

Effects of benthos on sediment transport: difficulties with functional grouping

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(Received 28 June 1983; in revised form 13 October 1983; accepted 16 November 1983)

Abstract—No consistent functional grouping of organisms as stabilizers vs destabilizers, respectively decreasing or enhancing erodibility, is possible. Benthic organisms can affect erodibility in particular—and sediment transport in general—via alternation (1) of fluid momentum impinging on the bed, (2) of particle exposure to the flow, (3) of adhesion between particles, and (4) of particle momentum. The net effects of a species or individual on erosion and deposition thresholds or on transport rates are not in general predictable from extant data. Furthermore, they depend upon the context of flow conditions, bed configuration, and community composition into which the organism is set. Separation of organism effects into these four categories does, however, allow their explicit incorporation into DuBoys-type and stochastic sediment dynamic models already in use and thus permits the specification of parameters whose measurement will enhance predictability of sediment transport modes and rates in natural, organism-influenced, marine settings.

If the variable of prime concern is the total amount of sediment transported, rather than the frequency of transport events or the spatial pattern of erosion and deposition, and if most transport occurs in rare but intense bouts (e.g., winter storms on boreal continental shelves), then it may be possible to ignore organism effects without major sacrifices in accuracy or precision. Under high transport rates, suspended load effects override organism-produced bottom roughness, abrasion removes adhesives from transporting grains, and transport rates (normalized per unit width of the channel or bed) exceed feeding and pelletization rates. Moreover, at high rates most material transports as suspended load, effectively out of reach of the benthos. The transport rates at which organism effects are overridden, however, remain to be determined. For lower transport rates, foraging theory promises to provide insights into organism effects.

INTRODUCTION

THE naming of biogenous sedimentary structures has evolved along with the study of stratigraphy until a consistent classification has emerged (FREY, 1973). Because the study of sediment transport is itself a comparatively young science, and the importance of organisms in influencing sediment dynamics is an even more recent realization, classifications of organism impacts on sediment transport are still evolving rapidly. It is our purpose here briefly to review existing classifications, to erect one of our own, and to examine qualitatively the compatibility of prevailing sediment transport models and ecological theory with this new scheme.

The simplest of classifications is dichotomous, and such a bipartite scheme has been erected to emphasize the divergent effects of organisms on sediment entrainment: organisms can either stabilize or destabilize sediments, that is make them less or more easily erodible

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than their abiotic counterparts. The processes by which these biogenous changes are made have been classed as 'binding' vs 'destabilizing' by RHOADS *et al.* (1978). Functional grouping of species as stabilizers and destabilizers (YINGST and RHOADS, 1978) at first appears to be a logical outgrowth of this classification and of the parallel dichotomy erected by BRENCHLEY (1981). Such grouping was presaged by earlier work in Rhoads' laboratory (RHOADS and YOUNG, 1970; RHOADS, 1974) and elsewhere (ROWE, 1974, Table 1).

Although dichotomies are a logical place to start, and the net effect of organisms must be stabilizing or destabilizing, it does not necessarily follow that individual species can be classed as stabilizers or destabilizers. Several inconsistencies in fact arise. For example, individual animal tubes and sparse arrays of such tubes projecting above the bottom increase erodibility by deflecting fluid of relatively high momentum onto the surrounding bed (ECKMAN *et al.*, 1981), while denser tube arrays are likely to stabilize the bed by shielding it from the faster flow above (RHOADS *et al.*, 1978; ECKMAN, 1983). Another sort of inconsistency arises for an organism that produces surficial crawling traces. If the surface microtopography initially is smooth, this activity enhances erodibility (NOWELL *et al.*, 1981). If, alternatively, the ambient microtopography already is rougher than the microtopography produced by the crawling species, then the production of crawling trails will act to smooth larger relief and so to decrease erodibility (MACILVAINE and ROSS, 1979). The 'fine sandpaper' of this smoothing or roughening process is provided by meiofauna (CULLEN, 1973). Depending on context (e.g., local abundance or initial conditions), the same individual engaged in the same activity may stabilize or destabilize the sediment surface.

It thus proves impossible to categorize individual species or even individual activities of species as being consistently stabilizing or destabilizing. Nor does this dichotomy give any insight into the mechanisms responsible. We choose instead to develop descriptions of four broad modes of organism effects on sediment transport. Doing so serves two purposes. First, it makes apparent the fact that, very few organism activities (and thus very few organisms) can be identified *a priori* as uniformly stabilizing or destabilizing. Most activities have several facets whose net impact on sediment transport can not yet be evaluated without ancillary data or experimentation. Second, it makes explicit the physical mechanisms whereby thresholds and transport rates can be altered by organisms and thereby permits us to present some preliminary ideas on how those physical mechanisms may be included in extant sediment transport models.

Because organism effects on incipient motion (on erosion thresholds, e.g., Shields' curve) have received the most experimental attention, we will treat organism effects on erodibility the most thoroughly. Data on deposition thresholds for fine abiotic materials are scarce, so that discussions of incipient deposition and net sediment transport rate under given organism influences must be largely conjectural. We hope that this conjecture helps to provoke relevant experiments. The general progression of experiments that we anticipate in arriving at a predictive knowledge of organism effects on sediment transport in the field is from the sorts of erodibility measures being conducted at present, through experiments on incipient deposition, to a coupling of erosion and deposition in evaluating biotic effects under conditions of steady transport, and, finally, to the field-relevant sorts of time-dependent experiments in which dominance of physical forcing and biotic activities may alternate. We will not approach the more general, time-dependent problem here. Also explicitly excluded, as our title implies, are the albeit sediment dynamically important (DEUSER *et al.*, 1983) impacts of planktonic organisms.

CLASSIFICATION OF ORGANISM EFFECTS ON SEDIMENT TRANSPORT

Alteration of fluid momentum impinging on the bed by biogenous or biological structures

Structures produced and maintained by organisms can either increase or decrease fluid momentum incident on the surrounding bed (Fig. 1A). We already have mentioned animal tubes in this regard. The effects of these and other biogenous and living roughness elements protruding into the flow are far from being well quantified. Only in the simplest cases, i.e., isolated, rigid tubes (ECKMAN, 1982; ECKMAN and NOWELL, in press) and hemispheres (PAOLA, personal communication) and for spatially uniform distributions of tubes (ECKMAN *et al.*, 1981; ECKMAN, 1983), have these effects been parameterized.

For inanimate, bluff bodies uniformly dispersed over a flume bottom, experiments indicate that the transition from bed destabilization to bed stabilization (due solely to hydrodynamic effects) occurs as approximately 8% cover of the bed by roughness elements is exceeded (WOODING *et al.*, 1973; NOWELL and CHURCH, 1979). Flume experiments (ECKMAN *et al.*, 1981) with the tube-building polychaete *Owenia fusiformis* at up to 4% areal cover (6.9×10^3 individuals m^{-2}), a tube density previously believed to be stabilizing (FAGER, 1964), show enhanced erosion. Although sediment-stabilizing densities of tubicolous species no doubt are reached in the field (MILLS, 1967; FEATHERSTONE and RISK, 1977), they have only recently (ECKMAN, 1983) been duplicated in the laboratory, where detailed flow measurements can confirm the supposed stabilizing effect. Previously published results suggesting stabilization (RHOADS *et al.*, 1978) do not separate stabilization via effects on near-bed flow vs via adhesive effects (see below). Continuing experiments (ECKMAN and NOWELL, in press) show that, in addition to areal coverage by tubes, aspect ratio (height:diameter) and tube roughness influence the extent and magnitude of local changes in bed shear stresses. Reliable quantification of analogous effects produced by biogenous or living structures having more complex geometries is even farther away. Nonetheless, clear instances of armoring of the bed (*sensu* GRAF, 1971, p. 101) against fluid shear by biological structures have been identified. Blanketing by macroalgae (FROSTICK and MCCAVE, 1979), by algal mats (NEUMANN *et al.*, 1970), and by seagrass blades (SCOFFIN, 1970) surely must reduce the incident fluid momentum locally. Even in these cases of obvious stabilization, however, scour may result from the channeling of flow at the edges of the armored patch of bed.

Biogenous or biological structures need not be discrete (roughness elements) or blanket-like to influence the spatial pattern and magnitude of fluid momentum impinging on the bottom. Any activity which produces microtopography approaching the thickness of the viscous sublayer in relief will suffice. Fluid stresses on the bed downstream (and a shorter distance upstream) of the structures would be altered. In FREY's (1973) ethological classification of structures, resting traces (cubichnia), crawling traces (repichnia), grazing traces (pasichnia), feeding structures (fodichnia), and dwelling structures (domichnia) would be included so long as they lend surface relief of sufficient magnitude. Topography of the relevant scales (i.e., greater than the viscous sublayer thickness), however, can be made by macrofauna (usually defined as organisms retained on a sieve of 0.5 or 1.0-mm meshes) and larger organisms only. Meiofauna (organisms passing the macrofaunal sieve but retained on one of approximately 0.05-mm mesh) can be important in degrading these structures (CULLEN, 1973) but not in producing them. It should be noted, however, that groups usually considered meiofaunal (e.g., Foraminifera) may have track- (BUCHANAN and HEDLEY, 1960) and test-producing (DELACA *et al.*, 1980) members that range into the macrofaunal size category.

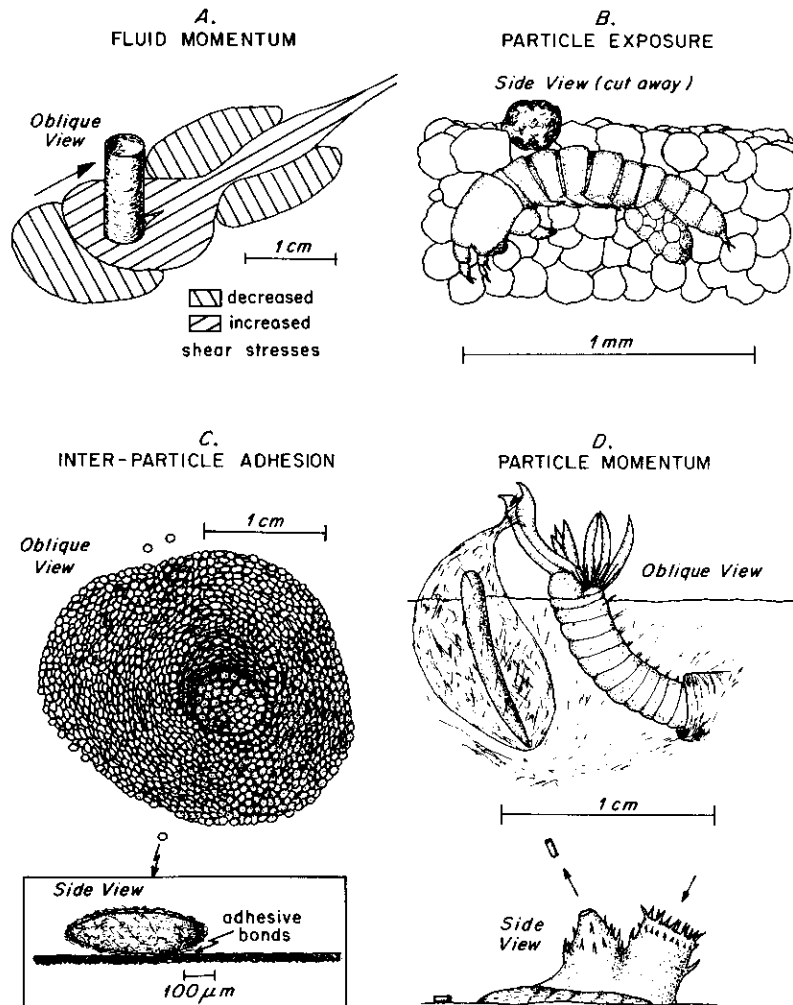


Fig. 1. Modes of organism influence upon sediment transport. Animal tubes (A) in a flow (direction indicated by arrow) typically cause local regions of increased and decreased bed shear stresses; adhesive and grain-exposure effects are also involved in tube construction. A burrowing harpacticoid copepod (*Huntemannia jadensis*) (B) has just moved the shaded sand grain into a position from which erosion is more likely; momentum imparted to the grain by burrowing may also be important. A conical mound of fecal pellets (C) produced by a burrowing tellinid bivalve (*Macoma nasuta*) combines adhesive effects with altered near-bed flow patterns and altered particle exposure to the flow; the exhalent siphon of the bivalve, positioned just below the crater in the mound, may also impart significant momentum to ejected pellets. *Amphicteis scaphobranchiata* (D, upper panel), a surface deposit feeding amphartetid polychaete, ejects fecal pellets from its feeding pit by use of a mucous sling attached to its two spatulate branchiae; besides imparting momentum to the particles comprising the pellet, this amphartetid affects near-bed flow via the geometry of its tube-pit complex, alters grain exposure, and secretes copious amounts of exopolymers. The cockle [*Clinocardium nuttalli*, (D) lower panel, with arrows indicating flow direction in the inhalent and exhalent siphons] removes microscopic particles from suspension, packages them into larger pellets, and ejects them into the flow, which may not be competent to hold these larger particles in suspension; adhesive effects are involved in the packaging, as is grain exposure.

Attention above has implicitly focused upon flow effects inducing erosion. Because bottom topography generates spatially varying bottom shear stresses and local recirculation regions, deposition also is influenced. For example, isolated tubes can produce sites of deposition in their immediate lee (ECKMAN, 1982, personal communication) and groups of closely spaced tubes can generate regions of enhanced net deposition (RHOADS, 1974; ECKMAN, 1983). It is widely accepted in the engineering literature that increased roughness enhances particle diffusion to the bed (BROWNE, 1974; WOOD, 1981), but there is no information available on biological effects in marine systems. SEHMEL (1979) shows that a factor of five increase in the roughness length causes a five-fold increase in particle "deposition velocity". A significant conclusion of Browne's work was that particle deposition rates are extremely sensitive to roughness, even when it is too small to produce hydraulically rough flow.

Alteration of particle exposure

The activities which produce any of these structures may also influence the exposure of individual sediment grains (Fig. 1B) or aggregates to the flow and thereby determine the fluid forces acting on these grains (PAINTAL, 1971; FENTON and ABBOTT, 1977). Without substantially changing the magnitude of fluid momentum impinging on the bed, organisms can place individual grains in positions from which they can be eroded either more or less easily. In flume experiments, the most stable beds vis-à-vis grain exposure (for sand and coarser materials) are formed by depositing material to make a flat bed at flow strengths just slightly below the critical erosion velocity (MANTZ, 1978). Moving grains from positions that they find under these conditions will, in general, enhance erodibility by increasing average grain exposure (MIDDLETON and SOUTHARD, 1978).

At the relevant scales for discussion of this means of sediment stabilization or destabilization, meiofaunal activities may have considerable impact. Near the other scale extreme in influencing exposure of particular grains are the activities of the frequently large and infaunal 'conveyor-belt' species christened by RHOADS (1974). These animals deposit feed at depth within the sediments but place their fecal material at or near the bed surface. Such feeding can produce graded beds of a decimeter or so in vertical extent (RHOADS and STANLEY, 1964) and thus may influence erosion rate and depth as erosion proceeds. More subtle grain exposure effects are produced during fecal deposition by both surface deposit feeders (NOWELL *et al.*, 1981) and suspension feeders (HAVEN and MORALES-ALAMO, 1966). Since grain exposure effects due to benthic organisms operate via alteration of the lift and drag (dominant forces in erosion) to which a grain is exposed, but can not alter gravity or Brownian motion (dominant forces in deposition) of particles in suspension, the importance of these influences is greater in erosion than in deposition.

Alteration of adhesive-cohesive bonding among particles

Virtually all organism activities are accompanied by the secretion of mucous exopolymers (FAZIO *et al.*, 1982), by the breaking of adhesive and cohesive bonds between particles, and by the formation of new adhesive and cohesive bonds between particles moved into proximity during these activities. We use 'cohesion' in the sense of electrochemical bonding directly between molecules of like chemical character and 'adhesion' in the sense of bonding of grains by an unlike substance (JUMARS *et al.*, 1982, Fig. 9), for example, an exopolymer secretion (which may or may not contain living bacteria) causing adhesion of two sediment grains. The

effect of such adhesive or cohesive bonds on erodibility of individual grains is visualized easily (Fig. 1C), but only recently has it been measured directly (A. R. M. NOWELL and J. WOLCOTT, personal communication). Because of the changing ratio of gravitational force (a function of particle volume) to adhesive-cohesive forces (functions of the number of grain-to-grain contacts and thus of particle surface area) with particle size, cohesive and adhesive forces play increasing roles in determining erodibility of individual grains as grain size decreases. Until recently (RHOADS *et al.*, 1978) it had been supposed that biogenous adhesion could be ignored in non-carbonate sediments of sand size and coarser. The simple but elegant field experiment of BOER (1981), showing significant microbial adhesion in the sand of an intertidal megaripple, lays this notion to rest. GRANT *et al.* (1982), further present the first detailed measurements of the critical entrainment stress, shown on a Shields plot, which suggest the magnitude of adhesive binding throughout the year on an intertidal sand flat; it appears that adhesive metabolites build up annually in this boreal environment, increasing critical shear stress by a factor of two, until episodes of mid-winter sediment transport remove them.

Bacteria (FAZIO *et al.*, 1982; UHLINGER and WHITE, 1983), benthic diatoms (HOLLAND *et al.*, 1974), macroalgae (NEWELL *et al.*, 1980), marine invertebrates (GRENON and WALKER, 1980), and marine vertebrates (PATEL *et al.*, 1980) all produce mucous exopolymers. Mucopolysaccharides are found on most surficial sediment particles at all water depths in the sea (WHITLATCH and JOHNSON, 1974; JOHNSON, 1977). Besides breaking adhesive and cohesive bonds as they move sediment grains, organisms also catabolize these compounds (HOBBIE and LEE, 1980; LINLEY *et al.*, 1981). Because both microbial and metazoan communities show strong vertical structure within sediments, adhesive effects are unlikely to remain constant with increasing erosion depth. Hence the net effect of an organism on erodibility via modifications of adhesion and cohesion may be difficult to measure, much less to predict *a priori*. A particularly insidious feature of microbial adhesion is that it will occur in laboratory flumes (REES, 1966) unless deliberate care is taken to exclude it. Bacteria and diatoms grow readily on experimental sediments in fresh or salt water over periods of hours to days.

The problem of evaluating adhesive-cohesive effects is further exacerbated by their almost invariable confounding with other organism impacts. Crawling traces of the suspension-feeding bivalve *Transenella tantilla*, for example, enhance erodibility of a smooth sand bed by altering both fluid momentum impacting the bed and grain exposure to it. However, the enhancement via these modes is not as great as would be predicted from the results of FENTON and ABBOTT (1977), and the difference appears to be due to mucus secreted by the animal during its crawling activity (NOWELL *et al.*, 1981).

Even more complex is the evaluation of adhesive effects resulting from deposit feeding. To pick up particles from the bed for ingestion, deposit feeders must break the adhesive and cohesive bonds between individual particles or groups of particles. Having done so and presumably having digested some of the initially present adhesives, deposit feeders frequently secrete some of their own exopolymers as binding agents for their fecal pellets. The resultant adhesive and cohesive forces within pellets may be sufficiently strong to allow pellets to transport for considerable distances as identifiable entities having their own hydrodynamic characteristics (RISK and MOFFAT, 1977; TAGHON *et al.*, 1984). Before this transport can occur, however, adhesive bonds between the pellets and the bed must be broken (NOWELL *et al.*, 1981; Fig. 1C).

The importance of adhesion and cohesion in deposition is explicit in the literature on particulate fouling (GUDMUNDSSON, 1981) and aerosol filtration (FRIEDLANDER, 1977).

Adhesion in these applications usually is parameterized as a 'stickiness coefficient', i.e., that fraction of contacts with the pipe wall, filter fiber, or bed that result in more or less permanent deposition. Exopolymer effects on this coefficient remain to be evaluated quantitatively, though casual flume observations (P. A. JUMARS, unpublished data) and the biology of suspension feeding (JORGENSEN, 1966; LABARBERA, 1984) make it apparent that mucus enhances deposition. Electrostatic attraction is also a factor in deposition of particles in waters of low salinity (GERRITSEN and PORTER, 1982), where it might be altered by biota.

Deposition appears, then, to be best approached as a two-stage process. The process consists of first, the probability of contact with the bed and subsequently, the conditional probability of adhesion given contact. Surface roughness (above) affects the first probability, whereas organic exopolymers can significantly alter the second probability.

Alteration of particle momentum

Alternatively, the organism may circumvent the problem of initial adhesive bond breakage or of initial motion in general by imparting substantial upward or horizontal momentum to sediment grains (Fig. 1D). *Amphicteis scaphobranchiata* (a tentaculate, tubicolous ampharetid polychaete), for example, ingests up to 30 mm³ of sediment per individual per hour and uses a mucous sling to eject fecal pellets from its feeding radius (NOWELL *et al.*, 1981; NOWELL *et al.*, 1984). Tellinid, deposit feeding bivalves, as another example, reject particles that are picked up initially but found unsuitable for ingestion. They inject these 'pseudofeces' as fluid-particle jets into the overlying water column (NEWELL, 1979). Although the animal uses fluid to impart particle momentum, we also list such mechanisms as fish burrowing or near-bottom swimming activity under this category of effects. The resuspension lasts only during the animal's activity. On a more subtle level, any organism activity (e.g., feeding, crawling, burrowing) which moves particles near the interface can alter the initial motion problem. Via their jostling during locomotion, even meiofauna may be important by virtue of imparting an analog of Brownian motion to particles (CULLEN, 1973; personal microscopic observation).

Conversely, organisms may capture particles in transport and deposit them. The phenomenon of suspension feeding accompanied by fecal and pseudofecal deposition is sufficiently well known to have been dubbed 'biodeposition.' This activity can double sedimentation rate locally (RHOADS, 1974). Particles in bedload transport may be captured and deposited in a similar manner (FAUCHALD and JUMARS, 1979; DAUER *et al.*, 1981).

DISCUSSION

Parameterization of organism effects in extant sediment transport models

Given this four-part scheme and the universal presence of organisms in marine sediments, it seems appropriate to ask which terms in extant sediment transport models will be influenced biologically and whether this influence can be made explicit. We will examine transport relationships only by general class, going from the most common to less frequently used formulations. The present level of information does not seem to warrant finer subdivision.

Virtually all bottom stress parameterizations in the marine environment depend on the law of the wall:

$$\sqrt{\tau_0/\rho} = u_* = \frac{U(z)}{\frac{1}{\kappa} \ln \frac{z}{z_0}}, \quad (1)$$

where τ_0 is shear stress at the bed, ρ is fluid density, u_* is boundary shear velocity, $U(z)$ is mean velocity at height z above the bed, κ is von Karman's constant (0.41), and z_0 is roughness length (qualitatively representing the height at which long-term average fluid velocity equals zero). From this formulation, it immediately is apparent that our first biological mode of effects enters the relationship as a determinant of roughness length; biogenous or biological structures alter fluid momentum impinging on the bed by altering z_0 in this simple, one-dimensional treatment. Using such a relationship (equation 1), the *local* skin friction can be related to the *local* sediment transport.

Assuming that biogenous roughness is uniform (*sensu* NIKURADSE, 1933), its effect is included implicitly in estimates of z_0 made from measured velocity profiles. If the roughness is non-uniform, showing non-stationarity or anisotropy ('patchiness' in the ecological jargon, e.g., GAGE and GEEKIE, 1973), this one-dimensional formulation will not be accurate. General, tractable, two- and three-dimensional formulations are not yet available, however.

The simplest and most widely used sediment transport equations that make use of these estimated τ_0 values are of the DuBoys type (O'BRIEN and RINDLAUB, 1934), i.e., of the form

$$q_s = a(\tau_0 - \tau_{0cr})^\beta, \quad (2)$$

where $\tau_0 > \tau_{0cr}$ (otherwise $q_s = 0$), q_s is bed material discharge rate per unit channel width, τ_{0cr} is shear stress just sufficient to initiate bed motion, and both a and β depend on particle parameters. The value of β varies between 1.4 and 1.8 for azoic silts and sands, based on USWES (1935) data. Simplistically, biogenous roughness enters this equation (as discussed above) in the τ_0 term, grain exposure and adhesion affect τ_{0cr} , adhesion (by virtue of altering effective grain-size, grain-shape, and grain-weight distributions) alters a and β as well as τ_{0cr} , and alteration of particle momentum (biodeposition or 'biosuspension') adds a constant (of unspecified sign) to the right-hand side of the equation. Moreover, it could be argued that the magnitude of biogenous effects in each of our four modes might depend on q_s , making both parameterization and estimation less tractable. Fortunately, there are reasons to believe that for arbitrarily high q_s these feedbacks become inconsequential. We must argue by deduction because data concerning organism effects on sediment transport at supercritical shear velocities are unavailable. We know of no laboratory data (stressed because only in the laboratory can these effects be identified and isolated with any facility) that allow determination of organism effects on sediment transport rates.

Above critical entrainment velocity, the rates of production of biogenous features and not just their accrued abundances would come into play. Transport would act, for example, to erase animal crawling traces or to replace them with other bedforms. Whether traces would influence sediment transport rates appreciably would then depend upon the rate of abiotic bedform growth and the rate of track production. At some rate of sediment transport, probably well below that needed to erode the crawling organism, trace production would stop entirely.

Effects of hydraulic roughness due to animal tubes also probably decrease with increasing sediment transport rates. Tubes built higher above the bottom expose the tube and protruding animal to increased drag forces. Spionid polychaetes, which suspension and bedload feed when horizontal particulate fluxes are sufficient (TAGHON *et al.*, 1980) decrease their tube heights as flow velocity and sediment transport rates increase (G. L. TAGHON, personal communication). Furthermore, the impact of both biogenous and abiogenous bottom roughness upon momentum transfer will decrease in general with increasing sediment transport, even if the physical nature of that roughness does not change. For example, tracking by the bivalve

Transenella tantilla doubles z_0 (NOWELL *et al.*, 1981), but z_0 increases by a factor of ten in the presence of strong bedload transport (SMITH and MCLEAN, 1977) or by two orders of magnitude in the presence of wave-current interactions (GRANT and MADSEN, 1982). Material in transport tends via stratification to stabilize the near-bottom water column and thus to impede the transfer of momentum from the outer flow to the bed (ADAMS and WEATHERLY, 1981).

Both in the field and in the laboratory, microbial cover of sediment grains, especially upon the exposed surfaces of contact points between moving grains, is reduced by abrasion (MEADOWS and ANDERSON, 1968). Presumably, then, microbial adhesion effects would decrease with increasing sediment transport rates. At some level of sediment transport, probably well below that necessary to erode and transport the animals responsible, animal activity levels would be expected to drop, with consequent decreases in grain-exposure, biodepositional or bioerosional effects. Many suspension-feeding bivalves, for example, are well known to be strongly affected by excessive suspended loads (LOOSANOFF and TOMMERS, 1948), which can clog their respiratory surfaces and lead to their replacement by other feeding guilds (RHOADS and YOUNG, 1970).

This sort of reasoning led us to pose the null hypothesis (JUMARS *et al.*, 1980; NOWELL and JUMARS, 1982) that organism impacts in general decrease with increasing sediment transport rates. Using the total load relationship of SHIELDS (1936) for a noncohesive, flat bed with grain roughness only (i.e., without bedforms) as a reference standard, we represented the relationship (Fig. 2E). Against this standard, the four modes of organism effects in theory can be resolved (Fig. 2A to D). At some transport rate, in theory, biological effects of benthos will

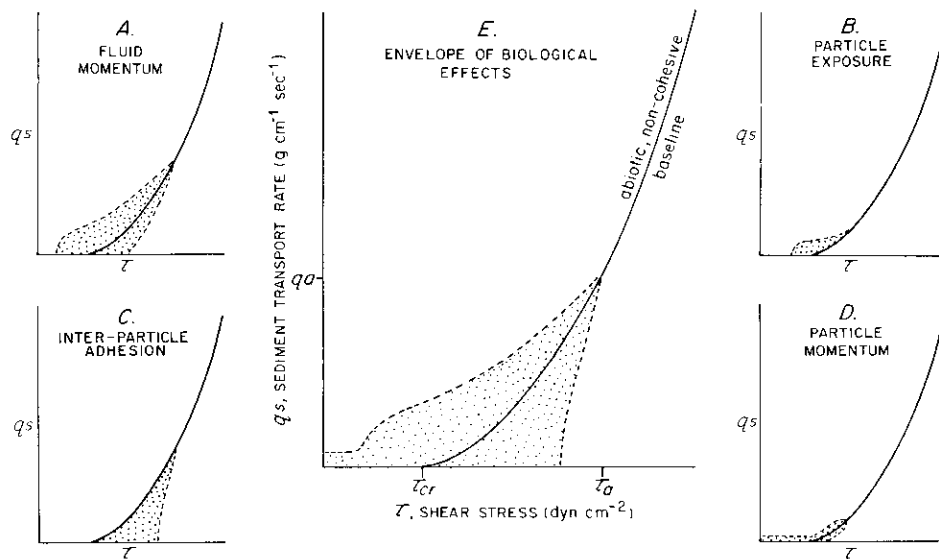


Fig. 2. Sediment transport rate, q_s , vs bed shear stress, τ , for an initially flat, non-cohesive, bed of abiotic sediments laid at a just subcritical flow velocity to create maximal stability with respect to grain exposure, biogenous scatter in the relationship indicated by stippling. Sediment transport begins at a critical shear value, τ_{cr} . It is conjectured that organism effects become inconsequential at some level of shear (τ_a) and sediment transport (q_a). Shapes and relative magnitudes of the stippled regions are also conjectural and are intended to apply only to the simplest case of well-sorted sediments in beds without vertical grading. Lettering corresponds with the modes of Fig. 1.

become quantitatively unimportant. That prediction, and we stress again that it is an untested one, also is supported by the fact that as the excess shear stress ($\tau_0 - \tau_{0cr}$) increases, more of the total load moves in suspension well above the bed—effectively out of reach of the benthos. An important and as yet unanswered question to address for the DuBoys-type relationship then is at what excess shear, for the environment and benthic community of concern, do organism effects drop to an inconsequential percentage of the transport rate? A preliminary answer for a hypothetical community living in medium sand might be obtained by utilizing the USWES (1935) data for transport rates of material and data on organism processing rates. Very approximately, when $\tau_0 \approx 1.15 \tau_{0cr}$, the transport rate of bedload exceeds the processing (feeding and pelletizing) rate of macrofauna [the latter calculated from the results of TAGHON and JUMARS (1984), coupled with realistic field densities of organisms]. However, this very crude answer ignores effects such as fecal pellet transport distances (TAGHON *et al.*, 1984), adhesive effects on τ_{0cr} , and interactions between deposit feeding and sediment transport.

Figure 2 also suggests why and when DuBoys-type relationships founded on the Shields curve can be reasonably successful. If the figure is accurate, then for an environment where most sediment transport occurs at very high excess shears, the best estimation technique for the model parameters α , β , and especially τ_{0cr} , is to establish the solid curve by dealing with sediments from which organism effects have been removed. It is easy to see (Fig. 2) that using a τ_{0cr} value from a biologically modified sediment readily could yield erroneous estimates of the curve's parameters. Unfortunately, stringent attention has not always been paid to the exclusion of microbes in 'abiotic' sediments (REES, 1966), making the abiotic 'baseline' difficult to specify. Even if our hypothesis of diminishing biological influence with increasing sediment transport rates is found to be true, however, there will be some range of sediment transport rates over which organism impacts can not be ignored.

We suggest, at least until experiments prove this approach inadequate, that these organism effects can be parameterized relatively easily with only minor modifications of the Einstein bedload transport equations.

To avoid the difficulties of determining a critical boundary stress, EINSTEIN (1950, 1964) developed a probabilistic entrainment model that assumes that the particles move in a series of steps (with step length proportional to particle size), with long rest periods (of varying duration) between steps. Thus, in any area of the bed there will be an exchange of particles, some being deposited and some being entrained; differing transport rates are then achieved by altering both the residence time between steps and the thickness of the moving layer. Here we shall state the key elements in the Einstein model and show how the four categories of organism effects may be incorporated into it.

The bedload equation of Einstein may be written as

$$P_1 = \frac{A_* \varphi}{1 + A_* \varphi}, \quad (3)$$

where P_1 is the probability of occurrence of at least one jump during time interval T .

$$A_* = \frac{k_1 k_3}{k_2 L} \quad \text{and} \quad \varphi = \left(\frac{i_s}{i_B} \frac{g_s}{\gamma_s} \frac{\rho}{\rho_s - \rho} \frac{1}{gd^3} \right)^{1/2}. \quad (4)$$

Here L is the jump length (which Einstein took to be a constant ≈ 100), k_1 and k_2 are coefficients of the weight and shape of the particle, and k_3 is a constant related to the settling velocity [following Einstein, but see YALIN'S (1977) discussion], and thus A_* should be an

empirical constant. The intensity of bedload transport (ϕ) represents the balance between deposition and entrainment; i_s and i_B represent the fractions of the bedload and bed material, respectively, of a given grain size (d); g_s is the bedload transport rate per unit width and time, and γ_s and ρ_s are the specific weight and density of the sediment. The probability P of entrainment is given by the ratio of the weight of the particle to the lift, which for entrainment must be less than unity, i.e.,

$$\frac{k_A(\rho_s - \rho)gd^3}{\frac{1}{2}C_L\rho k_1 x^2 u_b^2(1 + \eta)} < 1. \quad (5)$$

Here u_b is a 'bed velocity' equal to the velocity at $0.35x$, where x is a characteristic grain size incorporating an empirical correction curve for the ratio of particle size to the thickness of the viscous sublayer, C_L ; D_L is the lift coefficient which is a constant; and η is held to be a constant that includes the effects of fluctuations of the lift force. Two further corrections were included by Einstein, namely a hiding factor to allow for the fact that smaller grains are often hidden between larger ones, and second a pressure correction to allow for varying roughness.

The influence of organism activity, as represented by the four classes, may now be included. The effect of organisms altering the fluid momentum impinging on the bed enters the bedload model most directly through equation (5), in terms of x . The bed velocity is derived from the logarithmic velocity distribution (equation 1). We see that altering the boundary roughness by tube building, for example, will alter u_* and also affect x if the tube penetrates the viscous sublayer. Tracking effects, which are mainly a function of particle size: track ratio, may be included in the correction term for evaluating effective particle size or viscous sublayer thickness.

Altering grain exposure can affect the bedload relationship most directly through changing the effective particle diameter (x). If the bed material is of uniform size with no variations down through the bed, then altering grain exposure will have only a small effect on x . However, in natural beds there are distributions of particle sizes, and such size-frequency distributions often exhibit vertical gradations. Feeding selectivity may thus alter the grain size distribution in the topmost layers (RHOADS and STANLEY, 1964; TSUCHIYA and KURIHARA, 1980) and hence affect x (in equation 5) and d (in equation 4).

Inter-particle adhesion can be incorporated directly into the transport equation. As stated above (equation 5), the probability of entrainment depends on the ratio of weight of the particle to the instantaneous lift. Equation (5) may be modified so that

$$\frac{k_A(\rho_s - \rho)gd^3 C_A}{C_L \frac{1}{2} \rho k_1 u_b^2 x^2 (1 + \eta)} < 1. \quad (6)$$

Here, C_A is an adhesion coefficient (equal to unity for abiotic sediment) which will be a function of particle size and exopolymer abundance. If the adhesion is dominated by bacterial exudates, then measurements of mucus concentration [assayed by the amount of uronic acid present (cf. FAZIO *et al.*, 1982)] may yield a simple correlation with the lift required to break the adhesive bonds. Preliminary data, reported by NOWELL *et al.* (1981), suggest that including C_A will result in an apparent variation of a factor of 3 in C_L . Other adhesive effects, such as pelletization, result in a change in particle size and density and may be included most straightforwardly in equations (4) and (6).

Biodeposition can be included in the model by a change in d . However, it should be noted that we have concerned ourselves here chiefly with a bedload model, and much biodeposition occurs from suspended material. Bioerosion effects may be incorporated through the term η

in equation (7). In the original formulation, detachment of particles only occurs due to fluctuating forces, and the possibility of detachment due to viscous forces was excluded, but generalizations to include viscous forces have been developed of the form

$$\eta_1 = \eta f(u_* d/v)$$

(i.e., there is a dependence on roughness Reynolds number) which may be generalized to a first approximation (i.e., bioerosion is not affected by rate of bedload transport) as

$$\eta = \eta_0 + \eta_1,$$

where η_0 is a bioerosion constant determined by the activities of the organisms present.

We hesitate to suggest other formulations in any detail, especially more complex ones explicitly parameterizing organism influences, until the fit of the simple and relatively standard approaches above is examined. One additional approach that merits some mention, however, is rate process theory. GULARTE *et al.* (1980) show that such theory predicts reasonably well the effect of electrostatic cohesion on erosion rates of mineralogically pure, abiotic clays. Unfortunately, we know of no facile way of extending this approach to exopolymer adhesion or other organism effects. To date, rate process theory remains untested for natural, biologically modified sediments, and the prognosis for such testing is not very hopeful. Model coefficients in the rate process formulation generally are determined by varying flume temperature, a procedure that causes severe problems in the simultaneous dynamic scaling of biological rates (PLATT, 1981). Once again, however, the lack of data precludes confident conclusions.

An important first question which must be answered for application to a specific environment is whether organism effects must be considered at all. Since q_s is so strongly nonlinear with τ_0 (Fig. 2E), and if only the integrated transport rate is of concern, then occasional strong transport events (high τ_0) would be expected to dominate q_s . On boreal, non-carbonate shelves, transport seems to be dominated by just such infrequent but highly significant events (SMITH and HOPKINS, 1972). If only total transport is of interest, then perhaps in the situation dominated by episodic high transport, first-order approximations can safely ignore biogenous effects in estimating q_s . The relative unimportance of organisms in determining the total transport (if substantiated) would not be expected, however, to carry over into stratigraphic interpretation of the same transport events (NITTROUER and STERNBERG, 1981). For more subtle questions, such as how frequently sediment transport occurs, organism effects will have to be taken into account. Further, frequency of sediment transport is important as a feedback in determining benthic community structure (RHOADS and YOUNG, 1970; BRENCHLEY, 1981) and in controlling light transmissivity of continental shelf waters (ZANEVELD, 1977).

CONCLUSIONS

A tenable functional grouping clearly would be an asset in pursuing these more subtle effects. For reasons that we hope are now evident, grouping of organisms as stabilizers vs destabilizers has proven inconsistent. Unfortunately, no clear replacement of this classification, for use on continental shelves or elsewhere, is as yet possible. The experimental data simply are lacking for most taxa to determine the modes and magnitude of their impacts on transport thresholds and transport rates, much less to evaluate whether natural groupings of organisms according to their effects are possible. Flume experiments with a wide diversity of organisms are necessary before any definitive empirical grouping can result. Nonetheless,

some elements of a classification are beginning to emerge by virtue of their dramatic impacts. Adhesive-secreting microbes (RHOADS *et al.*, 1978; BOER, 1981), tube builders (ECKMAN *et al.*, 1981), and pelletizers (RISK and MOFFAT, 1977; MCCALL and TEVESZ, 1982; RHOADS and BOYER, 1982) will be major categories in any more complete classification of sediment transport effects.

Ideally, this empirical scheme could be coupled not only with sediment transport theory but also with ecological theory. Sediment transport effects surely could be more easily categorized and predicted if their adaptive (or exaptive *sensu* GOULD and VRBA, 1982) value to organisms could be identified. The body of ecological theory that shows the greatest potential in this regard is optimal foraging theory (PYKE *et al.*, 1977; HUGHES, 1980). Foraging theory already has proven useful in understanding the process of pelletization (LEVINTON and LOPEZ, 1977), selection of particles for incorporation into pellets (TAGHON *et al.*, 1978), patterns of deposit feeder movement (ROBERTSON *et al.*, 1980; SCHEIBLING, 1981), and rates of sediment processing by deposit feeders (TAGHON, 1981; TAGHON and JUMARS, 1984). We suggest that an enhanced effort to realize the potential for a closer coupling between foraging theory and sedimentological effects would be amply repaid.

Acknowledgements—This work was funded by Contract N00014-80-C-0252 with the Office of Naval Research. The manuscript benefited from critical reading by L. BLACK, D. C. MILLER, and R. F. L. SELF. R. FELLER kindly provided the photograph from which Fig. 1B was drawn. University of Washington Contribution No. 1346.

REFERENCES

- ADAMS C. E., JR. and G. L. WEATHERLY (1981) Suspended-sediment transport and benthic boundary-layer dynamics. *Marine Geology*, **42**, 1–18.
- BOER P. L. DE (1981) Mechanical effects of micro-organisms on intertidal bedform migration. *Sedimentology*, **28**, 129–132.
- BRENCHLEY G. A. (1981) Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *Journal of Marine Research*, **39**, 767–790.
- BROWNE L. W. B. (1974) Deposition of particles on rough surfaces during turbulent gas-flow in a pipe. *Atmospheric Environment*, **8**, 801–816.
- BUCHANAN J. B. and R. H. HEDLEY (1960) A contribution to the biology of *Astrorhiza limicola* (Foraminifera). *Journal of the Marine Biological Association of the United Kingdom*, **39**, 549–560.
- CULLEN D. J. (1973) Bioturbation of superficial marine sediments by interstitial meiobenthos. *Nature, London*, **242**, 323–324.
- DAUER D. M., C. A. MAYBURY and R. M. EWING (1981) Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, **54**, 21–38.
- DELACA T. E., J. H. LIPPS and R. R. HESSLER (1980) The morphology and ecology of a new large agglutinated Antarctic foraminifer (*Textulariina*: *Notodendroidea* nov.). *Zoological Journal of the Linnean Society of London*, **69**, 205–224.
- DEUSER W. G., P. G. BREWER, T. D. JICKELLS and R. F. COMMEAU (1983) Biological control of the removal of abiogenic particles from the surface ocean. *Science, Wash.*, **219**, 388–391.
- ECKMAN J. A. (1982) Hydrodynamic effects exerted by animal tubes and their importance to the ecology of soft-bottom, marine benthos. PhD. dissertation, University of Washington, Seattle, 275 pp.
- ECKMAN J. E. (1983) Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography*, **28**, 241–257.
- ECKMAN J. E. and A. R. M. NOWELL (in press) Boundary skin friction, particle deposition, and sediment entrainment about a protruding animal tube. *Sedimentology*.
- ECKMAN J. E., A. R. M. NOWELL and P. A. JUMARS (1981) Sediment destabilization by animal tubes. *Journal of Marine Research*, **39**, 361–374.
- EINSTEIN H. A. (1950) The bedload function for sediment transportation in open channel flows. *United States Department of Agriculture Technical Bulletin*, **1026**, 70 pp.
- EINSTEIN H. A. (1964) River sedimentation. In: *Handbook of hydrology*, V. T. CHOW, editor, McGraw-Hill, New York, pp. 79–105.
- FAGER E. W. (1964) Marine sediments: effects of a tube-building polychaete. *Science, Wash.*, **143**, 356–359.
- FAUCHALD K. and P. A. JUMARS (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review*, **16**, 193–284.

- FAZIO S. A., D. J. UHLINGER, J. H. PARKER and D. C. WHITE (1982) Estimations of uronic acids as quantitative measures of extracellular polysaccharide and cell wall polymers from environmental samples. *Applied and Environmental Microbiology*, **43**, 1151–1159.
- FEATHERSTONE R. P. and M. J. RISK (1977) Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology*, **47**, 446–450.
- FENTON J. and J. E. ABBOTT (1977) Initial movement of grains on a stream bed; the effect of relative protrusion. *Proceedings of the Royal Society of London*, **A352**, 523–537.
- FREY R. W. (1973) Concepts in the study of biogenic sedimentary structures. *Journal of Sedimentary Petrology*, **43**, 6–19.
- FROSTICK L. E. and I. N. MCCAVE (1979) Seasonal shifts of sediment within an estuary mediated by algal growth. *Estuarine and Coastal Marine Science*, **9**, 569–576.
- GAGE J. D. and A. D. GREEKIE (1973) Community structure of benthos in Scottish sea-lochs. II. Spatial pattern. *Marine Biology*, **19**, 41–53.
- GERRITSEN J. and K. G. PORTER (1982) The role of surface chemistry in filter feeding by zooplankton. *Science, Wash.*, **216**, 1225–1227.
- GRAF W. H. (1971) *Hydraulics of sediment transport*, McGraw-Hill, New York, 513 pp.
- GRANT W. D., L. F. BOYER and L. P. SANFORD (1982) The effect of biological processes on the initiation of sediment motion in non-cohesive sediments. *Journal of Marine Research*, **40**, 659–677.
- GRANT W. D. and O. S. MADSEN (1982) Movable bed roughness in unsteady oscillatory flow. *Journal of Geophysical Research*, **87**, 469–481.
- GRENON J.-F. and G. WALKER (1980) Biochemical and rheological properties of the pedal mucus of the limpet, *Patella vulgata* L. *Comparative Biochemistry and Physiology*, **66B**, 451–458.
- GOULD S. J. and E. S. VRBA (1982) Exaptation—a missing term in the science of form. *Paleobiology*, **8**, 4–15.
- GUDMUNDSSON J. S. (1981) Particulate fouling. In: *Fouling of heat transfer equipment*, E. F. C. SOMERSCALES and J. G. KNUDSEN, editors, Hemisphere Publishing Corporation, Washington, D.C., pp. 357–387.
- GULARTE R. C., W. E. KELLEY and V. A. NACCI (1980) Erosion of cohesive sediments as a rate process. *Ocean Engineering*, **7**, 539–551.
- HAVEN D. S. and R. MORALES-ALAMO (1966) Occurrence and transport of fecal pellets in suspension in a tidal estuary. *Sedimentary Geology*, **2**, 141–151.
- HOBBIE J. E. and C. LEE (1980) Microbial production of extracellular material: importance in benthic ecology. In: *Marine benthic dynamics*, K. R. TENORE and B. C. COULL, editors, University of South Carolina Press, Columbia, pp. 341–346.
- HOLLAND A. F., R. G. ZINGMARK and J. M. DEAN (1974) Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. *Marine Biology*, **27**, 191–196.
- HUGHES R. N. (1980) Optimal foraging in the marine context. *Oceanography and Marine Biology Annual Review*, **18**, 423–481.
- JOHNSON R. G. (1977) Vertical variation in particulate matter in the upper twenty centimeters of marine sediments. *Journal of Marine Research*, **35**, 273–282.
- JØRGENSEN C. B. (1966) *Biology of suspension feeding*. Pergamon Press, Oxford, 357 pp.
- JUMARS P. A., A. R. M. NOWELL and J. B. SOUTHARD (1980) The effects of deposit-feeding benthos on the entrainment and transport of fine sediments. Unpublished proposal to the United States National Science Foundation.
- JUMARS P. A., R. F. L. SELF and A. R. M. NOWELL (1982) Mechanics of particle selection by tentaculate deposit feeders. *Journal of Experimental Marine Biology and Ecology*, **64**, 47–70.
- LABARBERA M. (1984) Feeding currents and particle capture in suspension feeding animals. *American Zoologist*, in press.
- LEVINTON J. S. and G. R. LOPEZ (1977) A model of renewable resources and limitation of deposit-feeding benthic populations. *Oecologia*, **31**, 177–190.
- LINLEY E. A. S., R. C. NEWELL and S. A. BOSMA (1981) Heterotrophic utilization of mucilage released during fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). I. Development of microbial communities associated with the degradation of kelp mucilage. *Marine Ecology Progress Series*, **4**, 31–41.
- LOOSANOFF V. L. and F. D. TOMMERS (1948) Effect of suspended silt and other substances on the rate of feeding of oysters. *Science, Wash.*, **107**, 69–70.
- MACILVAINE J. L. and D. A. ROSS (1979) Sedimentary processes on the continental slope of New England. *Journal of Sedimentary Petrology*, **49**, 563–574.
- MANTZ P. A. (1978) Bed forms produced by fine cohesionless, granular and flaky sediments under subcritical water flows. *Sedimentology*, **25**, 83–103.
- MEADOWS P. S. and J. G. ANDERSON (1968). Micro-organisms attached to marine sand grains. *Journal of the Marine Biological Association of the United Kingdom*, **48**, 161–175.
- MIDDLETON G. V. and J. B. SOUTHARD (1978) *Mechanics of sediment movement*. Lecture notes for short course No. 3, Eastern Section, Society of Economic and Petroleum Geologists, 180 pp.
- MILLS E. L. (1967) The biology of an ampeliscid amphipod crustacean sibling species pair. *Journal of the Fisheries Research Board of Canada*, **24**, 305–355.

- NEUMANN A. C., C. D. GEBELEIN and T. P. SCOFFIN (1970) The composition, structure and erodibility of subtidal mats, Abaco, Bahamas. *Journal of Sedimentary Petrology*, **40**, 274–297.
- NEWELL R. C. (1979) *Biology of intertidal animals*. Marine Ecological Surveys, Faversham, Kent, U.K., 781 pp.
- NEWELL R. C., M. I. LUCAS, B. VELIMIROV and L. J. SEIDERER (1980) The quantitative significance of dissolved organic losses following fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). *Marine Ecology Progress Series*, **2**, 45–59.
- NIKURADSE J. (1933) *Stromungsgesetze in rauhen Röhren*. VDI-Forschungsheft 361, Beilage zu Forschung auf dem Gebiete des Ingenieurwesens Ausgabe B, 4.
- NITTROUER C. A. and R. W. STERNBERG (1981) The formation of sedimentary strata in an allochthonous shelf environment: the Washington continental shelf. *Marine Geology*, **42**, 201–232.
- NOWELL A. R. M. and M. A. CHURCH (1979) Turbulent flows in a depth-limited boundary layer. *Journal of Geophysical Research*, **84**, 4816–4824.
- NOWELL A. R. M. and P. A. JUMARS (1982) Measuring and modeling organism effects on sediment transport. *Geological Society of London, Newsletter*, **11**, 38–39 (abstract).
- NOWELL A. R. M., P. A. JUMARS and J. E. ECKMAN (1981) Effects of biological activity on the entrainment of marine sediments. *Marine Geology*, **42**, 133–153.
- NOWELL A. R. M., P. A. JUMARS and K. FAUCHALD (1984) The foraging strategy of a subtidal and deep-sea deposit feeder. *Limnology and Oceanography*, in press.
- O'BRIEN M. P. and B. D. RINDLAUB (1934) The transportation of bedload by streams. *Transaction of the American Geophysical Union*, **100**, 393–419.
- PAINTAL A. S. (1971) Stochastic model of bedload transport. *Journal of Hydraulic Research*, **9**, 527–554.
- PATEL B., J. EHRLICH, S. S. STIVALA and N. K. SINGH (1980) Comparative studies of mucopolysaccharides from marine animals: 1. *Raja eglanteria*. *Journal of Experimental Marine Biology and Ecology*, **46**, 127–136.
- PLATT T. (1981) Thinking in terms of scale: introduction to dimensional analysis. In: *Mathematical models in biological oceanography*, T. PLATT, K. H. MANN and R. E. ULANOWICZ, editors, UNESCO Press, Paris, pp. 112–121.
- PYKE G. H., H. R. PULLIAM and E. L. CHARNOV (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**, 137–154.
- REES A. I. (1966) Some flume experiments with a fine silt. *Sedimentology*, **6**, 209–240.
- RHOADS D. C. (1974) Organism–sediment relations on the muddy sea floor. *Oceanography and Marine Biology Annual Review*, **12**, 263–300.
- RHOADS D. C. and L. F. BOYER (1982) The effects of marine benthos on physical properties of sediments: a successional perspective. In: *Animal–sediment relations*, P. L. MCCALL and M. J. S. TEVESZ, editors, Plenum, New York, pp. 3–52.
- RHOADS D. C. and D. J. STANLEY (1964) Biogenic graded bedding. *Journal of Sedimentary Petrology*, **35**, 956–963.
- RHOADS D. C., J. Y. YINGST and W. ULLMAN (1978) Seafloor stability in central Long Island Sound. Part I. Temporal changes in erodibility of fine-grained sediments. In: *Estuarine interactions*, M. L. WILEY, editor, Academic Press, New York, pp. 221–244.
- RHOADS D. C. and D. C. YOUNG (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research*, **28**, 150–178.
- RISK M. J. and J. S. MOFFAT (1977) Sedimentological significance of fecal pellets of *Macoma balthica* in the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology*, **47**, 1425–1436.
- ROBERTSON J. R., K. BANCROFT, G. VERMEER and K. PLAISIER (1980) Experimental studies on the foraging behavior of the sand fiddler crab *Uca pugilator* (Bosc, 1802). *Journal of Experimental Marine Biology and Ecology*, **44**, 67–83.
- ROWE G. T. (1974) The effects of the benthic fauna on the physical properties of deep-sea sediments. In: *Deep-sea sediments: physical and mechanical properties*, A. L. INTERBITZEN, editor, Plenum Press, New York, pp. 381–400.
- SCHEIBLING R. E. (1981) Optimal foraging movements of *Oreaster reticulatus* (L.) (Echinodermata:Asteroidea). *Journal of Experimental Marine Biology and Ecology*, **51**, 173–185.
- SCOFFIN T. P. (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology*, **40**, 249–273.
- SEHMEL S. A. (1979) *Deposition and resuspension processes*. Battelle Pacific Northwest Laboratory, Richland, Washington, Report No. PNL-SA-6746, 47 pp.
- SHIELDS A. (1936) Anwendung der Ähnlichkeitsmechanik und Turbulenzforschung auf die Geschiebebewegung. *Mitteilungen der Preussischen Versuchsanstalt für Wasserbau und Schiffbau*, Heft 26, 70 pp.
- SMITH J. D. and T. S. HOPKINS (1972) Sediment transport on the continental shelf off of Washington and Oregon in light of recent current measurements. In: *Shelf sediment transport*, D. J. P. SWIFT, D. B. DUANE and O. H. PILKEY, editors, Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 143–179.
- SMITH J. D. and S. R. MCLEAN (1977) Spatially averaged flow over a wavy surface. *Journal of Geophysical Research*, **82**, 1735–1746.

- TAGHON G. L. (1981) Beyond selection: optimal foraging theory as a function of food value. *American Naturalist*, **118**, 202-214.
- TAGHON G. L. and P. A. JUMARS (1984) Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. *Ecology*, **65**, in press.
- TAGHON G. L., A. R. M. NOWELL and P. A. JUMARS (1980) Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science, Wash.*, **210**, 262-264.
- TAGHON G. L., A. R. M. NOWELL and P. A. JUMARS (1984) Transport and breakdown of fecal pellets: biological and sedimentological consequences. *Limnology and Oceanography*, in press.
- TAGHON G. L., R. F. L. SELF and P. A. JUMARS (1978) Predicting particle selection by deposit feeders: a model and its implications. *Limnology and Oceanography*, **23**, 752-759.
- TEVESZ M. J. S. and P. L. MCCALL (1982) Geological significance of aquatic nonmarine trace fossils. In: *Animal-sediment relations*, P. L. MCCALL and M. J. S. TEVESZ, editors, Plenum Press, New York, pp. 257-285.
- TSUCHIYA M. and Y. KURIHARA (1980) Effect of the feeding behaviour of macrobenthos on changes in environmental conditions of intertidal flats. *Journal of Experimental Marine Biology and Ecology*, **44**, 85-94.
- UHLINGER D. J. and D. C. WHITE (1983) Relationship between the physiological status and the formation of extracellular polysaccharide glycocalyx in *Pseudomonas atlantica*. *Applied and Environmental Microbiology*, **45**, 64-70.
- USWES (1935) Studies of river bed materials and their movement, with special reference to the lower Mississippi River. United States Waterways Experiment Station, Vicksburg, Mississippi, Paper 17, 115 pp.
- WHITLATCH R. B. and R. G. JOHNSON (1974) Methods of staining organic matter in marine sediments. *Journal of Sedimentary Petrology*, **44**, 1310-1312.
- WOOD N. B. (1981) A simple method for the calculation of turbulent deposition to smooth and rough surfaces. *Journal of Aerosol Science*, **12**, 275-290.
- WOODING R. A., E. F. BRADLEY and J. K. MARSHALL (1973) Drag due to regular arrays of roughness elements of varying geometry. *Boundary Layer Meteorology*, **5**, 285-308.
- YALIN M. S. (1977) *Mechanics of sediment transport*, 2nd edition, Pergamon Press, Oxford, 298 pp.
- YINGST J. Y. and D. C. RHOADS (1978) Seafloor stability in central Long Island Sound. Part II. Biological interactions and their potential importance for seafloor erodibility. In: *Estuarine interactions*, M. L. WILEY, editor, Academic Press, New York, pp. 245-260.
- ZANEVELD J. R. V. (1977) Bottom nepheloid layers and bottom mixed layers observed on the continental shelf off Oregon. *Journal of Geophysical Research*, **82**, 3921-3931.