

## Sediment destabilization by animal tubes

by James E. Eckman<sup>1</sup>, Arthur R. M. Nowell<sup>1</sup> and Peter A. Jumars<sup>1</sup>

### ABSTRACT

Laboratory flume experiments were conducted in order to test the influence on sediment erodibility of varying densities of the tube-building polychaete worm *Owenia fusiformis*. Experiments were performed on isolated individuals, in order to measure approximate spatial limits of isolated tube effects, and on arrays of individuals at densities reported previously to be associated with stable beds. The bed was destabilized at all densities of tubes tested, and this destabilization was more pronounced at the higher densities. In the field, stable beds persist despite the frequently destabilizing influence of animal tubes. We suggest that mucous binding of sediments by animals, diatoms and/or omnipresent bacteria explains this contradiction.

### 1. Introduction

Individual structures on an otherwise smooth sea bed (isolated roughness elements, in hydrodynamic terms) are known to cause local scour by deflecting fluid of relatively high momentum toward the bed. Such scour is seen around single blades of marine grasses (Neumann *et al.*, 1970; Scoffin, 1970), biogenous mounds and shell fragments (Young and Southard, 1978), and animal tubes (Gage, 1977).

In contrast to the sediment-destablizing effects of isolated roughness elements is the widely accepted notion that sediments are stabilized by arrays of seagrass blades and surface-evident tubes constructed by infauna. This notion has developed from both field observational studies (Sanders *et al.*, 1962; Fager, 1964; Galtsoff, 1964; Mills, 1967; Neumann *et al.*, 1970; Young and Rhoads, 1971; Daro and Polk, 1973; Bailey-Brock, 1979; McCall and Fisher, 1980) and laboratory flume studies (Rhoads *et al.*, 1978; Yingst and Rhoads, 1978).

It is widely believed that animal tubes stabilize sediments by altering the character of near-bed flow. At some density of tubes the interactions of flow perturbations created by individual tubes may produce a "skimming flow" (*sensu* Morris, 1955), effectively protecting the bed from erosion. In "skimming flow" the region of maximum turbulent kinetic energy and shear stress production occurs away from the bed. Unfortunately, empirical and theoretical means to predict the transitional tube density between that causing impingement of more kinetic energy, as in the

1. Dept. of Oceanography, University of Washington, Seattle, Washington 98195.

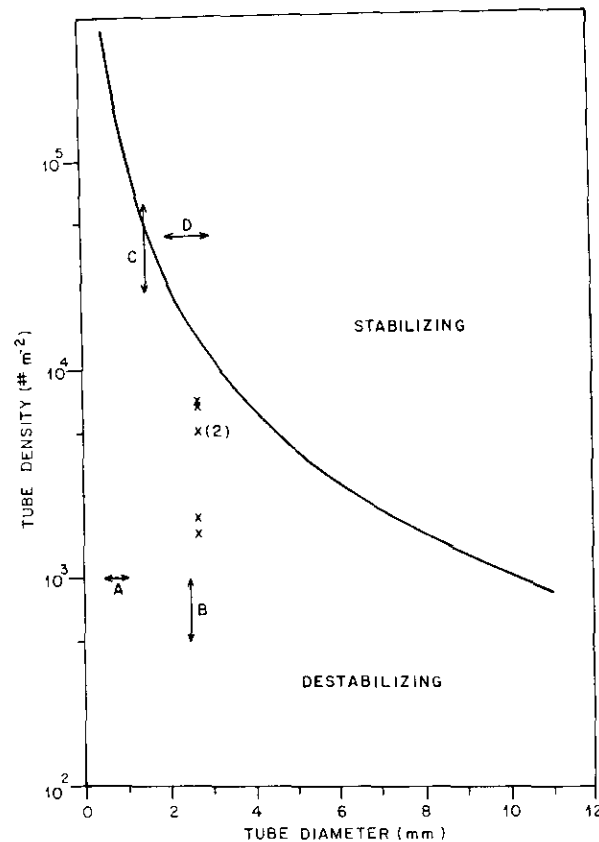


Figure 1. Minimum tube density required to stabilize sediments as a function of tube diameter, estimated from the results of Nowell and Church (1979). Also plotted are actual values from our experiments (x's) and from the following references: (A) McCall and Fisher (1980); (B) Fager (1964)—mean densities; (C) Bailey-Brock (1979)—chaetopterid mounds; (D) Mills (1967). Tube diameters are estimated for (A) through (D).

case of isolated tubes (above), versus that causing impingement of less kinetic energy upon the bottom are not yet well developed. The laboratory flume experiments of Nowell and Church (1979) suggest, however, that this transition likely will occur when roughly one-twelfth of the plan area of the bottom is occupied by roughness elements. Figure 1 expresses this "critical" ratio as a simple relationship between tube size and density. Surprisingly, densities of tubes reported from some studies of "stabilized" beds fall well within the range suggested by Nowell and Church (1979) to be hydrodynamically destabilizing.

There are many possible reasons for this apparent discrepancy (see also Discussion), including problems of dynamic and geometric scaling. Consequently, we have conducted laboratory flume experiments in order to test the influence on sediment

erodibility of varying densities of the tube-building polychaete worm *Owenia fusiformis*. We chose to work with *Owenia* for several reasons: (1) Fager's (1964) study of a population of this species is often cited as one of the earliest, definitive reports of sediment stabilization by animal tubes; (2) Fager reports field densities of this species encountered in "stable" (i.e., non-rippled) beds; and (3) we were able to obtain sufficient numbers of adults of this species to create equivalent densities in our flume studies. Experiments were performed on isolated individuals, in order to measure spatial limits of isolated tube effects, and on arrays of individuals at densities reported by Fager (1964) to be associated with stable beds. These densities, however, fall below the curve of Figure 1. Our objective, then, was to test directly the ability of *Owenia* tubes, at these densities, to stabilize sediments.

## 2. Methods

Experiments were performed in a recirculating seawater flume at the Friday Harbor Laboratories of the University of Washington. The plexiglass flume is 2.5 m long and 50 cm wide. The bed has a removable section (box) so that sediment cores 25 cm square and up to 20 cm deep may be placed coplanar with the surrounding flume bed. This box is located 1.75 m from the entrance to the flume. Further details regarding system design are found in Nowell *et al.* (in press).

In order to determine the mode of influence of isolated tubes on sediment transport and the areal extent of their effects, four adult *Owenia fusiformis* (collected from False Bay, Washington) were placed in a flume box that had been filled to approximately 2 cm below flume-bed level with a wetted foundry sand (median diameter = 169  $\mu\text{m}$ ). The four animals were inserted vertically into the sediments such that their tubes were below the sediment surface, and were arranged in a straight line oriented normal to flow direction. Distances between animals were at least 5 cm, which pretests showed was sufficient to avoid any significant flow interaction among tubes. The remainder of the box was then filled with foundry sand that had been thoroughly washed in fresh seawater less than three hours previously to minimize confounding effects of mucous binding. The box and surrounding flume bed (also covered with a thin sand layer) were then carefully leveled to create a visually smooth, flat surface.

The flume was run at a constant, low discharge rate (surface velocity  $\cong 2$  cm  $\text{sec}^{-1}$ , depth  $\cong 2$  cm) for 6 hours, long enough to allow all animals to surface and sweep out a characteristic pit (Plate 1A, see Results). Discharge was then increased slowly until initiation of sediment motion was noted in the vicinity of any tube. We define initial motion as rolling motion of individual grains to or on the bed outside of an animal's pit (where sediment was often moved by the animal itself). As soon as initial motion was noted, vertical profiles of flow velocity, from which boundary shear stress is calculated, were recorded (below) at several locations among and



Plate 1A. An erect *Owenia* tube with its characteristic circular pit. Pit diameter is approximately 1 cm; flow is from left to right.

immediately upstream of the tubes. The location of sediment motions relative to tubes/pits was also measured using a stereo-microscope (with ocular micrometer) mounted on an adjustable stand. Flume discharge was then increased until initial motion about each tube and "general bed motion" (below) on the smooth bed immediately upstream were attained sequentially. At each step velocity profiles and optical measurements were made. The experiment was replicated using four different adult *Owenia* and a new bed composed of freshly washed sands.

In order to test the influence of different tube densities on sediment stability, separate, replicated experiments were performed on beds of *Owenia* at densities of approximately 0.17, 0.50, and 0.70  $\text{cm}^{-2}$ . *Owenia* (average tube diameter 2.7 mm) were inserted vertically in the 25 × 25-cm flume box at randomly chosen coordinates. Procedures up to the initial increase in flume discharge are identical to those described above. The time of bed exposure to the constant, low flow varied among all experiments from 5.3 to 8 hours. Photographs of the bed were taken for determining the exact number of *Owenia* exposed.

As flume discharge was increased slowly, the bed was examined continuously by systematic sweeps with the stereo-microscope. Velocity profiles (below) were recorded as soon as initial motion was noted anywhere within the bed of tubes. Discharge was then increased until general bed motion, equivalent to "weak" transport (*sensu* USWES, 1935), was attained, sequentially, within the cluster of tubes and immediately upstream on the smooth bed. At the point of general bed motion, the entire bed appears to be in sporadic motion, when examined with the aid of a high-intensity, low-angle light, with particles rolling in contact with the bed.

To enable nonparametric testing of bed-activity differences among experiments we resorted to a means of measuring bed activity on an ordinal scale. As soon as general bed motion within the cluster of tubes was attained five visual sweeps of the bed were made with the stereo-microscope (10x, 2.2 cm wide field of view). Each sweep was centered along a straight line directed upstream/downstream and covered an area of the bed 25 cm long stream by 2.2 cm cross stream, chosen randomly and so as not to overlap other transects. All sweeps were made a minimum of 13.5 cm from the closest flume wall. Each sweep proceeded at an approximately constant rate of 1 cm sec<sup>-1</sup>. Where sediment motion was observed, the area of this "active" site was estimated using the calibrated ocular micrometer. The distance from the center of the active site to the nearest upstream *Owenia* tube was also recorded. Each experiment, then, produced five unbiased estimates of areal proportion of bed "active" at general bed motion. Vertical profiles of flow velocity (below) were recorded after sweeps were completed and, again, after general bed motion was attained on the smooth sand bed upstream of tubes. At each density experiments were replicated by rotating the flume box by 90° or 270° (chosen randomly) at the end of an experiment and resmoothing the bed after depositing a new layer of freshly washed sand.

Any instantaneous velocity ( $u$ ) may be expressed as a sum of two terms

$$u = \bar{u} + u' \quad (1)$$

where ( $\bar{u}$ ) is a mean velocity and ( $u'$ ) an instantaneous velocity fluctuation. We measured ( $\bar{u}$ ) and the streamwise turbulent kinetic energy, ( $\overline{u'^2}$ ), both with a 30-second integration time, using a hot-film anemometer (Thermo Systems TSI 1231 W conical quartz film). The horizontal and vertical positions of the probe were controlled by a traversing vernier stand that is accurate to 0.02 cm vertically. Further details on system properties and calibrations are found in Nowell *et al.* (in press).

Critical boundary shear stress ( $\tau_c$ ) may be expressed as a critical erosion velocity ( $u_{*c}$ ) by the expression

$$u_{*c} = (\tau_c/\rho)^{1/2}, \text{ where } \rho = \text{fluid density.} \quad (2)$$

Critical erosion velocity was determined from the log-profile relationship

Table 1. Bed-averaged erosion velocities ( $u_*$ ) at which initial motion and general bed motion within the cluster of tubes and on the smooth bed were noted. Values are reported for isolated individuals and for all densities tested. Ninety-five percent confidence limits for  $u_*$  are within  $\pm 1\%$  for all values.

Density (# cm <sup>-2</sup> )	Initial motion† (cm sec <sup>-1</sup> )	General bed motion within cluster of tubes† (cm sec <sup>-1</sup> )	General bed motion on smooth bed* (cm sec <sup>-1</sup> )
Isolated tubes (avg)	0.73 (24%)	—	1.48/1.53
0.163	0.68 (23%)	1.25 (76%)	1.43/1.49
0.187	0.71 (26%)	1.14 (67%)	1.39/ —
0.504	0.76 (33%)	1.04 (62%)	1.32/1.47
0.480	0.78 (33%)	0.96 (50%)	1.36/ —
0.672	0.69 (27%)	0.92 (50%)	1.32/1.46
0.694	0.76 (28%)	1.05 (54%)	1.43/ —

† Values in parentheses indicate percentages of bed-averaged critical shear stresses ( $\tau_c$ ) for the smooth bed ( $\tau_c \propto u_*^2$ ).

\* The two values represent, respectively, ( $u_*$ ) measured over the bed of tubes and ( $u_*$ ) measured over the smooth bed immediately upstream.

$$\frac{u(z)}{u_*} = \frac{1}{\kappa} \ln(z/z_0), \quad (3)$$

where ( $u(z)$ ) is the velocity at height ( $z$ ), ( $\kappa$ ) is von Karman's constant ( $= 0.4$ ), and ( $z_0$ ) is the roughness height, qualitatively representing the height at which long-term average velocity equals zero. For measurements made within the log layer a plot of ( $\bar{u}(z)$ ) vs.  $\ln(z)$  produces a straight line of slope ( $u_*/\kappa$ ). A minimum of six points from within the log layer was used in each regression ( $r^2 > 0.999$ , typically). This logarithmic region often extended to one-third of the boundary layer thickness (flow depth for a depth-limited boundary layer). No measurements were obtained within the viscous sublayer (approximately 1 mm thick).

### 3. Results

Although an *Owenia* can stand erect in even strong flow, the imbricated grains that form its tube (cf., Fager, 1964) allow the tube to flex freely. After surfacing from below the smoothed sand bed, an *Owenia* invariably creates a roughly circular pit (Plate 1A) by a sweeping action of the exposed section of its tube. This behavior was noted among isolated individuals and at all densities. An animal experiencing bedload transport actively maintains its pit by occasional sweepings. These pits serve as effective traps for materials moving as bedload (personal observations), and we have observed *Owenia* feeding on these trapped materials.

*a. Isolated tubes.* Initial sediment motion occurred in the vicinity of isolated tubes at bed-averaged erosion velocities significantly less than those at which "weak"

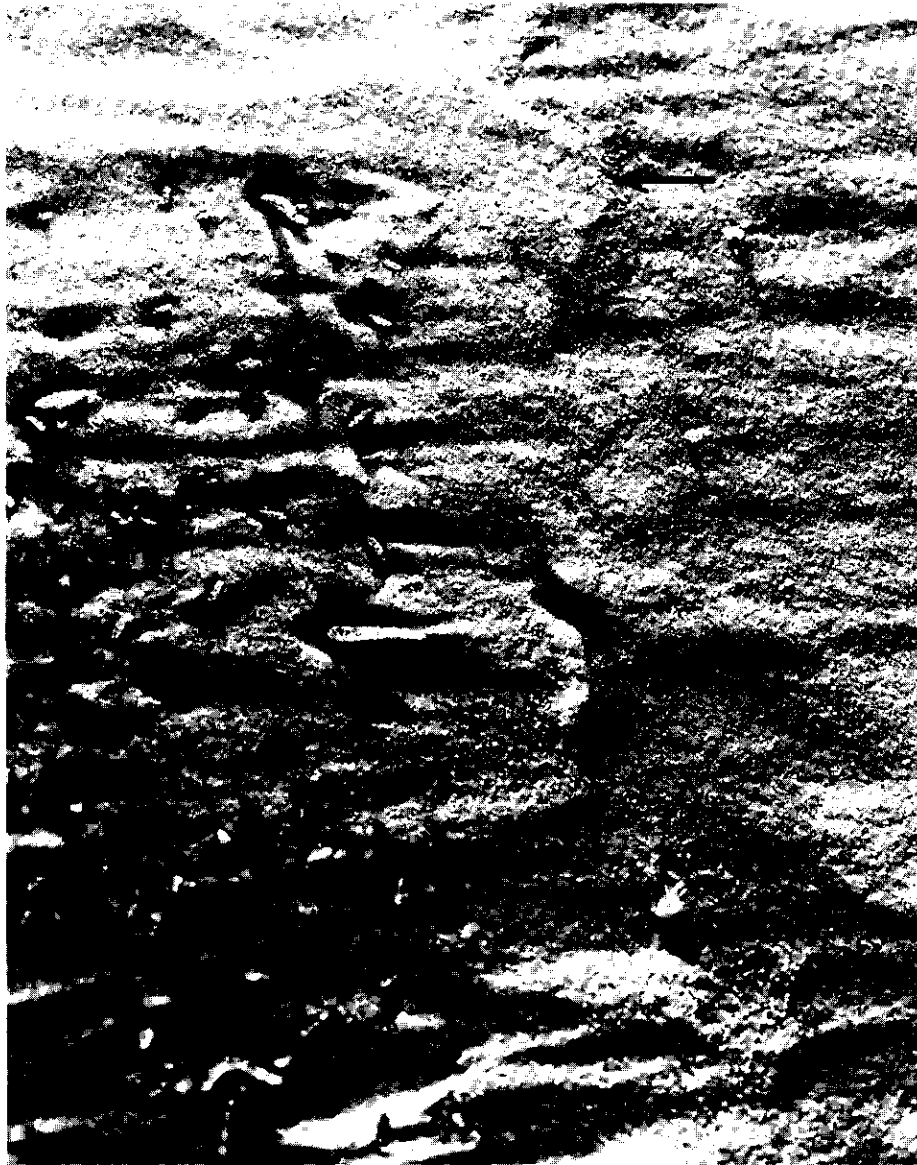


Plate 1B. Sediment grains transported from a bed containing *Owenia* cease moving immediately downstream of tubes and are deposited in a long (cross stream) ridge (note arrows) (flow is from left to right).

transport was noted on the smooth bed (Table 1,  $P \ll 0.001$ ). Local scour was noted always at an average boundary shear stress of less than 25% of the overall critical bed stress. Among all eight isolated individuals tested this local scouring

occurred in one of two manners: (1) grains would occasionally roll from the trailing (downstream) slope of the animal's pit and be advected downstream, and/or (2) an individual would move the tip of its flexible tube near the bed causing locally accelerated near-bed flow and consequent sediment motion. The range of isolated tube effects is limited by the exposed length of an individual's tube. The radii of individual pits created by the eight isolated *Owenia* averaged 5.45 mm ( $\pm 0.76$  mm, 95% confidence limits for the mean).

*b. Varying densities of tubes.* At all densities tested, initial sediment motion was first observed in the vicinity of no more than two to four animals. Initial motion occurred in the same manner as for isolated tubes (above) and at similar boundary shear stresses that varied among experiments from 23% to 33% of critical for the smooth bed (Table 1).

At all densities tested, general bed motion within clusters of tubes occurred at bed-averaged erosion velocities significantly less than that required to transport sediments on the smooth bed (Table 1;  $P \ll 0.001$ , each comparison; see also Plate 1B). This bed destabilization was more pronounced at the highest densities tested, where bed-averaged stresses at general bed motion were 50% to 62% of critical for the smooth bed.

At general bed motion no one experiment exhibited anomalous levels of bed activity (Table 2). For all treatments proportions of bed "active" within any one experiment cannot be distinguished from proportions measured within at least four of the remaining five experiments. The general similarity among treatments in levels of bed activity is not affected by normalization to numerical density (Table 2).

At general bed motion within a cluster of tubes, sediment motion still originated primarily from trailing slopes of animal pits and near tips of tubes venturing close to the bed. However, we also observed sediments being eroded from sections of smooth, flat bed as far as 2.2 cm from the nearest animal. These events were recorded at all densities tested with no obvious differences in frequency of occurrence.

The profiles of streamwise turbulent kinetic energy exhibit a simple monotonic decrease with distance from the wall (Fig. 2). The values have been scaled by  $u_*$ , as this is the velocity scale used in the similarity arguments to derive the logarithmic velocity profile (equation 3). The values near the bed are higher than those reported by Klebanoff (1955), but in close accord with measured values for beds that are in the transitional regime (Schlichting, 1968). At all densities tested, the maximum kinetic energy production and, therefore, the maximum shear stress production occurs at the bed. There is no evidence for skimming flow.

#### 4. Discussion

Figure 1, based on the results of Nowell and Church (1979), suggests that a density of at least 14,500 *Owenia*  $\text{m}^{-2}$  ( $1.45 \text{ cm}^{-2}$ ) would be required to stabilize

Table 2. Observed and normalized areal proportions of the bed "active" estimated for each density. Statistical comparisons of proportions among densities appear at the base of each column: two densities (capital letters) linked by a bar are not significantly different ( $\alpha = 0.05$ , experimentwise). Statistical significance is determined by multiple comparisons based on Kruskal-Wallis rank sums (Miller, 1966, as reported by Hollander and Wolfe, 1973, p. 124).

Tube density (# cm <sup>-2</sup> )	(I)	(II)
	Observed proportion of bed "active"	Normalized proportion of bed "active"*
(A) 0.163	0.0397	0.1690
	0.0056	0.0238
	0.0074	0.0315
	0.0056	0.0238
	0	0
(B) 0.187	0.0018	0.0067
	0	0
	0.0020	0.0074
	0.0012	0.0416
	0.0020	0.0074
(C) 0.504	0.0959	0.1321
	0.2106	0.2900
	0.0209	0.0288
	0.1216	0.1674
	0.0769	0.1059
(D) 0.480	0.0232	0.0335
	0.0598	0.0865
	0.0071	0.0103
	0.0326	0.0471
	0.0676	0.0977
(E) 0.672	0.0281	0.0290
	0.0546	0.0564
	0	0
	0.0460	0.0475
	0.0201	0.0208
(F) 0.694	0.0145	0.0145
	0.0009	0.0009
	0.0038	0.0038
	0.0125	0.0125
	0.0065	0.0065
	<hr/> B F A E D C	<hr/> F B E A D C

\* Values in column (I) are multiplied by a scaling factor to produce expected areas active if a standard *Owenia* density of 0.694 cm<sup>-2</sup> existed in all experiments. Bed activity is assumed to increase in direct proportion to numerical density.

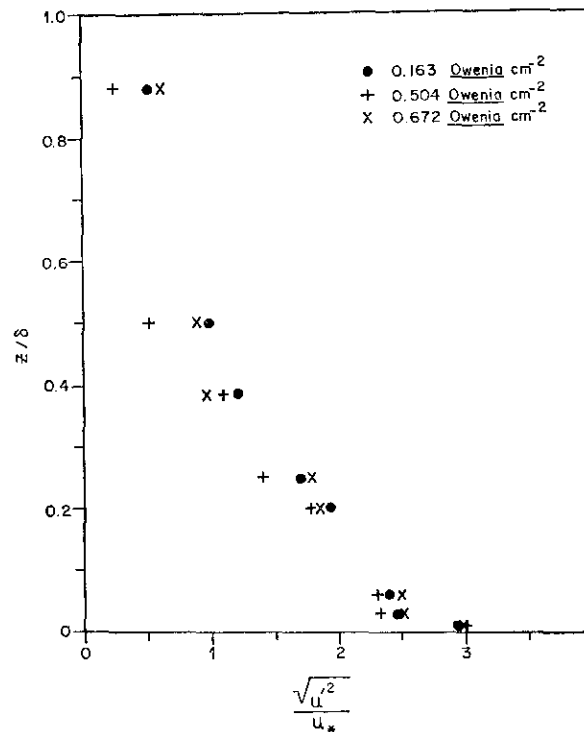
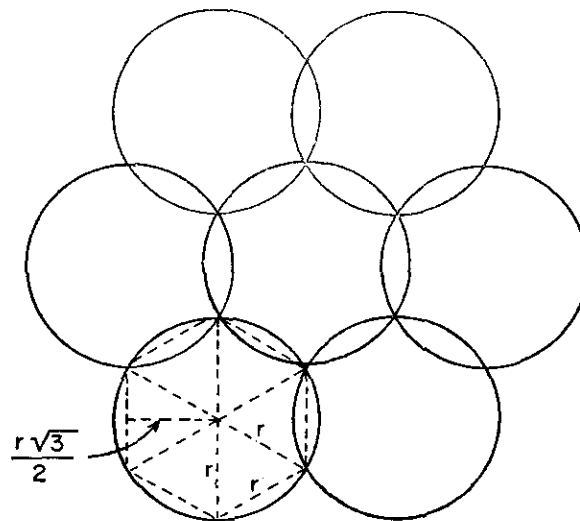


Figure 2. Streamwise turbulent intensity scaled by  $u_*$  (abscissa) plotted against distance from the bed scaled by the flow depth ( $\delta$ ) (ordinate) for three of the six densities tested.

sediments. This estimate assumes, however, that the mean tube diameter of 2.7 mm is the relevant length scale. Three length scales are needed to describe fully the roughness elements on the bed. Hydrodynamically, the frontal area of any bed obstruction is the most important parameter in determining flow resistance. However, numerical densities and tube diameters are often the only data reported from field observations. Figure 1, therefore, is calculated in terms of plan area. For *Owenia*, variations in tube heights, tube flexibility, and the presence of topographically complex scour pits make strict applicability of this density-tube diameter relationship less certain.

Our experiments enable us to estimate crudely a density below which sediment destabilization must occur. At all tube densities tested, initial sediment motion was the result of a local tube effect. Impingement on the bed of eddies shed from leading edges of pits or from erect tubes may induce sediment motion. Sediment grains frequently were transported from trailing slopes of pits where such impingement (flow reattachment) occurs. Sediment stabilization by animal tubes is possible only if such eddy impingement is prevented. Experiments on isolated *Owenia* and their attendant pits show that an individual's area of influence is approximately the size of its



$$A_{\text{hex}} = \frac{6r^2\sqrt{3}}{4}$$

$$(r = 0.545 \text{ cm})$$

$$A_{\text{hex}} = 0.7717 \text{ cm}^2$$

$$\text{TUBE DENSITY} = (A_{\text{hex}})^{-1} = 1.30 \text{ cm}^{-2}$$

Figure 3. The minimum hexagonal packing of evenly spaced, circular feeding pits that completely covers the bed. Tube density is the inverse of the unique hexagonal area. For *Owenia* pits of average radius 5.45 mm, a density of  $1.30 \text{ cm}^{-2}$  is obtained. Random spacing of individuals, as employed in our experiments, would increase the average density required to completely cover the bed.

scoured pit (see Results). We estimate that some eddy impingement must occur at densities below  $1.30 \text{ Owenia cm}^{-2}$  (Fig. 3), although we cannot predict with this method at what higher density eddy impingement would be prevented effectively and sediments would be stabilized.

By either estimate, however, densities of *Owenia* created in our experiments were well within the range expected to be destabilizing. The bed was strongly destabilized at all densities of tubes tested (Table 1), and this destabilization was more pronounced at the higher densities. At all densities tested, non-dimensionalized profiles of streamwise turbulent kinetic energy indicate the monotonic decrease in turbulent kinetic energy with distance from the bed expected for non-skimming flow (Fig. 2).

In his study of a shallow subtidal bed of *Owenia* off La Jolla, California, Fager (1964) noted that "In contrast to the surrounding sand there were no ripples in the sand where the animals were situated . . .". Fager estimated the average density of *Owenia* in this stable bed to be  $500\text{-}1000 \text{ worms m}^{-2}$  ( $0.05\text{-}0.10 \text{ cm}^{-2}$ ), although

densities reached a maximum of  $1.0\text{--}1.5\text{ cm}^{-2}$  near the seaward edge of the patch. All of the *Owenia* densities tested in our experiments (excluding experiments on isolated individuals), and found to be destabilizing, are well within the range that Fager (1964) associated with a stable bed. We must conclude that the presence of the tubes built by *Owenia* cannot, by itself, explain the bed stability that Fager noted. Fager reported that the tubes of most *Owenia* served as (subsurface) anchors for the anemone *Zaolutus actius* (Hand). The disc and tentacles of adult *Zaolutus* are 1 to 1.5 cm in diameter and, when exposed, may be held 0.5 to 1 cm above the bed (Fager, 1968). However, no information is offered regarding frequency of exposure of these animals. It is not possible to assess the hydrodynamic effects of this species on the sediments.

We suggest, instead, that an alternative process(es), that compensated for the destabilizing influence of the *Owenia* tubes, explains the bed stability that Fager (1964) noted. Production of mucus by bacteria (Webb, 1969; Rhoads *et al.*, 1978), benthic diatoms (Neumann *et al.*, 1970; Holland *et al.*, 1974), filamentous algae (Hommeril and Rioult, 1965; Gebelein, 1969), and seagrasses (Ginsburg and Lowenstam, 1958) may directly bind particles (see also Frankel and Mead, 1973; Frostick and McCave, 1979). By enhancing diffusional fluxes (e.g., Aller, 1980) tubes may well foster microbial growth and promote mucous binding of sediments. Fager (1964) reported the growth of a diatom film in the *Owenia* bed he studied, and he noted that such a film was uncommon elsewhere at similar depths. This film, moreover, is much stronger evidence of reduced sediment transport than is the absence of ripples (cf., Plate 1B). The observed bed stabilization may have been induced by mucus secretion and binding by the diatoms, by omnipresent bacteria, by the *Owenia*, by the commensal anemone *Zaolutus actius* (Hand), or by other unreported or undetected fauna.

Mucous binding may also explain other reported correlations between animal tubes and stabilized sediments. Sanders *et al.* (1962) noted that bed ripples disappeared with the appearance of tube-building deposit feeders. However, they also reported that "... with the disappearance of the rippling marks, the surface of the sediment stabilizes and, concurrently, a golden-brown hue appears on the surface. This coloration is brought about by the presence of benthic diatoms". Their quantitative measurements of sediment chlorophyll concentrations confirm this positive covariation.

Mills (1967) reported a dramatic drop in median grain size after a Barnstable (Massachusetts) flat was colonized by large numbers of tube-building ampeliscid amphipods. However, chlorophyll concentrations increased concurrently, possibly also due to the disappearance of the grazing mud snail *Nassarius obsoletus* (Say).

Similarly, Neumann *et al.* (1970) report that abundant animal tubes impart "... a considerable rigidity to the upper 1 cm of the sediment". However, they also

point out that benthic diatoms, filamentous algae, and animals all produce mucilage that directly binds the calcareous sands they studied.

We do not question the validity of the frequently reported association between the presence of tube-building infauna and stable beds. Neither do we doubt that animal tubes may sometimes reach densities sufficient to stabilize sediments purely by obstruction of near-bed flow. Our results and Figure 1, however, suggest that direct, hydrodynamic stabilization of sediments by tubes is the exception rather than the rule. It is especially difficult in field observational studies to reject or account precisely for the relative contributions of other sources of sediment stability. Additional controlled laboratory experiments and field manipulations to decipher cause from effect clearly are in order. The ability of animal tubes, at observed field densities, to stabilize sediments purely via alteration of near-bed flow has yet to be demonstrated.

*Acknowledgments.* This research was funded by Office of Naval Research Grant No. N00014-80-C-0252 Mod P00001. R. Self and T. Honkalehto assisted greatly in the collection of specimens from the field. We thank Drs. W. Grant and R. Feller; E. Gallagher, R. Self, and G. Taghon for reviewing earlier versions of this manuscript. We thank especially Dr. Eugene Kozloff, Acting Director, and staff of the Friday Harbor Laboratories, University of Washington, for providing us with laboratory facilities and most valuable support. This is contribution No. 1216 from the Department of Oceanography, University of Washington, Seattle, Washington 98195, U.S.A.

#### REFERENCES

- Aller, R. C. 1980. Relationships of tube-dwelling benthos with sediment and overlying water chemistry, in *Marine Benthic Dynamics*, K. R. Tenore and B. C. Coull, eds. Belle W. Baruch Library in Marine Science No. 11, Univ. So. Carolina Press, Columbia, 451 pp.
- Bailey-Brock, J. H. 1979. Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef. *J. Mar. Res.*, 37, 643-656.
- Daro, M. H. and P. Polk. 1973. The autecology of *Polydora ciliata* along the Belgian coast. *Neth. J. Sea Res.*, 6, 130-140.
- Fager, E. W. 1964. Marine sediments: effects of a tube-building polychaete. *Science*, 143, 356-359.
- . 1968. A sand-bottom epifaunal community of invertebrates in shallow water. *Limnol. Oceanogr.*, 13, 448-464.
- Frankel, J. and D. J. Mead. 1973. Mucilagenous matrix of some estuarine sands in Connecticut. *J. Sed. Petrol.*, 43, 1090-1095.
- Frostick, L. E. and I. N. McCave. 1979. Seasonal shifts of sediment within an estuary mediated by algal growth. *Estuar. Coast. Mar. Sci.*, 9, 569-576.
- Gage, J. D. 1977. Structure of the abyssal macrobenthic community in the Rockall Trough, in *Biology of Benthic Organisms*, B. F. Keegan, P. Ó. Céidigh and P. J. S. Boaden, eds. Pergamon Press, Oxford, 630 pp.
- Galtsoff, P. S. 1964. The American Oyster *Crassostrea virginica* Gmelin. U.S. Fishery Bull., Vol. 64, 480 pp.
- Gebelein, C. D. 1969. Distribution, morphology, and accretion rate of recent subtidal algal stromatolites, Bermuda. *J. Sed. Petrol.*, 39, 49-69.

- Ginsburg, R. N. and H. A. Lowenstam. 1958. The influence of marine bottom communities on the depositional environment of sediments. *J. Geol.*, 66, 310-318.
- Holland, A. F., R. G. Zingmark and J. M. Dean. 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. *Mar. Biol.*, 27, 191-196.
- Hollander, M. and D. A. Wolfe. 1973. *Nonparametric Statistical Methods*. John Wiley & Sons, New York, 503 pp.
- Hommeril, P. and M. Rioult. 1965. Étude de la fixation des sédiments meubles par deux algues marines: *Rhodothamniella floridula* (Dillwyn) J. Feldm. et *Microcoleus chthonoplastes* Thur. *Mar. Geol.*, 3, 131-155.
- Klebanoff, P. S. 1955. Characteristics of turbulence in a boundary layer with zero pressure gradient. N.A.C.A. Report 1247.
- McCall, P. L. and J. B. Fisher. 1980. Effects of tubificid oligochaetes on physical and chemical properties of Lake Erie sediments, in *Aquatic Oligochaete Biology*, R. O. Brinkhurst and D. G. Cook, eds. Plenum Press, New York, 529 pp.
- Miller, R. G., Jr. 1966. *Simultaneous Statistical Inference*, McGraw-Hill, New York.
- Mills, E. L. 1967. The biology of an ampeliscid crustacean sibling species pair. *J. Fish. Res. Bd. Can.*, 24, 305-355.
- Morris, H. M. 1955. A new concept of flow in rough conduits. *Trans. Amer. Soc. Civil Eng.*, 120, 373-398.
- Neumann, A. C., C. D. Gebelein and T. P. Scoffin. 1970. The composition, structure and erodibility [sic] of subtidal mats, Abaco, Bahamas. *J. Sed. Petrol.*, 40, 274-297.
- Nowell, A. R. M. and M. Church. 1979. Turbulent flow in a depth-limited boundary layer. *J. Geophys. Res.*, 84, 4816-4824.
- Nowell, A. R. M., P. A. Jumars and J. E. Eckman. 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.* (in press).
- Rhoads, D. C., J. Y. Yingst and W. J. Ullman. 1978. Sea floor stability in Long Island Sound. Part I. Temporal changes in erodibility of fine-grained sediments, in *Estuarine Interactions*, M. L. Wiley, ed. Academic Press, Inc., New York, 603 pp.
- Sanders, H. L., E. M. Goudsmit, E. L. Mills and G. E. Hampson. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.*, 7, 63-79.
- Schlichting, H. 1968. *Boundary Layer Theory*, 6th ed., McGraw-Hill, New York, 747 pp.
- Scoffin, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *J. Sed. Petrol.*, 40, 249-273.
- U.S.W.E.S. 1935. Studies of river bed materials and their movement, with special reference to the lower Mississippi River. Paper 17, U.S. Waterways Exp. Station, Vicksburg, Miss., 115 pp.
- Webb, J. E. 1969. Biologically significant properties of submerged marine sands. *Proc. Roy. Soc. Lond. B*, 174, 355-402.
- Yingst, J. and D. C. Rhoads. 1978. Seafloor stability in central Long Island Sound: Part II: Biological interactions and their potential importance for sea floor erodibility, in *Estuarine Interactions*, M. L. Wiley, ed. Academic Press, Inc., New York, 603 pp.
- Young, D. K. and D. C. Rhoads. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. *Mar. Biol.*, 11, 242-254.
- Young, R. N. and J. B. Southard. 1978. Erosion of fine-grained marine sediments: sea-floor and laboratory experiments. *Geol. Soc. Amer. Bull.*, 85, 663-672.

Received: 3 October, 1980; revised: 10 February, 1981.

Printed in U.S.A. for the Sears Foundation for Marine Research,  
Yale University, New Haven, Connecticut, 06520, U.S.A.  
Van Dyck Printing Company. North Haven, Connecticut, 06473, U.S.A.