

Sediment-to-water fluxes of particulate material and microbes by resuspension and their contribution to the planktonic food web

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ABSTRACT: Resuspension of bottom sediments by waves, currents, and biota is a potentially important mechanism by which particulate materials are introduced into the water column. Fluxes of particulate materials between sediments and overlying water were determined in the laboratory. Box cores of nearshore marine sediments were subjected to defined shear stresses in an annular flume. Sediment resuspension was detectable at shear velocities (u_*) of 0.95 to 1.35 cm s^{-1} in sediments ranging from fine to coarse sands. An average sediment subjected to shear velocities of 1.16 to 1.50 cm s^{-1} contributed 346 to 2312 $\text{mg particulate C m}^{-2} \text{ h}^{-1}$, 43 to 266 $\text{mg particulate N m}^{-2} \text{ h}^{-1}$, and 3.5×10^{11} to 2×10^{12} bacteria $\text{m}^{-2} \text{ h}^{-1}$. These fluxes would increase the concentrations of those substances in a 10 m homogeneously-mixed water column by 37 to 246 $\mu\text{g particulate carbon l}^{-1}$, 4.6 to 28.3 $\mu\text{g particulate N l}^{-1} \text{ h}^{-1}$, and 3.7×10^4 to 2.2×10^5 bacteria $\text{l}^{-1} \text{ h}^{-1}$, and would double typical water column concentrations in the field within a few hours. Shear stresses applied to sediments in these simulations represent mild field resuspension conditions (on the order of 0.5 m amplitude waves in 20 m water depth). Intense winter storms, which are not uncommon, would likely increase flux estimates according to the depth of sediment fluidization, and according to depth profiles of sedimentary physico-chemical parameters. Resuspension, in this study area, appears to play a greater role in relocating particulate than dissolved nutrients.

INTRODUCTION

Resuspension of marine sediments represents not only a loss of material from the benthos, but a gain of material to the water column and plankton. Hopkinson (1985) stated that 'Resuspension appears to control the relative amounts of organic carbon, as well as the sites and rates of organic matter degradation in the benthos and water column'. Fanning et al. (1982) concluded that resuspension may be an important provider of dissolved nitrogen compounds for phytoplankton, based on a combination of field data collected during a storm and laboratory stirring experiments. Wainright (1987) performed feeding experiments using heterotrophic microorganisms as consumers of resuspended sedimentary material, and found that planktonic microbial growth was stimulated by resuspended sediments within a few hours.

Further up the food chain, resuspended organic

matter may be a source of nutrition to filter-feeding organisms (Rhoads et al. 1975, Tenore 1977, Rhoads et al. 1984). Rhoads (1973) reported that transplanting oysters from a commercial bed of coarse-grained sediments to racks suspended above a muddy bottom subject to frequent resuspension produced higher meat yields than oysters grown in the commercial beds.

It is important to know the relationship between the magnitude of the resuspension flux of organic material and the erosional shear stress required to cause that flux. There have been a number of studies to determine the critical erosion velocities of sediments, i.e. the water velocity which produces movement of sediments (e.g. Rhoads et al. 1978, Grant et al. 1982, Grant & Gust 1987). However, data on critical resuspension velocities and the resulting material fluxes into the water column are rare. Gust & Morris (1989) give in situ estimates of bulk sediment fluxes. Wainright (1985, 1986) and Ferguson et al. (1987) were the first to directly estimate the magnitude of the microbial flux from the sediment to the water column at defined shear stresses.

This paper reports the critical shear velocity for

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resuspension (u_{*cr}) and resuspension flux estimates for particulate C and N, total seston, and microbes for a variety of nearshore sediments.

METHODS

Field sampling. Box cores of sediment were collected at 5 stations in the Georgia Bight off Savannah, Georgia, USA, in 20 m of water or less (Fig. 1). Sampling sites were chosen because of their widely varying sediment characteristics. Cores were quickly transported to the laboratory under temperature-controlled conditions. Stn OS (Offshore Sand) was sampled at each sampling period, to give a detailed picture of seasonal changes. Descriptions of sampling stations and sampling times are given in Table 1.

Sediment characteristics were determined from cores collected concurrently with those collected for flume experiments. Carbon and nitrogen analyses followed the method of Hedges & Stern (1984). The depth of the

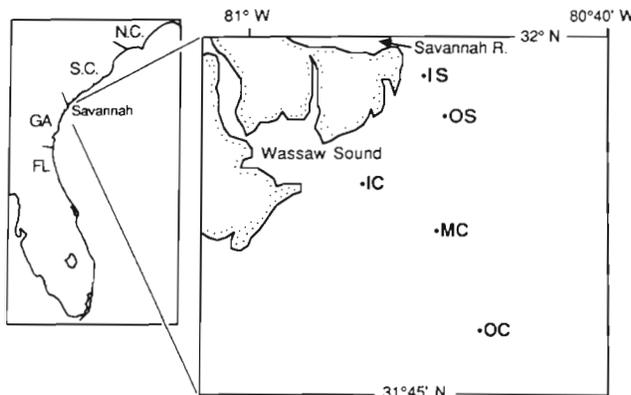


Fig. 1. The study area. Station coordinates are as follows: Inner Sand (IS), 31° 57.8' N, 80° 50.4' W; Outer Sand (OS), 31° 56.0' N, 80° 48.5' W; Inner Channel (IC), 31° 53.2' N, 80° 53.4' W; Mid Channel (MC), 31° 51.3' N, 80° 49.7' W; Outer Channel (OC), 31° 47.2' N, 80° 46.6' W

Table 1. Station descriptions and sampling periods

| Stn | Description ^a | Depth (m) | Sampling periods |
|-----|------------------------------------|-----------|-----------------------------------|
| OS | Fine sand, moderately sorted | 12 | Feb, Mar, May, Jun, Aug, Sep, Oct |
| IS | Fine sand, well sorted | 4 | Jun, Oct |
| IC | Shell gravel, mod. to well sorted | 6.5 | May |
| MC | Medium to coarse sand, mod. sorted | 12 | Aug |
| OC | Coarse sand, mod. to poorly sorted | 18 | Sep |

^a Based on Wentworth classification

Redox Potential Discontinuity (RPD) was estimated visually as the boundary between brownish surface sediments and deeper grey-black sediments. Chlorophyll content was determined by reverse-phase HPLC using a method modified from Bidigare et al. (1985). Solvents were 79:21 (v/v) methanol/water, 90:10 (v/v) methanol/water, 100% methanol, and 30:70 (v/v) isopropanol/methanol, all HPLC grade (Baker). The column (Alltech Assoc.) was a 100 × 4.6 mm cartridge containing Zorbax (Dupont) 7 μm, C₁₈-bonded spherical particles. Solvents were switched isocratically at 300, 550, 850, 1090 s respectively, with a starting pressure of 1950 psi (1.3 × 10⁷ Pa). Under these conditions, chlorophyll a eluted at 860 s, and phaeophytin a at about 1100 s.

Resuspension experiments. An annular flume (Fukuda & Lick 1980, P. A. Jumars & A. R. M. Nowell pers. comm.; Fig. 2) was used to experimentally determine the thresholds of sediment resuspension, and the ensuing flux of material from the sediments to the water column. The operating principle of the annular flume is, briefly, as follows (refer to Fig. 2): The cross-arm rotates, thereby rotating the ring which floats on the water in the channel. Shear stress between the ring and water induces circulation of the water in the channel. Shear velocities were determined with a flush-mounted skin friction sensor, similar in principle to one

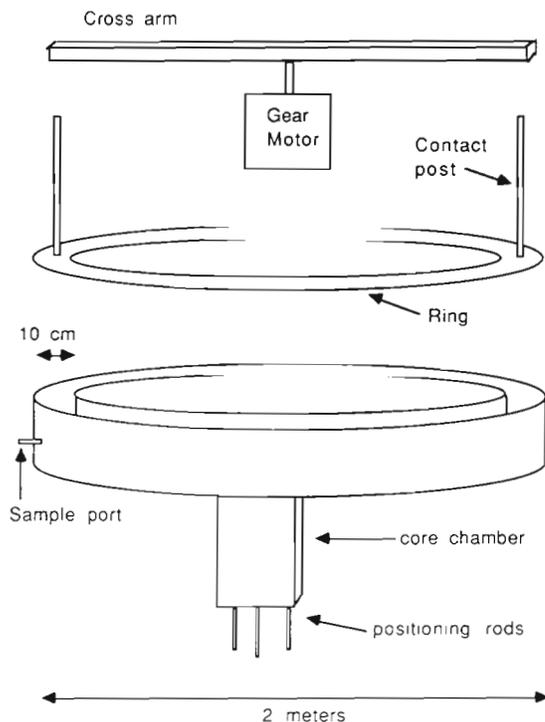


Fig. 2. Exploded view of the annular flume. The cross arm rotates, thereby rotating the ring, which floats on the water in the channel. Shear stress exerted on the water by the ring causes circulation of the water in the channel

described in Gust (1988), but using flat, beryllium oxide-coated thermistor elements (Victory Engineering Corp., Springfield, NJ, USA). Anemometer circuitry was a modification of that described by Vogel (1981). The sensors were calibrated against similar devices in the laboratory of G. Gust (University of South Florida). Cross-channel shear velocity variation was less than 19% of the mean (Wainright unpubl.).

In this paper, shear velocity (u_*) will be used instead of shear stress. The 2 quantities are related as:

$$\tau_b = \rho(u_*)^2 \quad (1)$$

where ρ = density of seawater = 1.025 g cm^{-3} ; and τ_b = boundary shear stress. The critical shear velocity for resuspension ($u_{*,cr-r}$) was operationally defined as that shear velocity which produced a flux significantly different from zero ($p \leq 0.05$).

The sediment-water interface for resuspension experiments was a box core of sediment that was inserted through a false bottom in the flume channel, into an acrylic chamber, to a level below that of the flume channel bottom. After insertion of the box core into the core chamber, the opening to the chamber was covered with an acrylic plate (to prevent resuspension during filling), and the flume channel filled with filtered ($0.2 \mu\text{m}$) seawater to a depth of 6 cm (60 l). Filling time was generally 1.25 h. The plate was then removed, and the core positioned flush with the flume channel bottom by means of positioning rods in the bottom of the core chamber.

Water flow was then started at a low shear velocity ($u_* = 0.1 \text{ cm s}^{-1}$). Following an equilibration period of 20 min, a sample of water was withdrawn through a port in the sidewall of the flume for determination of initial concentrations of particulate matter and microorganisms; this sample contained concentrations present in the filtered water plus those introduced by the small amount of water overlying the sediment core, and served as a blank. Sediment was resuspended by increasing the shear velocity in a stepwise manner. After each increase, the shear velocity was maintained for an equilibration period of 20 min and water samples withdrawn. This procedure was repeated until sediment was eroded enough to create serious artificial roughness elements (gullies).

Water column samples were collected for total suspended material (seston), particulate organic carbon (POC), particulate nitrogen (PN), and microorganisms. Bacteria/particle samples were fixed with acid-Lugol iodine solution (Nishino 1986) and refrigerated. Bacterial and particle counts followed Nishino's (1986) protocol for cellulose nitrate filters. Counts were made as follows: (1) Bacteria fell into 2 classes: $0.2 \mu\text{m}$ diam. cocci, and $0.6 \times 1.0 \mu\text{m}$ rods, and were counted separately. (2) Flagellated protozoans were enumerated at

either $125 \times$ or $500 \times$ magnifications, depending on cell size and abundance. (3) Particles were measured individually with an ocular micrometer, with the number of attached bacteria on each recorded. At least 50 particles, or the particles in 50 fields, were examined from each sample. Attached bacterial counts were multiplied by a factor of 2 to account for the reverse sides of particles (Kirchman 1983). Microbial volumes were calculated assuming cocci and spherical flagellates to be spherical, rods and ellipsoid protozoans to be ellipsoid. Average bacterial cell volumes were computed as weighted averages, based on the fraction of the total in each size class. Seston/CHN samples were collected at only 2 or 3 shear velocities in any given experiment because the relatively large volumes of water required for these analyses (several liters) dictated that few samples could be withdrawn before flow conditions were affected. Samples were filtered through precombusted, tared glass fiber filters (Reeve Angel 984H). After reweighing them, the filters were acidified, desiccated, reweighed, and subjected to CHN analysis (Wainright 1987).

Fluxes of materials from sediment to water column were calculated according to the relationship:

$$\text{Flux} = (C_f - C_i) V T^{-1} A^{-1} \quad (2)$$

where C_f and C_i = initial and final concentrations of the substance in the flume; T = time of exposure to a given shear velocity (u_*); V = volume of the flume; and A = surface area of the sediment core. (Note that fluxes at a particular shear velocity do not include material which had already been eroded at lower shear velocities, i.e. they are not cumulative.) Eroded sediment travels as bedload and suspended load. The latter was determined by weighing sediment which accumulated on the flume channel floor after a flume experiment. The percentage of the sedimentary material which was resuspendable was estimated as the amount of seston (the product of concentration and volume) compared to the total amount of sediment eroded.

RESULTS

Sedimentary characteristics

Brief descriptions of the study sites are given in Table 1. Sediments from the Inner Channel station (IC) were coarsest, a large fraction of the material being intact shells or large shell fragments. Stns IS and OS contained the finest sediments and were outwardly similar, both having approximately the same texture, but differing in several important respects. Stn OS had the highest organic C and N content of all stations (Table 2), while Stn IS had among the lowest. The

Table 2. Sedimentary characteristics at 5 sampling stations in the top 1 cm. Inorganic carbon (IC), total organic carbon (TOC), and particulate nitrogen (PN) are expressed as percent by dry weight. C:N is the ratio of carbon to nitrogen by atoms. Chl *a* is expressed as $\mu\text{g g}^{-1}$ dry wt. RPD is the depth of the Redox Potential Discontinuity. For stations sampled more than once, values are averages over all sampling periods. Means and standard errors (in parentheses) are based on numbers of replicates noted below

| Stn | % IC ^a | % TOC ^d | % PN ^a | C:N | Chl <i>a</i> ^b | RPD (cm) |
|-----------------|-------------------|--------------------|-------------------|----------------|---------------------------|----------|
| OS ^c | 0.58 (0.02) | 0.15 (0.005) | 0.02 (0.001) | 9.30 (0.67) | 1.21 (0.3) | 0.5–5 |
| IS ^d | 0.135 (0.005) | 0.066 (0.002) | 0.01 (0.001) | 7.95 (0.71) | 0.74 (0.14) | > 5–12 |
| IC ^e | 1.38 (0.282) | 0.109 (0.010) | 0.018 (0.002) | 7.18 (0.40) | 0.71 (0.11) | > 8 |
| MC ^e | 0.18 (0.024) | 0.032 (0.002) | 0.008 (0.001) | 5.12 (0.40) | 1.34 (0.18) | > 8 |
| OC ^e | 0.906 (0.065) | 0.127 (0.007) | 0.015 (0.002) | 9.88 (0.97) | 5.22 (0.45) | 2–3 |

^a To convert to g m^{-2} multiply by 156
^b To convert to mg m^{-2} multiply by 15.6
^c n = 30 for % IC, POC, PN, C:N; n = 41 for chl *a*
^d n = 8 for % IC, POC, PN, C:N; n = 12 for chl *a*
^e n = 4 for % IC, POC, PN, C:N; n = 6 for chl *a*

Middle Channel station (MC) and Stn IS had the lowest inorganic carbon contents. The Outer Channel station (OC) was a poorly-sorted mixture including shell fragments of all sizes. There was no consistent relationship between grain size and organic content. Sediments contained between 0.1 and 1.4 % inorganic carbon (1.1 to 11.5 % CaCO_3), mostly derived from bivalve shells.

The depth of the RPD varied between stations and seasonally. At Stn OS, the RPD was shallowest (0.5 to 1.5 cm) in July and deepest (2 to 5 cm) in February.

Sediment chlorophyll *a* concentrations were highest at Stn OC in September (Table 2). There was no significant correlation between particulate nitrogen (PN) or particulate organic carbon (POC) and chlorophyll *a* ($p \geq 0.05$) [although chlorophyll content was weakly correlated with the C:N ratio ($p = 0.078$)].

The atomic C:N ratio of the sediments did not consistently vary with depth down to 5 cm ($p = 0.57$), but it did vary seasonally ($p = 0.0002$), with highest ratios in October and lowest in August (2-way ANOVA). The C:N ratio of sediment approached that of phytoplankton (ca 5) in August (Stn MC), while the highest ratios (12.6 ± 2.7) occurred in February (Stn OS, 4 to 5 cm fraction), suggesting a more refractory pool of organic material.

Resuspension fluxes

Sediment-to-water fluxes of all materials showed similar patterns, i.e. measurable fluxes at $u_* = 0.95$ to 1.16 cm s^{-1} and much greater fluxes at higher shear velocities (Fig. 3). (The shear velocity reported in Wain-

right (1987), $u_* = 1.8 \text{ cm s}^{-1}$, was an overestimate. Experimental conditions were similar to the $u_* = 1.16 \text{ cm s}^{-1}$ reported here. Heated-thermistor velocity profiles, which were used to make the former

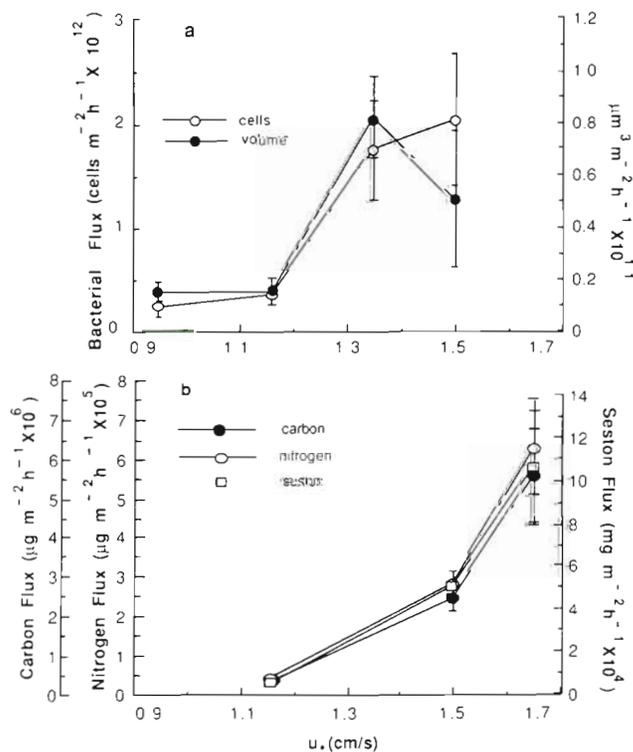


Fig. 3. (a) Bacterial fluxes from flume experiments, expressed on a numeric and on a volume basis. (b) Total seston, carbon and nitrogen fluxes from flume experiments. In all cases, plotted values are means of all runs combined; error bars are ± 1 standard error of the mean ($n = 41$)

estimates, are inferior to the shear stress sensors for this particular application.) $u_{*,cr-r}$, the shear velocity which produced a significant flux of sedimentary material into the flume water, was determined to be 0.95 cm s^{-1} when data from all stations were combined (Fig. 3). This flux of $2.3 \times 10^{11} \pm 7.7 \times 10^{10} \text{ cells m}^{-2} \text{ h}^{-1}$ is equivalent to an increase in the bacterial concentration in a homogeneously mixed 10 m water column of $2.4 \times 10^4 \pm 8.2 \times 10^3 \text{ cells ml}^{-1} \text{ h}^{-1}$. Estimates of increased cell concentration in 10 m of water may be obtained by dividing $\text{cells m}^{-2} \text{ h}^{-1}$ by 9.4×10^6 . The corresponding conversion factor for seston, C and N is 9.4×10^3 . During any particular sampling period $u_{*,cr-r}$ was between 1.16 and 1.35 cm s^{-1} . Insignificant fluxes at lower shear velocities were caused by high intrastation variability, making flux estimates insignificantly different from zero.

There were few detectable between-station, or seasonal differences regarding any flux parameter. An exception was particulate nitrogen at $u_* = 1.5 \text{ cm s}^{-1}$,

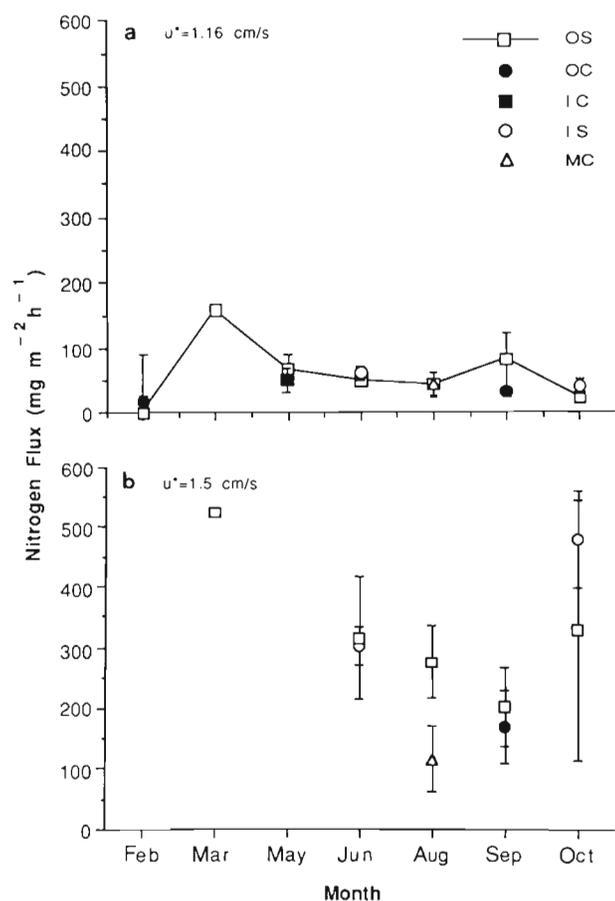


Fig. 4. Seasonal fluxes of particulate nitrogen at 2 shear velocities: (a) 1.16 cm s^{-1} ; and (b) 1.5 cm s^{-1} . Values are means ± 1 standard error of the mean. The plotted value of OS (Mar) is a single value, with no corresponding standard error. Error bar for Stn OC (Feb) at $u_* = 1.16 \text{ cm s}^{-1}$ actually extends below zero. No samples were collected during Apr, Jul

where Stn OS (March) and Stn IS (October) showed significantly greater N fluxes than Stns MC and OC in August and September, respectively (2-way ANOVA, $p < 0.05$; Fig. 4). Stn IS had a low nitrogen content (Table 2), and so its relatively large N flux must have been a result of unusually high erodibility, and thus high total seston flux. Although total seston flux at this station was higher than at several other stations, the difference was not significant ($p = 0.07$; 2-way ANOVA). Bacterial fluxes were significantly higher at Stn OS (February) at $u_* = 0.95$ and 1.16 cm s^{-1} (Fig. 5), suggesting that this station was more prone to erosion than average.

Bacterial fluxes from the sediments were highly correlated with the all other resuspension parameters ($p < 0.003$ or better; Table 3). The weakest correlation was between bacterial and particle abundances.

Samples were collected after 2 exposure times at 2 different shear velocities, to assess whether fluxes remained constant over a more extended period of

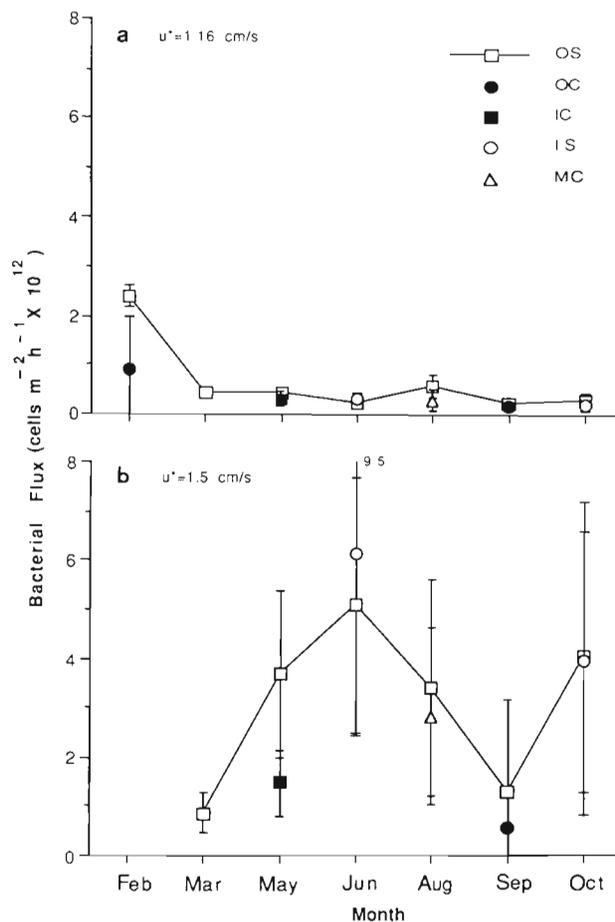


Fig. 5. Seasonal fluxes of bacteria at 2 shear velocities: (a) 1.16 cm s^{-1} ; and (b) 1.5 cm s^{-1} . Values are means ± 1 standard error of the mean. Error bar for Stn OC (Feb) at $u_* = 1.16 \text{ cm s}^{-1}$ actually extends off scale, as do those for Stns OS (Sep) and IS (Jun) at $u_* = 1.5 \text{ cm s}^{-1}$. No samples were collected during Apr, Jul

time. Fluxes of bacteria and particulate material collected after 12 min were not significantly different from those collected at 24 min at $u_* = 1.16$ or 1.5 cm s^{-1} . Thus fluxes remained constant for at least 24 min.

Characteristics of resuspended material

Sedimentary material was 0.16 to 1.61 % resuspendable on a dry weight basis (Table 4). Between 0.5 and

2.5 % of the resuspendable material was PN, while 4.3 to 16.5 % was POC, yielding atomic C:N ratios of 7 to 23. Resuspendable material at Stn OS generally had the lowest C:N ratio, while that from Stn IS (June) had the highest C and N contents. Lowest C and N contents were generally found at Stns IC and MC.

The percentage of bacteria that were attached to particles increased with shear velocity (Fig. 6a). Up to 80 % of the resuspended bacteria were attached to particles (Stn N, October), however, on average about

Table 3. Correlation matrix, with Pearson correlation coefficients between flux parameters. Significance is indicated as follows: *** $p < 0.001$; ** $0.001 < p < 0.01$

| Flux | Seston | N | C | Bacteria | Particles |
|-----------|----------|----------|----------|----------|-----------|
| Seston | 1.000 | | | | |
| N | 0.943*** | 1.000 | | | |
| C | 0.967*** | 0.955*** | 1.000 | | |
| Bacteria | 0.630*** | 0.541*** | 0.543*** | 1.000 | |
| Particles | 0.588*** | 0.589*** | 0.556*** | 0.234** | 1.000 |

n = 75 for the following correlations: seston × C, seston × N, C × N
n = 62 for the correlations: bacteria × seston, bacteria × N, bacteria × C, particles × seston, particles × C, particles × N
n = 173 for bacteria × particles

Table 4. Percent of eroded material resuspended, and its composition. Percent resuspended is based on the seston concentrations in flume water relative to sediment disappearance from the experimental box cores. Percent N, C and atomic C:N ratios are on a dry weight basis. nd: not determined. Numbers in parentheses are standard errors

| Stn, Month | u_* | % resusp | % N | % C | C:N |
|------------|-------|----------|-------------|--------------|--------------|
| OS, Feb | 1.16 | nd | 0.91 (0.23) | 6.69 (1.27) | 9.21 (1.47) |
| | 1.50 | | 1.70 | 10.31 | 7.09 |
| | 1.65 | nd | 0.77 (0.08) | 5.97 (0.37) | 9.29 (0.68) |
| May | 1.16 | | 1.50 (0.56) | 11.26 (3.54) | 9.89 (1.18) |
| | 1.65 | 1.61 | 0.79 (0.17) | 6.50 (0.78) | 10.61 (1.09) |
| Jun | 1.16 | | 1.16 (0.24) | 9.48 (1.98) | 9.89 (1.14) |
| | 1.50 | | 0.58 (0.06) | 5.02 (0.57) | 10.21 (0.81) |
| | 1.65 | nd | 0.58 (0.03) | 4.78 (0.36) | 9.53 (0.16) |
| Aug | 1.16 | | 0.77 (0.13) | 6.93 (1.00) | 12.28 (3.00) |
| | 1.50 | 1.47 | 0.67 (0.05) | 5.18 (0.32) | 9.12 (0.46) |
| Sep | 1.16 | | 1.65 (0.57) | 10.11 (2.35) | 8.13 (0.85) |
| | 1.50 | 0.67 | 0.74 (0.09) | 5.97 (0.50) | 9.56 (0.42) |
| Oct | 1.16 | | 0.65 (0.50) | 7.82 (1.63) | 16.01 (3.42) |
| | 1.50 | 0.66 | 0.64 (0.10) | 5.82 (0.76) | 10.70 (0.36) |
| IS, Jun | 1.16 | | 2.48 (0.98) | 16.49 (4.89) | 9.25 (1.51) |
| | 1.50 | nd | 1.01 (0.42) | 7.23 (1.34) | 11.49 (2.05) |
| Oct | 1.16 | | 0.84 (0.11) | 7.66 (1.02) | 10.73 (0.57) |
| | 1.50 | 0.16 | 0.50 (0.02) | 4.46 (0.26) | 10.44 (0.71) |
| OC, Feb | 1.16 | nd | 0.74 (0.08) | 7.11 (0.24) | 11.70 (0.91) |
| | 1.50 | | 0.78 (0.17) | 7.40 (1.37) | 13.34 (3.91) |
| Sep | 1.50 | 0.36 | 0.92 (0.16) | 7.69 (1.24) | 9.84 (0.34) |
| IC, May | 1.16 | | 0.55 (0.13) | 8.40 (0.99) | 22.96 (8.34) |
| | 1.35 | | 0.60 (0.06) | 7.12 (1.23) | 13.81 (1.07) |
| | 1.65 | 1.33 | 0.62 (0.04) | 5.58 (0.12) | 10.66 (0.76) |
| MC, Aug | 1.16 | | 0.64 (0.21) | 5.62 (1.64) | 9.24 (0.55) |
| | 1.50 | 0.29 | 0.47 (0.06) | 4.29 (0.34) | 10.94 (0.64) |

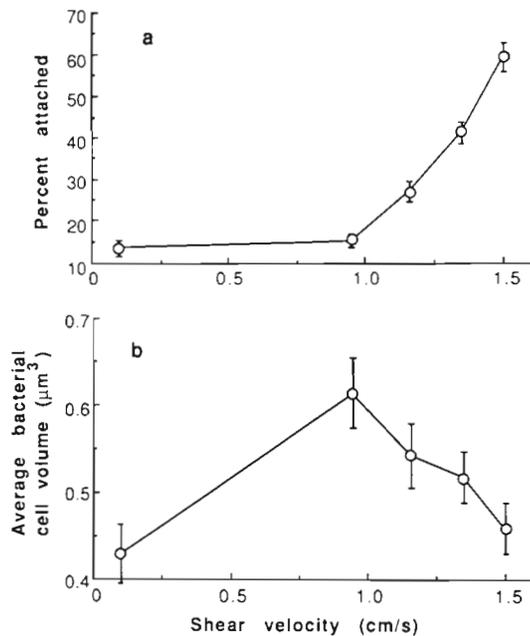


Fig. 6. (a) Percentage of resuspended bacteria attached to particles. Plotted values are means of all runs combined ($n = 41$) ± 1 standard error of the mean. (b) Average bacterial cell volumes of resuspended bacteria in flume experiments. Plotted values are means of all runs combined ($n = 41$) ± 1 standard error of the mean

60% of resuspended bacteria were attached to particles at the highest u_* examined.

Average bacterial cell volume (Fig. 6b) was typically maximum at or before the point where there was significant resuspension. Bacterial fluxes appeared to increase between $u_* = 1.35$ and 1.5 cm s^{-1} when viewed numerically, but decreased on a volume basis (Fig. 3). However, in both cases, fluxes at $u_* = 0.95$ and 1.16 cm s^{-1} were statistically indistinguishable from each other, as were those at $u_* = 1.35$ and 1.5 cm s^{-1} .

Flagellated protozoa (mostly 4 to 5 μm diameter)

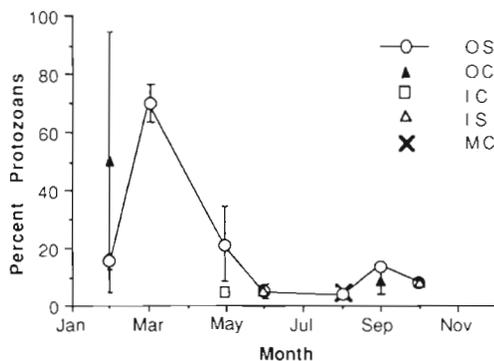


Fig. 7 Percentage of total microbial fluxes attributable to protozoans, on a volume basis. Plotted values are means and standard errors of fluxes from 2 to 4 cores per sampling period; each core's flux was itself a mean of fluxes from 4 shear velocities

were a significant component of the microbial biomass. These organisms were most numerous during February and March (Fig. 7), comprising 14 to 98% of microbial biovolume at both Stns OC and OS. However, protozoan volume was typically less than 10% of total microbial biovolume in all other resuspended microbial communities. Diatoms were infrequently observed, but in insufficient numbers to quantify.

DISCUSSION

Contribution of resuspended materials to the plankton

Resuspended sedimentary material may contribute very significantly to normal water column concentrations of all substances examined (Table 5). Using water concentrations of materials from the study area for comparison, estimates were made of the contribution of resuspended material to the average field concentrations of these substances. Measured laboratory fluxes could double typical planktonic field concentrations within an hour at $u_* = 1.5 \text{ cm s}^{-1}$ or a few hours at $u_* = 1.16 \text{ cm s}^{-1}$. While it was not possible to demonstrate a significant time-dependent reduction in the magnitude of resuspension fluxes on the order of 24 min, Fanning et al. (1982) found the greatest release of dissolved nutrients in the initial few minutes of their 'stirring experiment', despite the relatively small amount of sediment eroded. It is likely that this also applies to suspendable particulate nutrients, the implication being that once fluidized, sediments yield a diminishing return as resuspension persists.

Interestingly, attached bacteria comprised the bulk of the bacterial flux (Fig. 6a). While it is commonly thought that most planktonic bacteria are free-living, there are a number of reports of high proportions of attached bacteria in relatively turbid waters, in terms of both numbers and activity (e.g. Bell & Albright 1981, Schoenberg & McCubbin 1985, Plummer et al. 1987). Plummer et al. (1987) concluded that bacteria attached to resuspended particles were relatively unimportant compared with those attached to permanently suspended particles in estuaries, while Palumbo et al. (1984) stated that resuspension was an important determinant of the number of attached bacteria in the Georgia Bight.

The relationship between bacterial cell volume and shear velocity suggests a relationship between cell size and sediment depth. Bacteria resuspended first were larger than those resuspended later. Deeper sediment bacteria, which appeared in the water column only at greater shear velocities, had smaller average cell size. Reasons for smaller bacteria at depth may include the

Table 5. Comparison of increased seston, nitrogen, carbon and bacterial concentrations due to resuspension at 2 shear velocities with typical concentrations of those substances in the study area and surrounding area. Flume fluxes were converted to increased concentrations in a 10 m water column per hour, using box core surface area and flume volume, and assuming homogeneous mixing. For increased concentrations, units are $\text{mg l}^{-1} \text{h}^{-1}$ for seston, $\mu\text{g l}^{-1} \text{h}^{-1}$ for PN, POC, and $\text{cells ml}^{-1} \text{h}^{-1}$ for bacteria

| Substance | Typical field concentrations | Source | Range of increased concentrations | |
|-----------|--|--|-----------------------------------|----------------------------------|
| | | | at $u_* = 1.16 \text{ cm s}^{-1}$ | at $u_* = 1.5 \text{ cm s}^{-1}$ |
| Seston | 5–200 mg l^{-1} 2–15 | Oertel & Dunstan (1981) Wainright (unpubl.) | 0.1–0.9 | 1.8–10.1 |
| PN | 2–76 $\mu\text{g l}^{-1}$ 16–110 | Haines & Dunstan (1975) Wainright (unpubl.) | 0–15.9 | 11–52.4 |
| POC | 35–800 $\mu\text{g l}^{-1}$ 150–900 | Haines & Dunstan (1975) Wainright (unpubl.) | 0–70.4 | 107–433 |
| Bacteria | 10^5 – 10^6 cells ml^{-1} | Wainright (unpubl.) Pomeroy (1985) | 0.1 – 2.4×10^5 | 0.5 – 5×10^5 |

refractory nature of buried organic matter (although this was not evident in the C:N ratios), diffusion-limited uptake of oxygen and nutrients in subsurface sediments and reduced bacterial grazing in surface sediments.

Storm estimates

Shear velocities used in this study (0 to 1.5 cm s^{-1}), while exceeding $u_{*,\text{cr},T}$, were probably far lower than maximal shear velocities experienced in the study area during storms. A wave-current interaction model (Grant & Madsen 1979) was used to calculate shear velocities, using current and wave information as input. Shear velocities ranged from 1.5 to 6 cm s^{-1} (Table 6; T. F. Gross, Skidaway Institute of Oceanography, pers. comm.). Shallow areas are especially prone to resuspension (compare 4 m with 18 m run). Wiberg & Smith (1983) reported shear velocities as 4.5 to 5.2 cm s^{-1} during a storm at an 18 m station off Alaska. Other

Table 6. Expected shear velocities in the study area, computed using the Grant & Madsen (1979) wave-current interaction model. Default conditions are: $z = 12 \text{ m}$, roughness length (K_b) = 0.3 cm , current velocity 1 m off bottom = 20 cm s^{-1} , wave angle to current axis = 0° , wave period = 5 s , wave height ($1/2$ peak to trough) = 50 cm . In a given combination, only the indicated parameter has been changed from the default value

| Changed parameter | Resulting shear velocity (cm s^{-1}) |
|--|---|
| None; all default values | 2.44 |
| $z = 4 \text{ m}$ | 5.95 |
| $z = 18 \text{ m}$ | 1.50 |
| $K_b = 3 \text{ cm}$ | 3.98 |
| Current velocity = 2 cm s^{-1} | 2.04 |
| Wave angle = 90° | 2.09 |
| Wave period = 10 s | 3.76 |
| Wave height = 150 cm | 5.23 |

factors such as bottom roughness, wave height and wave period also have large effects on u_* . In the context of particle movement, u_* produced by steady unidirectional flow (as in the flume experiments) is equivalent to that produced by waves or wave-current interaction (Nowell & Jumars 1984); that is, particles would not distinguish between $u_* = 2 \text{ cm s}^{-1}$ produced by waves and $u_* = 2 \text{ cm s}^{-1}$ produced by currents.

Storm events show enormous potential for shifting pools of particulate organic matter from the benthos to the plankton. Hopkinson (1987) observed sediment fluidization down to 25 cm. While it is unknown exactly what values of u_* might produce sediment fluidization down to 25 cm, it is interesting to extrapolate my estimates of '% suspendable' to volumes of fluidized sediment reported by Hopkinson (1987). Assuming that fluidization releases all resuspendable material down to that depth, using a conservative value of 0.16% resuspendable (Table 4), and a sediment bulk density of 1.5 g cm^{-3} , 600 g of material would be resuspended per m^2 . This is probably an underestimate, since the u_* capable of this sort of erosion would likely have a higher '% resuspendable' value associated with it. Multiplying the dry weight of resuspendable sediment by 7.7% carbon and 0.8% nitrogen (Table 4) yields 46.2 g C and 4.8 g N m^{-2} . The overall release ratios are $1.23 \times 10^{-4} \text{ g POC g}^{-1}$ sediment (0.0123%) and $1.3 \times 10^{-5} \text{ g PN g}^{-1}$ sediment (0.0013%). Assuming homogeneous mixing in a 10 m water column, this becomes about 4.9 mg C and 0.51 mg N l^{-1} (compare with Table 5). To make a similar estimate of the increase in bacterial concentration in a 10 m water column, the regression equation which describes resuspended bacteria as a function of resuspended nitrogen may be used [bacteria = $8464 (N) - 3.4 \times 10^4$; $r^2 = 0.292$, $p = 0.0001$, where N is in $\mu\text{g N l}^{-1}$, bacteria are expressed as cells ml^{-1}]. The result is an increase in the bacterial concentration of $4.3 \times 10^6 \text{ cells ml}^{-1}$ (release ratio = $1.08 \times 10^8 \text{ cells g}^{-1}$ sediment). These estimates

of post-storm concentrations are similar to concentrations observed during a storm in October 1987: up to 2.7 mg C l^{-1} , 0.39 mg N l^{-1} , $3 \times 10^6 \text{ cells ml}^{-1}$ (Griffith et al. unpubl.).

Quality vs quantity

The quantity of any substance resuspended depends strongly on at least 3 factors: the concentration of the substance in the sediment, the erodibility of the sediment, and the shear velocity. The first 2 factors are determined by a complex interaction of physical and biological factors including grain size distribution, hydrodynamic history, organic content, and resident biota (see e.g. Eckman et al. 1981, Grant et al. 1982, Grant & Gust 1987). Given similar sedimentation inputs, sediments which are resuspended on each tidal cycle (such as at Stn MC) or as a result of frequent wave action (such as at Stn IS) might be expected to be organically poorer than those remaining stationary for an extended period.

In terms of resuspended carbon, the resuspension of large quantities of low-C material may have the same net effect as the resuspension of a small amount of organically rich, but less erodable sediment. Stn IS sediments were relatively low in organic content (Table 2); however, the resuspendable portion was comparable to or higher in organic content than that from other stations (Table 4). Assuming that resuspendable material from all stations had similar organic contents, and using data from October in the '% resuspended' column of Table 4, $0.66/0.16 = 4.125$ times the sediment at Stn IS must be eroded to produce the same amount of resuspended carbon as at Stn OS. In fact, the amount of sediment eroded at $u_* = 1.5 \text{ cm s}^{-1}$ was 6.5 times greater at Stn IS than at OS (data not shown). Thus, the opposing effects of organic content vs erodibility seemed to balance each other in this case.

Sedimentary organic matter is widely believed to be of relatively low quality, however some simple calculations suggest that this is not necessarily so. Chlorophyll content (Table 2) provides an indication of the quality of the sedimentary organic matter. Using a factor of 50:1 for converting chlorophyll a to organic C [this value is toward the lower range of values given in Parsons et al. (1977) and Mann (1982) for phytoplankton], $50 \mu\text{g C g}^{-1}$ of sediment, or 5 % of sedimentary organic C content, is attributable to phytoplankton. To this can be added organic C contributed by bacteria [assuming $10^9 \text{ cells g}^{-1}$, mean cell volume = $0.5 \mu\text{m}^3$, $106 \text{ fg C } \mu\text{m}^{-3}$ (Nagata 1986)] which brings the contribution of labile organic C to 10 %. This excludes protozoans (which may contribute substantially to microbial biomass; Fig. 7), other meiofauna, macrofauna,

and unknown quantities of unidentified labile organic matter. Also excluded are dissolved organic C or dissolved inorganic nutrients released during resuspension, each of which may stimulate pelagic production (Fanning et al. 1982, Hopkinson 1987). Thus it is probable that the resuspension of sediments which contain a fully developed community may contribute significantly to pelagic pools of labile organic carbon.

Particulate vs dissolved

Resuspension apparently plays a much larger role in redistributing particulate nutrients than dissolved nutrients in this study area. Using porewater concentrations of NH_4^+ , NO_3^- , and PO_4^{3-} from Hopkinson (1987: 100, 20, and $45 \mu\text{M}$, respectively), assuming 100 % release of those substances when 25 cm of sediment is fluidized, and averaging the result over a 10 m water column, the water column concentration would increase by ca $1.13 \mu\text{M NH}_4^+$, $0.23 \mu\text{M NO}_3^-$, and $0.51 \mu\text{M PO}_4^{3-}$, respectively, with release ratios of $5.5 \times 10^{-7} \text{ g N g}^{-1}$ sediment and $2.0 \times 10^{-7} \text{ g P g}^{-1}$ sediment. These results compare with typical field concentrations of $0.5 \mu\text{M NH}_4^+$, $0.25 \mu\text{M NO}_3^-$, and $0.7 \mu\text{M PO}_4^{3-}$ (Hopkinson 1987). The percentage increase in dissolved nutrients as a result of sediments being fluidized to a depth of 25 cm is similar to the percentage increase in particulate substances in just a few hours at a u_* of 1.16 or 1.5 cm s^{-1} (Table 3).

Do flume results mimic nature?

Up to ca $u_* = 1.2 \text{ cm s}^{-1}$, the flume mimics conditions on a flat sand-bed quite well. At shear velocities greater than about $u_* = 1.2 \text{ cm s}^{-1}$ gullies began to develop at the corners of some box cores. Flux estimates at higher shear velocities may therefore overestimate resuspension on a flat sand bed, a situation which might be argued to be atypical in nature. Erosion at these higher shear velocities may more closely mimic that which might occur near a rock, sand ripple, reef edge, or biotic structures such as sea urchins and polychaete tubes (Eckman et al. 1981, Carey 1983). I have frequently observed the following roughness elements in the study area: onuphid and oweniid polychaete tubes (up to $7 \times 0.5 \text{ cm}$, densities of several hundred m^{-2}), sea urchins, sand dollars, large mollusc shells, rocks and sand ripples.

Annular flumes have several advantages over other flume designs for use in resuspension experiments: (1) they are recirculating in that the same water passes over the sediment core repeatedly, leading to relatively high concentrations of suspended material; (2) unlike

straight-channel recirculating flumes, water is not passed through a water pump which might physically alter suspended particles and associated organisms, and the chemical composition of the water; (3) the boundary layer is fully developed throughout the flume, unlike in a straight channel where the boundary layer grows in a downstream direction; (4) the use of intact sediment has obvious advantages when results are to be extrapolated to nature. A disadvantage of the annular design is the secondary circulation pattern associated with the shape of the channel, which creates non-uniform shear velocities across the sediment surface, and makes calibration both difficult and laborious. The calibration problem was largely overcome by the use of flush-mounted skin friction sensors (Wainright unpubl.).

CONCLUSIONS

These results and extrapolations support Hopkinson's (1985) contention that resuspension may be a major influence on organic matter cycling in shallow-water marine environments. Resuspension can shift the major pools of particulate organic matter from the benthos to the water column. A significant part of this organic matter may be labile, and thus of immediate nutritive value to filter-feeding organisms. Previous work on this topic (Wainright 1987) showed that the longer-term impact of resuspended sediments on planktonic microbes could be very significant, even when the initial microbial contribution to the water column was indistinguishable from background. Measured fluxes in the present study exceeded those used in Wainright's (1987) study, and were themselves probably conservative estimates of field conditions during storms. Thus, the long-term stimulatory effect of resuspension fluxes on planktonic microbes should be even greater. Resuspension appears to be an important influence on the cycling of particulate carbon and nitrogen which persists much longer (days to weeks) than the resuspension event itself.

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LITERATURE CITED

- Bell, C. R., Albright, L. J. (1981). Attached and free-floating bacteria in the Frazer River Estuary, British Columbia, Canada. *Mar. Ecol. Prog. Ser.* 6: 317–327
- Bidigare, R. R., Kennicutt, M. C. II, Brooks, J. M. (1985). Rapid determination of chlorophylls and their degradation products by high-performance liquid chromatography. *Limnol. Oceanogr.* 30: 432–435
- Carey, D. A. (1983). Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes. *Can. J. Fish. Aquat. Sci.* 40 (Suppl. 1): 301–308
- Eckman, J. E., Nowell, A. R. M., Jumars, P. A. (1981). Sediment destabilization by animal tubes. *J. mar. Res.* 39: 361–374
- Fanning, K. A., Carder, K. L., Betzer, P. R. (1982). Sediment resuspension by coastal waters: a potential mechanism for nutrient re-cycling on the ocean's margins. *Deep Sea Res.* 29: 953–965
- Ferguson, R. L., Davis, W. R., Draxler, A. F. J., Jacobsen, T. R. (1987). Erodibility of benthic bacteria in wastewater sludge enriched coastal sediments. *Eos (Abstract)* 68: 1775
- Fukuda, M. K., Lick, W. (1980). The entrainment of cohesive sediments in freshwater. *J. geophys. Res.* 85 (C5): 2813–2843
- Grant, J., Gust, G. (1987). Prediction of coastal sediment stability from photopigment content of mats of purple sulphur bacteria. *Nature, Lond.* 330: 244–246
- Grant, W. D., Boyer, L. F., Sanford, L. P. (1982). The effects of bioturbation on the initiation of motion of intertidal sands. *J. mar. Res.* 40: 659–677
- Grant, W. D., Madsen, O. S. (1979). Combined wave and current interaction with a rough bottom. *J. geophys. Res.* 84 (C4): 1797–1808
- Gust, G. (1988). Skin friction probes for field applications. *J. geophys. Res.* 93 (C11): 14121–14132
- Gust, G., Morris, M. J. (1989). Erosion thresholds and entrainment rates of undisturbed in situ sediments. *J. coastal Res. Special Issue* 5: 87–99
- Haines, E. B., Dunstan, W. M. (1975). The distribution and relation of particulate organic material and primary productivity in the Georgia Bight, 1973–1974. *Estuar. coast. mar. Sci.* 3: 431–441
- Hedges, J. I., Stern, J. H. (1984). Carbon and nitrogen determinations of carbonate-containing solids. *Limnol. Oceanogr.* 29: 657–663
- Hopkinson, C. S. Jr (1985). Shallow-water benthic and pelagic metabolism: evidence of heterotrophy in the nearshore Georgia Bight. *Mar. Biol.* 87: 19–32
- Hopkinson, C. S. Jr (1987). Nutrient regeneration in shallow-water sediments of the estuarine plume region of the nearshore Georgia Bight, USA. *Mar. Biol.* 94: 127–142
- Kirchman, D. (1983). The production of bacteria attached to particles in a freshwater pond. *Limnol. Oceanogr.* 28: 858–872
- Mann, K. H. (1982). *Ecology of coastal waters: a systems approach.* University of California Press, Berkeley
- Nagata, T. (1986). Carbon and nitrogen content of natural planktonic bacteria. *Appl. environ. Microbiol.* 52: 28–32
- Nishino, S. F. (1986). Direct acridine orange counting of bacteria preserved with acidified Lugol iodine. *Appl. environ. Microbiol.* 52: 602–604
- Nowell, A. R. M., Jumars, P. A. (1984). Flow environments of aquatic benthos. *Ann. Rev. Ecol. Syst.* 15: 303–328
- Oertel, G. F., Dunstan, W. M. (1981). Suspended-sediment distribution and certain aspects of phytoplankton production off Georgia, U.S.A. *Mar. Geol.* 40: 171–197
- Palumbo, A. V., Ferguson, R. L., Rublee, P. A. (1984). Size of

- suspended bacterial cells and association of heterotrophic activity with size fractions of particles in estuarine and coastal waters. *Appl. environ. Microbiol.* 48: 157–164
- Parsons, T. R., Takahashi, M., Hargrave, B. (1977). *Biological oceanographic processes*, 2nd edn. Pergamon, New York
- Plummer, D. H., Owens, N. J. P., Herbert, R. A. (1987). Bacteria-particle interactions in turbid estuarine environments. *Cont. Shelf Res.* 7 (11–12): 1429–1433
- Pomeroy, L. R. (1985). The microbial food web of the southeastern U.S. continental shelf. In: Atkinson, L. P., Menzel, D. W., Bush, K. A. (eds.) *Oceanography of the southeastern U.S. continental shelf*. Am. Geophys. Union, Washington, D. C., p. 118–129
- Rhoads, D. C. (1973). The influence of deposit-feeding benthos on water turbidity and nutrient recycling. *Am. J. Sci.* 273: 1–22
- Rhoads, D. C., Tenore, K., Brown, M. (1975). The role of resuspended bottom mud in nutrient cycles of shallow embayments. In: *Estuarine research*, Vol. 1: Chemistry, biology and the estuarine system. Academic Press, New York, p. 653–679
- Rhoads, D. C., Boyer, L. F., Welsh, B. L., Hampson, G. R. (1984). Seasonal dynamics of detritus in the benthic turbidity zone (BTZ); implications for bottom-rack molluscan mariculture. *Bull. mar. Sci.* 35 (3): 536–549
- Rhoads, D. C., Yingst, J. Y., Ullman, W. J. (1978). Seafloor stability in central Long Island Sound: Part 1. Temporal changes in erodibility of fine-grained sediments. In: Wiley, M. L. (ed.) *Estuarine interactions*. Academic Press, New York, p. 221–244
- Schoenberg, S. A., McCubbin, A. E. (1985). Relative feeding rates on free and particle-bound bacteria by freshwater macrozooplankton. *Limnol. Oceanogr.* 30: 1084–1090
- Tenore, K. R. (1977). Food chain pathways in detrital feeding benthic communities: a review, with new observations on sediment resuspension and detrital recycling. In: Coull, B. C. (ed.) *Ecology of marine benthos*. University of South Carolina Press, Columbia, p. 37–53
- Vogel, S. (1981). *Life in moving fluids: the physical biology of flow*. Princeton Univ. Press, Princeton, NJ
- Wainright, S. C. (1985). Fluxes of particulate material and associated bacteria from sediments to the water column in the nearshore zone: laboratory estimates. *Eos* 66: 1315–1316 (Abstract)
- Wainright, S. C. (1986). Sediment to water flux of particulate material and associated bacteria in the nearshore zone off Georgia, U.S.A.: laboratory estimates. In: Wildish, D. J. (ed.) *Fluxes of particulate matter across benthic boundaries: a workshop report*. Can. Tech. Rep. Fish. Aquat. Sci. 1458: 12–13
- Wainright, S. C. (1987). Stimulation of heterotrophic microplankton production by resuspended marine sediments. *Science* 238: 1710–1712
- Wiberg, P., Smith, J. D. (1983). A comparison of field data and theoretical models for wave-current interactions at the bed on the continental shelf. *Cont. Shelf Res.* 2: 147–162

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