

## Fluid and Sediment Dynamic Effects on Marine Benthic Community Structure<sup>1</sup>

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**SYNOPSIS.** Fluid and sediment dynamics affect benthic community dynamics and structure in manifold ways. We single out three community-structuring processes that are both strongly affected and amenable to controlled manipulation: microbial population growth, faunal recruitment, and particle feeding. Attachment and colony growth rates of microbes depend on the details of near-bed fluid exchange. Their emigration and colony growth rates are affected by erosion of microbial films and by abrasion during sediment transport. Recruitment and successional patterns of metazoans, especially those resulting from the settlement of weakly swimming, small larvae and juveniles, also are very sensitive to local variations in boundary layer flow pattern and strength. While the importance of particle fluxes to suspension feeders has long been apparent, the foraging patterns of a growing number of surface deposit feeders are being found to reflect a dependence upon sediment transport.

Although these three processes have spatial and temporal scales amenable to both laboratory and field experimentation, proper dynamic scaling of laboratory model flows may not always be easy. Even the simplest two-phase (particles plus liquids, where particles can be bacteria, flocs, larvae, or sediments) flows must match appropriate laboratory and field Reynolds number, Froude number, particle-fluid density (weight per unit volume) ratio, and the ratio of boundary layer thickness to particle size, if the laboratory flow model is to provide accurate results.

### INTRODUCTION

Our long-term biological goal is the same as that of many biological oceanographers—to understand underlying processes well enough to predict accurately what organisms, and in what abundances, will be found where and when within the sea. Our predilection has been for the soft-sediment marine environments that cover most of the globe. The focus of our contribution thus differs from others in this symposium volume: Our ultimate concern is with community-level organization, and our physically oriented tools and approaches are drawn largely from the field of sediment dynamics (*e.g.*, Graf, 1971; Yalin, 1977; Middleton and Southard, 1978).

Fluid and particle motions affect benthic community structure on manifold scales in numerous ways. Patterns of oceanic circulation dictate broad-scale biogeography (*e.g.*, Ekman, 1967). Turbidity flows and

storm surges decimate communities and restart successional sequences (*e.g.*, Boesch *et al.*, 1976; Yeo and Risk, 1979). Rather than attempt a balanced review, we will limit ourselves to the oceanic microscale (as opposed to meso- or general circulation scales) and will examine only three biological processes, microbial population growth, faunal recruitment, and particle feeding, all as functions of bottom boundary-layer fluid and particulate transport. What these three processes have in common are strong implication in the control of community dynamics and amenability to manipulative experimentation both in the laboratory and in the field. Our primary goal in this essay is to make the implications explicit and to highlight open questions for future research.

Interactions of fluid dynamics and living organisms on longer time scales or larger spatial scales than those involved in these three processes are for the most part inaccessible to accurate dynamic scaling in microcosms or mesocosms. The problem is a simultaneous dependence of both fluid viscosity (and to a lesser extent, fluid density) and biological rates on temperature

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(Platt, 1981). It is exacerbated by a general inability to use exotic fluids (of varying viscosities and densities) together with living organisms. This comment is in keeping with our subsidiary goal of pointing out potential methodological pitfalls, particularly in laboratory flow tanks or flumes.

#### METHODOLOGY AND TERMINOLOGY

For simplicity of discussion, we will limit ourselves to steady, unidirectional (in the mean), turbulent flows. In the absence of flow obstructions (*e.g.*, animal tubes or organisms themselves) and enough suspended matter to cause fluid (bulk density) stratification, then, mean velocity varies only as a function of height ( $z$ , cm) above the bed. For this case, the "law of the wall" generally applies and is conveniently summarized as follows:

$$U(z) = \frac{u_*}{\kappa} \ln\left(\frac{z}{z_0}\right), \text{ where}$$

$U(z)$  = mean downstream velocity at height  $z$  above bottom (cm sec<sup>-1</sup>),  
 $\kappa$  = von Karman's constant (=0.41)  
 $z_0$  = roughness height (cm), and  
 $u_*$  = boundary shear velocity (cm sec<sup>-1</sup>).

If one plots  $\ln z$  versus  $U$ , a straight line results, with slope  $u_*/\kappa$  and intercept  $z_0$ . In practice,  $u_*$  and  $z_0$  usually are estimated by taking suitably time-averaged measures of  $U$  at various heights  $z$  for regression against  $\ln z$  (*e.g.*, Nowell *et al.*, 1981, Fig. 5). Note that even in this simplest of all turbulent boundary layer situations, velocity measurement at one arbitrary height is insufficient to characterize the flow in the vicinity of the bed. Because  $z_0$  is estimated by extrapolation (as the height at which mean velocity would drop to zero if the logarithmic velocity profile were to hold, *i.e.*, no viscous sublayer existed), its statistical confidence limits (and those for  $u_*$ ) are extremely broad unless velocity is measured at about six or more heights. The quantity  $u_*$  in this relation is called a boundary shear velocity because it is not a true velocity. Rather, it is a boundary shear stress in disguise (Middleton and Southard, 1978, p. 5.7):  $u_* = (\tau_0/\rho)^{1/2}$ , where  $\tau_0$  = boundary shear stress (g cm<sup>-1</sup> sec<sup>-2</sup>) and

$\rho$  = fluid density (g cm<sup>-3</sup>). The fact that it is shear stress that is responsible for momentum, nutrient, and particle flux at the bed, makes  $u_*$  perhaps the best single "velocity-like" parameter to use in describing near-bottom flow effects.

For  $u_*$  and  $z_0$  alone to characterize the flow adequately, the flow must be one dimensional, *i.e.*, both  $\partial U/\partial x$  and  $\partial U/\partial y$  must equal zero (as must be true of all derivatives of mean quantities [except pressure] in the downstream and cross-stream directions). Neither condition is strictly achievable in a flume of finite dimension. One must then work far enough downstream from the flume inlet for an equilibrium boundary layer to have developed to a thickness greater than the flow depth of interest (Schlichting, 1968) and far enough from the sidewalls that the bottom boundary fully dominates the flow. Otherwise, elaborate measurements and corrections are required (*e.g.*, Grant *et al.*, 1982) to obtain accurate  $u_*$  and  $z_0$  estimates. In practice, flume length must be tailored to the problem at hand, but serious sidewall problems are likely unless the flume width exceeds about seven times the bottom boundary layer thickness (seven times the flow depth in the most common laboratory situation of depth-limited boundary layer development).

We will deal explicitly with two-phase (particles plus liquids) flows. The particles may be bacteria, larvae, organic flocs, or sediments. The appropriate dynamic scaling parameters may not be self-evident for this case; dimensional analysis isolates seven relevant parameters and usually groups them into four dimensionless ratios as follows (Southard *et al.*, 1980):

$$\frac{\rho U d}{\mu}, \text{ a bulk flow Reynolds number;}$$

$$\frac{U}{(gd)^{1/2}}, \text{ a Froude number;}$$

$$\frac{\rho_s}{\rho}, \text{ a density ratio; and}$$

$$\frac{d}{D}, \text{ a size ratio; where}$$

$d$  = boundary layer thickness (=flow

- depth in many laboratory flumes) (cm),  
 $U$  = mean (vertically averaged) flow velocity (cm sec<sup>-1</sup>),  
 $D$  = particle diameter (cm),  
 $\rho$  = fluid density (g cm<sup>-3</sup>),  
 $\mu$  = fluid viscosity (g cm<sup>-1</sup> sec<sup>-1</sup>),  
 $\rho_s$  = particle density (g cm<sup>-3</sup>), and  
 $g$  = gravitational acceleration (cm sec<sup>-2</sup>).

Whenever this strict scaling is followed (*i.e.*, all four ratios are equal in the laboratory and field flows being compared) and the flow is long and wide enough, dynamic similarity is assured, even when ripples develop (Southard *et al.*, 1980) and the near-bed flow departs from one-dimensionality. Whenever this scaling is not followed, it is imperative to identify the departures and to resolve their consequences for the flows of interest. The importance of proper Reynolds number scaling has been emphasized elsewhere (*e.g.*, Vogel, 1981, p. 81 *ff.*), as related to the relative importance of inertial (numerator) and viscous (denominator) effects. Analogously, the density ratio can be viewed as a ratio of (particle *versus* fluid) inertial effects or as a relative measure of fluid buoyancy, and there is probably little temptation to alter it.

Probably the greatest temptation, due to cost limitations in flume wall materials and pumps, is to reduce  $d/D$ . If the bed is more or less flat and the problem is one of incipient sediment motion (*e.g.*, Nowell *et al.*, 1981) or simply of creating a desired  $\tau_0$ , so long as  $d/D$  remains large there may be little problem in comparing laboratory and field results. As soon as the reduction causes deformation of the free (water) surface or when suspended sediment is involved, however, the consequences can be serious. The Froude number is the ratio of mean fluid velocity to surface (gravity) wave speed. Fluid accelerations due to gravity waves can dominate fluid shear stresses. With respect to suspended sediments, let us say arbitrarily that the flow depth in the laboratory is halved but that  $\tau_0$  is sufficient to erode the same depth of sediment in the laboratory and field flows. The laboratory

flow will then have twice the average field suspended sediment concentration. The severity of such consequences, once again, can only be weighed against their impacts on the problem at hand.

For the sake of clarity and brevity, we will intercolate the few additional methods and parameterizations that we need directly in the text. While recent advances in the physical modeling and measurement of flows over two-dimensional (wavy or rippled) beds, of unsteady (*i.e.*, oscillatory) flow over both flat and wavy beds, and of flow stratification effects by suspended sediments have been nothing short of spectacular (reviewed by Nowell, 1983), the biological data now available and the flow tanks now accessible to biological oceanographers do not yet warrant our inclusion of this level of complexity. Such additions are sure to be desirable in the future.

#### PROCESSES AFFECTED

##### *Microbial population growth*

Microbial population growth occupies a central role in the prevailing view of energy and carbon flow within the soft-bottom benthos. Microbes make otherwise refractory detrital material available to higher trophic levels (*e.g.*, Tenore, 1977) and renew the food value of material that has passed once or more through the guts of deposit feeders (*e.g.*, Newell, 1965). In a closed system, the renewal rate of this food value puts a natural limit on environmental carrying capacity for deposit feeders (Levinton and Lopez, 1977). Furthermore, habitat selection by faunal recruits on both soft and hard substrata is influenced strongly by bacterial cover (*e.g.*, Wilson, 1955; Kirchman *et al.*, 1982).

The documented and potential roles of fluid and particle dynamics in modulating bacterial population growth are made more evident by separating local population growth into its four components: birth, mortality, immigration, and emigration. In the absence of over-grazing or light limitation (in the subset of photosynthetic autotrophs), microbial cell growth rate and hence birth (division) rate on submerged surfaces often is limited by the rate of sup-

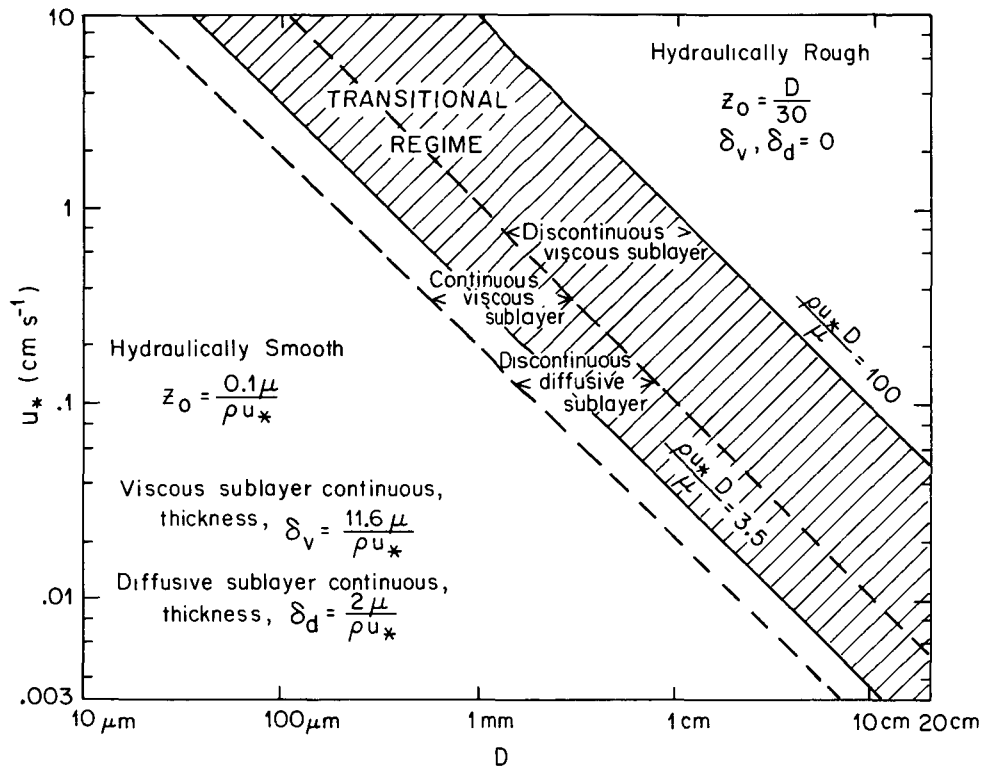


FIG. 1. A plot of the qualitative changes observed in near-bed fluid dynamic behavior (roughness Reynolds number) as a function of shear velocity ( $u_*$ ) and bed grain diameter ( $D$ ) for a flat (unrippled) bed of uniform grain size. The diagram encompasses the full range of  $u_*$  and  $D$  values generally encountered in oceanic and riverine conditions. Viscosity ( $\mu = 0.01$  poise [ $\text{g cm}^{-1} \text{sec}^{-1}$ ]) and fluid density ( $\rho = 1.0 \text{ g cm}^{-3}$ ) are taken to be constants for simplicity of illustration. Their ranges of variation are small in comparison with those of  $u_*$  and  $D$ .

ply of dissolved nutrients (*e.g.*, Admiraal *et al.*, 1981; Characklis, 1981). As we have done implicitly up to now, we will explicitly simplify discussion by assuming an impermeable bed and hence no supply from below. (We know this assumption to be inaccurate in some cases, *e.g.*, Rutgers van der Leoff, 1981.) The rate of nutrient supply from above, in turn, is strongly a function of the hydrodynamic nature of near-bed flow, which can be characterized without resort to the full suite of four dimensionless variables above.

Nikuradse (1933) introduced the boundary roughness Reynolds number,  $Re_r = \rho u_* D / \mu$ , to characterize boundary-layer flow over a flat (no ripples or other large, relative to  $D$ , projections) but granular bed as hydrodynamically (or hydraulically)

smooth ( $Re_r < 3.5$ ), fully rough (rough-turbulent,  $Re_r > 100$ ) or transitional ( $3.5 \leq Re_r \leq 100$ ). Note that no new parameters have been introduced in  $Re_r$ , but that those parameters especially relevant to flow very near the bed (*i.e.*, boundary shear velocity and microtopography) have been isolated. In the hydraulically smooth region, the flux of dissolved nutrients toward the boundary is limited by the diffusive sublayer thickness, approximated by  $2\mu / u_* \rho$ . Through this sublayer (approximately  $1/5$  of the thickness of the more extensive viscous sublayer, *cf.* Davies, 1972), the flux is set by the concentration gradient,  $dC/dz$ , times the coefficient of molecular diffusion ( $K_m \cong 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$ ). In the hydraulically rough region, no continuous diffusive sublayer exists, and the

flux of dissolved material is set by the concentration gradient times the near-bed eddy diffusion coefficient ( $K_e \cong 10^1 \text{ cm}^2 \text{ sec}^{-1}$ ). Turbulent eddy diffusion is so efficient at transporting dissolved materials that in the latter case, for all practical purposes, the microbial cells are bathed in nutrients of the average boundary layer concentration. In the little studied transitional regime, the flux of dissolved nutrients to the bed likely is controlled by the frequency of exchange of near-bed water parcels with the fluid above. In this regime, the diffusive sublayer is patchy in space and time (Fig. 1).

While monotonically increasing cell division rate as a function of increasing  $Re_r$  is thus a reasonable prediction for nutrient-limited cells already attached to the bed, the effects of flow on microbial immigration (attachment) rate are more difficult to foresee. Two factors are of concern, namely the frequency of contact with the bed and the probability of adhesion upon contact. For particles in general, their velocity toward the bed can be decomposed into six component vectors due to: (1) gravity, (2) Brownian motion, (3) electrostatic forces, (4) self propulsion, (5) fluid motion, and (6) inter-particle interaction. In a sense, we have turned the aerosol filtration problem (Rubenstein and Koehl, 1977) on its side, with the bed as filter. Characklis (1981) argues that, for a flagellated bacterium ( $\rho_s = 1.07 \text{ g cm}^{-3}$ ,  $D = 1 \text{ } \mu\text{m}$ , swimming speed =  $40 \text{ } \mu\text{m sec}^{-1}$ ), arrival at the bed through a diffusive sublayer will be dominated by Brownian motion and self propulsion. Frequency of contact with the bed in the hydraulically rough case, on the other hand, will be dominated by turbulent water motions. Bacterial adsorption to surfaces, like that of algal spores (Charters *et al.*, 1973), requires a finite time to achieve firm or permanent attachment (Floodgate, 1972). While the frequency of bacterial-bed contact probably increases monotonically with  $Re_r$ , the residence time of any one bacterium near the bed probably decreases with increasing  $Re_r$  above 100. Although experiments under carefully controlled flow conditions (set  $Re_r$  values) remain to be done, there is some sugges-

tion (Daniels, 1981, p. 20) that maximal attachment flux (cells attaching  $\text{cm}^{-2} \text{ sec}^{-1}$ ) would occur at intermediate  $Re_r$ .

For bare substrata placed in seawater under initially hydraulically smooth flow, there is clear evidence that initial bacterial population growth (immigration plus birth) rate is a monotonically non-decreasing function of flow velocity (Characklis, 1981; Pedersen, 1982). In predator-free systems, Characklis (1981) found that an equilibrium population size was attained when the microbial film thickness grew to exceed the diffusive sublayer thickness. At that point, erosion of the film (emigration) began to balance immigration plus birth. None of Characklis' (1981) or Pedersen's (1982) experiments began, however, with fully rough flow. In this case, we would expect rapid achievement of an attached population in dynamic equilibrium, probably concentrated in the niches between individual "grains."

For the very central question of microbial renewal of sediment food value, we are unaware of any experiments concerning fecal pellet repopulation modulation by flow. Does immigration or growth of residual cells dominate initial growth? Do the necessary microbial nutrients come from within the pellets or from the flow above? Do microbes growing on the outsides of pellets ablate with the mucous coating (Nowell *et al.*, 1981) and become unavailable to deposit feeders locally? Do immigrant microbes (and their nutrients) come from the fluid or from the ubiquitous organic flocs (*e.g.*, Kajihara *et al.*, 1974; Eisma *et al.*, 1980) that transport actively at almost any shear velocity?

Likewise there is scant evidence upon the influence of sediment ( $\rho_s = 2.65 \text{ g cm}^{-3}$  for quartz particles) transport itself on microbial population growth. Once sediment transport begins, particles impact each other and "sand blast" populations of microbes off the exposed edges of sediment grains (Meadows and Anderson, 1968; Weise and Rheinheimer, 1978). In open systems with intense sediment transport (*i.e.*, wave-exposed beaches), much of the local microbial production is exported as a result of such abrasion (Steele, 1976).

What are the consequences for microbial population dynamics when sediment transport is less severe in either open or closed systems? Does weak sediment transport, by exposing grains to a higher nutrient flux and to abrasion, have a stimulatory effect analogous to that of low-level grazing pressure (Hargrave, 1970)? When ripples form and migrate (for quartz grains with an equilibrium height of about  $100D$ , a wavelength of about  $1,000D$ , and a migration velocity of about  $0.01u_*$  [Yalin, 1977]), overturning (grain by grain) sediment to a depth of one ripple height, what are the consequences? Is this overturn capable of preventing blooms in attached autotrophs by mixing them below the level (in the sediments) of sufficient light (Fenchel and Straarup, 1971) for net production? What are the microbial impacts of the fact that  $\tau_0$ , and consequently nutrient flux, varies as a function of (crest-to-trough) position on the surface of a rippled bed?

Thus, there is obvious need for simplified (but well controlled) experiments over beds of varying (but uniform) roughness. Let us now introduce the realistic complexity of what fluid dynamicists call an isolated "roughness element," an object on the bed that causes divergence of streamlines (and is larger than the ambient grain size). The most frequent such element on the seabed is the tube of an animal. In altering the streamlines of flow about itself, such a projection will produce local regions of varying  $\tau_0$  on the surrounding bed (e.g., Eckman, 1983, Fig. 2). One might intuit that an additional useful scaling parameter in this case would be the cylinder Reynolds number,  $Re_c = \rho UL/\mu$ , where  $L$  is the cylinder diameter. At least for hydraulically smooth flow encountering a tube on an immovable bottom (the only case investigated empirically to date; Eckman, 1982 and in preparation), the height to which the tube protrudes into the boundary layer (i.e., the gradient, with  $z$ , of velocity encountered by the tube) is even more important in determining the intensity and spatial scale of changes in the surrounding bed shear stress. In general, localized regions both of increased and of decreased  $\tau_0$  are observed about a tube, but the for-

mer predominate. A tube projecting one quarter (Bowden, 1978) or more of the way through the viscous sublayer effectively pokes a hole through it and produces local regions where no diffusive sublayer exists. These regions may (Eckman, 1982) foster enhanced microbial growth rates. Nearby areas of decreased  $\tau_0$  may be sites of local deposition (Eckman, 1982) or decreased fluid exchange. Again, the effects on local microbial populations remain to be determined.

As the numerical (areal) density of roughness elements, such as tubes, increases, fluid momentum reaching the bed remains elevated—until roughly  $1/12$  of the plan area of the bed is covered by these projections (Nowell and Church, 1979; Eckman *et al.*, 1981, Fig. 1). As the density of roughness elements increases further, a "skimming" flow (*sensu* Morris, 1955) ensues, in which the site of maximal turbulence intensity rises above the tops of the roughness elements and mean  $\tau_0$  on the remaining bed decreases. Eckman *et al.* (1981) have suggested that the enhanced fluid exchange in beds of sparse ( $<1/12$  plan area cover) tubes may lead to increased microbial growth rates, but substantiating or discrediting experiments have yet to be carried out.

#### *Faunal recruitment*

There are many homologies and analogies to be drawn between faunal and microbial recruitment to the seabed; we leave most of them to the reader. The major difference is that the faunal recruits are larger, suggesting greater relative contributions from gravity and self propulsion and a lesser contribution from Brownian motion in determining the frequency of larval contact with the bed. The small value for  $\rho_s/\rho$ , however, still suggests a major role for fluid motions in the hydraulically rough regime. The landmark work in this field is that of Crisp (1955), who showed that barnacle species differ in their optimal near-bed velocity gradients (and hence  $\tau_0$ ) for initial substratum exploration behavior. Previous workers (e.g., Smith, 1946; Doochin and Smith, 1951) had been concerned primarily with maximal current

velocities (measured at some arbitrary height over a boundary of undefined roughness or averaged over some arbitrary volume) for settlement but had neither calculated nor measured flow conditions at the bed where larvae settle. In view of Crisp's early results, it is surprising that recent hard-substratum manipulative experiments (e.g., Dean, 1981) have not focused greater attention on the fluid dynamic consequences of their procedures. The implicit importance of fluid dynamics, especially of the roughness Reynolds number, awaits explicit discovery.

The potential sensitivity of recruits to flow variation was demonstrated dramatically by Eckman (1979) who showed that both tanaids and sabellid polychaetes in the intertidal community he studied recruited selectively to the sites of individual simulated tubes (sewing needles <1 mm in diameter) implanted in the sand flat. Most macrofaunal species, in turn, showed relict periodicities in their spatial dispersion patterns, consistent with (spatially) periodic recruitment to past ripple fields. Hogue and Miller (1981) discovered similar, ripple-related spacing patterns in nematodes, and sediment dynamics has now been implicated much more generally in both meiofaunal (Palmer and Brandt, 1981) and macrofaunal (Grant, 1981) recruitment.

Evidence for the extreme importance of fluid and particle dynamics in recruitment phenomena is growing at a rapid rate. Hannan and Grant (in preparation) have carefully evaluated the biases of various designs of sediment traps. Theirs are the first such experiments to use realistic dynamic scaling, showing strong biases of various trap geometries for or against particles as a function of flow about the trap (its cylinder Reynolds number) and particle settling velocity ( $w_s$  = gravitational settling velocity in the absence of convective fluid motions). In addition, they measured  $w_s$  of various (narcotized) larvae. From these two sets of data and field flow measurements, Hannan and Grant have accurately predicted relative efficiency of larval collection by traps of various designs *in the field*.

Eckman (1983) concentrated on events

closer to the bed. First, he characterized flow in and over tube arrays of varying spacings in a laboratory flume. He used these results to predict, *a priori*, relative rates of passive larval recruitment to field arrays of artificial tubes at equivalent areal densities (Eckman, 1983, Fig. 8). Eckman (1983) suggests that recruits of several species behaved as would passive tracer particles, of low (relative to quartz sand)  $w_s$ , and he shows conclusively that fluid dynamics strongly influences recruitment in the majority of species encountered. Although they experienced *severe* Froude number scaling problems in attempting quantification of the flow, we would interpret the results of Fonseca *et al.* (1982) to suggest that increasing shoot density (for the flexible seagrass *Zostera marina*) decreases within-bed  $\tau_0$ . If so, then their field results for faunal recruitment (Homziak *et al.*, 1982) also can be interpreted as generally conforming to expectations for passive particles of low  $w_s$ . The results of Gallagher *et al.* (1983), in turn, show clearly that the roles of biological interactions in soft-bottom benthic succession cannot be resolved without proper hydrodynamic controls.

While recruitment as passive particles makes a convenient null hypothesis against which to resolve important recruitment behaviors, it also emphasizes the need for direct observation of potential recruits under locally varying but precisely controlled flow conditions. Do recruits indeed get concentrated (and remain) passively in regions of reduced  $\tau_0$ , for example about an adult tube? How divergent are the effects of fluid and sediment dynamics upon recruitment across environments and across taxa?

#### *Particle feeding*

The importance of fluid motions to aquatic suspension feeders is unquestioned, as is the reason for the general lack of subaerial suspension feeders. Wind (*vis-à-vis*  $\rho_s/\rho$ ) is competent to suspend only dry, small soil particles of little nutritive value (*i.e.*, dust and sand). The closest terrestrial analogues of aquatic suspension feeders appear to be carnivores or granivores that

take advantage of wind-transported organic matter having its own means (*e.g.*, insect wings and seed parachutes) of "suspension" enhancement.

Nonetheless we have avoided study of suspension feeders as a first step in our evaluation of the impacts of sediment transport on biota. The dynamic complexities are subtle and difficult to quantify. Take a tube-dwelling or cylindrical suspension feeder, for example. The flow patterns around it will be at least as complex as those seen by Eckman (1982 and in preparation) about perfect cylinders. The induced flow will be very sensitive to the height to which the suspension feeder (or its inhalent stream) extends above the bottom. Serious artifacts, both in terms of detailed flow patterns and Froude number, can result if the laboratory animal height : flow depth ratio departs from that in the field. Inanimate scale models, together with exotic fluids or temperature manipulation, may help in this regard (Taghon, in preparation).

Still more subtle is the problem of vertical gradients in suspended material, which must be combined with the vertical gradients of velocity to determine horizontal suspended fluxes. A useful scaling parameter in this regard is  $w_s/u_*$  (*e.g.*, Middleton and Southard, 1978, Fig. 6.15). For  $w_s/u_* \cong 1$ , most material in transport moves as bedload, saltating or rolling within approximately five grain diameters ( $D$ ) of the bottom. What little material is suspended, however, produces a very strong gradient in suspended matter concentration in the immediate vicinity of the bed. For  $w_s/u_* \cong 0.1$ , more material is suspended, and the concentration gradient is strong all the way to the top of the boundary layer. Only when  $w_s/u_*$  drops to about 0.01 or below is the suspended concentration more or less uniform throughout the boundary layer. For natural, sediment-transporting flows, these three steps in  $w_s/u_*$  are observed, respectively (and approximately) in sands, silts and clays. In those laboratory situations where uniform suspension is desired, then, one should adjust  $w_s/u_*$  to fall at 0.01 or below.

Slightly less obvious than the difference

in importance of suspension feeders in aquatic *versus* subaerial environments is the difference in importance of surface deposit feeders. In the marine realm, there are few locations above abyssal depths where surface deposits are not rummaged through on a more or less continuous basis by abundant surface deposit feeders. Typically, as many deposit feeders forage right at the sediment-water interface as on all the layers below combined (Jumars and Fauchald, 1977). Some at this symposium might suggest that part of the reason is mechanical, *e.g.*, that hydraulically operated, sticky tentacles would be difficult to deploy subaerially. We would argue, however, that fluid and sediment dynamics are implicated strongly in supplying the resources utilized by surface deposit feeders. Microbial growth modulation was discussed above. Surface deposits are also frequently resuspended and mixed with relatively new products of photosynthesis (*e.g.*, Rhoads *et al.*, 1975). Nor is the importance of advective inputs limited to shallow water (*e.g.*, Yingst and Aller, 1982).

Surface deposit feeders are situated ideally to take advantage of transported material. We (Nowell, Jumars, and Fauchald, 1984) have identified one surface deposit feeding polychaete species, *Amphicteis scaphobranchiata*, that takes great care to build and feed from a sediment trap, a depression in the bed. Due to reduced  $\tau_0$  levels, sediment deposits selectively in these pits, *i.e.*, food supply rate to the animal appears to be enhanced by pit construction. When sediment transport is excluded artificially in a laboratory setting, grossly aberrant (large and deep) pits result. A central issue for deposit feeders in general (*e.g.*, Levinton, 1979; Jumars *et al.*, 1984) is the degree to which individuals are limited by the rate of food supply. The results of Taghon *et al.* (1980), showing switching between deposit and suspension feeding on the basis of suspended flux, highlight the potential sensitivity of foraging behavior to rate of supply.

Figure 2 focuses on this issue and integrates the three processes that we have chosen to cover. First, the foraging location is set by recruitment or, more gen-

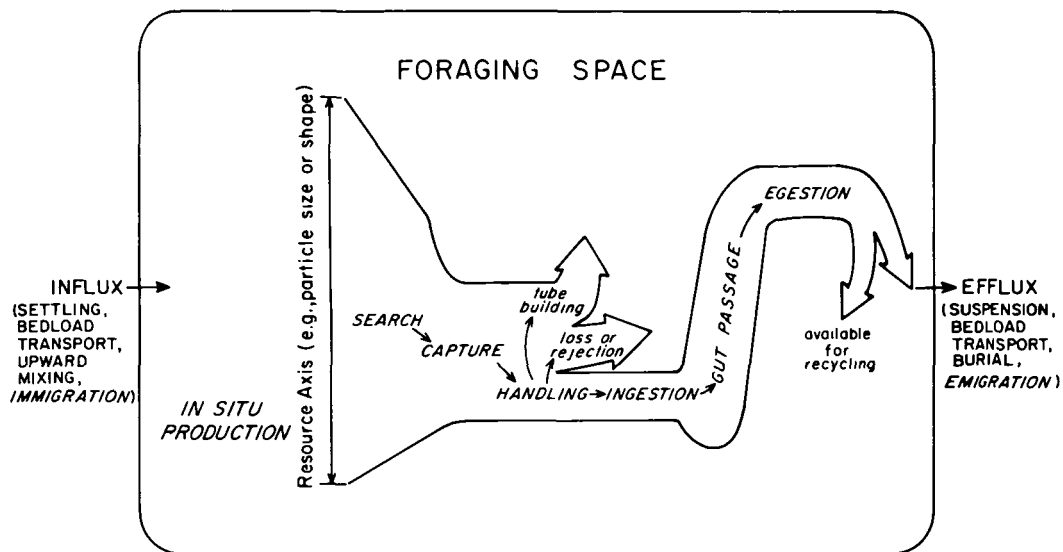


FIG. 2. A simple conceptual model of the interaction of fluid and particulate fluxes with feeding in a benthic deposit feeder. Biological processes are listed in italics. Note that only a selected fraction of available particles normally is utilized.

erally, by habitat selection, as impacted by fluid and particle dynamics. Microbial growth within an individual's foraging area is mediated by flow and particle transport. Lastly, particle supply rate is a function of sediment transport rate. Note also the impact that sediment transport can have on the issue of particle selection and resource overlap; standing stocks of different particle types within the foraging area may give poor indication of their relative rates of supply.

A major remaining question is the degree to which the foraging spaces of "typical" deposit feeders in a suite of benthic environments are closed versus open systems with respect to the food-resource impacts of fluid and sediment dynamics over time scales relevant to the deposit-feeding process. Our laboratory (D. Miller, in preparation) has systematized the search for an answer by subjecting the combined biological and physical system to the technique of dimensional analysis (e.g., Platt and Silvert, 1981). We eagerly await the organisms' answers.

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