North America Geology) scale. The palynological data are from the sources cited in (*11*) and (*17*), as interpreted here, except for new data (A. Traverse, unpublished) on the Culpeper and South Georgia basins. It should also be noted that Ediger (*7*) states that the oldest sediments of the Richmond-Taylorsville basins are of late Ladinian age. If this is correct, the oldest sediments of the Deep River Basin would also be Ladinian, as they contain similar palynofloras.
19. The shale samples studied were all prepared by HF maceration, $ZnCl_2$ solution (specific gravity 2.2) gravity separation, and Schulze's mixture (1:1) oxidation.
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Swept Away: Resuspension of Bacterial Mats Regulates Benthic-Pelagic Exchange of Sulfur

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Filaments and extracellular material from colorless sulfur bacteria (*Beggiatoa* spp.) form extensive white sulfur mats on surface sediments of coastal, oceanic, and even deep-sea environments. These chemoautotrophic bacteria oxidize soluble reduced sulfur compounds and deposit elemental sulfur, enriching the sulfur content of surface sediment fivefold over that of deeper sediments. Laboratory flume experiments with *Beggiatoa* mats from an intertidal sandflat (Nova Scotia) demonstrated that even slight erosion of sediment causes a flux of 160 millimoles of sulfur per square meter per hour, two orders of magnitude greater than the flux produced by sulfur transformations involving either sulfate reduction or sulfide oxidation by benthic bacteria. These experiments indicate that resuspension of sulfur bacterial mats by waves and currents is a rapid mechanism by which sediment sulfur is recycled to the water column. Benthic communities thus lose an important storage intermediate for reduced sulfur as well as a high-quality bacterial food source for benthic grazers.

MICROBIAL MATS CONSISTING OF various sulfur bacteria are ubiquitous in marine intertidal and subtidal sediments and have gained recent attention as the base of the food web at deep-sea hydrothermal vents (*1*). Extracellular mucus, produced by microorganisms in the mats, binds the substrate, stabilizes the sediment surface, and influences the exchange of particles between the sediment and the water column (*2*). Despite the widespread occurrence of such biogenic mats, their effect on the exchange of nutrients between the sediment and the water column has rarely been considered (*3*). To examine this process we have used a laboratory flume to simulate tidal flow, sediment transport, and resuspension of benthic mats consisting mainly of the colorless sulfur bacteria *Beggiatoa* spp.

Beggiatoa oxidizes soluble sulfide to elemental sulfur and sulfate for chemoautotrophic fixation of CO_2 (*4*). Through gliding motility these bacteria maintain a vertical position in the sediment at the H_2S/O_2 interface (*4, 5*). In shallow waters, sulfur bacterial mats are abundant wherever organic enrichment occurs (estuaries, harbors, upwelling regions) (*1, 6*). On Eastern Passage sandflat, Halifax Harbor, mats are apparent as white sulfur coatings (up to 4 mm thick) on the sediment surface where reducing conditions and black, sulfide-rich sand occur (*7*) (Fig. 1).

Although the morphology of *Beggiatoa* and its production of extracellular slime have been studied in laboratory cultures (*6*), little is known about the intact mat structure and its potentially stabilizing effect on particle flux. Scanning electron microscopy (*8*) of intact samples from Eastern Passage demonstrated the presence of a complex mat structure with extensive connections of extracellular material between sand grains (Fig. 2A). A variety of organisms, detrital substrates, and flocculation reactions contribute to the amorphous appearance of the mat (*8, 9*). Both filamentous and circular growth forms (*6*) of the *Beggiatoa* trichomes were observed (Fig. 2, B through D).

In an active sulfuretum, internal deposition of elemental sulfur by *Beggiatoa* (*6*) allows use of total sediment sulfur as a tracer of these bacteria (*10*). We first examined the effects of sediment transport on benthic sulfur fluxes in a "control" sediment sample lacking *Beggiatoa* mats (April). Using a small box corer (18 by 18 cm), we collected undisturbed field cores from Eastern Passage after a storm. These cores had black reducing sand at the surface with some tan oxidized sand at ripple crests; ripples were 6 cm in wavelength and 0.5 cm in crest-trough height. The box core sample was placed in the fitted corewell of a flow-through laboratory flume, the sediment surface flush with the flume bed (*11*). Flowing water, measured with thermistor anemometers (*11*), was gradually applied until the initiation of sediment movement on the ripple crests (critical friction velocity, $u_{*\mathrm{crit}}$). Gentle erosion for 0.5 hour produced only a minor change in the total sulfur content (*12*) of the upper millimeters of sediment (Table 1). When sulfur mats were absent, erosion exposed underlying sediments, which had a sulfur content similar to that of surface sand (for example, due to iron sulfides), and no flux was apparent.

Cores with similar ripples collected after extended calm weather (May) had a white surface and about twice the total sulfur content of post-storm black sediments (Table 1). Later summer samples (July) of the bacterial mats showed that sulfur enrichment of surface sediments was undoubtedly due to *Beggiatoa* mats; mat-free sand from surface-oxidized sediments or deeper black sediments lacked high concentrations of sulfur (Fig. 3). When intact sediment cores with mats were eroded in the flume, white aggregates of sand, mucus, and *Beggiatoa* in the upper 2 to 3 mm of sand were visibly resuspended.

Erosion caused the severance of bacterial trichomes because sediment transport disrupted grain-grain contacts (Fig. 2D). Almost 50% of the sulfur content was resuspended (*5*), creating a mottled black-white surface and exposing an underlying reducing layer similar in sulfur content to the mat-free April core (Table 1). Variation in ripple morphology may affect $u_{*\mathrm{crit}}$ more than the binding action of microbial mucus (*2, 8*). However, the effect of sediment transport on resuspension of *Beggiatoa* mats was consistent for both cores. Even mild erosion in the flume (that is, nonstorm transport) produced major changes in total sediment sulfur similar to those caused by a storm event in the field (Table 1).

On the basis of an erosion depth of 3 mm and a bulk density for the sediment of 1.39 g cm^{-3}, the resuspension of *Beggiatoa* from cores in the flume is equivalent to a sulfur

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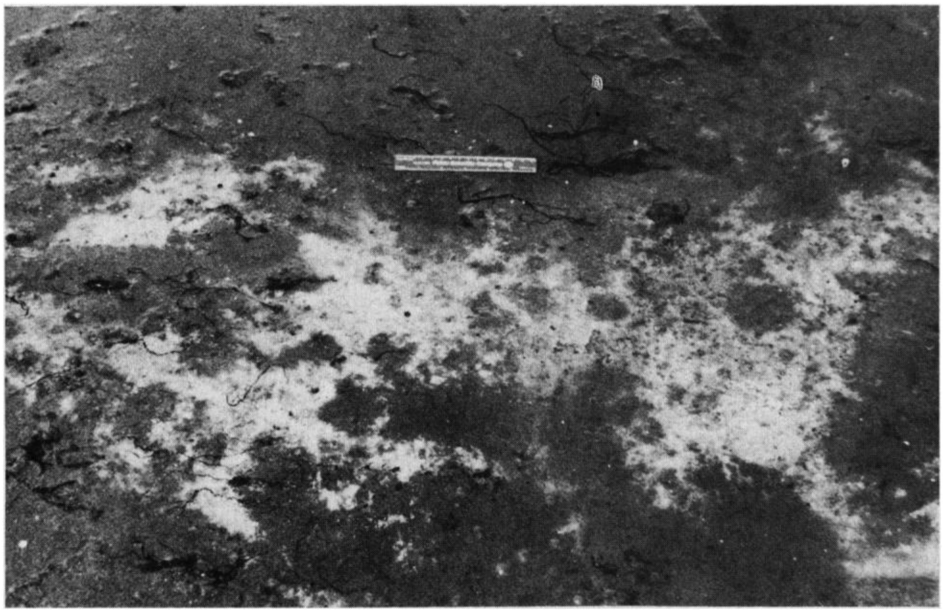

Fig. 1. White sulfur mats of colorless sulfur bacteria (*Beggiatoa*) in the intertidal zone, Eastern Passage, Nova Scotia (July). Ruler is 15 cm. Surrounding dark strands are the green alga *Enteromorpha*, abundant only in summer. These bacterial mats are in an area without ripples and are spatially more heterogeneous than mats used in the flume experiments. The surrounding sediment is oxidized on the surface, but the sediment just beneath the mats is black reducing sand. Other mats (for example, Table 1) are surrounded by reducing sand at the sediment surface.

flux of 160 mmol m^{-2} hour $^{-1}$. The relative magnitude of this process can be seen if we compare it to the estimated rates of bacterial sulfate reduction and sulfide oxidation in these sediments. Anaerobic community respiration in Eastern Passage sediments (May, 6°C) is 3.3 mmol of carbon per square meter per hour (*13*). If all anaerobic metabolism is due to sulfate reduction (*14*) and the stoichiometry of sulfate reduction to CO_2 production is 1:2, sulfate reduction would produce 1.6 mmol of sulfur per square meter per hour, comparable to literature values (*15*). Some of the H_2S released in sulfate reduction forms sulfide minerals (pyrite) at ~10% the rate of sulfate reduction (*15*). Because *Beggiatoa* can outcompete chemical oxidation, the remaining H_2S flux (1.4 mmol of sulfur per square meter per hour) is available for biological oxidation to elemental sulfur and sulfate (*4*). Therefore, a single gentle resuspension event of 0.5-hour duration causes a sulfur flux two orders of magnitude greater than concurrent bacterial sulfur transformations. After a storm the mats are usually lost, but more frequent nonstorm conditions with minimal sediment transport can drive the advective processes.

Because the sulfur content in mat-free sediments is similar to that of post-erosion mats (Table 1), sulfur lost during resuspension of mats (~0.6 mg per gram of sediment) is presumably *Beggiatoa* biomass. At the above rate of biological sulfide oxidation, the film represents a minimum sulfur accumulation of 2 days (excluding removal by grazers; see below). Thicker mats (Fig. 3) represent undisturbed production of at least 6 days. During May, extended calm periods at Eastern Passage would easily allow such an accumulation. However, when resuspension occurs, it can have a major impact on sulfur cycling and the benthic community at Eastern Passage. *Beggiatoa* is an important intermediary in the sediment sulfur cycle because stored elemental sulfur conserves the energy contained in reduced sulfur compounds; elemental sulfur can be both oxidized (for example, by *Beggiatoa*) and reduced by various types of bacteria (*10*). When *Beggiatoa* mats are resuspended by sediment transport, the capacity for bacterial conservation of chemical energy is lost.

Beggiatoa biomass and extracellular material (Fig. 2) may be a high-quality source of organic matter for benthic grazers such as gastropods (*16*). On the basis of a minimum growth yield for *Beggiatoa* (2.1 g of dry biomass per mole of H_2S for S^0 end product) and a cell dry weight of 50% carbon (*4*), the above rate of sulfide oxidation allows chemosynthesis of 0.13 mmol of carbon per square meter per hour. This production could contribute substantially to the

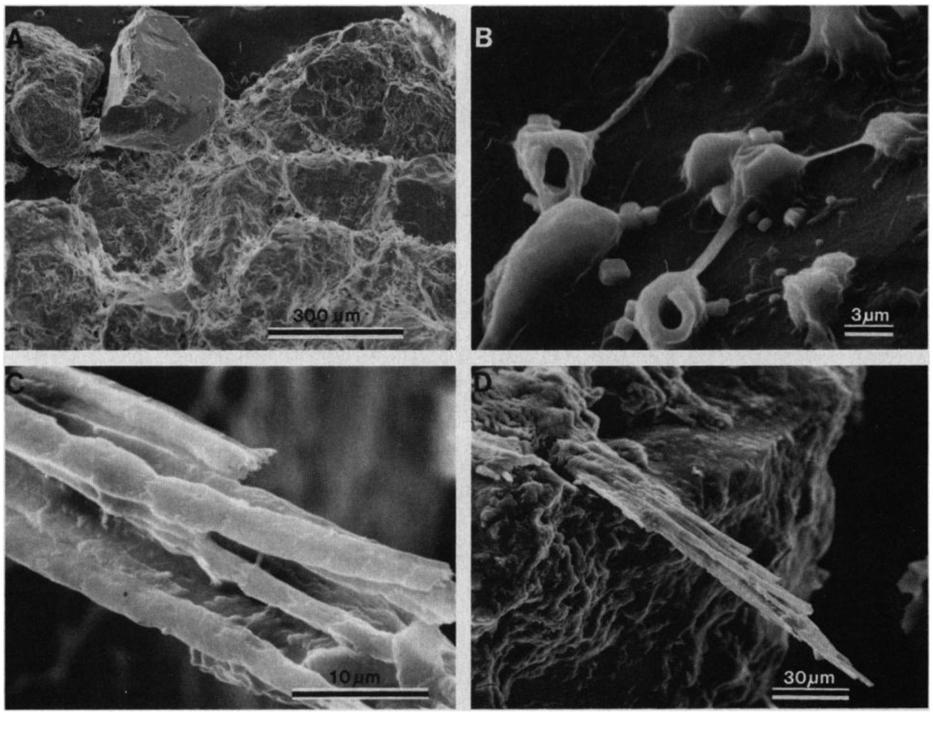

Fig. 2. Scanning electron micrographs from the mats of colorless sulfur bacteria, Eastern Passage sandflat. (**A**) Overview of sand grains from surface sediments bound in amorphous mucus, presumably extracellular bacterial slime. Note the clean appearance of the unbound grain in upper left of center. (**B**) Circular growth form of *Beggiatoa* trichomes on a sand grain. Note the intercellular mucus connections. (**C**) Filamentous growth form of *Beggiatoa* or bundled filaments of related *Thioploca*. (**D**) Overview of a portion of (**C**), showing the erosion of the bacterial mat in the laboratory flume. The trichome remains attached to one grain but is severed at the other end as a result of grain movement.

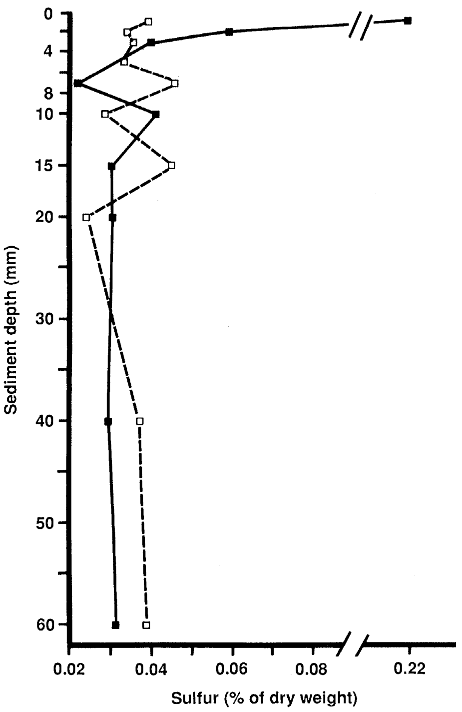

Fig. 3. Vertical profile of total sediment sulfur in field cores, Eastern Passage sandflat (July 1986). Dashed line is from sediments with a 1-cm layer of tan oxidized sand on the surface (no bacterial mats) and black reducing sediments beneath. Solid line is from sediments with well-developed white mats of *Beggiatoa* (see Fig. 1) covering the sediment surface (up to a depth of 4 mm), and overlying black reducing sediments. For the entire oxidized profile and in the subsurface (>5 mm) mat profile, replicate values varied by an average of 20%. For the surface mat sediments, the variability in sulfur content is given in Table 1.

Table 1. Changes in the total sulfur content (percentage of dry sediment weight) of surface sediments (to a depth of 3 mm) during erosion of intact box cores in a laboratory flume channel. The 2 April core had a black reducing sediment surface with no visible microbial mat. The 7 May cores had a white sediment surface due to *Beggiatoa* mats. Field and flume values are means (CV, coefficient of variation) of samples collected continuously across the ripple train. CV values reflect spatial heterogeneity due to ripple morphology (*2*, *8*). Each sediment sample (for example, ripple crest) contains two to three subsamples obtained with a spatula over a path of several centimeters. Field sulfur samples came from a homogeneous area of mat <2 m^2. Box cores for the flume were collected in adjacent undisturbed mat sediments. After erosion in the flume, the number of sediment samples was limited by the size of the box core.

Core	$u_{*\text{ crit}}$ applied 0.5 hour (cm sec^{-1})	Mean sulfur (CV) as percentage of dry sediment weight	
		Pre-erosion (field)	Post-erosion (flume)
2 April 1985 (black)	1.05	0.068 (20%) (n = 12)	0.058 (10%) (n = 4)
7 May 1985 (white)	1.38	0.130 (19%) (n = 10)	0.073 (19%) (n = 4)
7 May 1985 (white)	0.66	0.130 (19%) (n = 10)	0.076 (37%) (n = 4)

estimated carbon requirements (0.13 to 0.50 mmol m^{-2} hour^{-1}) of benthic grazers at Eastern Passage (*3*). However, amounts of chemoautotrophic production available to benthic consumers that have accumulated over days can be immediately removed by a single sediment transport event.

Benthic microbial mats generally stabilize the sediment surface against erosion (*2*), although aggregates projecting above the bed may be destabilizing (*17*). In any case, mucus production by *Beggiatoa* (Figs. 1 and 2) does not curtail the exchange of material between the sediment and the water column. To the contrary, sulfur oxidation by *Beggiatoa* concentrates particulate sulfur at the sediment-water interface [Fig. 3; (*10*)], thus enhancing the effect of resuspension on the release of benthic nutrients. Marine habitats may have tens of square kilometers of areal coverage of sulfur bacterial mats (*1*), which may account for the enrichment of sulfate that has been observed in estuarine waters (*18*). The disruption of *Beggiatoa* mats by sediment transport provides a rapid mechanism by which these sulfur species are returned to the water column.

Studies of nutrient cycling in estuarine sediments have concentrated on rates of biological transformation such as the decomposition of organic matter. Despite the obvious impact of water and sediment movement in the marine environment, the effect of advection has rarely been incorporated into these studies. Examination of sediment bacterial mats under controlled laboratory flow conditions demonstrates the magnitude of advection as a pathway in nutrient flux. An understanding of the biogeochemical coupling between sediments and the water column will require further work on physical transport and its interaction with biological processes.

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