may be manipulated to test specific *a priori* hypotheses on processes such as larval settlement, recruitment and succession in the deep sea (e.g., Desbruyères *et al.*, 1985; Grassle and Morse-Portcous, 1987; Snclgrove *et al.*, 1992, 1994). However, because small-scale hydrodynamic processes are now known to play an important role in larval recruitment under certain conditions, it is critical that the mudbox structure only minimally affect the natural near-bed hydrodynamic regime. Otherwise, collections of infaunal invertebrates in mudboxes may be biased by the unusual flows generated by the mudbox structure, yielding uninterpretable or ambiguous results.

The objectives of this study were to measure, in a laboratory flume, the types of flows that might be expected to occur over mudbox sediments elevated above the ocean floor compared with flows over the adjacent seabed, to identify specific hydrodynamic effects that may influence colonization of mudbox sediments, and to offer alternative mudbox designs to minimize or eliminate these effects. Although our emphasis is on mudboxes, similar flow considerations apply to any sampling



Figure 1. Diagram showing a natural bottom boundary layer profile (left) and where the free vehicle or mudbox structure intercepts this profile (right). Stippled areas indicate sediment in mudbox structure or natural scabed. Also shown is the boundary layer that attaches to the leading edge of the mudbox structure and grows downstream (compare  $\delta_1$  to  $\delta_2$ ; as the boundary layer thickens downstream, the shear near the mudbox sediment surface decreases).

device that protrudes above the bottom and remains *in situ* over a significant period of time, for example, respirometer chambers (e.g., Smith, 1978) and *in situ* core incubations (e.g., Wirsen and Jannasch, 1986).

#### 2. Conceptualization of the problem

a. Boundary-layer flow. As a fluid moves across a solid boundary such as the sea floor, the drag of the boundary on the flow retards the fluid motion. This produces a region of vertically sheared velocity referred to as the "boundary layer," where horizontal velocity u is zero at the sediment-water interface, and increases with increasing distance z above the bottom to a distance  $\delta$ , where the bottom has minimal influence on the flow and u = U, the mean-stream flow speed (Fig. 1a). General descriptions of boundary-layer flows in oceanic habitats are given by Komar (1976), Madsen (1976), Wimbush (1976), Nowell (1983), and Grant and Madsen (1986), and only a few relevant boundary-layer characteristics are reiterated here. A fundamental feature of boundary-layer flow over an hydrodynamically smooth bed is that in the lower  $\sim 20\%$  of the boundary layer, the flow is independent of total water depth and U such that the velocity profile can be described adequately by the parameters  $u/u_*$  and



Figure 2. Diagrams of the Old Free Vehicle showing a side view (left) and a top view (right), drawn approximately to scale. Sediment in trays is shown in black, and ocean bottom in side view is shown in hatched lines. Arrows and "A" in top view indicate position from which side view was drawn. Dashed lines delineate section used in model for flume simulation.

 $u_*z/v$  (e.g., Clauser, 1956), where  $u_*$  is the boundary shear velocity and v is kinematic viscosity of the fluid. For these flows, it is thus possible to create dynamically similar conditions between a laboratory flume flow and the field by maintaining similar  $u_*$  (e.g., Nowell and Jumars, 1987).

b. The mudbox case. We here compare flow over a free vehicle ("Old Free Vehicle," Fig. 2) and a submersible-deployed mudbox ("Raised Mudbox," Fig. 3) that were not designed with specific regard for potential flow disturbances, with flow over a free



Figure 3. Diagram of the Raised Mudbox.



Figure 4. Diagrams of the New Free Vehicle, showing a side view (left) and a top view (right), drawn approximately to scale. Sediment in trays is shown in black and ocean bottom is indicated by stippled area. Arrows and "A" in top view indicate position from which side view was drawn. Dashed lines delineate section used in model for flume simulation.

vehicle ("New Free Vehicle," Fig. 4) and submersible-deployed sediment tray ("Flush Sediment Tray," Fig. 5) specifically designed to minimize potential hydrodynamic biases. In the older tray designs, the mudbox sediment surface is raised above the seafloor and is exposed to higher oncoming flow speeds than natural bottom sediments (refer to Fig. 1b). Also, because mudbox sediments are themselves a boundary to the flow, a second boundary layer forms above the mudbox sediments. Furthermore, bluff body effects of the mudbox structure on the flow may result in flow separation, where recirculating eddies are shed into the flow and the boundary layer eventually reattaches downstream. Flow velocities over these structures thus result from a boundary layer within a boundary layer, and may be very different from flows over the natural bottom.

We attempted to circumvent these problems in two different ways. (1) The New Free Vehicle was designed so that a new boundary layer would not form over the mudbox sediments, although the flow was still expected to accelerate moderately as it moved over the mudbox structure. (2) The Flush Sediment Tray was designed to be placed flush with the bottom, so that flow would not be altered by the presence of the tray. In this study, we compared velocity characteristics within a simulated natural bottom boundary layer with velocity characteristics observed over the four different mudbox designs.



Figure 5. Diagram of the Flush Sediment Tray showing separated components.

#### 3. Materials and methods

a. Characterization of natural flow. To evaluate flow over free vehicles and colonization trays, it was necessary to recreate flow conditions approximating those that might be expected to occur naturally. Given that many deep-sea colonization experiments have been conducted on the Atlantic continental slope and rise off New Jersey (e.g., Grassle, 1977; Grassle and Morse-Porteous, 1987; Maciolek *et al.*, 1987; Snelgrove *et al.*, unpublished data), flume flows were selected to mimic typical current regimes within this region. The Flush Sediment Tray has been deployed south of St. Croix, U.S.V.I. at 900 m depth (Snelgrove *et al.*, 1992, 1994) and flow conditions within this region are roughly comparable to those that occur on the New Jersey slope (C. A. Butman, unpublished data).

The boundary shear velocity can be calculated from vertical profiles of horizontal current speed taken within the log layer over an hydrodynamically smooth bed given that the following assumptions are satisfied (e.g., Gross and Nowell, 1983). (1) There is quasi-steady, uniform, neutrally stratified flow over the bed. (2) The bed is uniform over large horizontal distances relative to the height above the bed where velocities are calculated. (3) Bottom roughness is small compared with boundary-layer thickness. In addition to these assumptions, information must be available on velocities

occurring at some height above the bottom within the log layer and on bottom roughness characteristics. These assumptions are satisfied, at least periodically, at the mudbox deployment sites on the Atlantic continental slope and rise and on the slope south of St. Croix, and deviations from these assumptions are unlikely to affect the first-order results of this study.

Given the range of near-bed flow speeds and bottom types expected at the study sites, values of the roughness Reynolds number  $Re_*$  ( $u_*k_b/\nu$ , where  $k_b$  is the bottom grain size) are roughly 0.1 for the New Jersey slope and 1.1 for the St. Croix slope. These values fall within the range for hydrodynamically smooth-turbulent flow. Using the log-layer equation for hydrodynamically smooth-turbulent flows (Schlichting, 1979), where  $\kappa$  is Von Karman's constant,

$$\frac{u}{u_*} = \frac{1}{\kappa} \ln \frac{zu_*}{\nu} + 5.5$$

a  $u_*$  of 0.49 cm s<sup>-1</sup> was calculated for v = 0.01 cm<sup>2</sup> s<sup>-1</sup> and for u = 15 cm s<sup>-1</sup> at z = 500 cm, a typical velocity for flows expected to occur at these and other deep-sea sites (e.g., Grassle and Morse-Porteous, 1987; Mullineaux and Butman, 1990).

b. The free vehicles. The Old Free Vehicle (Fig. 2) has been used in colonization studies on the mid-Atlantic slope (Maciolek et al., 1987) and consists of a square fiberglass frame (1.52 m by 1.42 m) containing six identical polyethylene trays (30 cm by 40 cm by 7.5 cm deep) that are filled with sediment. A fiberglass lid covers the trays and retains sediment during transport to and from the bottom. An aluminum support structure bears the flotation, the transponder release, and the pelican hook release. The frame is raised on feet such that the tray sediments are  $\sim 10$  cm above the bottom on a hard surface, but the frame sinks slightly into a natural muddy bottom, depending on the consistency of the sediments. When the free vehicle rests on the bed, the lid is raised  $\sim 43$  cm above the top of the trays so that it does not interfere with flow over the sediment surface. Steel plates attached to the underside of the center of the frame make the free vehicle negatively buoyant; upon acoustic release, the plates are dropped and the vehicle rises from the bottom, meets the lid to seal the sediments within the tray, and continues a free ascent to the water surface for recovery. A square, rubber gasket  $(1 \text{ cm} \times 1 \text{ cm})$  spans the lip of each of the trays and, with the aid of magnets around the lid and mudbox perimeter, seals the trays against the lid during deployment and recovery.

The New Free Vehicle (Fig. 4), which was designed to reduce flow disturbance (see Discussion), consists of a round sediment tray (80 cm in diameter) located at the center of a large, radially symmetrical, smooth, flat disc (224 cm in diameter) which slopes gently to the seabed at its perimeter. The central sediment tray is filled with sediment flush with the disc surface. The disc is made from molded plastic (0.64 cm thick), and support structures underneath the disc hold the structure rigid. The New

Free Vehicle utilizes a weighting and acoustic release mechanism similar to those used in the Old Free Vehicle design, except that the weights, release mechanism and flotation are at the periphery of the vehicle. As in the Old Free Vehicle design, the tray floats up to meet the lid; a gasket located on the lid and magnets (recessed in the disc and protruding from the lid) seal the lid against the disc during deployment and recovery. The sediment surface is  $\sim 10$  cm above the natural seabed.

c. The colonization trays. The Raised Mudbox (Fig. 3), is deployed by submersible and has been used in several deep-sea studies (e.g., Grassle, 1977; Grassle and Morse-Porteous, 1987). A thin lip (width of 3 cm) extends around the periphery of a single fiberglass tray (12.7 cm in height, 50 cm in width and 50 cm in length), which is filled to within 1 cm of the lip with sediment. A PVC (polyvinylchloride) lid is attached with a hinge to one side, and flips down over the tray to seal it during transport to and from the bottom. A sealing gasket is attached to the lid rather than to the box itself. Because some deep-sea experiments were conducted with a screened version of this mudbox (Grassle and Morse-Porteous, 1987), flume simulations were also performed with Nytex screen (2 mm square openings) covering the sediment surface. As in the original deployments, the screening material was not rigid, and formed gentle contours which occasionally touched the sediment surface. For flume simulations, the lid was oriented downstream of the flow.

A second type of submersible-deployed colonization tray, the Flush Sediment Tray (Fig. 5), was designed to eliminate hydrodynamic bias (Snelgrove *et al.*, 1992) and has been used in deep-sea (Snelgrove *et al.*, 1992, 1994) and shallow-water (Snelgrove, 1994) colonization studies. This tray consists of a central cup (11.2 cm diameter) that is fastened to a Delrin plastic plate with a central opening of the same diameter. This results in a central well 10 cm deep that is filled with sediment, sealed with a lid, and carried to the bottom by submersible (or divers in shallow water). It is then placed flush with the seafloor and the sealing lid is removed. Posts at the periphery of the tray allow attachment of deployment and recovery lids and cause minor flow disruption, but they are located sufficiently far away from the sediment cup in the center of the tray so that the flow recovers before it passes over the sediment (see Results). This colonization tray is described in more detail in Snelgrove *et al.* (1992).

d. The flume. Experiments were performed in the 17-Meter Flume, a recirculating, temperature-controlled, seawater flume located at the Coastal Research Laboratory of the Woods Hole Oceanographic Institution (flume described in Butman and Chapman, 1989; Trowbridge *et al.*, 1989). Velocity measurements were made with a laser-Doppler velocimeter (LDV), which allows non-intrusive flow measurements and where the measurement volume is very small—0.3 mm in diameter by 1 mm long permitting detailed velocity profiles (e.g., Agrawal and Belting, 1988). The LDV sampled at 32 Hz, and 6-min averages are reported here.

The channel width of the flume is 60.5 cm, which made it necessary to modify the free vehicles for placement in the channel. Model sections of both free vehicles, completely spanning the flume width, were made for flow characterization in the flume. In the case of the Old Free Vehicle, the section was taken parallel to the longest dimension of the individual trays, which included two complete trays with their long axes parallel to the flow (see Fig. 2). For the New Free Vehicle, a 60-cm wide section was built from PVC to mimic the center of the tray, encompassing most of the central sediment area (see Fig. 4). On the model, the upstream sloping perimeter of the tray was carefully reproduced to the downstream edge of the sediments only-that is, the model terminated just behind the sediment areabecause the nature of the downstream flow in this unidirectional, steady flow simulation is irrelevant. In addition, because of the sizes of the structures relative to the size of the flume, peripheral attachments such as the sealing lid, flotation spheres and acoustic release could not be used in flume simulations. Preliminary data collected using a larger flume (with water depth of 1.2 m) indicated no difference in flow near the sediment over the "Old Free Vehicle" with and without the sealing lid present (Maciolek et al., 1987) because of the large distance between the lid and the sediment tray. In addition, based on the size of the pipes comprising the support frame for these structures, flow disturbances generated by the support frame itself are expected to be substantially less than those resulting from elevating the mudbox sediments above the bottom.

For both free-vehicle designs, the structures completely blocked the lower 10 cm of the flume flow, forcing the flow to move over, rather than around, the mudboxes. This enhanced flow acceleration, of about 50%, over the model free vehicles is unrealistic for the field. The situation was identical for both free vehicle designs, however, and other than exaggerated flow acceleration over the trays, the essential fcatures of the vertical velocity profiles, and their along-channel variation, were expected to be a reasonably accurate simulation of flow over the central portion of the structures. Allowing flow around the sides of the free vehicles in the flume would likely have created more serious flow artifacts because the morphology of the boxes would be incorrect (i.e., sharp edges that do not occur in the full-scale designs).

The Raised Mudbox was only 50 cm in width and therefore could be placed directly in the flume without any modification. However, to create a similar, flow-blockage effect to the other designs (i.e., for between-structure comparisons) and to eliminate funneling of flow along the sides of the mudbox, a thin (3 mm) PVC plate was placed at the corners of the leading edge of the mudbox. The plates were cut to fit just under the lip of the sediment tray to seal it against the flume walls.

For flume runs with the Flush Sediment Tray, a section of the flume bottom was removed and replaced with a 50-cm square by 50-cm deep box, which was filled with sediment so that it was flush with the floor of the flume. The sediment tray was then

buried in this box so that the tray sediment surface could be specifically positioned relative to the surrounding sediment bed—that is, flush with the sediment bed, as during an ideal ocean deployment, or tipped slightly relative to the bed to simulate a less-ideal deployment (see Fig. 13).

A limitation to the flume simulations was the height of the free vehicles and the Raised Mudbox relative to the flume water depth. The Raised Mudbox reached to a height of slightly more than 12 cm from the bottom, with the contained sediments therefore  $\sim 11$  cm above the bottom. Although the upper frame (i.e., parts of the free vehicles higher than the sediment trays) were removed to allow placement in the flume, both free vehicles, as well as their sediment surfaces, reached to a height of  $\sim 10$  cm from the bottom. It was therefore necessary to maintain a water depth of  $\sim 23$  cm above the flume bottom to quantify a reasonable portion of the flow over the structures. This water depth was maintained for all experiments, and although slight fluctuations in water level occurred, this had a negligible effect on results during the course of a profiling series. In instances where depth fluctuations exceeded 3%, the flume run was terminated and the measurement series was repeated.

Ideally, flume simulations of one-dimensional, open-channel flow should maintain a minimum width to depth ratio of at least five to avoid significant secondary circulation effects associated with boundary layer growth along the flume walls (e.g., Nowell and Jumars, 1987). Unfortunately, it was impossible to satisfy this criterion and still quantify a reasonable portion of the flow over structures as large as these mudboxes in this particular flume. Thus, secondary flow effects may have occurred. Such secondary flows generally consist of several cells of recirculating fluid in the cross-stream direction. However, for a width to depth ratio of order three, as in this study, the magnitude of the velocities of such secondary flows is expected to be small compared with the along-channel flow (e.g., Henderson, 1966; also our own measurements, e.g., Butman et al., 1994). Therefore, because the goal of the flume simulations was to quantify downstream changes in flow over the sediment surface of a mudbox relative to a flat bottom, flow measurements were confined to vertical profiles taken in one along-channel transect (along the flume channel centerline) both with and without the mudboxes in place. Thus, for this particular application, cross-stream flow effects are largely irrelevant.

The fluid-dynamic environment associated with all of the mudbox designs was quantified at a  $u_*$  of about 0.4 cm s<sup>-1</sup> (hereafter called "slow flow"), where the near-surface water velocity was about 10 cm s<sup>-1</sup>, and the two free vehicles were also tested at a  $u_*$  of about 0.6 cm s<sup>-1</sup> (hereafter referred to as "fast flow"), where the near-surface water velocity was about 15 cm s<sup>-1</sup>. These flows bracket the  $u_*$  of 0.49 cm s<sup>-1</sup> calculated for typical deep-sea flows over muddy bottoms where mudboxes have been deployed (Section 3a.), and they also fall within the range of tidal flows expected for shallow-water, coastal embayments (e.g., Butman, 1986a).

the Nytex screening that was used in field experiments for predator exclusion (Grassle and Morse-Porteous, 1987). This comparison was designed to document potential effects of the screens on flow over the mudbox. In both Raised Mudbox simulations, the sides of the mudbox were cut away to allow profiling down to the sediment surface (i.e.,  $\sim 1$  cm below the lip of the tray). In the screened mudbox, however, the screen was not rigid and formed wavy contours such that the mesh blocked the laser beams of the LDV, making it impossible to profile below the screen close to the sediment surface. For the Flush Sediment Tray, simulations were conducted with the tray flush with the flume bottom and also with the leading edge of the tray purposely exposed (i.e., tipped up into the flow). Thus relatively "good" (=flush) and "poor" (=tipped) deployments were simulated.

Theoretical calculations indicated that the log layer in the open-channel flow section of the flume was between approximately 0.3 and 5.0 cm above the bottom. Therefore, 10 profile points in the vertical were roughly logarithmically spaced within this region and five more points were evenly spaced above the log layer. Because the nature of flow over the mudboxes was unknown and may have been more complex than in the flume channel, 10 vertical profile points were roughly evenly spaced above the mudbox structure. Fifteen point profiles were taken in areas where greater resolution was desired. Along-channel positions of vertical profiles over the mudboxes were dictated by visual observations of flow separations and other boundary-layer flow features which we sought to resolve.

The sediment used in the Old Free Vehicle, New Free Vehicle and Raised Mudbox simulations was obtained from the U.S. Mid-Atlantic slope at 2100 m where colonization experiments have been conducted (Maciolek et al., 1987; Grassle and Morse-Porteous, 1987). Despite slight differences in the actual heights of the mudboxes, the sediment surface in each case was about 10 cm above the floor of the flume, except for the Raised Mudbox, where it was about 11 cm above the flume floor. The Flush Sediment Tray was filled with sediment from the St. Croix site, where this type of tray had been used previously (Snelgrove et al., 1992, 1994). Although this sediment is somewhat coarser than the muddy sediment from the Mid-Atlantic slope, the roughness is not sufficiently large to extend above the viscous sublayer in hydrodynamically smooth-turbulent flow, and therefore both sediments would be expected to have a similar effect on the vertical shear, mixing and shape of the velocity profile. The position of the mudboxes along the flume channel was such that the front edge of the sediment in each tray was 10.1 m downstream from the flume entrance. Therefore, the leading edge of the New Free Vehicle extended 6 cm further upstream than that of the Old Free Vehicle. Also, because the fiberglass rim of the Raised Mudbox was relatively small, it did not extend quite as far upstream as the Old Free Vehicle (leading edges differed by 9 cm).



Figure 6. Velocity profiles taken at three points along the flume axis encompassing the test section where measurements were made in slow (left) and fast (right) flow. Boundary shear velocities  $(u_*)$  were calculated with a semi-empirical expression for the mean velocity in a steady, open-channel flow above a smooth bottom, as described in Trowbridge *et al.* (1989) and Butman and Grassle (1992).

#### 4. Results

To validate the assumption of one-dimensional open-channel flow in the region where mudboxes were tested, measurements were made at widely-spaced intervals along the channel before the mudboxes were added. Profiling was done at points along the flume channel corresponding to the location of the leading edge of the New Free Vehicle, the leading edge of the Old Free Vehicle, and a position near the furthest downstream measurement location. In both slow and fast flow, the shear velocities and shapes of profiles were similar at each along-channel location (Fig. 6) as predicted from theoretical considerations (e.g., Nowell and Jumars, 1987). Thus, the flow was essentially fully developed, in terms of mean horizontal velocity, at the leading edges of the mudboxes. Furthermore, a comparison of the flume flows and a typical deep-sea flow (Fig. 7) reveals that the mudbox leading edges would intercept the velocity profiles within the log layer of the flow in all cases and that the highest shear region, the viscous sublayer, is well below the interception point.

a. The free vehicles. In the slow-flow simulation, flow approaching the sediment tray in the Old Free Vehicle differed markedly from flow over the flat flume bed (compare Fig. 8 to Fig. 6a). Directly above the fiberglass lip at the leading edge of the tray, negative velocities were observed adjacent to the lip, with positive velocities occurring only at heights >1 cm above the lip, suggesting that an eddy formed upstream of the rubber gasket. Above the region of flow separation, velocities of about 9 cm s<sup>-1</sup> were observed, much as predicted for a natural deep-sea boundary



Figure 7. A theoretical, hydrodynamically smooth-turbulent velocity profile in a typical deep-sea, muddy habitat, calculated for u = 15 cm s<sup>-1</sup> at z = 500 cm (e.g., see Butman, 1986a).

flow (Fig. 7) and the hydrodynamically smooth-turbulent flume flow (Fig. 6). Several centimeters downstream from the gasket, over the upstream portion of the sediment surface, negative velocities were again observed. Within  $\sim 1$  cm of the sediment surface, flows were negative at a distance 4 cm downstream from the gasket, suggesting that an eddy (or eddies) had formed just behind the gasket. Further downstream, negative velocities were not observed, as the boundary layer reattached and began to grow over the sediment surface. Note that the generally higher flow speeds observed over the tray compared with the open channel case is partly due to the mudbox blocking the flume flow, resulting in enhanced acceleration (see Section 3d.); this would be much less pronounced in nature.

The two-dimensional velocity field over the Old Free Vehicle in fast flow (Fig. 9) was qualitatively similar to that observed in slow flow (Fig. 8). The size of the eddy that formed downstream of the gasket appeared to be slightly larger than in slow flow, given that negative velocities were observed 6 cm downstream of the gasket compared with 4 cm in slow flow. Not surprisingly, under these flow conditions, velocities were generally faster in all cases; however, the shapes of the profiles at corresponding locations were similar in the slow and fast flows.

For the New Free Vehicle, changes to the natural velocity profile as the flow moved over the mudbox structure were much less pronounced (Fig. 10). Although the shape of the profile changed as flow moved past the leading edge of the disc up onto the raised surface where the sediment was contained, flow separation was not



Figure 8. Velocity profiles measured at different positions along the Old Free Vehicle upstream of the sediment surface (left) and directly over the sediment surface (right) for slow flow conditions. Letters refer to along-channel positions of the profiles, as indicated in the diagram beneath the plots.

observed. The absence of negative velocities downstream from the leading edge also suggests that eddies did not form anywhere over the mudbox structure. Flow was reduced near the mudbox surface, particularly just before the crest of the leading edge (profile C in Fig. 10). Most importantly, however, flow over the sediment surface did not change appreciably in the along-channel direction, and at least qualitatively resembled flow in the open-channel case (Fig. 6). Although flow acceleration was observed relative to the open channel, this was again, in part, a result of structure-induced flow accelerations in the flume, and such accelerations would be expected to be smaller in nature where the flow is free to move around as well as over the structure. As with the Old Free Vehicle, velocity profiles above the New Free Vehicle under fast flow conditions (Fig. 11) were similar to those under slow flow (Fig. 10).

b. The colonization trays. In general, flow over the Raised Mudbox (Fig. 12) was similar to that over the Old Free Vehicle (Figs. 8 and 9). Although there was no



Figure 9. Velocity profiles measured at different positions along the Old Free Vehicle for fast flow conditions. Letters refer to along-channel positions of the profiles, as indicated in the diagram beneath the plots.

gasket at the upstream edge of the Raised Mudbox, negative velocities indicative of eddy formation were observed just above the overhanging lip at the leading edge (profile A in Fig. 12); evidently, the overhanging lip created a complex hydrodynamic disturbance. At the upstream edge of the sediment surface, just behind the lip, negative velocities (and thus, eddy formation) were again observed (profiles B and C in Fig. 12). Further downstream, a secondary boundary layer appeared to develop over the sediment surface, and vertical profiles varied considerably as the flow progressed downstream (profiles D and E in Fig. 12). Relative to these other flow effects, differences between screened and unscreened case mudboxes were modest, at least in the region where measurements could be obtained. Nonetheless, higher velocities were generally observed close to the sediment surface in the screened case, and the eddy in the upstream region of the contained sediment was somewhat larger in the unscreened case.

The Flush Sediment Tray was designed to be placed flush with the ocean bottom, and not surprisingly, the flow over the tray (Fig. 13) was virtually identical to that in the open-channel case (Fig. 6). Exposing the leading edge of the Flush Sediment



Figure 10. Velocity profiles measured at different positions along the New Free Vehicle upstream of the sediment surface (left) and directly over the sediment surface (right) for slow flow conditions. Letters refer to along-channel positions of the profiles, as indicated in the diagram beneath the plots.

Tray resulted in modest changes to the velocity profiles as flow passed over the sediment surface. These changes were minor, however, compared with alongchannel changes in velocity profiles observed over the sediment surfaces of any of the other mudbox designs. This orientation also represents a worst-case scenario because it is generally possible for a submersible or divers to place the trays more flush with the sediment surface (authors' pers. obs.).

#### 5. Discussion

Within recent years, small-scale hydrodynamic processes have been recognized as an important source of benthic biological heterogeneity (e.g., see reviews by Jumars and Nowell, 1984; Butman, 1987; Snelgrove and Butman, 1994). Despite the fact that many different processes such as nutrient supply, organic flux, sediment deposition and erosion, and larval supply may all be heavily influenced by the near-bed flow regime, benthic experimental structures or instruments generally have not been designed to minimize flow disturbance or artifacts. Studies specifically evaluating flow effects on infaunal larval settlement and recruitment in natural habitats (e.g., Eckman, 1979, 1983; Butman, 1989; Snelgrove, 1994) and in laboratory flumes (e.g., Pawlik *et al.*, 1991; Jonsson *et al.*, 1991; Butman and Grassle, 1992; Grassle *et al.*, 1992b; Pawlik and Butman, 1993; Snelgrove *et al.*, 1993) have produced strong



Figure 11. Velocity profiles measured at different positions along the New Free Vehicle for fast flow conditions. Letters refer to along-channel positions of the profiles, as indicated in the diagram beneath the plots.

evidence that hydrodynamic processes have an important effect on larval or postlarval distributions both in the water column and on the bottom. Such results dictate a re-evaluation of colonization studies where sediments were raised above the seafloor both in shallow water (e.g., McCall, 1977; Zajac and Whitlatch, 1982) and in the deep sea (Grassle, 1977; Desbruyères *et al.*, 1980, 1985; Levin and Smith, 1984; Grassle and Morse-Porteous, 1987; Maciolek *et al.*, 1987).

One means of eliminating potential flow artifacts in benthic colonization studies is to place sediments flush with the natural bottom, an approach which has been successfully adopted in intertidal habitats (Eckman, 1983; Gallagher *et al.*, 1983). Indeed, the Flush Sediment Tray tested here has been successfully used in shallow water (Snelgrove, 1994) and the deep sea (Snelgrove *et al.*, 1992, 1994). The flume simulations summarized here (see also Snelgrove *et al.*, 1992) indicate that flow disturbance generated by Flush Sediment Trays is minimal, even when the leading edge of the tray is exposed, and that the flow across the tray closely approximates that predicted for the natural environment. Unfortunately, it is not always logistically possible to place trays flush with the ambient sediment, particularly in marginally accessible habitats such as the deep sea. Thus, it is sometimes unavoidable to have structures protruding above the sediment surface, and efforts must then be directed toward minimizing, rather than eliminating, hydrodynamic disturbance.



Figure 12. Velocity profiles measured at different positions along the Raised Mudbox upstream of the sediment surface and over the sediment surface for screened (left) and unscreened (right) trays in slow flow. Letters refer to along-channel positions of the profiles, as indicated in the diagram beneath the plots.

Instruments that extend above the ocean bottom and into the benthic boundary layer create flow disturbance in several different ways, and the potential flow artifacts are exemplified by the mudbox examples. The flow must accelerate as it moves over and around a mudbox which protrudes above the bottom. In unbounded flows, this effect is somewhat minor, however, compared with other potential hydrodynamic effects. By raising the sediment contained in the mudbox up into the boundary layer flow, relatively fast flows will move past the mudbox sediment compared with flow over the sediment-water interface (Fig. 1b). The result is that a second boundary layer develops on the sediment surface, creating complex, constantly changing flow conditions over the mudbox sediments. Furthermore, if the drag of the mudbox on the flow is sufficiently large, the boundary layer may separate such that eddies are shed at various places along the sediment surface, potentially creating regions of enhanced shear and of local deposition.

These types of flow disturbances were observed in the Old Free Vehicle and Raised Mudbox flow simulations (Figs. 8, 9, 12). Qualitatively, flows over these two



Figure 13. Velocity profiles measured at different positions along the Flush Sediment Tray upstream of the sediment surface and over the sediment surface for flush (left) and partially exposed (right) trays in slow flow. Letters refer to along-channel positions of the profiles, as indicated in the diagram beneath the plots.

types of mudbox were similar. Because the sediment surface is raised well above the natural seabed, relatively high flow speeds approached the sediment. Over the mudbox sediment and within the natural bottom boundary layer, a thin boundary layer grew over the sediment surface, increasing in thickness as the flow moved downstream. Eddies formed in front of and behind the gasket of the Old Free Vehicle, and although a gasket was absent from the Raised Mudbox, the sediment surface was lower than the rest of the tray and a similar flow effect (i.e., eddy production) resulted from the tray itself. Thus, an area of relatively low shear was produced both in front of and behind the gasket, creating potential depositional areas upstream of the gasket and at the leading edge of the sediment surface.

In unidirectional flows, the eddy in front of the gasket may reduce the number of larvae, adults, sediment grains, or food particles that encounter the sediment tray, because this area of very slow flow may cause passively transported material to fall out of suspension. Those particles that make it over the gasket may tend to be entrained in the small eddy behind the gasket. Moreover, the boundary layer over the sediment in this design grows considerably as the flow progresses across the sediment. Thus, because boundary-layer characteristics constantly change in the alongchannel direction, the flow regime is not uniform over the sediment surface. This along-channel variation in boundary-layer characteristics thus imposes an additional variable over the mudbox sediments that could confound interpretation of effects due to sediment treatments alone. Furthermore, these measurements were made with flow at right angles to the sediment tray. Flow approaching at an angle, across the corners of the tray, may be even more complex. Clearly, characteristics of flow moving across the Old Free Vehicle and the Raised Mudbox were very different from those expected to occur over natural, muddy deep-sea bottoms.

In designing the New Free Vehicle, many of these potential problems were considered. The gasket was attached to the lid rather than to the sediment trays, eliminating the eddy effect. The sloping edge of the disc surrounding the sediment tray was designed to minimize disturbance to the natural boundary layer, and to avoid eddy shedding downstream of the leading edge. Based on the flume simulations shown here, these design goals appear to have reduced hydrodynamic biases considerably. Velocity profiles changed comparatively little across the sediment surface of the New Free Vehicle, and there were no areas of enhanced deposition and shear resulting from eddies. The net effect was that flow across the sediment tray closely mimicked predictions for flow over the natural seafloor.

The two major improvements of the New Free Vehicle were the elimination of flow separations and the production of a relatively uniform flow across the sediment surface. These improvements are critical given the growing evidence that even relatively small-scale flow alterations influence settling larvae. Given that typical swim speeds for larvae may be exceeded by mean horizontal flow speeds at distances of only a few millimeters above the bottom (e.g., Butman, 1986a; Gross et al., 1992), it is not surprising that results of several field studies suggest that larvae may be passively entrained in relatively small-scale bottom features, such as depressions (e.g., Savidge and Taghon, 1988; Snelgrove, 1994). Although these organisms may be actively responding to organic material that has accumulated in depressions (e.g., VanBlaricom, 1982), there is evidence that passive entrainment may occur for at least some taxa. In flume experiments with larvae of the polychaete Capitella sp. I and the bivalve Mulinia lateralis, for example, enhanced settlement was observed in small depressions compared with flush treatments of a similar sediment type (Snelgrove et al., 1993). In fact, M. lateralis larvae, in particular, were often observed to make a "poor choice," settling in depressions containing an unfavorable substrate, probably because of hydrodynamic entrainment. The spatial scale of eddies created in the small depressions in the Snelgrove et al. (1993) flume experiments was roughly comparable to the eddies generated in the mudbox simulations described here. Moreover, although larvae of Capitella sp. I and M. lateralis are capable of active habitat selection, settlement may be modified by near-bed hydrodynamics (Butman

and Grassle, 1992; Grassle *et al.*, 1992a,b; Snelgrove *et al.*, 1993). Likewise, because transport of passive particles such as fine-grained sediments and detritus clearly can be modified by near-bed flow processes (e.g. Stolzenbach *et al.*, 1992; Yager *et al.*, 1993) sediment properties may vary over small scales within the Old Free Vehicle and Raised Mudbox sediments and larvae may respond actively to this variation.

Mudbox-type experiments can also be criticized for physically isolating the experimental sediments from the surrounding sediment. Indeed, Smith and Brumsickle (1989), working in an intertidal system, found that patch size and sediment isolation influenced colonization rates of species and the time required for treatments to return to background composition. The relative effects of elevating the sediment above the surrounding bottom and placing sides on the sediment plugs in this study were unclear, but the high numbers of post-larval individuals that were observed in their treatments do suggest that physical isolation of sediments represents a poor mimic of a natural, small-scale disturbance, at least in this environment. Still, if the goal of a given experiment is to mimic a large-scale disturbance where withinsediment migration is less likely to be important, or to isolate effects of specific variables on colonization (e.g., sedimentary organic composition; Snelgrove *et al.*, 1992; 1994) from confounding variables, such as presence or absence of different adults, then mudbox-type experiments can be a valuable tool.

Although these flume simulations were motivated by an interest in potential hydrodynamic effects on settling larvae, the types of flow disturbances that have been documented here may be relevant to many different fields of oceanographic research. These demonstrated alterations to the boundary-layer flow caused by mudbox structures are presented to facilitate the design of hydrodynamically unbiased benthic experimental gear for use in other areas of benthic ecology, chemistry, geology, and engineering.

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#### REFERENCES

- Agrawal, Y. C. and C. J. Belting. 1988. Laser velocimetry for benthic sediment transport. Deep-Sea Res., 35, 1047–1067.
- Amos, C. L., J. Grant, G. R. Daborn and K. Black. 1992. Sea Carousel—A benthic, annular flume. Est. Coast. Shelf Sci., 34, 557–577.

Butman, C. A. 1986a. Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom velocity profiles, *in* Marine Interfaces Ecohydrodynamics, J. C. J. Nihoul, ed., Elsevier Oceanogr. Ser., 42, Elsevier, Amsterdam, 487–513.

— 1986b. Sediment trap biases in turbulent flows: Results from a laboratory flume study. J. Mar. Res., 44, 645–693.

- 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging rôle of hydrodynamical processes. Oceanogr. Mar. Biol. Ann. Rev., 25, 113–165.
- 1989. Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters. J. Exp. Mar. Biol. Ecol., 134, 37–88.
- Butman, C. A. and R. J. Chapman. 1989. The 17-Meter Flume at the Coastal Research Laboratory. Part 1: Description and User's Manual. WHOI Technical Report 89-10, 31 pp.
- Butman, C. A., M. Fréchette, W. R. Geyer and V. R. Starczak. 1994. Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. Limnol. Oceanogr., 39, 1755–1768.
- Butman, C. A. and J. P. Grassle. 1992. Active habitat selection by *Capitella* sp. I larvae. I. Two-choice experiments in still water and flume flows. J. Mar. Res., *50*, 669–715.
- Clauser, F. H. 1956. The turbulent boundary layer. Adv. Appl. Mech., 4, 1-51.
- Dayton, P. K. and J. S. Oliver. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments, *in* Marine Benthic Dynamics, K. R. Tenore and B. C. Coull, eds., University of South Carolina Press, Columbia, 93–120.
- Desbruyères, D., J. Y. Bervas and A. Khripounoff. 1980. Un cas de colonisation rapide d'un sédiment profond. Oceanologica Acta, 3, 285–291.
- Desbruyères, D., J. W. Deming, A. Dinet and A. Khripounoff. 1985. Réactions de l'écosystème benthique profond aux perturbations: Nouveaux résultats expérimentaux, *in* Peuplements profonds du golfe de Gascogne, L. Laubier and C. Monniot, eds., IFREMER, 193–208.
- Eckman, J. E. 1979. Small-scale patterns and processes in a soft-substratum intertidal community. J. Mar. Res., 37, 437–457.
- 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr., 28, 241–257.
- Emerson, C. W. and J. Grant. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnol. Oceanogr., *36*, 1288–1300.
- Gallagher, E. D., P. A. Jumars and D. D. Trueblood. 1983. Facilitation of soft-bottom benthic succession by tube builders. Ecology, *64*, 1200–1216.
- Grant, W. D. and O. S. Madsen. 1986. The continental-shelf bottom boundary layer. Ann. Rev. Fluid Mech., 18, 265–305.
- Grassle, J. F. 1977. Slow recolonisation of deep-sea sediment. Nature, 265, 618-619.
- Grassle, J. F. and L. S. Morse-Porteous. 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Res., *34*, 1911–1950.
- Grassle, J. P., C. A. Butman and S. W. Mills. 1992a. Active habitat selection by *Capitella* sp. I larvae. II. Multiple-choice experiments in still water and flume flows. J. Mar. Res., 50, 717–743.
- Grassle, J. P., P. V. R. Snelgrove and C. A. Butman. 1992b. Larval habitat choice in still water and flume flows by the opportunistic bivalve *Mulinia lateralis*. Neth. J. Sea Res., 30, 33–44.
- Gross, T. F. and A. R. M. Nowell. 1983. Mean flow and turbulence scaling in a tidal boundary layer. Cont. Shelf Res., 2, 109–126.
- Gross, T. F., F. E. Werner and J. E. Eckman. 1992. Numerical modeling of larval settlement in turbulent bottom boundary layers. J. Mar. Res., 50, 611–642.

- Hannan, C. A. 1984. Planktonic larvae may act like passive particles in turbulent near-bottom flows. Limnol. Oceanogr., 29, 1108–1116.
- Haury, L. R., D. E. Kenyon and J. R. Brooks. 1980. Experimental evaluation of the avoidance reaction of *Calanus finmarchicus*. J. Plank. Res., 2, 187–202.
- Henderson, F. M. 1966. Open Channel Flow, Macmillian Publishing Co., New York, 522 pp.
- Hulberg, L. W. and J. S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. Can. J. Fish. Aquat. Sci., 37, 1130–1139.
- Jonsson, P. R., C. André and M. Lindegarth. 1991. Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: evidence for near-bottom confinement. Mar. Ecol. Prog. Ser., 79, 67-76.
- Jumars, P. A. and A. R. M. Nowell. 1984. Fluid and sediment dynamic effects on marine benthic community structure. Am. Zool., 24, 45–55.
- Komar, P. D. 1976. Boundary layer flow under steady unidirectional currents, *in* Marine Sediment Transport and Environmental Management, D. J. Stanley and D. J. P. Swift, eds., John Wiley and Sons, New York, 91–106.
- Levin, L. A. 1990. A review of methods for labeling and tracking marine invertebrate larvae. Ophelia, 32, 115–144.
- Levin, L. A. and C. R. Smith. 1984. Response of background fauna to disturbance and enrichment in the deep sea: a sediment tray experiment. Deep-Sea Res., 31, 1277–1285.
- Maciolek, N., J. F. Grassle, B. Hecker, P. D. Boehm, B. Brown, B. Dade, W. G. Steinhauer, E. Baptiste, R. E. Ruff, and R. Petrecca. 1987. Study of biological processes on the U.S. North Atlantic slope and rise. Final Report Prepared for U.S. Department of the Interior, Minerals Management Service, Washington, D.C. 20240, 358 pp.
- Madsen, O. S. 1976. Wave climate of the continental margin: elements of its mathematical description, *in* Marine Sediment Transport and Environment, D. J. Stanley and D. J. P. Swift, eds., John Wiley and Sons, New York, 66–87.
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res., 35, 221–266.
- Mullineaux, L. S. and C. A. Butman. 1990. Recruitment of encrusting benthic invertebrates in boundary-layer flows: A deep-water experiment on Cross Seamount. Limnol. Oceanogr., 35, 409–423.
- 1991. Initial contact, exploration and attachment of barnacle (*Balanus amphitrite*) cyprids settling in flow. Mar. Biol., *110*, 93–103.
- Mullineaux, L. S. and E. D. Garland. 1993. Larval recruitment in response to manipulated field flows. Mar. Biol., 116, 667–683.
- Nowell, A. R. M. 1983. The benthic boundary layer and sediment transport. Rev. Geophys. Space Physics, 21, 1181–1192.
- Nowell, A. R. M. and P. A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst., 15, 303–328.

— 1987. Flumes: Theoretical and experimental considerations for simulation of benthic environments. Oceanogr. Mar. Biol. Ann. Rev., 25, 91–112.

- Pawlik, J. R. and C. A. Butman. 1993. Settlement of a marine tube worm as a function of current velocity: Interacting effects of hydrodynamics and behavior. Limnol. Oceanogr., 38, 1730–1740.
- Pawlik, J. R., C. A. Butman and V. R. Starczak. 1991. Hydrodynamic facilitation of gregarious settlement of a reef-building tube worm. Science, 251, 421–424.
- Savidge, W. B. and G. L. Taghon. 1988. Passive and active components of colonization following two types of disturbance on intertidal sandflat. J. Exp. Mar. Biol. Ecol., 115, 137–155.

Schlichting, H. 1979. Boundary-layer Theory, 7th ed, McGraw-Hill, New York, 817 pp.

Singarajah, K. V. 1969. Escape reactions of zooplankton: The avoidance of a pursuing siphon tube. J. Exp. Mar. Biol. Ecol., *3*, 171–178.

— 1975. Escape reactions of zooplankton: Effects of light and turbulence. J. Mar. Biol. Assoc. U.K., 55, 627–639.

- Smith, C. R. 1985. Colonization studies in the deep sea: Are results biased by experimental design?, *in* Proceedings of the Nineteenth European Marine Biology Symposium, P. E. Gibbs, ed., Cambridge University Press, Cambridge, England, 183–190.
- Smith, C. R. and S. J. Brumsickle. 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. Limnol. Oceanogr., 34, 1263–1277.
- Smith, K. L., Jr. 1978. Benthic community respiration in the N.W. Atlantic Ocean: in situ measurements from 40 to 5200 m. Mar. Biol., 47, 337–347.
- Smith, K. L., Jr., G. A. White, M. B. Laver, R. R. McConnaughey and J. P. Meador. 1979. Free vehicle capture of abyssopelagic animals. Deep-Sea Res., 26, 57–64.
- Snelgrove, P. V. R. 1994. Hydrodynamic enhancement of invertebrate larval settlement in microdepositional environments: colonization tray experiments in a muddy habitat. J. Exp. Mar. Biol. Ecol., 176, 149–166.
- Snelgrove, P. V. R. and C. A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. Oceanogr. Mar. Biol. Ann. Rev., 32, 111–177.
- Snelgrove, P. V. R., C. A. Butman and J. P. Grassle. 1993. Hydrodynamic enhancement of larval settlement in the bivalve *Mulinia lateralis* (Say) and the polychaete *Capitella* sp. I in microdepositional environments. J. Exp. Mar. Biol. Ecol., 168, 71-109.
- Snelgrove, P. V. R., J. F. Grassle and R. F. Petrecca. 1992. The role of food patches in maintaining high deep-sea diversity: Field experiments using hydrodynamically unbiased colonization trays. Limnol. Oceanogr., 37, 1543–1550.

- Stolzenbach, K. D., K. A. Newman and C. S. Wong. 1992. Aggregation of fine particles at the sediment-water interface. J. Geophys. Res., 97, 17,889–17,898.
- Trowbridge, J. H., W. R. Geyer, C. A. Butman and R. J. Chapman. 1989. The 17-Meter Flume at the Coastal Research Laboratory. Part II: Flow Characteristics. WHOI Technical Report 89-11. 37 pp.
- VanBlaricom, G. R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecol. Monogr., *52*, 283–305.
- Walters, L. J. 1992. Field settlement locations on subtidal marine hard substrata: Is active larval exploration involved? Limnol. Oceanogr., *37*, 1101–1107.
- Wimbush, M. 1976. The physics of the benthic boundary layer, *in* The Benthic Boundary Layer, I. N. McCave, ed., Plenum Press, New York, 3–10.
- Wirsen, C. O. and H. W. Jannasch. 1986. Microbial transformations in deep-sea sediments: free-vehicle studies. Mar. Biol., 91, 277–284.
- Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. Ecol. Monogr., *44*, 171–187.
- Yager, P. L., A. R. M. Nowell and P. A. Jumars. 1993. Enhanced deposition to pits: A local food source for benthos. J. Mar. Res., 51, 209–236.
- Young, R. A. 1977. Seaflume: a device for *in-situ* studies of threshold erosion velocity and erosional behavior of undisturbed marine muds. Mar. Geol., 23, M11–M18.
- Zajac, R. N. and R. B. Whitlatch. 1982. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. Mar. Ecol. Prog. Ser., *10*, 1–14.

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<sup>— 1994.</sup> Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. J. Mar. Res., 52, 345–369.