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Flow disruption by an animal-tube mimic affects sediment bacterial colonization

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ABSTRACT

Simple flume experiments demonstrate that local flow perturbations by a protruding animal-tube mimic can cause a significant increase in bacterial colonization at the sediment-seawater interface. The occurrence and extent of this increase depend on properties of the viscous sublayer adjoining the bed—specifically, its spatial and temporal continuity, and its thickness relative to tube height. In the field homologous tube effects on bacterial colonization and abundances are likely to be common. These effects are postulated to be important to larval recruitment, community composition, the nutrition of deposit feeders, and sediment dynamics.

1. Introduction

Protruding animal tubes or tests are widespread in soft-substratum marine and estuarine environments (e.g., Fager, 1964; Mills, 1967; Heezen and Hollister, 1971; Jumars, 1975a; Woodin, 1978; Rhoads and Boyer, 1982). Arrays of tubes are known to perturb flow near the sediment-seawater interface sufficiently to affect both sediment erodibility (see summaries in Eckman *et al.*, 1981; Rhoads and Boyer, 1982) and the composition of animal communities inhabiting the surrounding substratum (Bailey-Brock, 1979; Eckman, 1979, 1983). These results have prompted recent quantitative studies of the flow perturbations created by tubes (Carey, 1983; Eckman and Nowell, 1984).

Eckman and Nowell (1984) conducted a detailed study of the transfer of fluid momentum and the spatial distribution of boundary skin friction (local drag force exerted per unit area of bed) about a protruding tube. They noted one effect common to any tube that projects beyond the viscous sublayer into fully turbulent flow; such a structure strongly increases boundary skin friction within a horseshoe-shaped region adjoining its upstream and lateral margin (Fig. 1). This increase in boundary skin friction about the base of a tube derives primarily from the locally enhanced downward transport of higher momentum fluid toward the bed and subsequent formation of a highly rotational horseshoe vortex (see Eckman and Nowell, 1984, Fig. 1). This

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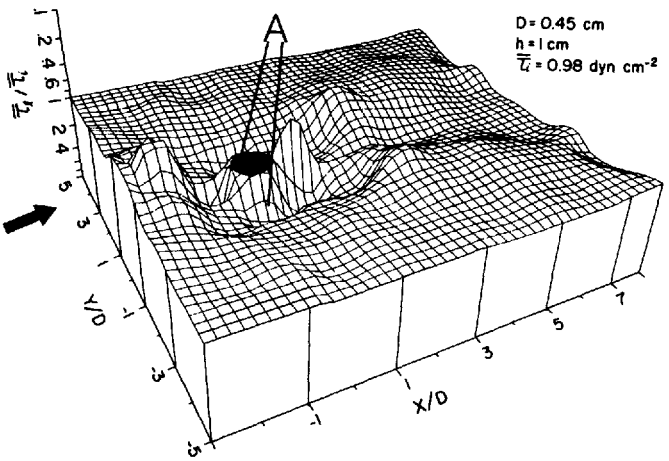

Figure 1. Distribution of skin friction (τ_1), normalized to the imposed shear stress (τ_i = 0.98 dyn cm^{-2}), about a tube mimic (solid circle) of 0.45 cm diameter and 1 cm height, as described in Eckman and Nowell (1984). Flow direction is indicated by the arrow. The figure is scaled to cylinder diameter in the horizontal plane. A horseshoe-shaped region of increased skin friction (indicated by a depression in the surface) occurs immediately upstream and lateral to the tube's margin, and trails several diameters downstream. Nitex® squares were placed at location A.

penetration of higher momentum and highly rotational fluid close to the boundary causes a local thinning of the viscous and diffusional sublayers adjoining the bed (e.g., Schlichting, 1979, pp. 603–604, 612–613). Thus, mass exchange between the overlying water and sediments may be expected to be enhanced in the vicinity of a tube.

This fluid-dynamic effect of a tube may influence microbial colonization and population growth locally. Jumars and Nowell (1984) predict that turbulent-advective and diffusional fluxes of solutes (or microbial recruits) from and to seawater in motion over a stationary boundary will determine rates of benthic microbial growth and attachment *in situ* (see also Characklis, 1981). Some empirical evidence exists to support this prediction (Pedersen, 1982).

Because of the widespread occurrence of tubes in soft-sediment environments, and the strong importance of microflora and bacteria to the ecology of benthic communities and to sediment dynamics, these potential flow-microbe links deserve careful investigation. This report describes initial experiments designed to assess the impact of flow disruption by a protruding tube on bacterial colonization at the sediment-seawater interface. Attention was focused on the horseshoe-shaped region of increased boundary skin friction (Fig. 1) that exists adjacent to any tube projecting into turbulent regions of the boundary layer. Bacterial colonization within this near-tube region and within nearby control areas experiencing no tube effects was compared at several values of imposed shear velocity and at different levels of bed roughness. These two parameters

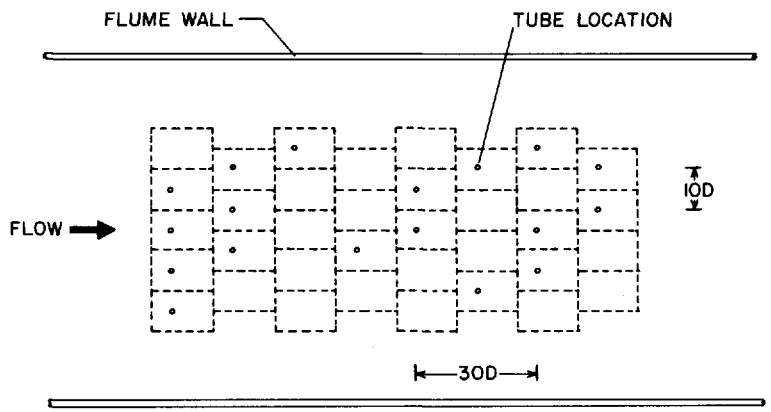

Figure 2. Schematic representation of experimental layout. Thirty-six contiguous 6 cm × 9 cm subareas (defined and relocated non-invasively) were established within the 50 cm-wide flume. Randomly chosen locations of tube mimics are shown for the high shear-smooth bed experiment. Nearest tube neighbors always were separated by at least 10 diameters (10 D) directly cross-stream and 30 diameters (30 D) directly downstream.

determine properties of the viscous and diffusional sublayers (e.g., Schlichting, 1979, pp. 603–604, 612–613) that may limit fluxes of critical solutes or microbial recruits (cf. Jumars and Nowell, 1984).

2. Methods

All experiments were conducted in a 2.5 m-long × 50 cm-wide seawater flume described in detail by Nowell *et al.* (1981). Tripping devices (5 mm height) spanned the width of the flume at the entrance. Work was confined to a region ranging from 1.2–1.8 m downstream of the flume entrance, and within 15 cm of the flume centerline. Flow depths varied from 4.5–5.0 cm. From equations describing growth of a turbulent boundary layer on a smooth, flat plate (Schlichting, 1979, p. 638) it was calculated that in all cases studied (below) flow was fully developed (i.e., uniform in both the longstream and cross-stream directions) within this working area. These calculations were confirmed empirically by velocity profiles made with a hot-film probe (Thermo Systems, Inc. model 1231W); the flow was always fully turbulent and no systematic variations in velocity profiles were noted within this working area.

Thirty-six contiguous 6 cm × 9 cm subareas were defined within the working area (Fig. 2). In each experiment, half of these subareas were selected at random to receive a single tube mimic (plastic cylinder: 6 mm in diameter, 1 cm in height); the other half were used as no-tube controls. Inert tube mimics were used to produce approximately the flow disruption of a protruding animal tube but to preclude attendant biological effects of the tube dweller that might simultaneously affect microbial colonization and population growth (e.g., respiratory pumping and mucous secretion). Each tube mimic

was separated from its nearest neighbor by at least 10 tube diameters cross-stream (Fig. 2); the nearest mimic directly downstream was at least 30 tube diameters distant. This separation ensured that each tube existed essentially in isolation (i.e., flow was not characterized by significant tube-interaction effects—cf., Paola, 1983; Eckman and Nowell, 1984).

Four separate bacterial colonization experiments were performed. In three of these experiments, a thin (≈2 mm), smooth bed of sieved, oxic, marine sand (61 μm < D < 210 μm, taken from False Bay, San Juan Island, Washington) was deposited in the flume before tube mimics were set in place. Natural marine sand was used to provide a potential source population of bacteria for colonization in addition to bacteria occurring naturally in the seawater system. The three smooth-bed experiments differed in the rate of flume discharge (i.e., in shear velocity imposed). A roughened bed was created in the fourth experiment. Roughness was established by depositing a layer of gravel (1 mm < D < 4 mm) on the flume bed prior to deposition of the natural marine sand. The rough-bed experiment was run at the same flume discharge that characterized the high shear-smooth bed experiment.

In all experiments bacterial colonization was monitored on a series of 5 mm × 5 mm squares of initially sterile (autoclaved) Nitex® mesh (350 μm mesh size). Sterilized Nitex® squares were placed flush with the sediment-seawater interface either immediately adjacent to a tube mimic's lateral face (Fig. 1, region A), or at an equivalent location within subareas designated as no-tube controls. Thus, each square was either confined to the horseshoe-shaped region of increased skin friction about a tube mimic (Fig. 1), or was far removed from a tube's flow disruption (no-tube control subareas). Autoclaved Nitex® was chosen as a substratum for colonization because: (1) it is placed flush with the sediment-seawater interface and subsequently sampled with minimal disturbance, (2) it is porous and thus permits exchange between the natural sand bed and the overlying seawater, and (3) it offers a substratum for colonization that is identical among treatments, times and replicates. It thus eliminates much of the extreme heterogeneity characterizing natural sediment particles at bacterial scales (e.g., Weise and Rheinheimer, 1978). As a consequence the counting variance is minimized (see below) and a more powerful statistical test of the influence of flow perturbation on bacterial colonization at the sediment-seawater interface is realized. It should be noted, however, that due to differences in their surface properties (e.g., wettability), absolute rates of bacterial colonization on Nitex® mesh and on natural sediment particles would be expected to differ (e.g., Dexter *et al.*, 1975).

In the first experiment (low shear-smooth bed) Nitex® squares were sampled from eight subareas (chosen in a stratified random scheme to select 4 tube and 4 no-tube squares) 24, 48, 72 and 96 hours after their immersion. This sampling scheme was altered in the three subsequent experiments in order to increase sample coverage of the initial colonization period. In these three experiments, Nitex® squares were sampled from twelve subareas (stratified random selection: 6 tube, 6 no-tube squares) approxi-

mately 10, 20 and 30 hours after immersion. In all experiments the sampled Nitex® squares were placed immediately in a filter-sterilized (0.22 μm) solution of 2% formaldehyde in seawater. Bacteria directly attached to Nitex threads were enumerated within 6 days by acridine orange direct counts. For each Nitex® square sampled, bacteria were counted within 32–40 haphazardly located 924 μm^2 grids. At the high magnification employed (1250×) the threads appeared as broad, two-dimensional surfaces. Counts were made always on the upper surface of the mesh (i.e., the face exposed to moving seawater) and uniformly on sections of thread far removed from thread junctions.

From subsequent counts of the fixing solution it was estimated that approximately 10% of the bacteria detached from Nitex® threads during fixation, storage (in the dark at 4°C), staining and slide preparation. Since the permanent attachment of marine bacteria to a substratum is known to involve biosynthesis of a sticky exopolymer network (e.g., Marshall *et al.*, 1971; Fletcher and Floodgate, 1973; Costerton *et al.*, 1978) it is likely that these detached cells included only those which were reversibly adsorbed onto threads at the time of sampling (including passively adsorbed dead cells). Only bacterial cells counted on Nitex® threads were included in statistical analyses.

Bacterial abundance data were analyzed using a mixed model, nested analysis of variance. Log-transformed counts (to homogenize variances) were fit to the model:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + C_{ijk} + \epsilon_{ijkl},$$

where Y_{ijkl} = log-transformed bacterial count per 924 μm^2 grid; μ = grand mean; α_i = fixed treatment (tube/no-tube) effect; β_j = fixed time effect; $(\alpha\beta)_{ij}$ = fixed treatment-time interaction effect; C_{ijk} = random Nitex®-square (replicate) effect nested within treatment i and time j; and ϵ_{ijkl} = independent, normally distributed "error" term. The significance of each coefficient (i.e., significance of tube/no-tube [α], time [β], tube-time interaction [$\alpha\beta$], and nested replicate [C] effects) was assessed using BMDP program BMDP3V (Jennrich and Sampson, 1981).

3. Results

a. Low shear-smooth bed experiment. The condition of the boundary layer near the sediment-seawater interface is characterized by the roughness Reynolds number (Re_*), defined as

$$Re_* = \frac{u_* k_s}{\nu},$$

where u_* = imposed shear velocity; k_s = scale of particles governing bed roughness (here, grain size); and ν = kinematic viscosity of seawater. The low shear velocity (u_* = 0.12 cm s^{-1}, estimated from velocity profiles measured within the viscous

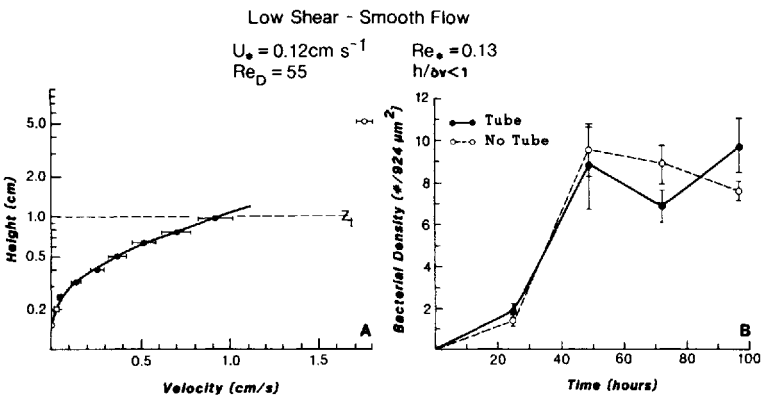

Figure 3. Results of the low shear-smooth bed experiment. Re_D refers to the cylinder Reynolds number of the tube mimic, calculated using velocity measured at its tip (z_t = 1 cm). h/δ_v defines the ratio of tube-mimic height (h) to viscous-sublayer thickness (δ_v). The spatially averaged velocity profile is shown in (A). The concave shape of the profile extending at least to z_t = 1 cm (tube height) is characteristic of the viscous sublayer. u_* was calculated from values indicated by filled circles. Bacterial colonization is summarized in (B). Circles indicate grand means of bacterial abundance within each treatment-time locus. As one indicator of variance among replicates, "error bars" show one standard error of the 4 replicate means.

sublayer) and smooth sand bed (average $k_s \approx 150$ μm) in this experiment produce an $Re_* = 0.13$, well within the range of values characterizing hydraulically smooth flow (Schlichting, 1979, pp. 616–617). Thus, the sediment-seawater interface was immersed within a continuous viscous sublayer (a region adjoining the boundary wherein fluid motions become governed by viscous damping; within the viscous sublayer viscous shear stresses dominate over turbulent shear stresses). The spatially averaged (semi-log) profile of fluid velocity (Fig. 3A), measured using a hot-film anemometer, clearly exhibits the concave shape characteristic of the viscous sublayer (Clauser, 1956; Grant *et al.*, 1982; Chriss and Caldwell, 1984) to a height of at least 1 cm. Thus, in this experiment the 1 cm-high tube mimics were immersed within the viscous sublayer ($h/\delta_v < 1$).

Figure 3B shows patterns in bacterial colonization. For Nitex® squares both adjacent to and distant from tube mimics, early colonization proceeded at a seemingly exponential rate. Bacterial abundances on squares reached an asymptotic limit within 45 hours of their immersion. Analysis of variance (Table 1) indicates that there was no demonstrable difference in bacterial abundances between tube and no-tube treatments ($P = 0.160$). There was a strong time effect ($P < 0.0005$), and there was significant variation among replicate squares sampled within each treatment-time locus ($P < 0.0005$).

b. Intermediate shear-smooth bed experiment. At the shear velocity characterizing this experiment ($u_* = 0.85$ cm s^{-1}, estimated from velocity profiles measured within

Table 1. Results of mixed model, nested ANOVA's. The level of variation termed *Treatment* refers to tube/no-tube effects. Replicate squares are nested within the higher levels of *Treatment* and *Time*.

Level of Variation	χ^2	d.f.	P
Low Shear-Smooth Bed			
Treatment	1.979	1	0.160
Time	56.779	2	<0.0005
Treatment × Time	2.189	2	0.335
Replicate Square	14.770	1	<0.0005
Intermediate Shear-Smooth Bed			
Treatment	18.734	1	<0.0005
Time	47.081	2	<0.0005
Treatment × Time	0.835	2	0.659
Replicate Square	26.583	1	<0.0005
High Shear-Smooth Bed			
Treatment	31.958	1	<0.0005
Time	64.317	2	<0.0005
Treatment × Time	0.539	2	0.764
Replicate Square	16.428	1	<0.0005
High Shear-Rough Bed			
Treatment	1.619	1	0.203
Time	3.402	2	0.183
Treatment × Time	0.918	2	0.632
Replicate Square	108.80	1	<0.0005

the logarithmic layer) $Re_* = 0.95$. This value indicates a hydraulically smooth flow (Schlichting, 1979); the sediment-seawater interface again was immersed within a continuous viscous sublayer. However, at heights exceeding 0.25 cm spatially averaged velocities exhibit the linear profile (Fig. 4A) characterizing the turbulent logarithmic layer (Clauser, 1956; Grant *et al.*, 1982; Chriss and Caldwell, 1984). Thus, in this experiment tube mimics extended through the thinner viscous sublayer into the higher velocity and fully turbulent flow characterizing the logarithmic layer ($h/\delta_\nu \approx 5$).

Figure 4B and Table 1 reveal a highly significant treatment effect ($P < 0.0005$). At all times mean bacterial abundances on squares adjacent to tube mimics were approximately twice (range: 1.8–2.7) mean abundances on no-tube control squares. Table 1 also indicates that significant variation occurred among replicate squares sampled within each treatment-time locus ($P < 0.0005$).

c. High shear-smooth bed experiment. The roughness Reynolds number ($Re_* = 1.2$) indicates that the viscous sublayer again was continuous and was thinner than in the intermediate shear-smooth bed experiment (Schlichting, 1979). The spatially averaged velocity profile (Fig. 5A) indicates that the logarithmic layer penetrated to less

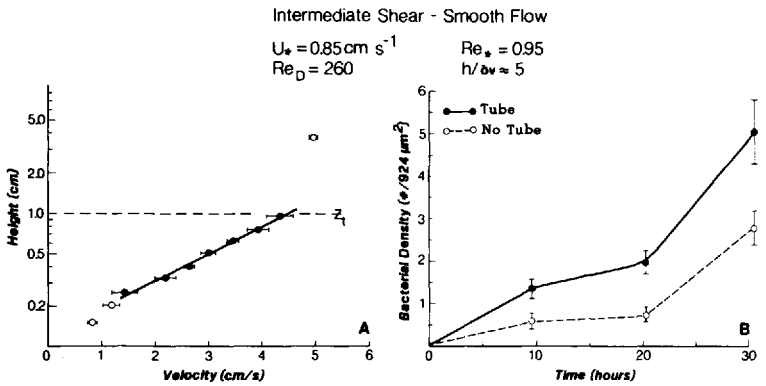

Figure 4. Results of the intermediate shear-smooth bed experiment. Interpretation as in Figure 3. (A) The linear velocity profile beginning approximately at $z = 0.25$ cm is characteristic of the logarithmic layer. (B) "Error bars" show one standard error of the 6 replicate means.

than 0.2 cm above the bed; the 1 cm-high tube mimics again extended into the fully turbulent logarithmic layer ($h/\delta_v \approx 7$). A comparison of Figures 4A and 5A indicates that, in this experiment, tube mimics were exposed to a higher mean velocity than in the intermediate shear-smooth bed experiment.

The treatment effect was highly significant ($P < 0.0005$, Table 1). After 9.0 hours, mean bacterial abundances on squares adjacent to the tube mimics were 4.0 times greater than abundances on no-tube control squares (Fig. 5B). This ratio decreased monotonically to 1.9 by 29.7 hours. There was significant variation among replicate squares sampled at each treatment-time locus ($P < 0.0005$, Table 1).

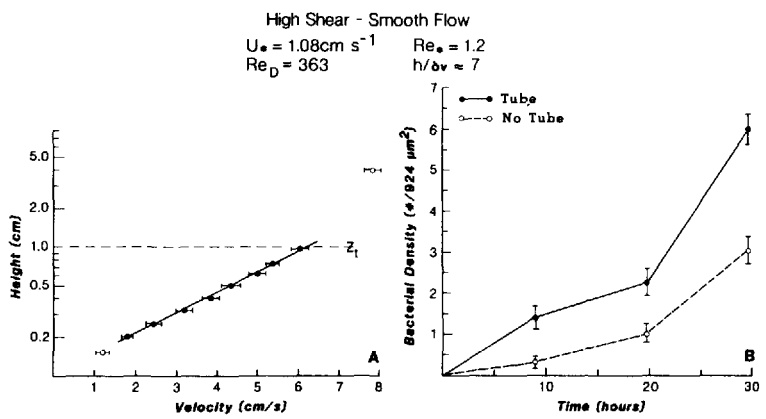

Figure 5. Results of the high shear-smooth bed experiment. Interpretation as in Figure 3. (A) The logarithmic layer begins at $z \leq 0.2$ cm. (B) "Error bars" show one standard error of the 6 replicate means.

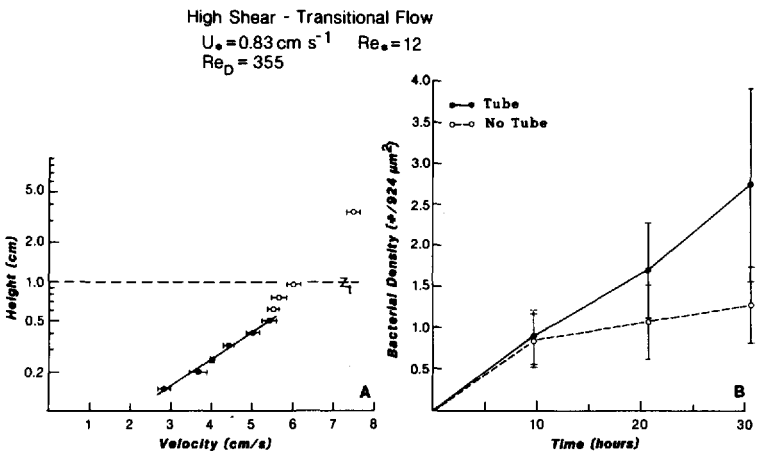

Figure 6. Results of the high shear-roughened bed experiment. Interpretation as in Figure 3. (A) The logarithmic layer begins at $z \leq 0.1$ cm. (B) "Error bars" show one standard error of the 6 replicate means.

d. High shear-rough bed experiment. The scale of the gravel underlayer determines the roughness Reynolds number. Its value ($Re_* = 12$) reveals that flow was hydraulically transitional indicating that the viscous sublayer was spatially and temporally discontinuous (Schlichting, 1979). Tube mimics were exposed always to higher velocity, fully turbulent flow (Fig. 6A).

This increased heterogeneity of the sediment-seawater interface produced highly significant differences among replicate squares sampled within each treatment-time locus (note the large χ^2 value in Table 1; note also the relative magnitudes of "error bars" in Figure 6B vs. Figures 3B–5B). Squares adjacent to tube mimics tended to contain higher mean bacterial abundances beyond 10 hours immersion, and exhibited an apparent higher rate of increase (Fig. 6B). However, the large variance in abundances at any treatment-time locus rendered both time ($P = 0.183$) and treatment ($P = 0.203$) effects undetectable statistically (Table 1).

4. Discussion

These simple experiments show that local flow disruption by a tube mimic may increase bacterial colonization at the sediment-seawater interface. Under conditions of hydraulically smooth flow at the intermediate and high shear velocities sterile Nitex® squares placed adjacent to tube mimics accumulated significantly greater numbers of bacteria (2–4×, $P < 0.0005$) than did no-tube control squares (Table 1; Figs. 4B, 5B). The similar patterns of bacterial colonization observed in these two experiments may be explained by the roughly concordant boundary conditions established. Velocity profiles (Figs. 4A and 5A) and the similar values of Re_* and (h/δ_v) indicate that, in

both experiments, tube mimics projected through a viscous sublayer that otherwise completely overspread the sediment-seawater interface. The significant enhancement in bacterial numbers observed about tube mimics is unquestionably related to this boundary condition. Eckman and Nowell (1984) show that a tube projecting beyond the viscous sublayer deflects turbulent, higher momentum fluid toward the bed and increases skin friction immediately adjacent to the tube's margin (Fig. 1). This fluid-dynamic effect can be expected to enhance vertical mass transfer locally. The increase in bacterial colonization demonstrated within this region suggests that a protruding tube may perturb flow sufficiently to enhance a bacterial colonization process in some manner limited by diffusional flux(es) through the viscous and diffusional sublayers to or from seawater overlying the bed.

This suggestion of diffusion-limited colonization is supported by results of the high shear-rough bed experiment. In this experiment the gravel-sized roughness of the sediment-seawater interface was sufficient to disrupt the viscous sublayer episodically in both space and time (as indicated by $5 < Re_* < 70$; Schlichting, 1979), exposing the bed to episodic impingement by turbulent eddies. At microbial scales strong local gradients in fluid-momentum and mass transfers would have been produced by the topographic complexity of the gravel bed. This spatial heterogeneity in vertical fluxes at scales relevant to bacteria likely was responsible for the relatively great variance in counts observed among replicate squares (note relative magnitude of "error bars" in Fig. 6B vs. Figs. 3B–5B). This increased variance was sufficient to render both time and treatment effects statistically undetectable (Table 1). Moreover, the episodic impingement of turbulent eddies on the boundary likely lessened the relative impact of tube-induced flow perturbations on bacterial colonization.

Unfortunately, it is not possible to compare absolute colonization rates or absolute bacterial abundances *among* experiments. At all times the flume utilized fresh (nonrecirculating) seawater. Consequently, external conditions likely to affect rates of colonization, including concentrations of suspended bacteria, dissolved nutrients, etc., potentially varied among experiments. The experimental and statistical design accounts completely only for *within*-experiment variability; thus, comparisons among experiments must be confined to discussion only of differences in patterns of colonization noted within experiments.

Results of these four experiments suggest that enhancement of bacterial colonization about protruding tubes may occur commonly in many marine environments. Tubes and tests often will extend into the turbulent logarithmic layer that begins within a few millimeters to ≈ 1 cm above even an hydraulically smooth boundary (cf., Komar, 1976). Despite the presence of ubiquitous small-scale roughness (e.g., fecal castings, tracks), a spatially and temporally continuous viscous sublayer may overlie the sediment-seawater interface in widespread marine environments. For example, Caldwell and Chriss (1979) and Chriss and Caldwell (1984) present highly detailed *in situ* measurements of an outer shelf boundary layer (199 m depth, maximum $u_* =$

0.48 cm s^{-1}, no larger bedforms) that confirm an hydraulically smooth flow. This condition is certain to exist in deeper waters where shear velocities typically are much lower than those on the shelf (e.g., Komar, 1976; Wimbush, 1976; Hayes, 1979) and, consequently, where the pervasive roughness features characterizing the sediment-seawater interface must exceed 0.5–1 cm in scale in order to disrupt the viscous sublayer (i.e., produce $Re_* > 5$).

One might suggest that the potential impact of flow disruption by tubes on bacterial colonization would be lessened in higher energy marine boundary layers (e.g., in some shallower water environments). In regions characterized by a relatively high imposed shear velocity ($u_* \gg 1$ cm s^{-1}) the increased skin friction about the base of a tube may induce sediment scour (Eckman *et al.*, 1981; Eckman and Nowell, 1984). Such erosive events would quickly destroy any local enhancements of microbial populations. Moreover, a spatially and temporally continuous viscous sublayer is unlikely to exist in regions where larger bedforms (e.g., transverse ripples) persist due to periodic or episodic sediment transport events. In addition, short-period oscillatory flows (e.g., caused by passage of gravity waves) decrease boundary layer thickness substantially (Grant and Madsen, 1979; Grant *et al.*, 1984) and likely would lessen the degree of diffusional limitation of bacterial colonization.

Nevertheless, field evidence indicates that these caveats cannot be used to dismiss structure-induced flow perturbations as unimportant to bacterial colonization in shallow-water environments. Thistle *et al.* (1984) have shown that at 1 m depth in the Gulf of Mexico sediments about isolated seagrass (*Syringodium*) shoots and about inert shoot mimics both contain roughly doubled bacterial biomass and increased bacterial growth potential relative to unvegetated sediments nearby. They attribute these increases to a flow-perturbation effect of the shoot structure.

Although tube mimics used in the present experiments were widely spaced, the results can be applied similarly to appropriate field situations ($Re_* < 5$, $h/\delta_v > 1$) where tubes exist in denser arrays. Despite wake-interaction effects at closer structure spacings (e.g., Nowell and Church, 1979; Brayshaw *et al.*, 1983; Paola, 1983), the horseshoe-shaped region of increased skin friction adjacent to a tube will in most cases persist; it derives from a strong and essentially independent pressure gradient established along the tube's upstream face (Eckman and Nowell, 1984). This pressure gradient can be expected to exist in similar form so long as tubes are not so densely packed as to establish a "skimming flow" (*sensu* Morris, 1955; see also Eckman *et al.*, 1981, Fig. 1). As an estimate, flow perturbations about bases of tubes in the field can be expected to be qualitatively similar to those established in this study so long as the tubes occupy less than 1/16 of the bed in plan area (equivalent to strong "wake-interaction" flow discerned by Nowell and Church, 1979). Appropriately "low" densities of tubes are common *in situ* (e.g., Eckman *et al.*, 1981, Fig. 1).

These experimental results have important ecological implications. In the field increased microbial abundances about tubes may significantly influence recruitment.

Settling larvae, dispersing juveniles and adults of many species are known to respond positively to the presence of bacteria on substrata (Wilson, 1955; Gray, 1974; Kirchman *et al.*, 1982). In light of results reported herein, such responses could help explain the enhanced recruitment observed about individual tubes and tube mimics *in situ* (Eckman, 1979; Gallagher *et al.*, 1983) as well as the increased macrofaunal and meiofaunal abundances commonly noted among tube arrays (e.g., Sanders *et al.*, 1962; Jumars, 1975b; Woodin, 1978, 1981; Thistle, 1979).

Feeding and growth of deposit feeders also may be influenced by a local increase in microbial colonization about tubes. Benthic microbes are known to be an important food resource for many deposit feeders (e.g., Newell, 1965; Fenchel, 1970; Lopez and Levinton, 1978; Levinton and Bianchi, 1981). Levinton and Lopez (1977) present a model that identifies microbial renewal (= colonization) as a key process potentially limiting deposit-feeder growth. More recently, Miller *et al.* (1984) analyzed the suite of variables likely to affect microbial abundances on sediment particles. They show that rates of *in situ* regeneration are likely to significantly affect microbial abundances only at relatively low rates of particle advection (i.e., horizontal sediment transport). Thus, it is possible that in environments where the rate of advection of "new" organic material is low, an increased colonization (regeneration) of bacteria about tubes may benefit feeding and growth of resident surface deposit feeders.

Results of these experiments also have important sedimentological implications. In the field, sediments among tube arrays commonly are more resistant to erosion, despite the hydrodynamically destabilizing flow perturbations often caused by the tubes (Eckman *et al.*, 1981). The increased bacterial colonization about tube mimics demonstrated herein supports Eckman *et al.*'s suggestion that this apparent contradiction may be explained by increased microbial abundances among tube arrays, with a resultant increased mucous binding of sediments.

Clearly, the likelihood that flow perturbation causes increased bacterial (and possibly microfloral) colonization and standing stocks about tubes *in situ* is potentially of great importance. Careful field studies and additional laboratory experiments both are demanded in order to assess the extent of these effects. Such studies need to address a suite of important questions, including:

(1) To what extent is the tube-induced enhancement in bacterial (or microfloral) colonization and abundances compromised by the presence of larger bedforms and the occurrence of high-frequency oscillatory flows common in many shallow-water environments? Is the detectability of such enhancement effects dependent upon the frequency of sediment transport events? To what vertical depths in the sediments are flow-induced enhancement effects detectable?

(2) How do *in situ* patterns of microbial colonization and standing stock relate to other known patterns of flow about a tube? In a tube's complex wake region are colonization rates and abundances dependent upon tube height—specifically, the height-governed capacity to induce either particulate deposition or scour (cf., Eckman and Nowell, 1984)?

(3) To what extent do wake-interaction effects (cf., Nowell and Church, 1979; Brayshaw *et al.*, 1983; Paola, 1983) characterizing flow among structures within denser arrays alter the basic pattern of bacterial colonization noted about a relatively isolated structure?

(4) To what extent are flow-perturbation effects of microbial colonization and abundances augmented by (or countered by) activities of the tube-dwelling organism? For example, does respiratory pumping affect microbiota via its effects on pore-water fluxes (cf., Aller, 1980; Aller *et al.*, 1983), and how do such disparate effects compare in magnitude?

This study has documented an important effect of a common flow perturbation on benthic bacterial colonization—measured as the temporal pattern of increasing bacterial abundances. Bacterial abundances have both ecological and sedimentological relevance, as standing stock will be pertinent to recruitment of larvae that key on bacterial cues, to bacterivore nutrition, and to the degree of mucous binding of sediments. Colonization, however, is a process that reflects the sum of bacterial growth, attachment and detachment processes (Caldwell *et al.*, 1981, 1983). Determining, separately, the dependence of growth, attachment and detachment rates on vertical flux to and from seawater overlying the boundary (and, therefore, on flow perturbation) represents an important topic in benthic microbial ecology. However, it is unclear whether methods proposed for their measurement, based on observed frequencies of dividing cells (e.g., Newell and Christian, 1981; Caldwell *et al.*, 1983; Malone and Caldwell, 1983), may be applied accurately to marine benthic bacteria (Newell and Fallon, 1982; Fallon *et al.*, 1983). Such questions may perhaps be addressed via measurement of thymidine uptake (Fuhrman and Azam, 1982) or via relatively sophisticated biochemical estimates of physiological status (White *et al.*, 1979; Findlay and White, 1983; see also Thistle *et al.*, 1984).

5. Conclusions

Flow perturbations created by an animal-tube mimic protruding above an hydraulically smooth bed cause a significant increase in bacterial colonization at the sediment-seawater interface. Boundary conditions necessary to produce an enhancement of bacterial colonization about tubes *in situ* are likely to occur in widespread marine and estuarine, soft-sediment environments. This effect is not likely to be altered significantly by flow-interaction among tubes at most field densities encountered. Based on results of previous studies it is postulated that increased microbial colonization and abundances about a tube may be significant to the nutrition of resident surface-deposit feeders, and may serve as an attracting cue to settling larvae and/or other motile, deposit-feeding fauna in the community. Active responses to such a microbial cue may help explain the increased macrofaunal and meiofaunal abundances often noted among tubes. Increased microbial abundances about a tube also may explain the seemingly paradoxical association of "stabilized" sediments with structures known to

increase local drag exerted on the boundary (cf., Eckman *et al.*, 1981). Because of these potentially important ecological and sedimentological consequences, extensive field and laboratory studies are demanded in order to determine the importance of flow perturbation to microbial colonization and abundances *in situ*.

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