

FLOW ENVIRONMENTS OF AQUATIC BENTHOS

A. R. M. Nowell and P. A. Jumars

School of Oceanography, WB-10, University of Washington, Seattle,
Washington 98195

INTRODUCTION

Appreciation of the importance of fluid and particle motions to aquatic organisms is a precept of limnology and biological oceanography. The incentives to understand the details of these motions near sea, river, and lake beds, as well as around particles settling through the water column, are growing steadily. The recruitment of microbes and invertebrate larvae to surfaces of all kinds is controlled or strongly modulated by boundary-layer flow dynamics (18, 21, 30). The fluxes of dissolved nutrients and wastes to and from attached algae depend on the details of the flow regime (55, 134). The survival and growth of suspension feeders hinge upon the near-bottom—horizontal as well as vertical—flux of particles; less obviously, the same is true of many kinds of deposit feeders (80). The ability to track scents (60, 140) or detect vibrations (53, 91) also depends upon the details of near-bed fluid motions. Furthermore, any organism protruding above the bed must withstand forces whose magnitudes and directions depend on the details of the local flow (131, 132).

The scales of these ecological phenomena range from that occupied by a single individual to that inhabited by a small population. On the smaller end of the scales we will treat, viscous flows predominate, and progress is being made, for example, in studying the important details of the flow around feeding appendages (2). On the larger end, there is a voluminous literature on geophysical flows (98). It is especially difficult, however, to find literature relevant to the intermediate scales and to extract those parts with strong ecological implications. The need to do so is critical for both designing and interpreting manipulative laboratory and field experiments—including those with microbes—which are largely conducted on an intermediate scale.

Our aim is threefold. First, we hope to provide access to the ecologically relevant fluid dynamic literature concerning the above range of scales. Second—and most importantly—we wish to emphasize the parameters that need to be measured or controlled in order to describe or simulate a natural flow regime adequately. Few ecologists would attempt to characterize a normal distribution without specifying both a mean and a variance, yet many aquatic scientists try to characterize complex flows using single velocity measurements or, at best, single Reynolds numbers. Before beginning an ecologically oriented, fluid dynamic study, it is essential to determine the number and nature of the critical flow parameters (Figure 1). Otherwise, reproducibility (i.e. dynamical similarity; see 67) is difficult to achieve. Third, we will review the literature establishing the ecological significance of benthic flow environments and microenvironments. Due to space limitations, our intent is to provide representative and selective, rather than exhaustive, coverage and to highlight fertile areas for future research.

We will begin by placing benthic microenvironments in context by summarizing what is known in general about bottom-boundary-layer structure, including flow around settling particles as a special case. We then treat the major categories of flow microenvironments within bottom-boundary layers: flow around obstacles (e.g. stones or animal tubes), flow around and through meshes (e.g. grass beds and cages), and flow over and in depressions (e.g. stingray feeding pits or feeding depressions produced by deposit feeders). For each category and for the macroenvironments, we characterize the flow, establish its ecological relevance (e.g. to processes of recruitment or feeding), and discuss both its laboratory simulation and its bearing upon past and future field manipulations. The characterizations are not fully derived herein; we refer the interested reader to the cited literature. We also caution that we follow the oceanographic rather than the engineering convention for symbols (see Appendix 1) and assume a familiarity with simple Reynolds numbers and the terms in them (130).

BOTTOM-BOUNDARY-LAYER STRUCTURE

Fully Developed, Uniform, Steady Flow

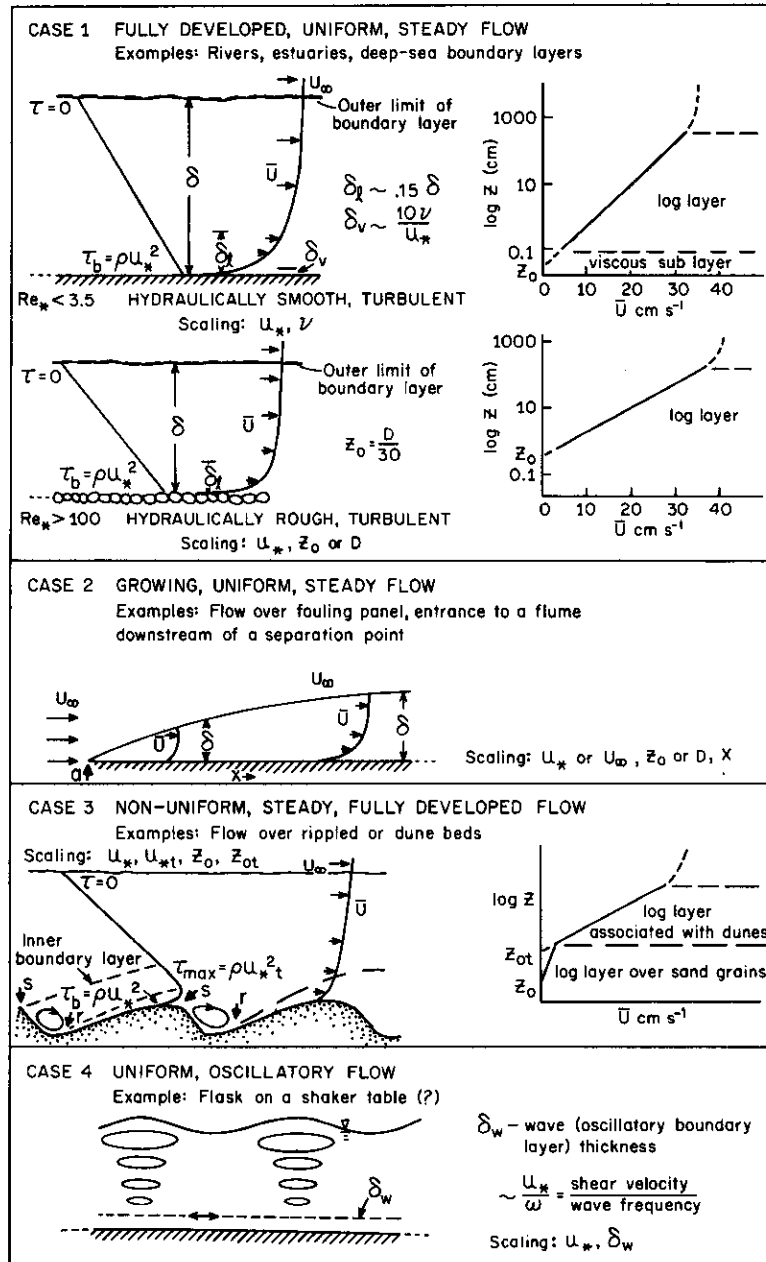
Analytic solutions of the (Navier-Stokes) equations that describe the flow near a solid boundary exist only for the simplest situation of steady (no temporal variation in the outer flow forcing), uniform (no spatial variation in the properties of the boundary), entirely laminar flow (107). Virtually all boundary-layer flows of aquatic interest are turbulent, at least over most of their regions. Even approximate solutions of the equations for turbulent cases require strict assumptions. The simplest case is based on an assumption of

strictly one-dimensional flow with no temporal variation (i.e. the mean of turbulent velocity fluctuations is zero), where gradients in velocity exist only in the z direction. One length and one velocity scale are needed to describe the flow (136). Both for consistency and for ease of conversion into a measure of the shear stress acting on the bed (Figure 1), the friction velocity, u_* , is typically used as the velocity parameter. For a flat bed, the grain diameter, D , is the obvious choice for a length scale, since it is the grain roughness that extracts momentum from the fluid. These parameters combine naturally into a roughness Reynolds number, Re_* , that is fully adequate to characterize such simple flows near the bed. That flow velocity at one height alone is insufficient is illustrated by the matching velocities at 10 cm above the two beds in Figure 1, Case 1.

An alternate means of characterizing these flows comes from what is usually the most practical means of estimating u_* , namely regression. Mean velocity, measured at a series of distances from the bed, is plotted against the logarithm of z (e.g. Figure 5 in 89); the z intercept is labelled z_0 and is called the hydraulic roughness, boundary roughness, or simply roughness length. The slope of this plot can be used to estimate u_* (89). Intuitively, z_0 is the height at which the mean velocity would drop to zero if the log-linear relation between z and U held so close to the bed. Only at high Re_* 's is there a simple linear relationship between D and z_0 (Figure 1).

A sublayer next to the bed and present only for small Re_* 's is characterized by long periods of quiescent, viscous flow interrupted occasionally by injections and eruptions of turbulent fluid as the large, energetic eddies in the outer part of the turbulent boundary layer penetrate all the way to the bed (13). In the viscous sublayer, the velocity is proportional to the distance from the bed, and the stress is constant. In the lowermost portion of the viscous sublayer, there is a diffusive sublayer, and the only vertical motion in it occurs via molecular diffusion. Above the viscous sublayer or throughout boundary layers with high Re_* 's, flow is dominated by turbulent eddies, with high exchange rates of momentum and consequently high rates of mixing and diffusion. This near-bed, turbulent layer—the logarithmic region (or inertial layer; cf 119)—has a level of turbulent shear stress that decreases linearly with distance from the bed (Figure 1).

When the roughness of the boundary increases (z_0 gets larger) or the overlying flow velocity rises, the region of viscous influence shrinks and eventually disappears altogether (when $Re_* > 100$, i.e. when there is fully rough, turbulent flow). High rates of momentum and contaminant exchange predominate, and the stresses in the fluid are entirely turbulent, in contrast to the viscous stresses that dominate the momentum flux in a viscous sublayer. This hydraulically rough flow is common in fluvial boundary layers and occurs most frequently in the ocean during periods of active sediment transport. Close to the



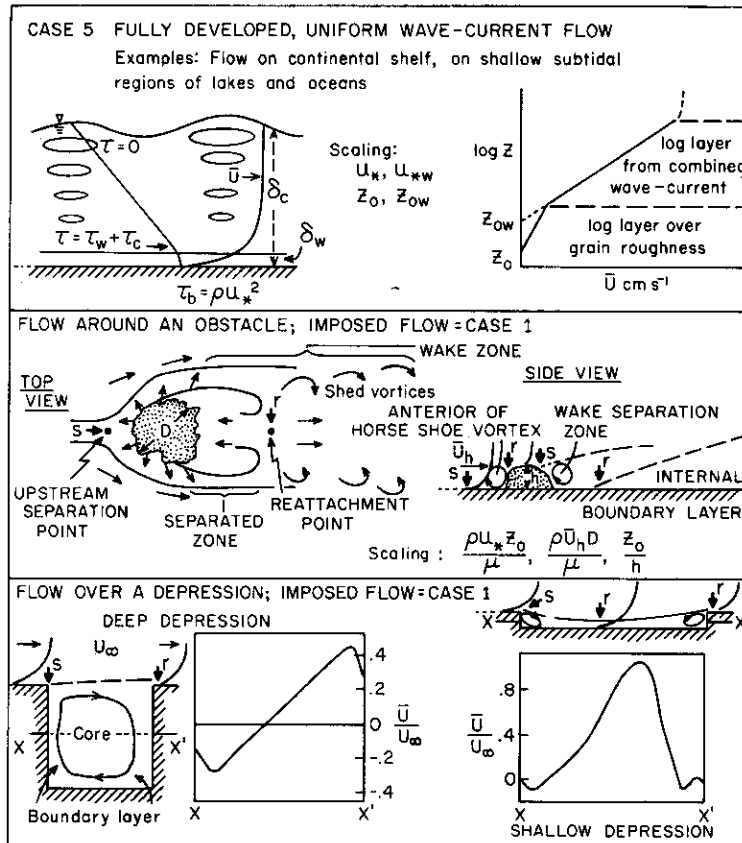


Figure 1 Examples of the five types of boundary-layer flows for the two classes of microenvironments observed in marine and freshwater environments. Note that not even in Case 1 will measurements of velocity at a single height adequately characterize the flow, especially the shear exerted on the boundary. Flow separation and reattachment (127) are observed in most aquatic boundary layers and have dramatic effects on fluxes near the bed.

bed, there are strong velocity gradients in all directions as the flow accelerates and decelerates over and around obstacles. Thus, within approximately three particle diameters ($3D$) of the boundary, the fluid is no longer characterized by a one-dimensional model, and the simple logarithmic profile cannot be expected to hold (87). To measure the boundary friction velocity under these circumstances, one must resort to velocity profiles made within the logarithmic region, using enough measurement points to achieve respectable confidence limits on the regression parameters of interest, namely u_* and z_0 (48). In gravel streams, the boulders often extend all the way through the flow depth, or the flow in riffles is less than three boulder scales thick. While there are methods for estimating u_* under such circumstances, average boundary skin friction

would probably be much less relevant to any organism on a boulder than would the complex, three-dimensional flow pattern induced by the surrounding topography.

Flows of the simplest type, namely uniform, steady, fully developed, turbulent boundary layers, are easily generated in the laboratory and provide the simplest fluid dynamic environment in which to examine the postulated relations among momentum flux, particulate flux, and organism growth or behavior. Because we are dealing with the flow within a few meters of the bed, the inherent length scales are small enough to allow us to ignore Coriolis effects due to rotation of the earth. Hence, flow over a flat surface is similar to flow in a pipe. This similarity allows us to make many simplifications, as it is easy to determine u_* in a pipe by measuring the pressure drop (67). Nikuradse (86) developed the basic data set relating D and z_0 over a range of Re_* 's using pipe flow (107; C. E. Long & A. R. M. Nowell, submitted for publication). Estimating u_* over a flat surface in either the laboratory or the field requires measurements of the velocity within the viscous sublayer (Figure 1) or several measurements within the logarithmic region (48). Obviously, one measurement of velocity at an arbitrary height over a region of inadequately described roughness will be of little value. An alternate technique, using a flush-mounted sensor in the bed, works well—but only when the flow is hydraulically smooth (6) and when no particulate material is present to alter the sensor's heat-transfer characteristics. In order to simulate a one-dimensional boundary layer, the flume or flow channel must be wide enough ($> 7 \delta$) to prevent the secondary circulation induced by the sidewalls from dominating the flow and long enough ($> 50 \delta$) to allow the boundary layer to grow to its equilibrium thickness (see below).

Many empirical studies indicate that there is a correlation between Re_* and benthic community structure. Perhaps the most frequent generalization about both marine and freshwater benthos is that community structure varies with sediment type (58, 73, 84, 95). The level (and temporal pattern) of u_* determines, to a substantial extent, grain size and sorting (137). While the implicit chain of cause and effect is generally from flow regime through sediment type to community structure, there is no reason to believe that this sequence is the only one possible. The flow regime (Re_*) can affect the community structure much more directly, even in the absence of sediment transport, by altering the fluxes of dissolved materials to organisms on and in the bed (141). Organisms can, in fact, significantly change both z_0 and the response of sediments to an imposed shear stress (66), making assumptions regarding cause and effect even more risky.

Studies that succeed in establishing a mechanism for flow effects on benthos are far rarer than correlative approaches. Most notably, nutrient supply and uptake rate in attached algae have been shown to be strongly dependent (135)

upon near-bed turbulent mixing rates (Re_*). Pipe flow has been used to show that there is an optimal u_* for the initial substratum-exploration behavior of barnacle cyprids and that this optimum differs among species (21). Pipe flow has also been used to simulate flow and its interactions with fouling bacteria in a heat exchanger (18). Results from pipe flow should be generalizable to one-dimensional boundary layers in the field. For bare substrata in an initially hydraulically smooth flow ($Re_* < 3.5$), bacterial population growth (i.e. immigration plus birth) is a function of u_* (18, 97). In a predator-free system, an equilibrium microbial film thickness is established (with birth and immigration balancing erosive emigration), which decreases with increasing u_* (18). It would be extremely interesting to follow up these experiments under a range of boundary roughnesses and to use techniques that resolve microbial immigration from local colony growth (9, 69).

Field manipulation of boundary-layer structure is in a primitive state. Grain diameter, D , is the easiest parameter to vary, altering z_0 and Re_* in a predictable fashion. One must alter a sufficiently large area and work far enough from the edge of the region to ensure that the flow is fully developed and uniform. We are unaware of any experiments based on deliberate alteration of the soft-sediment grain size aimed at monitoring changes in the boundary-layer structure and the consequent, flow-mediated effects on biota. Dredge-spoil disposal frequently produces such modifications, but it has many other confounding effects. Using substrata with varying surface roughnesses has been a relatively frequent practice in successional studies of aquatic fouling communities (36, 100, 115). Consequent modifications of fluid boundary-layer structure have not been monitored, and procedures have often confounded changes in chemical composition with changes in hydraulic roughness. Surface chemistry plays a strong role in the initial phases of adhesion to substrata (4). Controlled experiments that begin with a constant surface chemical composition and then vary surface roughness in order to monitor the effects on boundary-layer structure and ensuing colonization would be especially informative. Blinn et al.'s (7) finding that enhanced early colonization is correlated with greater surface roughness (z_0), and hence turbulent exchange, among three natural (but chemically disparate substrata) is particularly tantalizing.

Devices that modify near-bed flow velocity have also been used. The prototypes have been relatively short, open-ended, and primitively instrumented with respect to flow measurement. Nonetheless, they have provided valuable data on sediment entrainment (138) and have led to more sophisticated devices—in terms of both flow manipulation and measurement of the resulting flow structure—for in situ use (88). All of these devices use energy provided by pumps. Where current directions are reasonably predictable, it is also possible to emplace simple weirs or channels that alter the local flow's geometry and intensity. J. E. Eckman (personal communication) used

such a device to increase u_* locally and produce ripple migration in a small section of an intertidal sand flat. No data have been published yet on the ecological consequences of such in situ modifications, but the potential is great.

Growing, Uniform, Steady Flow

Boundary layers require finite distances to grow to equilibrium thicknesses (107). Fouling plates with an edge facing upstream; many sections of topographically rough, natural bottoms; and short ($< 50 \delta$) flumes or flow tanks thus have boundary-layer characteristics that vary with downstream distance as well as with distance from the boundary. Hence Re_* and an additional length scale, namely, the distance (x) downstream from the point at which boundary-layer growth begins, are needed to characterize the flow. Growing, turbulent boundary layers exhibit a growth rate of $(x/\delta)^{0.8}$ (99, 124). At any fixed downstream distance within the boundary layer, the flow is characterized by the same parameters as in the one-dimensional case. The boundary shear stress decreases rapidly, however, from a maximum at the leading edge (or at the point where boundary-layer growth begins) to the equilibrium value that develops approximately 50 (equilibrium) boundary-layer thicknesses downstream.

Sudden changes in boundary roughness, from smooth to rough or vice versa, are common in marine and fluvial environments. The momentum field takes a certain distance to relax to the new boundary conditions, and the transition from smooth to rough occurs more rapidly than the converse (3, 124). In the field, a sufficient upstream distance of uniform roughness must exist before the flow can be characterized by only u_* and z_0 , and this distance increases the further one is from the bed. Cummins & Lauff's (23) data require reinterpretation in light of this fact. They found that some species of stream invertebrates' apparent preference for settlement in certain particle sizes depends on the upstream-downstream order of the trays of graded sediments in their laboratory flow tank. They also ran some experiments with varying sediment structures in the cross-stream direction (silt on one side of the tray but not on the other); this pattern of varying roughness can cause subtle but important changes in near-bed fluid circulation (78).

The growing boundary layer presents problems in the laboratory. In order to measure the drag on an obstacle fixed on the bed—the drag equals the integral of the momentum extracted by the obstacle—the ratio of the obstacle height to the boundary-layer thickness must be similar to that found in the field. In the architectural aerodynamics literature, examples abound where the drag on simulated high-rise buildings has been miscalculated because an adequate ratio of boundary layer thickness to obstacle height was not maintained (cf comments by Gartshore (40) on Lee & Soliman (72)). When a flume less than 50δ

long is used (1, 26), the results of a one-dimensional characterization are not reliable quantitatively.

Growing boundary layers have the most immediate ecological applications to the design and interpretation of fouling experiments. The effect of area on species diversity is an important case in point. It often has been assumed that the only difference among fouling plates of different dimensions is the area available for colonization (93). Small fouling plates, however, may never develop a boundary layer of equilibrium thickness, and boundary-layer edge effects will cover a proportionately large area (61). One ecologically important consequence is that microbes or suspension feeders near the leading edge of a plate will not experience diffusional limitations of dissolved or particulate nutrients, while organisms hidden within a fully developed diffusive sublayer may (51).

A fouling plate dipped down in the flow (i.e. whose downstream edge is higher than its upstream edge) at angles less than 10° off the horizontal will produce a negative pressure gradient and accelerate the flow within the boundary layer over the plate. The boundary layer will thin, and the shear stress on the upper surface of the plate will be greater than that on a plate parallel to the flow. If the plate tips up at shallow angles, there will be a deceleration, but as this angle gets larger the flow will tend to separate; no simple boundary layer model can be used to describe such a momentum regime (17). Such arbitrarily complex and ill-characterized flow regimes and the sedimentation patterns they produce are likely to be more important (77, 114) than the substratum angle per se (52) in determining directions and rates of colonization. Orientation effects (i.e. of bare substrata relative to the flow) are well established in the periphyton literature (82, 125), but the degree to which streamwise variations in boundary-layer thicknesses are involved has yet to be determined.

A less obvious but perhaps ecologically more important implication of growing boundary layers is related to the cost-benefit trade-offs of microbes' attachment to particles or surfaces. Without *extreme* measures (e.g. water jacketing and the exclusion of any open surfaces that might lead to evaporation), convective circulations are set up in most containers of fluids. A boundary layer grows from the point at which a circulation cell meets the wall of the container to the point at which it detaches, but due to the small size of most containers and of the even smaller convection cells, this boundary layer is generally thin. Thus, microbes attached to the walls enjoy enhanced rates of nutrient supply and waste diffusion. We suspect that this essentially passive means of continuing gain explains the major portion of the so-called solid surface effect in aquatic microbiology (62). Similarly, microbes attached to particles can experience relatively large fluxes of nutrients and wastes (96). Flow past a small, isolated particle (e.g. one that is settling or that projects into fully rough, turbulent flow) can generate only a thin boundary layer, but

particles of the size and specific gravity of bacteria have virtually no gravitational or inertial motion with respect to the surrounding fluid, and their own swimming velocities usually are not high enough to yield substantial nutrient gains over those provided by molecular diffusion (103).

A related problem plagues the interpretation of field results from benthic flux chambers or bell jars. Such chambers are generally equipped with pumps or stirring motors to prevent stagnation (139). The motors again set up circulation cells that are small compared with the distance required for growth of a boundary layer of equilibrium thickness over the bottom, biasing the measured fluxes upward. The relative insensitivity of measured fluxes to stirring speed (105, Figure 7) is thus a weak argument for accuracy. Designs for flux chambers that produce more natural boundary-layer structure are now available (88), but they have yet to be applied to geochemical flux measurements.

Nonuniform, Steady, Fully Developed Flow

As the flow field becomes more complicated over a more complex boundary, the number of independent scaling parameters rises. Hence, the number of measurements required to characterize such a complex environment adequately also increases. In recent years, considerable theoretical work has been devoted to describing nonuniform flow fields, which are common in nature. The flow over sand waves is a well-studied case of nonuniform turbulent flow, and in many fluvial and marine environments, the additional conditions of steady and fully developed flow are adequately met (111). The extra scaling parameters come from increased resistance by the large obstacles to flow. Flow over dunes separates from the bottom. The lee region has a recirculating flow (Figure 1), and this separation increases the drag on the flow. At the same time, the individual grains of the bed still extract momentum, and thus two roughness lengths and two shear velocities can be identified. Far away from the bed, the resistance to flow is produced primarily by the large-scale separation flow over the dunes, and hence we find large u_{*r} values. Within the 1000 grain diameters of the bed the velocity profile will yield a shear velocity, u_{*b} , that is determined, as in simpler boundary layers, by skin friction on the sediment grains. By using spatial averages over the dominant topographic scale (say the wavelength of a dune), the flow field can be simplified (111).

Flow over dune fields oriented normal to the flow exhibits predictable velocities and momenta. The boundary shear stress profiles over dunes have been investigated in detail, though the structure of the diffusive sublayer has not been. The abundances of megafauna (123), macrofauna (28) and meiofauna (54, 106) vary spatially with a periodicity comparable to that of the local bedforms, which implies that they have some ecological link with bedform (42)

or flow dynamics, but cause and effect have not been clearly identified and verified.

Ambühl (1) used flow visualization techniques that resolve the u and w components of velocity over objects and series of objects mounted on the bottom of a flume. Qualitatively, his results resemble those for flows over dunes. His quantitative results are difficult to interpret or generalize, however, because the flume was not long enough to allow equilibrium boundary-layer development.

Fully Developed, Uniform, Oscillatory Flow

The simplest case of this class of flow is a wave boundary layer developed over a flat bottom under a train of monochromatic waves (15, 43). The extra length scale that turns up is the thickness of the oscillatory boundary layer. For typical high frequency waves, say 5-sec waves and commonly observed shear velocities of 1 cm sec^{-1} , the total oscillatory boundary layer is only 2 mm thick. Thus, there will be strong velocity gradients, high shear stresses, and high rates of sediment resuspension. Purely oscillatory boundary layers rarely exist in the field, however. If one thinks of the tidal boundary layer as an oscillatory flow with a frequency of $2 \times 10^{-4} \text{ sec}^{-1}$, the boundary layer will be of order 20 m thick, and hence, the near-bed flow can be treated as quasi-steady (48).

One well-quantified study of the effects of oscillatory flow (19) examined the effects of wave surge on algal spore adhesion. A more common laboratory application of oscillatory flow is the so-called shaker table. The container's size and shape may keep the boundary layer from full development, but a maximum boundary-layer thickness can be calculated for a given oscillation frequency. If we assume that the motion is purely oscillatory at a frequency of 75 min^{-1} (11) and that u_* equals 0.1 cm sec^{-1} , the *entire* boundary layer over the bottom of the flask can not be any more than $400 \mu\text{m}$ thick. Attached microbes will thus experience much greater nutrient flux than freely floating ones in the same kind of container, providing a facile fluid dynamic explanation of Bright & Fletcher's (11) results. It is certainly an oversimplification to regard flow in a flask on a shaker table as purely oscillatory, but this technique is used so frequently that it would be worth the effort to characterize such flows more accurately. Quantification of oscillatory flows may be easier, however, in simple apparatuses of alternative design (118).

Fully Developed, Uniform, Wave-Current Flow

In the presence of a steady mean flow and an oscillatory component due to either surface or internal waves, the momentum field exhibits a complex form. Within the current boundary layer, there is a thinner boundary layer created by the oscillatory flow. This wave boundary layer increases the roughness (i.e. by

extracting momentum from the flow) felt by the outer part of the flow, and thus the velocity profiles are segmented, with differing slopes showing the differing momentum flux regions (Figure 1). Obviously, if there are too few measurement heights to detect the complex shape of the profile or if an inappropriate time scale is used for averaging, the actual boundary friction velocity (u_*) cannot be evaluated. The modeling techniques and measurement difficulties in dealing with such flows have been reviewed by Grant & Madsen (43, 44).

This advance in modeling wave-current boundary layers has occurred too recently to have been adopted in ecological applications, but some historical information suggests that such applications will be profitable. Shelford (110, p. 27), for example, notes that faunas of shallow lake bottoms exposed to strong, wave-generated oscillatory flows (plus unspecified but probably slow mean flows) closely resemble those of swiftly flowing streams. It would be interesting to compare the net u_* values in these kinds of environments to see whether they are roughly equal.

Particle Behavior in Bottom Boundary Layers

Proper analysis and dynamic scaling of two-phase flows—made up of fluid plus particles, where the particles may be resuspended sediments, food for suspension feeders, bacteria, or larvae—is inherently more difficult and involves more parameters than examination of fluid flows alone (112). A thorough treatment of the problem would fill a textbook (41, 79, 137), but much ecologically useful information can be gained from examining one simple nondimensional scaling, i.e. the still-water particle settling velocity, w_s , divided by u_* (65).

Suspended load and particle behavior in the lowermost 5% of the bottom boundary layer has not been studied extensively. While theories of suspended load transport have been verified (137), most require measurement of particle concentration at some reference height, usually set arbitrarily at 5% of the boundary layer thickness above the bottom. These theories do not predict particle behavior below the reference height. Suspended load in the region occupied by suspension feeders thus has not been well characterized in either the theoretical or practical literature on sediment transport; the only exception is the elegant pair of papers by Sumer and his coworkers (116, 117). Another recent, ecologically important contribution is by Nielsen (85), who showed that particles can be trapped readily and hence concentrated in vortical circulation patterns, such as those existing in steady flow over dunes (Figure 1). The degree of concentration depends on the angular rotation rate of the vortex relative to w_s . Local concentrations of particles produced by this mechanism may well be important for both passive and active suspension feeders.

Despite the paucity of information on near-bed particle behavior, Grant & Madsen (44) have recently made a major contribution to ecologically relevant

sediment transport theory. They focused on unsteady, oscillatory flow that was produced near the bottom by gravity waves passing overhead. They showed that w_s/u_* is still an excellent index of particle behavior under waves or combined currents and waves. Specifically, they calculated the response times of sediment particles to wave-produced unsteadiness and found them, for all practical purposes, to be instantaneous. Thus, while waves add a great deal to the magnitude of u_* , particles resuspend no differently than one would expect in a steady flow of sufficient velocity to produce an equivalent u_* . Net horizontal flux is determined by net horizontal velocity, coupled with the concentration gradient; but the flux of import to a passive, benthic suspension feeder will lie somewhere between this net horizontal flux and the gross flux calculated by taking the scalar sum of steady and oscillatory components.

In summary, although much can be said about patterns over the entire boundary layer, there is a major gap in knowledge of suspended sediment transport in a region of primary ecological concern, i.e. the near bottom layer controlling nutrition of suspension and deposit feeders and the settlement of larvae and bacteria. This gap is not crucial to field scientists interested in sediment transport itself, who can now predict net rates of sediment transport without these details (because the bulk of net transport occurs well above the bottom in major transport events). Rapid progress in closing this gap will require the attention of ecologists concerned with the near-bottom region. Workers interested in sediment transport *can* be relied upon to identify the minimal suite of particle and flow characteristics that need to be measured in the field and controlled in the dynamic scaling of laboratory analog systems. In the simplest abiotic case, this set includes δ , u_* , ρ , μ , D , ρ_s , and g (112). In designing measurements, it must also be borne in mind that the strong shear within the bottom boundary layer can both significantly affect the particle aggregation of cohesive materials (74) and bias sediment-trap catches (49).

MICROENVIRONMENTS WITHIN THE BOTTOM BOUNDARY LAYER

Flow and Sedimentation Around Objects on the Bottom

It might at first seem logical to take the vast literature on flow around spheres and cylinders (17) and use it directly in predicting flow patterns around objects on the bottom. The problem is that this literature is largely based upon flow around objects far from any boundary. Objects within a boundary layer experience a gradient of incident velocities, producing much more complex flow patterns than one might at first suppose. This complication, for example, invalidates the otherwise elegant approach by O'Neill (92), who used airfoil theory to infer flow patterns around sand dollars. Only two simple shapes of objects attached to a bed have been investigated in any quantitative detail,

namely erect cylinders (29, 31) and hemispheres (10, 94). The ecological equivalents of these shapes are, respectively, animal tubes or macrophyte stalks and sediment mounds or protruding stones.

Qualitatively, simple dye studies or other visualization techniques will reveal distinct regions in the flow about an arbitrarily shaped object attached to the bottom (Figure 1). Upstream-downstream asymmetry grows in concert with imposed Re_* . Qualitative patterns of bottom shear stress about such objects are similar for cylinders and hemispheres and accord with one's intuition from observing flow and scour about a piling. Quantitatively, however, pilings provide poor analogs of shorter objects attached to the bottom. Pilings generally extend through and beyond the entire boundary layer, while animal tubes and mounds usually reach only the lowest part of the logarithmic layer. The flow velocity gradient is steepest close to the boundary, making small changes in the heights of objects exceedingly important in that region. For the same reason, the structure of the boundary layer incident on the object must be well specified for any quantitative study.

The full range of parameters for cylinders has not been investigated. Eckman & Nowell (31) explored only hydraulically smooth flow incident on a cylinder, selecting this case because a cylinder is likely to have the strongest effect when it is the only object protruding through the diffusive sublayer. Likewise, only a narrow range of parameters has been investigated for hemispheres (94). Flows about objects of more complex geometries, about flexible objects (e.g. sea-grasses), and about any class of objects in an unsteady bottom boundary-layer flow setting remain essentially uncharacterized. One generalization emerging from the measurements to date is that an isolated, rigid object that protrudes through the viscous sublayer increases the spatially integrated shear stress on the immediately surrounding bed. In terms of the effects on bed structure, one can expect scour and deposition to reflect these patterns of bed shear stress (31).

When objects are sparsely distributed on the bottom, their effects on the flow will remain essentially isolated, and group effects can be treated as the sum of individual flow disturbances. For cylinders that project well into the boundary layer, the minimal spacing to avoid significant flow interactions is approximately 2 cylinder diameters upstream, 5 cross-stream, and 20 downstream. When arbitrarily shaped objects are more closely spaced, flow within and around the cluster of objects cannot be characterized without detailed measurements (10). Flow interactions among frames or plates plague interpretations in many fouling studies (128). If the rigid objects in a group attached to the bed are similar in height, are randomly or evenly dispersed over the bottom, and the group is sufficiently expansive to allow the boundary layer to equilibrate with it (i.e. to develop fully), then some bulk properties of the flow, if not the local details, can be specified. In this situation, turbulence levels in the fluid among the objects are higher than those prevailing in the absence of the structure, up to

a density of objects that equals approximately one twelfth of the cover of the bed's plan area (87). Natural densities of tube builders usually fall below this threshold, ruling out hydrodynamic stabilization (32) as a cause of the frequently observed correlation (34) between the presence of the tube builders and sediment stability. At areal densities above the threshold, a skimming flow (*sensu* 81) is observed; the fluid "finds it easier" to flow over rather than through the field of structures, and both flow velocities and turbulence levels among the objects decrease.

Colonization rates and species compositions differ among the various portions of the flow structure produced by objects attached to the bed (37, 110), but the mechanisms accounting for these differences have rarely been identified and substantiated experimentally. In one simple but elegant experiment on caddis-fly larvae, Edington (33) showed (by moving the obstacle to flow) that the larvae behaviorally select—on a species-specific basis—particular flow environments about rocks. Periphyton colonization experiments employing bare substrata generally show enhanced initial colonization of the upper leading and trailing edges of objects attached to the bed (70, 82). The roles of direct interception (104), variation in boundary-layer thickness, vortex concentration (85) of propagules, and wake recirculation remain to be unraveled experimentally.

There are other incentives for understanding the details of flow around and among objects protruding from the bed. Bacterial swimming speeds typically fall near $50 \mu\text{m sec}^{-1}$ (101), while those of invertebrate larvae generally fall below 10 mm sec^{-1} (Hsueh-tze Lee, personal communication). Their likelihoods of reaching particular locations on the bottom and of being able to maintain their positions once having arrived must therefore be influenced strongly by the details of flow about natural biogenous or abiotic topography. J. E. Eckman (personal communication) has recently demonstrated that bacterial population growth on initially sterile substrata is enhanced in the horseshoe vortex region surrounding isolated tubes, supporting his (32) hypothesis that tubes may enhance sediment stability by stimulating microbial growth and its contribution to adhesion between sedimentary grains. The importance of this process in the field and to the next trophic level has also been established (D. Thistle, unpublished manuscript). Some preliminary data suggest that the flow pattern in the lee of a facultatively suspension-feeding polychaete enhances the flux of suspended particles to its feeding tentacles, which are situated near the top of its nearly cylindrical tube (14). The way that capitellid polychaete larvae are trapped in vortices and caught in sediment traps indicates that they apparently behave as passively settling particles (50). A similar vortex concentration mechanism may be used by passive suspension feeders (M. Patterson & K. L. Sebens, personal communication). Experiments designed to dissect the contributions of passive and active particle behavior in settlement as well as in

feeding would be amply repaid. We do not know at present, for example, whether larvae tend to "sediment" or stay preferentially in any of the various subregions of flow about an obstruction (Figure 1).

Laboratory simulation of flow about objects on the bed must be undertaken carefully. First, the boundary layer incident upon the organism or structure must be tailored to the situation of interest, i.e. a sufficient upstream expanse ($> 50 \delta$) of the proper Re_* is necessary to ensure that an equilibrium boundary-layer thickness has evolved. Next, the flow must be deep enough; if it is less than three times the object's height, its field will be strongly affected by induced deflections of the free surface. Perhaps the most insidious problem in laboratory modeling of flow about an object or group of objects is flow blockage. If the object or group of objects occupies more than 25% of the channel width, then the fluid will have a greater tendency to go over (rather than around) the object(s) than in a comparable field situation without sidewalls, making interpretation of results difficult, if not impossible (35). Similarly, if objects are brought within about 5 diameters of a sidewall or if interacting clusters of objects are brought within about 3 cluster diameters of the sidewall, the circulation patterns induced by the object(s) and the sidewall are likely to interact. These considerations place serious constraints on the sizes of the objects or arrays that can be investigated quantitatively in existing flow facilities (30).

The clearest implications of fluid dynamics in community ecology have come from intentional reproduction in the field of flow regimes that have been characterized in the laboratory. At present, such manipulations are limited to individual cylinders and hemispheres or to expansive arrays of objects. Eckman (28) clearly demonstrated that isolated cylinders less than a millimeter in diameter and protruding less than a millimeter into the water column of an intertidal sand flat significantly enhance the recruitment of some species to the cylinder's immediate vicinity (28). By producing large arrays of artificial tubes spanning the threshold for skimming flow, he (30) showed that a wide variety of recruits increase over time in a pattern that is consistent with their passive sedimentation (109) into the tube arrays. Equally importantly, he identified a few species that do not fit this pattern.

The inclusion of proper fluid dynamic controls in manipulative experiments also reveals the effects of flow on community structures. Rigorous attention to such controls allows one to evaluate the potential importance of fluid and sediment dynamic effects before deciding whether it is possible or necessary to characterize them. Eckman's (28) results led Gallagher et al (38) to avoid any unnaturally protruding structures in their manipulations. Fluid dynamic controls were still necessary, however, in order to determine whether the effects that implanted tube builders have on succession are due to the effects of their tubes on flow and sedimentation or (at least in part) to first-order biological interactions. Artificial tubes were implanted in the same spatial configurations

and areal densities as the manipulated tube builders. While the fluid and sediment dynamic effects of such arbitrary arrays are difficult to characterize, these simple controls did demonstrate that much of the tube builders' facilitative effect on succession in this sand flat community was due to the physical effects of the tubes.

Dean & Hurd (25) similarly produced inanimate mimics of early colonists on hard substrata and found that they have strong effects on subsequent successional events. We suggest that these effects, which Dean (24) labels simply structural, are predominantly mediated by induced changes in fluid and particle fluxes to and from the settling plate, much as J. E. Eckman (personal communication) demonstrated for bacterial recruitment at the bases of simulated tubes in soft substrata. It is difficult, in fact, to conceive of a mechanism whereby a new recruit could perceive or respond to this "structure" except via modification of flow patterns and shear stresses on the plate. This idea could be tested by attaching isolated objects whose fluid dynamic effects have been characterized (i.e. erect cylinders or hemispheres) to large ($> 50 \delta$) settling plates oriented parallel to the flow.

Thus, extreme caution should be used in interpreting data from litter bags (5), settling chambers (27), and sediment boxes or baskets (45, 68, 133), or from areas near other solid obstructions (16, 76) set on the bottom. These structures exert arbitrary, and to date uncharacterized, effects on near-bed flow. Current findings (28, 38) suggest that the flow artifacts can still be large if *any* artificial structure remains exposed. The techniques of implanting abiotic cores flush with the sediment surface (38) or of producing an area devoid of macrofauna via asphyxiation (J. F. Grassle, personal communication) are much more acceptable from a fluid dynamics viewpoint.

Flow Through Meshes

Meshes' dominant effects on flow are easily visualized: They do not allow flow structures (e.g. vortices) larger than the mesh size to pass through unaffected. Conversely, they produce flow structures of scales comparable to the mesh size and to the "wire" diameter of the mesh material. The geometry and spacing of natural "meshes" vary considerably, as the simple contrast between gorgonians (47) and grass beds (12) demonstrates.

Meshes are used for a wide variety of purposes in laboratory flows. At the upstream end of flow tanks or flumes, they are utilized to break up undesired cross-stream or vertical circulation in order to produce well-characterized, steady flows. The most effective meshes here are bundles of tubes or "hexcell" material aligned with the stream (108). Conversely, meshes are often used to generate fully three-dimensional turbulence by oscillating a grid or screen in a tank (121). This technique produces well-characterized, turbulent flow fields that have dominant temporal and spatial scales (71). We know of only one study that quantifies the effects of flow about and through meshes attached to

the bed (i.e. a snow fence; see 63), though there are qualitative appraisals in aquatic environments (22, 129). In the sparsest of meshes, individual vertical elements should act much like isolated tubes, while the effects of denser meshes will approach the flow blockage and flow separation effects induced by similarly shaped solid bodies (Figure 1).

By far the most frequent use of meshes in ecological field manipulation is in predator inclusion and exclusion experiments. To institute a control including fluid dynamic effects, the standard procedure is to use topless or sideless cages (20). A long history of attempts to devise traps for bedload transport estimation (56) indicates that these controls are woefully inadequate. Friction with any object, even one with an open weave, slows the flow through it and accelerates the flow around it. Upstream-facing (i.e. front-less) "cages" produce underestimates of the gravel transport rate of as much as 50% (8); gravel hops over and around them.

Cages, in turn, have been used most frequently on hard substrata at shallow depths. Here, due to surface waves, near-bed flows usually have a strong oscillatory component. Hence cages provide a crude analog of the laboratory turbulence grid. If the sides are removed in a control, the orientation of the remaining meshes to the oscillatory flow will be of paramount importance. Fortunately, due to the rough texture of many hard substrata and the rapid accelerations produced by oscillatory flow, the fluid surrounding the cages also tends to be turbulent. In such settings, the flow artifact of caging should be relatively small. On hard substrata where or when flow is steady and weak, cages may, however, act primarily to impede prevailing currents, thus increasing the residence times of water parcels in regions under cages. Thus, cages on hard substrata do produce artifacts (74).

On soft substrata, the artifacts should vary widely in direction and magnitude. Where oscillatory flow components are strong (e.g. in shallow water on exposed coasts), turbulence generation may be the prevailing effect, producing scour in and around the cage. Where currents are steady and weak, there should be enhanced sedimentation (perhaps including larvae) under a cage. If oscillatory and steady flows are very weak, however, as may occur in regions of lakes and ponds, cages may impede passive recruitment (122). Unless the cage protrudes above the level of the grass or has an extremely close weave, relatively small caging artifacts would be expected in grass beds where flow already encounters "meshes." The greatest problems should occur in areas with otherwise low Re_* 's, i.e. in flat and featureless bottoms in low-energy environments. Here, warnings about caging artifacts must be taken seriously (28, 38, 57).

Exclusion and inclusion experiments are so useful that it would be foolish to recommend their discontinuation. There is an abundant and obvious need, however, to carry out laboratory modeling and field measurements with proper dynamic scaling for the purposes of (a) characterizing flow and sediment

transport within and about cages, (b) designing cages with minimal flow perturbations, and (most importantly) (c) designing controls that closely simulate the flow modifications produced by cages or at least err in the conservative direction of accentuating the flow artifacts.

Flow and Sedimentation in a Depression

Qualitatively, a depression has the opposite effect from an object protruding above the bottom. Since there is more cross-sectional area for it to fill, the flow must slow down as it flows over and into a depression. Consequently, a depression is an area of reduced shear stress and enhanced deposition or residence time of suspended material. Once again, there are comparatively few quantitative studies (64, 113) and even fewer generalizations.

Pits are common in nature. They result primarily from the foraging activities of animals feeding either on sediments or on animals or plants buried within them. Subsurface deposit feeding in a localized area often leads to slumping. In some species, this slumping leads to characteristically shaped depressions and the functional group label of "funnel feeders" (83). Surface-deposit feeding species that place fecal material outside their feeding areas must also produce pits (90). A diverse group of more mobile animals feeds on buried plant (39) or animal (46) material. Its members make pits ranging in spatial scales from the beak widths of shorebirds to the jaw dimensions of bottom-feeding whales. The ecological importance of pits produced in deposit feeding is clear: Sedimentation, especially of flocculent and presumably nutritious aggregates, is enhanced because of reduced shear, increasing both the quantity and quality of food that is available to the deposit feeder without moving. Removal of plants or animals from the deposit and the associated production of a pit alter the path of succession by making both space and food resources available (120).

Pits have received little ecological attention in the laboratory. Nowell et al (90), working with an ampharetid polychaete, and D. M. Dauer (personal communication), working with a spionid polychaete, found that these animals have a greater propensity to move to a new feeding area if they are placed in an artificial laboratory situation excluding sediment transport. When sediment transport is reproduced in a laboratory flume, each species remains sessile, making use of material sedimenting into its feeding pit. Both of these studies are anecdotal, partly because the flumes presently available to benthic ecologists and oceanographers cannot accurately stimulate a steady supply rate of natural flocs. Material is generally forced through a pump or other region of unnaturally high shear in existing recirculation systems. Thus, the relationships among pit morphology, flow patterns, and the sedimentation rates of particulate food or of new recruits still need to be quantified. One of a number of interesting questions that remain to be answered concerns the degree to which the sedimentation process into pits is selective for particles of differing characteristics (e.g. varying w_s).

Field manipulation of depressions, on the other hand, has primarily been limited to creating analogs of those produced by fish feeding and has been aimed at successional questions. The importance of pits in affecting directions and rates of succession varies from one environment to the next (102, 126). VanBlaricom (126) emphasized active selection of pits by the recruits of pit opportunists as an important component of the successional pattern observed. A viable alternative, however, is that recruits have transport characteristics (e.g. w_s ; see 49, 50) similar to those of the food resources they utilize. In VanBlaricom's (126) study area, flow was strongly oscillatory due to swell, while at Reidenauer & Thistle's (102) site, it was not. How fluid flow and particulate (including larval) transport differ in these two flow regimes and pit morphologies is not known, again highlighting the need for parameterization and characterization of fluid and particle trajectories in and around pits.

CONCLUSIONS AND PROSPECTUS

The importance of flow to the ecology of aquatic benthos is unquestionable. Fluid dynamic parameters are important in microbial and metazoan recruitment and in the supply of particulate food to both deposit and suspension feeders. At a minimum, fluid dynamics must be considered in the design of experiments and controls on benthic community structure and processes, even when biological interactions are the prime targets of the experiments. Despite the weight of the evidence, mechanisms responsible for ecologically important flow effects remain poorly identified, poorly parameterized, and largely unquantified. Given this state of affairs, experiments with well-characterized boundary layers (one of the categories noted above) and geometrically simple flows seem much more promising than deployments of experimental devices of arbitrary design in poorly characterized flows. The sequential elucidation of flow effects in well-controlled laboratory models, coupled with subsequent manipulation and evaluation of their ecological significance in the field, will continue to be profitable.

Quantitatively, our perusal of the literature suggests that boundary-layer flows in rivers, streams, and oceans have been relatively well parameterized and characterized by the simple formulations we have summarized. Some of these formulations (e.g. those for wave-current interactions) have been derived comparatively recently and have opened the way for a great deal of new, ecologically relevant, and exciting work. Far less is known about bottom-boundary-layer structure in lakes, and the existing data suggest that fluid dynamics are often dominated by episodic events (59) and therefore may not be susceptible to the simple (i.e. steady or periodic) modeling and measuring approaches we have outlined.

Flow microenvironments within boundary layers are inherently difficult to characterize quantitatively because they result from perturbations of already

strong gradients in velocity. It is therefore imperative to determine the number and nature of measurements required to quantify adequately the flow in the microenvironment of ecological concern. Given adequate parameterization, there is an impressive list of questions in physiological ecology, population dynamics, and community dynamics that await refined measurements of benthic flow microenvironments.

ACKNOWLEDGMENTS

This review (contribution no. 1388 from the School of Oceanography, University of Washington) was supported by NSF grant OCE-8117397. We thank D. C. Miller, D. Penry, R. F. L. Self, and R. Strathmann for their contributions and revisions.

APPENDIX 1

a	Attachment point (start of boundary layer)
D	Grain diameter, cm
g	Gravitational acceleration, cm sec^{-2}
r	Reattachment point
Re_*	Roughness Reynolds number, $u_* D/\nu$
s	Separation point
u_*	Shear or friction velocity, cm sec^{-1}
u_{*t}	Shear velocity associated with topography, cm sec^{-1}
\bar{U}	Mean velocity at one elevation, cm sec^{-1}
U_h	Mean velocity at height of obstacle, cm sec^{-1}
U_∞	Free-stream velocity, or velocity at water surface, cm sec^{-1}
w_s	Settling velocity of a particle, cm sec^{-1}
x, y, z	Coordinate system with z vertical, x along stream, and y across stream
z_0	Roughness length (due to sediment grains or surface texture), cm
z_{0t}	Roughness length due to bedforms, cm
z_{0w}	Roughness length due to oscillatory current, cm
δ	Boundary-layer thickness, distance at which $\bar{U} = .99 U_\infty$, cm
δ_c	Boundary-layer thickness generated by mean current, cm
δ_l	Logarithmic-layer thickness, cm
δ_v	Viscous-sublayer thickness, cm
δ_w	Wave boundary-layer thickness, cm
μ	Dynamic viscosity, g cm sec^{-1}
ν	Kinematic viscosity, μ/ρ , $\text{cm}^2 \text{sec}^{-1}$
ρ	Fluid density, g cm^{-3}
ρ_s	Particle density, g cm^{-3}
τ_b	Shear stress on the bed, $\text{g cm}^{-1} \text{sec}^{-2}$
τ_c	Shear stress generated by mean current, $\text{g cm}^{-1} \text{sec}^{-2}$
τ_w	Shear stress generated by oscillatory current, $\text{g cm}^{-1} \text{sec}^{-2}$

Literature Cited

1. Ambühl, H. 1959. Die Bedeutung der Strömung als ökologischer Factor. *Schweiz. Z. Hydrol.* 20:133-264
2. Andrews, J. C. 1983. Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. *Can. J. Fish. Aquat. Sci.* 40:1293-1302
3. Antonia, R. A., Luxton, R. E. 1972. The response of a turbulent boundary layer to a step change in surface roughness. Part 2. Rough to smooth. *J. Fluid Mech.* 53: 737-57
4. Baier, R. E. 1980. Substrate influences on adhesion of microorganisms and their resultant new surface properties. In *Adsorption of Microorganisms to Surfaces*, ed. G. Bitton, K. C. Marshall, pp. 59-104. New York: Wiley. 439 pp.
5. Bärlocher, F., Schweizer, M. 1983. Effects of leaf size and decay rate on colonization by aquatic hyphomycetes. *Oikos* 41:205-10
6. Bellhouse, B. J., Schultz, D. L. 1966. Determination of mean and dynamic skin friction, separation and transition in low-speed flow with a thin-film heated element. *J. Fluid Mech.* 24:379-400
7. Blinn, D. W., Fredericksen, A., Korte, V. 1980. Colonization rates and community structure of diatoms on three different rock substrata in a lotic system. *Br. Phycol. J.* 15:303-10
8. Bogardi, J. 1978. *Sediment Transport in Alluvial Streams*. Budapest: Akademiai Kiado. 826 pp.
9. Bott, T. L., Brock, T. D. 1970. Growth and metabolism of periphytic bacteria: Methodology. *Limnol. Oceanogr.* 15: 333-42
10. Brayshaw, A. C., Frostick, L. E., Reid, I. 1983. The hydrodynamics of particle clusters and sediment entrainment in coarse alluvial channels. *Sedimentology* 30:137-43
11. Bright, J. J., Fletcher, M. 1983. Amino acid assimilation and respiration by attached and free-living populations of a marine *Pseudomonas* sp. *Microb. Ecol.* 9:215-26
12. Burke, R. W. 1982. *Free surface flow through salt marsh grass*. PhD thesis. Woods Hole Oceanogr. Inst./MIT, Woods Hole, Mass. 252 pp.
13. Cantwell, B. J. 1981. Organized motion in turbulent flow. *Ann. Rev. Fluid Mech.* 13:457-515
14. Carey, D. A. 1983. Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes. *Can. J. Fish. Aquat. Sci.* 40:301-8 (Suppl. 1)
15. Carstens, T. 1968. Wave forces on boundaries and submerged bodies. *Sarsia* 34:37-60
16. Chandler, G. T., Fleeger, J. W. 1983. Meiofaunal colonization of azoic estuarine sediment in Louisiana: Mechanisms of dispersal. *J. Exp. Mar. Biol. Ecol.* 69:175-88
17. Chang, P. K. 1970. *Separation of Flow*. London: Pergamon. 777 pp.
18. Characklis, W. G. 1981. Microbial fouling: A process analysis. In *Fouling of Heat Transfer Equipment*, ed. E. F. C. Somerscales, J. G. Knudsen, pp. 251-91. Washington DC: Hemisphere. 743 pp.
19. Charters, A. C., Neushul, M., Coon, D. 1973. The effect of water motion on algal spore adhesion. *Limnol. Oceanogr.* 18: 884-96
20. Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31:61-104
21. Crisp, D. J. 1955. The behaviour of barnacle cyprids in relation to water movement over a surface. *J. Exp. Biol.* 32:569-90
22. Crowley, P. H., Pierce, C. L., Johnson, D. M., Bohanan, R. E. 1983. An enclosure for experimental manipulation of lentic littoral and benthic communities. *J. Freshwater Ecol.* 2:59-66
23. Cummins, K. W., Lauff, G. H. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* 34:145-81
24. Dean, T. A. 1981. Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *J. Exp. Mar. Biol. Ecol.* 53:163-80
25. Dean, T. A., Hurd, L. E. 1980. Development of an estuarine fouling community: The influence of early colonists on later arrivals. *Oecologia* 46:295-301
26. Décamps, H., Capblanq, J., Hirigoyen, J. P. 1972. Étude des conditions d'écoulement près du substrat en canal expérimental. *Verh. Int. Ver. Limnol.* 18: 718-25
27. Desbryères, D., Bervas, J. Y., Khripounoff, A. 1980. Un cas de colonisation rapide d'un sédiment profond. *Oceanol. Acta* 3:285-91
28. Eckman, J. E. 1979. Small-scale patterns and processes in a soft-substratum, intertidal community. *J. Mar. Res.* 37:437-57
29. Eckman, J. E. 1982. *Hydrodynamic effects exerted by animal tubes and marsh grasses and their importance to the ecol-*

- ogy of soft-substratum marine benthos. PhD thesis. Univ. Wash., Seattle. 275 pp.
30. Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* 28:241-57
 31. Eckman, J. E., Nowell, A. R. M. 1984. Boundary skin friction and sediment transport about an animal-tube mimic. *Sedimentology*. In press
 32. Eckman, J. E., Nowell, A. R. M., Jumars, P. A. 1981. Sediment destabilization by animal tubes. *J. Mar. Res.* 39:361-74
 33. Edington, J. M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *J. Anim. Ecol.* 37:675-92
 34. Fager, E. W. 1964. Marine sediments: Effects of a tube-building polychaete. *Science* 143:356-59
 35. Fonseca, M. S., Fisher, J. S., Ziemann, J. C., Thayer, G. W. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine Coastal Shelf Sci.* 15:351-62
 36. Foster, M. S. 1975. Regulation of algal community development in a *Macrocystis pyrifera* forest. *Mar. Biol.* 32:331-42
 37. Fritsch, F. E. 1929. The encrusting algal communities of certain fast flowing streams. *New Phytol.* 28:165-96
 38. Gallagher, E. D., Jumars, P. A., Trueblood, D. D. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology* 64:1200-16
 39. Garbisch, E. W. Jr., Waller, P. B., McCallum, R. J. 1975. *Salt Marsh Establishment and Development*, US Army Corps of Eng. Tech. Memo. 52. 110 pp.
 40. Gartshore, I. S. 1977. Discussion of B. E. Lee and B. F. Soliman. *J. Fluids Eng.* 99:510
 41. Graf, W. H. 1971. *Hydraulics of Sediment Transport*. New York: McGraw-Hill. 513 pp.
 42. Grant, J. 1983. The relative magnitude of biological and physical sediment reworking in an intertidal community. *J. Mar. Res.* 41:673-89
 43. Grant, W. D., Madsen, O. S. 1979. Combined wave and current interaction with a rough bottom. *J. Geophys. Res.* 84:1797-1808
 44. Grant, W. D., Madsen, O. S. 1982. Movable bed roughness in unsteady oscillatory flow. *J. Geophys. Res.* 87:469-81
 45. Grassle, J. F. 1977. Slow recolonization of deep-sea sediment. *Nature* 265:618-19
 46. Gregory, M. R., Ballance, P. F., Gibson, G. W., Ayling, A. M. 1979. On how some rays (Elasmobranchia) excavate feeding depressions by jetting water. *J. Sediment. Petrol.* 49:1125-30
 47. Grigg, R. W. 1972. Orientation and growth form of sea fans. *Limnol. Oceanogr.* 17:185-92
 48. Gross, T. F., Nowell, A. R. M. 1983. Mean flow and turbulence in a tidal boundary layer. *Cont. Shelf Res.* 2:109-26
 49. Hannan, C. A. 1984. *Initial settlement of marine invertebrate larvae: The role of passive sinking in a near-bottom turbulent flow environment*. PhD thesis. Woods Hole Oceanogr. Inst./MIT, Woods Hole, Mass. 517 pp.
 50. Hannan, C. A. 1984. Planktonic larvae act like passive particles in turbulent near-bottom flows. *Limnol. Oceanogr.* In press
 51. Hargrave, B. T., Phillips, G. A. 1977. Oxygen uptake of microbial communities on solid surfaces. In *Aquatic Microbial Communities*, ed. J. Cairns Jr., pp. 445-587. New York: Garland. 624 pp.
 52. Harris, L. G., Irons, K. P. 1982. Substrate angle and predation as determinants in fouling community succession. In *Artificial Substrates*, ed. J. Cairns Jr., pp. 131-74. Ann Arbor, Mich: Ann Arbor Sci. 279 pp.
 53. Hawkins, A. D., Rasmussen, K. J. 1978. The calls of gadoid fish. *J. Mar. Biol. Assoc. UK* 58:891-911
 54. Hogue, E. W., Miller, C. B. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *J. Exp. Mar. Biol. Ecol.* 53:181-91
 55. Horner, R. R., Welch, E. B. 1981. Stream periphyton development in relation to current velocity and nutrients. *Can. J. Fish. Aquat. Sci.* 38:449-57
 56. Hubbell, D. W. 1964. *Apparatus and Techniques for Measuring Bedload*. US Geol. Surv. Water Supply Pap. 1748. 74 pp.
 57. Hulberg, L. W., Oliver, J. S. 1980. Caging manipulations in marine soft-bottom communities: Importance of animal interactions or sedimentary habitat modifications. *Can. J. Fish. Aquat. Sci.* 37:1130-39
 58. Hynes, H. B. N. 1970. *The Ecology of Running Waters*. Liverpool: Liverpool Univ. Press. 555 pp.
 59. Imboden, D. M., Lenmin, U., Joller, T., Shurter, M. 1983. Mixing processes in lakes: Mechanisms and ecological relevance. *Schweiz. Z. Hydrol.* 45:11-44
 60. Ingram, C. L., Hessler, R. R. 1983. Distributional and behavioral patterns of

- scavenging amphipods from the central North Pacific. *Deep-Sea Res.* 30:683-706
61. Jackson, J. B. C. 1977. Habitat area, colonization, and development of epibenthic community structure. In *Biology of Benthic Organisms*, ed. B. F. Keegan, P. O. Ceidigh, P. J. S. Boaden, pp. 349-58. New York: Pergamon. 630 pp.
 62. Jannasch, H. W., Pritchard, P. H. 1972. The role of inert particulate material in the activity of aquatic microorganisms. *Mem. Ist. Ital. Idrobiol. Dott Marco de Marchi Pallanza Italy* 29:289-308 (Suppl.)
 63. Jensen, M. 1954. *Shelter Effect*. Copenhagen: Danish Tech. 74 pp.
 64. Johnston, J. P. 1960. On the three-dimensional turbulent boundary layer generated by secondary flow. *ASME J. Basic Eng.* 82:233-48
 65. Jumars, P. A., Nowell, A. R. M. 1984. Fluid and sediment dynamic effects on marine benthic community structure. *Am. Zool.* 24:45-55
 66. Jumars, P. A., Nowell, A. R. M. 1984. Effects of benthos on sediment transport: Problems with functional grouping. *Cont. Shelf Res.* 3:115-30
 67. Kay, J. M. 1963. *An Introduction to Fluid Mechanics and Heat Transfer*. Cambridge: Cambridge Univ. Press. 327 pp. 2nd ed.
 68. Khalaf, G., Tachet, H. 1980. Colonization of artificial substrata by macro-invertebrates in a stream and variations according to stone size. *Freshwater Biol.* 10:475-82
 69. Kieft, T. L., Caldwell, D. E. 1983. A computer simulation of surface microcolony formation during microbial colonization. *Microb. Ecol.* 9:7-13
 70. Korte, V. L., Blinn, D. W. 1983. Diatom colonization on artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. *J. Phycol.* 19:332-41
 71. Laws, E. M., Livesy, J. L. 1978. Flow through screens. *Ann. Rev. Fluid Mech.* 10:247-66
 72. Lee, B. E., Soliman, B. F. 1977. An investigation of the forces on three dimensional bluff bodies in rough wall turbulent boundary layers. *J. Fluids Eng.* 99:503-9
 73. Macan, T. T. 1974. *Freshwater Ecology*. New York: Wiley. 343 pp. 2nd ed.
 74. Marshall, J. J., Rowe, F. W. E., Fisher, R. P., Smith, D. F. 1980. Alterations to the relative species-abundance of ascidians and barnacles in a fouling community due to screens. *Aust. J. Mar. Freshwater Res.* 31:147-53
 75. McCave, I. N. 1984. Size spectra and aggregation of suspended particles in the deep ocean. *Deep-Sea Res.* 31: In press
 76. McClatchie, S., Juniper, S. K., Knox, G. A. 1982. Structure of a mudflat diatom community in the Avon-Heathcote Estuary, New Zealand. *NZ J. Mar. Freshwater Res.* 16:299-309
 77. McDougall, K. D. 1943. Sessile marine invertebrates of Beaufort, North Carolina. *Ecol. Monogr.* 13:321-74
 78. McLean, S. R. 1981. The role of non-uniform roughness in the formation of sand ribbons. *Mar. Geol.* 42:49-74
 79. Middleton, G. V., Southard, J. B. 1978. *Mechanics of Sediment Movement*. Lect. Notes for Short Course No. 3, Sponsored by East. Sect. Soc. Econ. Paleontol. & Mineral, Binghamton, NY, March 29-30, 1977. 231 pp.
 80. Miller, D. C., Jumars, P. A., Nowell, A. R. M. 1984. Effects of sediment transport on deposit feeding: Scaling arguments. *Limnol. Oceanogr.* In press
 81. Morris, H. M. 1955. A new concept of flow in rough conduits. *Trans. Am. Soc. Civ. Eng.* 120:373-98
 82. Munteanu, N., Maly, E. J. 1981. The effect of current on the distribution of diatoms settling on submerged glass slides. *Hydrobiologia* 78:273-82
 83. Myers, A. C. 1977. Sediment processing in a marine subtidal bottom community. *J. Mar. Res.* 35:609-47
 84. Nowell, R. C. 1970. *Biology of Intertidal Animals*. London: Elek. 555 pp.
 85. Nielsen, P. 1984. On the motion of suspended sand particles. *J. Geophys. Res.* 89:616-26
 86. Nikuradse, J. 1933. Laws of flow in rough pipes. *Nat. Advis. Comm. Aeronaut. Tech. Memo. 1292*. 62 pp. (Transl. from German, 1950)
 87. Nowell, A. R. M., Church, M. A. 1979. Turbulent flow in a depth-limited boundary layer. *J. Geophys. Res.* 84:4816-24
 88. Nowell, A. R. M., Hess, F. R., Zaneveld, J. R. V., Bartz, R., McCave, I. N., Winget, C. L. 1984. Instrumentation in HEBBLE. *Mar. Geol.* In press
 89. Nowell, A. R. M., Jumars, P. A., Eckman, J. E. 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.* 42:133-53
 90. Nowell, A. R. M., Jumars, P. A., Fauchald, K. 1984. Foraging strategy of a subtidal and deep-sea deposit feeder. *Limnol. Oceanogr.* 29:645-49
 91. Ockelmann, K. W., Vahl, O. 1970. On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. *Ophelia* 8:275-94
 92. O'Neill, P. L. 1978. Hydrodynamic

- analysis of feeding in sand dollars. *Oecologia* 34:157-74
93. Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecol. Monogr.* 47:37-63
 94. Paola, C. 1983. *Flow and skin friction over artificial rough beds*. PhD thesis. Woods Hole Oceanogr. Inst./MIT, Woods Hole, Mass. 347 pp.
 95. Parsons, T. R., Takahashi, M., Hargrave, B. 1977. *Biological Oceanographic Processes*. Oxford: Pergamon. 332 pp.
 96. Pasciak, W. J., Gavis, J. 1975. Transport limited nutrient uptake rates in *Ditylum brightwellii*. *Limnol. Oceanogr.* 20:604-17
 97. Pedersen, K. 1982. Factors regulating microbial biofilm development in a system with slowly flowing seawater. *Appl. Environ. Microbiol.* 44:1196-1204
 98. Pedlosky, J. 1979. *Geophysical Fluid Dynamics*. New York: Springer-Verlag. 624 pp.
 99. Peterson, E. W. 1969. Modification of mean flow and turbulent energy by a change in surface roughness under conditions of neutral stability. *Q. J. R. Meteorol. Soc.* 95:561-75
 100. Pomeroy, C. M., Weiss, C. M. 1946. The influence of texture and composition of surface on the attachment of sedentary marine organisms. *Biol. Bull.* 91:57-65
 101. Purcell, E. M. 1977. Life at low Reynolds number. *Am. J. Phys.* 45:3-11
 102. Reidenauer, J. A., Thistle, D. 1981. Response of a soft-bottom harpacticoid community to stingray (*Dasyatis sabina*) disturbance. *Mar. Biol.* 65:261-67
 103. Roberts, A. M. 1981. Hydrodynamics of protozoan swimming. In *Biochemistry and Physiology of Protozoa*, ed. M. Levandowsky, S. Hutner. 4:5-66. New York: Academic. 213 pp.
 104. Rubenstein, D. I., Koehl, M. A. 1977. The mechanisms of filter feeding: Some theoretical considerations. *Am. Nat.* 111: 981-94
 105. Santschi, P. H., Bower, P., Nyffeler, U. P., Azevedo, A., Broecker, W. S. 1983. Estimates of the resistance to chemical transport posed by the deep-sea boundary layer. *Limnol. Oceanogr.* 28:899-912
 106. Schafer, C. T. 1971. Sampling and spatial distribution of benthic Foraminifera. *Limnol. Oceanogr.* 16:944-51
 107. Schlichting, H. 1968. *Boundary-Layer Theory*. New York: McGraw-Hill. 658 pp. 6th ed.
 108. Schubauer, G. B., Spangenberg, W. G., Klebanoff, P. 1950. Aerodynamics of damping screens. *NACA Tech. Note 2001*. 16 pp.
 109. Scoffin, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *J. Sediment. Petrol.* 40:249-73
 110. Shelford, V. E. 1918. Conditions of existence. In *Fresh-Water Biology*, ed. H. B. Ward, G. C. Whipple, 2:21-60. New York: Wiley. 1111 pp.
 111. Smith, J. D., McLean, S. R. 1977. Spatially averaged flow over a wavy boundary. *J. Geophys. Res.* 82:1735-46
 112. Southard, J. B., Boguchwal, L. A., Romea, R. D. 1980. Test of scale modeling of sediment transport. *Earth Surf. Process.* 5:17-23
 113. Squire, H. B. 1956. Note on the motion inside a region of recirculation (cavity flow). *J. R. Aeronaut. Soc.* 60:203-5
 114. Stevenson, R. J. 1983. Effects of current and conditions stimulating autogenically changing microhabitats on benthic diatom immigration. *Ecology* 64:1514-24
 115. Straughan, D. 1972. Ecological studies of *Mercierella enigmata* Fauvel (Annelida: Polychaeta) in the Brisbane River. *J. Anim. Ecol.* 41:93-136
 116. Sumer, B. M., Deigaard, R. 1981. Particle motions near the bottom in turbulent flow in an open channel. Part 2. *J. Fluid Mech.* 109:311-37
 117. Sumer, B. M., Oğuz, B. 1978. Particle motions near the bottom in an open channel. *J. Fluid Mech.* 86:109-27
 118. Svoboda, A. 1970. Simulation of oscillating water movement in the laboratory for cultivation of shallow water sedentary organisms. *Helgol. Wiss. Meeresunters.* 20:676-84
 119. Tennekes, H., Lumley, J. L. 1972. *A First Course in Turbulence*. Cambridge, Mass: MIT Press. 300 pp.
 120. Thistle, D. T. 1981. Natural physical disturbances and communities of marine soft bottoms. *Mar. Ecol. Prog. Ser.* 6: 223-28
 121. Thompson, S. M., Turner, J. S. 1975. Mixing across an interface due to turbulence generated by an oscillating grid. *J. Fluid Mech.* 67:349-68
 122. Thorp, J. H., Bergy, E. A. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. *Ecology* 62:365-75
 123. Thum, A. B., Allen, J. C. 1975. Distribution and abundance of the lamp urchin *Echinolampas crassa* (Bell) 1880 in False Bay, Cape. *Trans. R. Soc. S. Afr.* 41:359-73
 124. Townsend, A. A. 1966. The flow in a turbulent boundary layer after a change in surface roughness. *J. Fluid Mech.* 26: 255-66

125. Tuchman, M. L., Stevenson, R. J. 1980. Comparison of clay tile, sterilized rock and natural substrate diatom communities in a small stream in southeastern Michigan, U.S.A. *Hydrobiologia* 75:73-79
126. VanBlaricom, G. R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.* 52:283-305
127. Van Dyke, M. 1982. *An Album of Fluid Motion*. Stanford, Calif: Parabolic. 176 pp.
128. Vandermeulen, H. DeWreede, R. E. 1982. The influence of orientation of an artificial substrate (transite) on settlement of marine organisms. *Ophelia* 21:41-48
129. Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58:1199-1217
130. Vogel, S. 1981. *Life in Moving Fluids*. Boston: Grant. 352 pp.
131. Wainwright, S. A., Koehl, M. A. R. 1976. The nature of flow and the reaction of benthic Cnidaria to it. In *Coelenterate Ecology and Behavior*, ed. G. O. Mackie, pp. 5-21. New York: Plenum. 579 pp.
132. Welch, P. S. 1935. *Limnology*. New York: McGraw-Hill. 471 pp.
133. Welch, P. S. 1948. *Limnological Methods*. New York: McGraw-Hill. 381 pp.
134. Whitford, L. A. 1960. The current effect and growth of freshwater algae. *Trans. Am. Microsc. Soc.* 79:302-9
135. Whitford, L. A., Shumacher, G. J. 1961. Effect of current on mineral uptake and respiration by a freshwater alga. *Limnol. Oceanogr.* 6:423-25
136. Yaglom, A. M. 1979. Similarity laws for constant-pressure and pressure-gradient turbulent wall flows. *Ann. Rev. Fluid Mech.* 11:505-40
137. Yalin, M. S. 1977. *Mechanics of Sediment Transport*. New York: Pergamon, 307 pp. 2nd ed.
138. Young, R. A., Southard, J. B. 1978. Erosion of fine-grained sediments: Seafloor and laboratory experiments. *Geol. Soc. Am. Bull.* 89:663-72
139. Zeitzschel, B. 1980. Sediment-water interactions in nutrient dynamics. In *Marine Benthic Dynamics*, ed. K. R. Tenore, B. C. Coull, pp. 195-218. Columbia: Univ. SC Press. 451 pp.
140. Zimmer-Faust, R. K., Case, J. F. 1983. A proposed dual role of odor in foraging by the California spiny lobster, *Panulirus interruptus* (Randall). *Biol. Bull.* 164: 341-53
141. Zimmerman, P. 1961. Experimentelle Untersuchungen über die ökologische Wirkung der Stromgeschwindigkeit auf die Lebensgemeinschaften des fliessenden Wassers. *Schweiz. Z. Hydrol.* 23:1-81