

Resuspension of phytodetritus from the sea floor: A laboratory flume study

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Abstract

Mass settling of phytoplankton can result in the accumulation of a layer of phytodetritus on the sea floor. In order to determine the fate of this organic matter, we must know whether the phytodetritus may be returned to the water column by resuspension. This study was designed to measure the critical bed shear stress (τ_{ocrit}) for resuspension of phytodetritus and to test whether τ_{ocrit} differs (1) among types of phytodetritus with different phytoplankton species composition and (2) within type among ages. Phytodetritus was created from cultured *Skeletonema costatum* and from natural assemblages dominated by *Chaetoceros* spp., collected near the end of diatom blooms in Cape Cod Bay and Woods Hole, Massachusetts. Resuspension of phytodetritus decomposed 1- to 11-d was measured in a laboratory flume. Overall, τ_{ocrit} for the diatom-derived detritus ranged by a factor of four (0.018–0.068 N m⁻²), with significant differences in τ_{ocrit} among types and ages of phytodetritus. Reasons for these differences are suggested, such as species-specific differences in size, shape, porosity, and stickiness of the detrital matrix, as well as changes in these parameters that occurred during decomposition. Values for critical shear velocity, which ranged from 0.4 to 0.6 cm s⁻¹ for *Chaetoceros*-derived detritus and from 0.5 to 0.8 cm s⁻¹ for *Skeletonema*-derived detritus, validated indirect estimates from field studies. An interesting finding with special relevance in lake and coastal systems was the importance of wave-forced resuspension, suggesting that coupling of settled phytodetritus and other sticky organic flocs to the water column is enhanced by waves.

Phytoplankton, especially chain-forming planktonic diatoms, can settle en masse, yielding a pulse of organic matter to the sea floor. Ephemeral, fluffy, green carpets of phytodetritus may cover the sea bed in areas with low flow energy, including sandy beds at slack tide. These “fluff” layers have been observed in lakes (e.g., Carrick et al. 1993), shallow marine systems (e.g., Davies 1975; Williams et al. 1998), and the deep sea (e.g., Lampitt 1985; reviewed by Beaulieu 2002). Sedimentation of relatively short-lived phytoplankton blooms may result in a significant percentage of the annual carbon input to the benthos in some systems (e.g., Goedkoop and Johnson 1996; Keller et al. 1999). To evaluate the carbon budget in such systems, we must know the fate of phytodetritus on the sea floor. Local processes may occur such as microbial decomposition, consumption by benthic fauna, dissolution, or burial into the sediments. However, phytodetritus also may be resuspended and advected laterally,

forming a major source of near-bottom suspended matter in the shallow and deep sea (e.g., Lampitt 1985; Jago et al. 1993).

Resuspension of phytodetritus increases its residence time above the sediment–water interface, delaying burial and enhancing remineralization (e.g., Jago et al. 2002). Thus, transport of phytodetritus after its initial deposition may lead to the burial of more refractory organic matter elsewhere. Resuspension and the lateral transport of phytodetritus appear to be important processes for the advection of organic carbon to deeper areas of the Baltic Sea (Leipe et al. 2000), the North Sea (Van Raaphorst et al. 1998), and the Northwest European continental margin (Thomsen and van Weering 1998). Recent studies indicated that flocs of phytodetritus were advected very near the bed rather than whisked high into the water column in the shallow (Leipe et al. 2000) and deep sea (Thomsen and van Weering 1998). This transport in proximity to the bed has implications for the redistribution of phytodetritus as food for benthic suspension feeders (e.g., Grant et al. 1997). Also, bedload transport may contribute to localized focusing of phytodetritus in depressions, redistributing food to deposit feeders (Yager et al. 1993).

In addition to balancing carbon budgets, there are many ecologically important reasons for quantifying the physical forces required to resuspend phytodetritus. Phytodetritus decomposing as a layer on the sea floor may alter chemical fluxes across the sediment–water interface (e.g., Conley and Johnstone 1995) and lead to anoxia at the sea bed (e.g., Davies 1975; Jago et al. 1993). In addition, the deposition of fine inorganic particles may be enhanced by a fluff layer overlying more consolidated sediments (Stolzenbach et al. 1992). The resuspension of phytodetritus may seed the water column with viable cells for further primary production (e.g., Carrick et al. 1993), a process that may be important in the life history of some diatoms (Smetacek 1985). Resuspension

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of phytodetritus also may be a transport mechanism for organisms or organic contaminants (Leipe et al. 2000) associated with the fluff.

Resuspension of particles from the sea floor is controlled by the bottom (bed) shear stress (τ_0). Shear stress often is described in terms of shear velocity (u_{*}), given by $\tau_0 = \rho u_{*}^2$ (in which ρ is fluid density). Critical shear stress (τ_{0crit}) and critical shear velocity (u_{*crit}) generally are defined at the threshold required to initiate particle transport. Initial motion is a function of the sediment (density, size, shape, packing, sorting, and stickiness), the fluid (density and viscosity), and the flow conditions (mean flow, oscillatory flow, turbulence; list modified from Miller et al. 1977). As flow speed and, consequently, τ_0 increase, particle transport occurs as bed-load or by resuspension into the water column. Although several recent studies examined the transport of organic particles (e.g., Huettel and Rusch 2000; Thomas et al. 2001), studies that quantify u_{*crit} for organic particles are rare. The only studies that directly determined u_{*crit} for organic detritus reported values for walnut shells, beans, and acorns (Fisher et al. 1983), fragments of cordgrass (Fisher et al. 1979), organic-rich aggregates on the surface of cores taken in the field (Thomsen and Gust 2000), and a sediment/phytodetritus mixture (Thomsen and van Weering 1998).

The present study was designed to measure the threshold for entrainment of recently deposited phytodetritus into the water column. The primary objective was to quantify the critical bed shear stress (τ_{0crit}) for phytodetritus that would result from a diatom bloom. Because initial motion is a function of the sediment matrix, it was hypothesized that τ_{0crit} (1) depends on species composition of the phytodetritus and (2) changes over time during decomposition of the organic material. The first hypothesis was drawn from knowledge that diatom aggregation is altered by species composition—particular species may form chains, and the shape and stickiness of individual cells differs broadly among species (e.g., Kiorboe and Hansen 1993; Alldredge et al. 1995). The second hypothesis was based on observations of phytodetrital decomposition—early phases include bacterial colonization and detritus aggregation, but later phases involve disaggregation and dissolution (Biddanda and Pomeroy 1988). Results from the experiments are applicable in lake and marine systems in which diatoms settle and accumulate on the bed.

Methods

Experimental treatments—Phytodetritus was created from cultured diatoms and from natural phytoplankton assemblages collected from net tows in Cape Cod Bay and Woods Hole, Massachusetts. For the initial and exploratory flume experiments in April 1999, phytoplankton were collected from Cape Cod Bay at the end of the winter/spring diatom bloom. The phytoplankton assemblage was almost entirely diatoms, dominated by *Chaetoceros socialis* (94% of cells). Glass carboys were incubated with 10-L volumes at $\sim 20^{\circ}\text{C}$ with air bubbling until the day before each flume run.

For the flume experiments in July 1999, an (initially) axenic culture (CCMP 1332 isolated from Long Island Sound) of *S. costatum*, a species that flocculates into marine snow

(e.g., Kiorboe and Hansen 1993), was used to inoculate glass carboys with 10 L of 0.2- μm filtered seawater spiked with f/2 medium (plus silicate). The cultures were maintained at a constant light intensity at $\sim 15^{\circ}\text{C}$ with air bubbling and checked daily for growth with fluorometer readings calibrated to cell counts. After the cultures reached stationary phase, with cell concentrations $\sim 4 \times 10^5$ cells ml^{-1} , carboys were kept shaded (without bubbling) at 15°C . Four sets of inoculations yielded a total of 14 carboys, each intended for a single flume run.

For the final flume experiments, phytoplankton were collected in Woods Hole during February 2000, near the end of the winter diatom bloom. Samples were collected on 2 days, yielding two sets of carboys with diatom cell concentrations of 3.6×10^5 cells ml^{-1} and 3.9×10^5 cells ml^{-1} , respectively. Almost all cells were diatoms, and both days had similar species composition, dominated by *Chaetoceros* spp. other than *C. socialis* (set 1: 67%; set 2: 66%) and *S. costatum* (set 1: 7%; set 2: 7%). A total of six carboys with ~ 10 L of concentrated cells were kept in the dark (without bubbling) at 5°C . Each carboy was used for three replicate flume runs.

Phytodetritus was decomposed up to 11 d, an appropriate time scale based on laboratory (Biddanda and Pomeroy 1988) and in situ observations of the longevity of phytodetrital fluff layers (Beaulieu 2002). On the day before each flume run, top water was siphoned from the carboys, leaving ~ 1 L of concentrated phytodetritus that was poured into graduated cylinder(s) and allowed to settle overnight. On the following morning, top water was withdrawn to ~ 300 ml, and aliquots of the concentrated phytodetritus were withdrawn for chlorophyll, bacteria, and (for *S. costatum*) carbohydrate analyses to assess decay of the diatoms. The remainder of the phytodetritus was introduced into the settling box in the flume (described below).

For chlorophyll analysis, aliquots (0.3 or 0.5 ml) were filtered in triplicate over 3- μm nitrocellulose filters. Filters were extracted in 10 ml of 90% acetone for 24 h, and fluorescence was measured with a Turner Designs fluorometer. For microscopic analysis, 1-ml aliquots were preserved to 4% glutaraldehyde. Subsamples (10 μl) were diluted with particle-free water, treated with Tween-80 (Sigma), and sonicated (Yoon and Rosson 1990). Duplicate 0.2- μm black polycarbonate filters were prepared with DAPI for counting bacteria under a Zeiss epifluorescence microscope at $\times 1,250$ (Porter and Feig 1980). For the cultured *S. costatum* detritus, a phenol-sulfuric acid assay (Dubois et al. 1956) was used to analyze bulk carbohydrates of 5-ml aliquots retained on precombusted GF/F filters. Each sample was analyzed on a HP 8452A spectrophotometer and calibrated via a standard curve of absorption versus glucose concentration.

Analysis of critical shear stress—Critical bed shear stresses (τ_{0crit}) were measured in a 17-m-long, 60-cm-wide, open-channel flume at Woods Hole Oceanographic Institution (Butman and Chapman 1989). A removable bottom panel with a recessed 20- \times 20- \times 2-cm deep box was placed in the flume, centered at 12.9 m downstream. The box was filled with sieved sand (250–500 μm), leveled ~ 1 –2 mm

below flush to create the test bed. At the beginning of each experiment, the flume was filled to 12-cm water depth with 10- μm filtered seawater, moving at the slowest possible flow speed ($\sim 3 \text{ cm s}^{-1}$). An acrylic fence, covered with plastic wrap, was placed around the test bed, and a wide-mouthed pipette was used to introduce phytodetritus into the enclosed volume. To simulate settling during a tidal cycle, the phytodetritus was given 3 h to accumulate into a layer on the sand bed. The analysis of critical shear stress began when the fence was removed, exposing the phytodetrital layer to the overlying flow.

The test bed surface was illuminated from above with a light sheet ($\sim 2 \text{ cm}$ wide at the bed), and a video camera recorded a section of the flow directly above the test bed. As the flow speed was increased in the flume, the following visual criteria were used for determining thresholds for three stages of particle transport: initial motion—when particles (i.e., phytodetrital flocs) started rolling; bedload—when most particles were rolling and some were saltating; resuspension—when particles were lifting from and not returning to the bed. The threshold criterion for initial motion has been defined in many ways (e.g., Miller et al. 1977; Lavelle and Mofjeld 1987). The heterogeneous sizes and shapes and unknown specific gravity of phytodetrital flocs precluded using a more objective criterion for initial motion (e.g., Yalin 1977, p. 100–102).

Mean shear stress ($\bar{\tau}_0$) at each stage of particle transport was estimated by analyzing profiles of mean along-channel velocity, measured with a laser Doppler velocimeter. Flow profiles were 4-min records at each of 10 points between 0.9 and 8.0 cm above bottom. These measurements were fit to a model consisting of the Prandtl–Von Karman law of the wall plus the Coles wake correction,

$$\bar{u}(z) = u_* \left[f \left(\frac{u_* z}{\nu} \right) + \frac{2\Pi}{\kappa} \sin^2 \left(\frac{\pi z}{2h} \right) \right] \quad (1)$$

which is accurate in smooth-turbulent, open-channel flow (Nezu and Rodi 1986; Trowbridge et al. 1989). Here, \bar{u} is mean velocity, z is height above bottom, $u_* = (\bar{\tau}_0/\rho)^{1/2}$, f is an empirical expression for the log layer (e.g., Von Reichardt 1951), ν is kinematic viscosity, Π is Coles parameter, κ is Von Karman's constant, and h is water depth. Due to the limited amount of phytodetritus on the test bed and the length of time required for a complete flow profile, in some experiments, only \bar{u} at $z = 8 \text{ cm}$ was measured, and u_* was estimated via a drag law ($u_* = 0.0419\bar{u}_8 + 0.0574$; $n = 84$ profiles, $r^2 = 0.999$).

Spectral analysis of the flow records revealed that most of the variance was at a 30-s period, likely due to standing waves in the flume (Trowbridge et al. 1989). An estimate of the thickness of the wave boundary layer was of the same order of thickness as the phytodetrital layer. The importance of waves in mobilizing phytodetritus at low flow speeds is demonstrated visually in Web Appendix 1 (<http://www.aslo.org/lo/toc/vol.48/issue.3/1235a1.html>). Therefore, each estimate of critical shear stress (τ_{ocrit}) included a wave-induced component in addition to a mean component. The following model for an oscillatory bound-

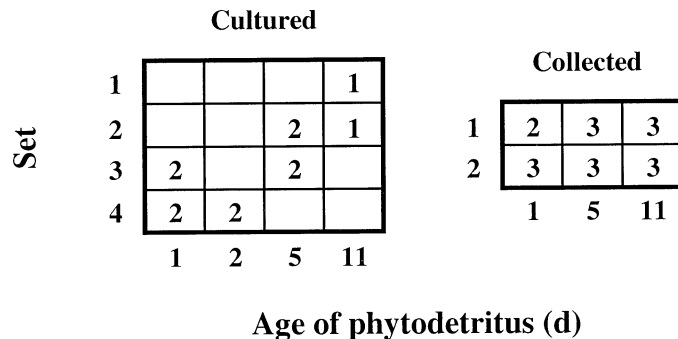


Fig. 1. Factorial designs resulting from flume experiments. Left: incomplete 4×4 design for flume runs with cultured *Skeletonema costatum*. Right: fully crossed 2×3 design for flume runs with phytoplankton collected from Woods Hole in February 2000. Number of replicates is listed in each cell.

ary layer was used to estimate time series of wave-forced bottom stress:

$$\frac{\partial \tilde{u}}{\partial t} = \frac{\partial \tilde{U}}{\partial t} + v \frac{\partial^2 \tilde{u}}{\partial z^2} \quad (2)$$

in which

$$\tilde{\tau}_0 = \rho \nu \left(\frac{\partial \tilde{u}}{\partial z} \right)_{z=0} \quad (3)$$

(Batchelor 1967). Here, $\tilde{u}(z, t)$ is wave-induced along-channel velocity within the wave boundary layer, t is time, $\tilde{U}(t)$ is wave-induced along-channel velocity above the wave boundary layer, and $\tilde{\tau}_0(t)$ is wave-induced bottom stress. To solve the partial differential equation, an input time series of horizontal velocity at 1.2 cm above bottom was transformed to the frequency domain by fast Fourier transform. An inverse Fourier transform then was applied to obtain a time series of $\tilde{\tau}_0(t)$. (Matlab routines for the estimation of mean and wave-forced bottom stress are available from the author.) Critical shear stress then was estimated as $\tau_{\text{ocrit}} = \bar{\tau}_0 + \max(\tilde{\tau}_0(t))$ and critical shear velocity as $u_{*\text{crit}} = (\tau_{\text{ocrit}}/\rho)^{1/2}$. The technique for estimating $u_{*\text{crit}}$ was checked by running additional experiments with the test bed filled with sand of the following grain sizes: 125–250 μm , 250–500 μm , and 500–1,000 μm . Estimates of $u_{*\text{crit}}$ for initial motion of sand compared well with the expected threshold values (Miller et al. 1977).

Experimental design and statistics—One-way analysis of variance (ANOVA) was used to compare τ_{ocrit} among the three types of phytodetritus (at the same age), with planned multiple comparisons by the least significant difference (LSD) procedure. Assumptions of ANOVA were checked with normal probability plots and Bartlett's test for homogeneity of variances. Experimental designs to determine whether τ_{ocrit} differed among ages (within type) of phytodetritus were constrained by the maximum number of flume runs per day, which required the preparation of at least two "sets" of carboys of phytodetritus in order to obtain more replicate measurements (Fig. 1). Although one replicate was lost due to technical complications, the experimental design

Table 1. Summary of critical shear velocities for resuspension of phytodetritus in flume experiments.

| Type of phytodetritus | Age of phytodetritus (d) | No. of flume runs | Critical shear velocity, u_{*crit} (cm s ⁻¹) | |
|---|--------------------------|-------------------|--|-----------|
| | | | Mean | Range |
| Collected from Cape Cod Bay in Apr 1999 | 5 | 1 | 0.45 | n/a |
| | 7 | 2 | 0.45 | 0.42–0.48 |
| Cultured <i>Skeletonema costatum</i> | 1 | 4 | 0.68 | 0.63–0.75 |
| | 2 | 2 | 0.73 | 0.64–0.82 |
| | 5 | 4 | 0.55 | 0.52–0.59 |
| | 11 | 2 | 0.61 | 0.58–0.63 |
| Collected from Woods Hole in Feb 2000 | 1 | 5 | 0.55 | 0.52–0.58 |
| | 5 | 6 | 0.50 | 0.46–0.54 |
| | 11 | 6 | 0.51 | 0.47–0.54 |

for the phytoplankton collected in February 2000 was fully crossed (Fig. 1) and was analyzed by two-way ANOVA with age and set as factors. Planned comparisons by LSD were conducted for the age effect. Due to the labor-intensive demands of maintaining large culture volumes as well as technical complications with the flume, the resulting factorial design for cultured *S. costatum* was incomplete (Fig. 1). The pattern of missing data precluded comparison of τ_{0crit} for *S. costatum* detritus as a two-way ANOVA.

In addition to the above statistical tests, the nonparametric Spearman's rank correlation coefficient (r_s) was used to examine the correlation of u_{*crit} and biochemical content to age (within type) of phytodetritus. Pearson's product-moment correlation coefficient (r) was used to examine the correlation of u_{*crit} to biochemical content (within type) of the phytodetritus. Statistics were conducted with Statistica 5.1 software, tested for significance at $\alpha = 0.05$, and are described by Sokal and Rohlf (1981).

Results

Critical shear stress for resuspension—Overall, τ_{0crit} for resuspension of phytodetritus ranged over a factor of four

(0.018–0.068 N m⁻²), with values for critical shear velocity (u_{*crit}) ranging from 0.42 to 0.82 cm s⁻¹ ($n = 32$ flume runs; Table 1). Critical shear stresses for initial motion and bed-load transport of phytodetritus, respectively, ranged from 30 to 50% and 50 to 70% of τ_{0crit} for resuspension. For some flume runs with collected, natural assemblage phytodetritus, initial motion occurred at the lowest bed stress that could be tested in the flume (~ 0.009 N m⁻²). The wave-forced component contributed 12–32% of the critical shear stress for resuspension of phytodetritus in the flume.

Among types of phytodetritus, the cultured *S. costatum* detritus was the most difficult to resuspend from the bed, with u_{*crit} measurements greater than all measurements for *Chaetoceros socialis* collected in April 1999 and most measurements for the mainly *Chaetoceros* spp. collected in February 2000 (Table 1). The mean τ_{0crit} estimates for resuspension of 5-d detritus (including 7-d *C. socialis*) differed significantly ($F_{2,10} = 10.65$, $P = 0.003$), and planned comparisons indicated that all types differed from each other. Qualitatively, the *S. costatum* detritus was composed of dense, discrete aggregates; the February 2000 *Chaetoceros* spp. detritus was the most fluid; and the April 1999 *C. socialis* detritus (easiest to resuspend) was loose with fluffy, discrete aggregates.

Critical shear stresses for resuspension also differed within type, among ages of phytodetritus. These differences were most dramatic for the cultured *S. costatum* detritus (Fig. 2), for which u_{*crit} decreased with age ($r_s = -0.63$, $P = 0.03$). Ignoring the “set” (i.e., inoculation) effect altogether, a one-way ANOVA revealed a significant age effect ($F_{3,8} = 4.74$, $P = 0.03$). However, the incomplete factorial design precluded more appropriate analysis with both age and set effects. The lowest u_{*crit} value for *S. costatum* detritus resulted from 5-d detritus rolling upon itself in clumps (~ 1 -cm diameter) that projected into the flow. On one occasion, 2-d *S. costatum* detritus appeared to adhere to the sand grains in the test bed, yielding the highest u_{*crit} value for all the flume runs.

For the natural assemblage collected in February 2000 (mainly *Chaetoceros* spp.), τ_{0crit} for resuspension also was

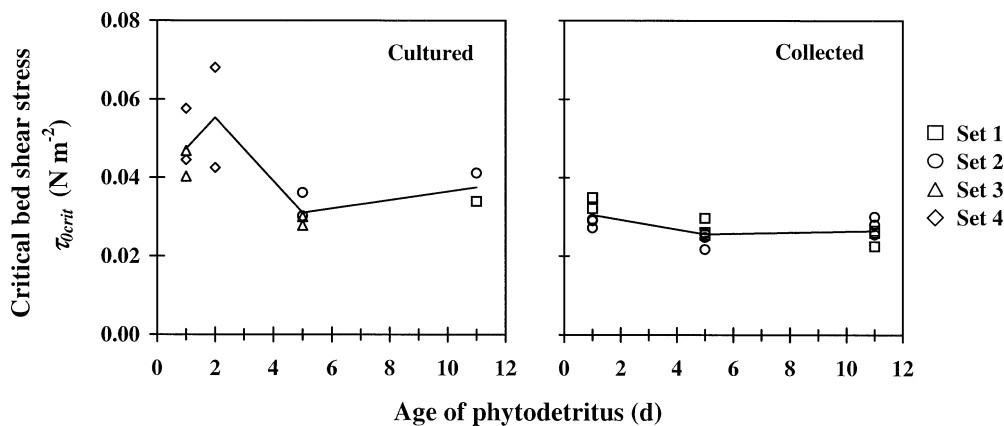


Fig. 2. Critical bed shear stress (τ_{0crit}) for resuspension of phytodetritus in flume experiments. Left panel: cultured *Skeletonema costatum*; right panel: phytoplankton collected from Woods Hole in February 2000. Symbols indicate single estimate for each individual flume run. Lines connect the mean for each age.

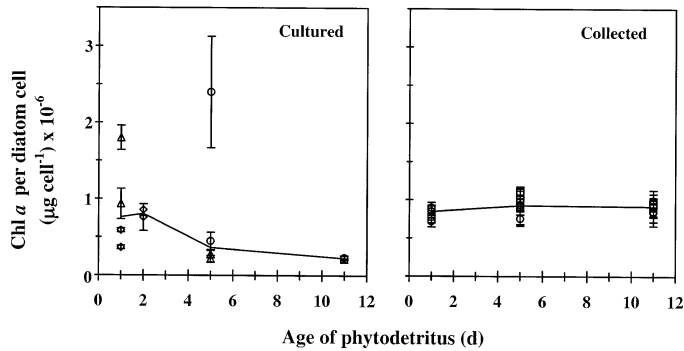


Fig. 3. Chlorophyll *a* normalized to initial diatom cell concentration in phytodetritus. Panels and symbols as in Fig. 2. Symbols indicate mean and error bars standard deviation of three replicate measurements. Lines connect the median for each age.

greatest for the fresh, 1-d phytodetritus (Fig. 2), although the correlation of $u_{s,crit}$ with age was not significant ($r_s = -0.43$, $P = 0.11$). The mean $\tau_{0,crit}$ for set 1 decreased with age, while set 2 had a minimum $\tau_{0,crit}$ at 5-d. Age and interaction effects in the two-way ANOVA were significant for differences in the mean $\tau_{0,crit}$ values (age: $F_{2,11} = 10.60$, $P = 0.003$; set: $F_{1,11} = 2.86$, $P = 0.12$; interaction: $F_{2,11} = 5.57$, $P = 0.02$). Although the difference among ages in $\tau_{0,crit}$ for resuspension was significant, the magnitude of this difference was much less than for *S. costatum* detritus. Planned comparisons for the age effect indicated that the 5- and 11-d samples grouped together, with $\tau_{0,crit}$ less than 1-d detritus. During the flume runs with the 5-d (and some 11-d) detritus, resuspension occurred when particles were pulled off bumps (2–3 mm high) that developed in the fluid detrital layer.

Biochemical analyses—In order to compare quantitatively the composition of phytodetritus among experimental treatments, chlorophyll, bacteria, and carbohydrate concentrations were normalized to initial diatom cell concentration (at age = 0 d). For the cultured *S. costatum* detritus, chlorophyll content tended to decrease with age ($r_s = -0.59$, $P = 0.04$; Fig. 3). Qualitatively, the *S. costatum* detritus changed markedly with age, with 1- and 2-d samples having intact cells in chains and 5- and 11-d samples having progressively more

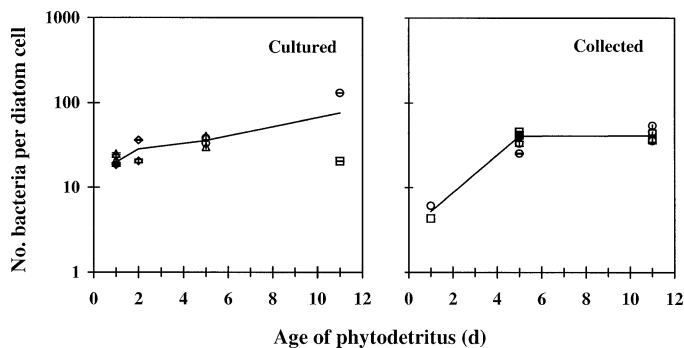


Fig. 4. Bacteria counts normalized to initial diatom cell concentration in phytodetritus. Panels and symbols as in Fig. 2. Symbols indicate mean and error bars range of two replicate counts. Lines connect the median for each age.

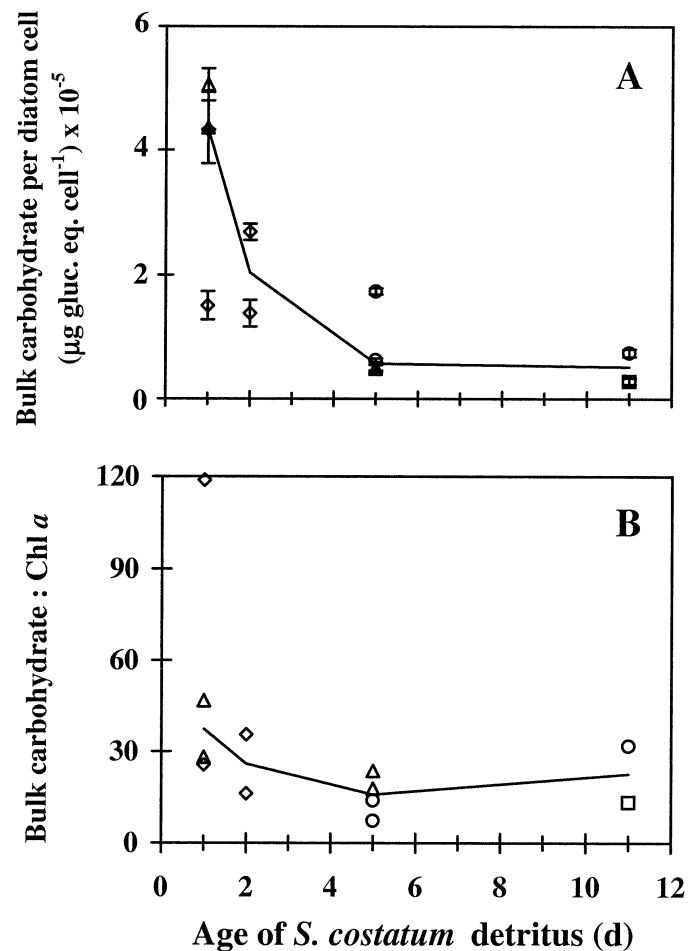


Fig. 5. Carbohydrate content of *Skeletonema costatum* detritus. Symbols as in Fig. 2. Lines connect the median for each age. (A) Bulk carbohydrate concentration normalized to initial diatom cell concentration. Symbols indicate mean and error bars range of two replicate measurements. “Gluc. eq.” is an abbreviation for “glucose equivalent.” (B) Bulk carbohydrate concentration normalized to chlorophyll *a* concentration. These ratios are derived from mean values.

broken chains and disintegrated frustules. In contrast, there was no change in chlorophyll content with age for the natural assemblage (mainly *Chaetoceros* spp.) collected in February 2000 (Fig. 3). Values for chlorophyll content were similar to the 1- and 2-d *S. costatum* detritus and, qualitatively, there was very little to no change over time in general appearance of the cells under the microscope.

The number of bacteria generally increased with age for both the *S. costatum* ($r_s = 0.57$, $P = 0.05$) and the February 2000 *Chaetoceros* spp. phytodetritus ($r_s = 0.52$, $P = 0.06$; Fig. 4). Arguably, bacterial populations may have declined in the 11-d *S. costatum* detritus (set 1) or stabilized for the 11-d *Chaetoceros* spp. phytodetritus. Under the microscope, 5- and 11-d *S. costatum* detritus appeared to have bacteria associated tightly with aggregates of degrading diatom cells. Clearly, bulk carbohydrate content decreased with age of the *S. costatum* detritus, particularly between 1 and 5 d ($r_s = -0.81$, $P = 0.001$; Fig. 5A). The chlorophyll weight-specific

carbohydrate concentration (i.e., the bulk carbohydrate-to-chlorophyll ratio) also was correlated negatively with age of the *S. costatum* detritus ($r_s = -0.59$, $P = 0.04$). However, the median carbohydrate-to-chlorophyll ratio was at a minimum for 5-d detritus (Fig. 5B).

Critical shear velocity (u_{*crit}) was not correlated significantly with the chlorophyll or bacteria content of either the cultured or collected phytodetritus. In addition, u_{*crit} was not correlated significantly with bulk carbohydrate content or the carbohydrate-to-chlorophyll ratio of *S. costatum* detritus, although the patterns in Figs. 2 and 5B are similar in showing minimums for 5-d detritus.

Discussion

Differences in critical shear stress—The original hypotheses, that both species composition and age would affect the erodibility of phytodetritus, were confirmed by the results of flume experiments. The differences in critical shear stress likely resulted from differences in the composition of the detrital (i.e., sediment) matrix. The initial motion of sediment is known to be a function of such parameters as density, size, shape, sorting, packing (or porosity), and stickiness (list modified from Miller et al. 1977). As suggested below, size, shape, porosity, and stickiness may have played the major roles in determining τ_{ocrit} for resuspension of phytodetritus. Differences in the density of diatom cells as individual sediment grains were assumed to play a minor role. Sorting may have played a minor role for the natural assemblage collected in February 2000, which was composed of several diatom species.

Phytodetritus composed mainly of *Chaetoceros* species resuspended more readily than *S. costatum* detritus, potentially due to species-specific differences in the size and shape of cells, chains, and aggregates. *S. costatum* has small cells arranged in straight chains, with frustules on the order of 10 μm and no setae (spines). *C. socialis*, which dominated the assemblage collected in April 1999, had similar sized cells with spines and chains associated in tight spherical colonies (colony diameter up to 1 mm). The mixed assemblage of mostly *Chaetoceros* spp., collected in February 2000, included cells much larger than *S. costatum*, with spines and a variety of chain structures. The larger size of the *Chaetoceros* spp. cells (and *C. socialis* colonies) as well as their spines likely enhanced drag on the bed, making the *Chaetoceros* detritus more susceptible to resuspension. The actual size of flocs (aggregates) was difficult to categorize due to the fluid nature of the phytodetrital layer. However, it appeared that aggregates that projected into the flow (i.e., the bumps in the 5-d *Chaetoceros* spp. phytodetrital layer) were mobilized at lower bed stresses. The *Chaetoceros* spines also may have enhanced erodibility by increasing the porosity (i.e., bulk water content) of the detrital matrix. Increased porosity has been shown to increase the entrainment rate of cohesive sediments (e.g., Sanford 1994). Porosities for newly formed diatom flocs composed mainly of *Chaetoceros radicans* have been reported in excess of 99.9% (Logan and Alldredge 1989).

Species-specific differences in stickiness also may have

led to differences in τ_{ocrit} for resuspension. Stickiness may be due to extracellular polymeric substances (EPS; Hoagland et al. 1993) attached to the diatom frustules or released as transparent exopolymer particles (TEP; e.g., Alldredge et al. 1995). Marine snow aggregates can be held together by a matrix of EPS and TEP (e.g., Alldredge et al. 1995; Heissenberger et al. 1996). Diatom species produce different types and amounts of EPS (Hoagland et al. 1993). For example, some studies have found particular species of *Chaetoceros* to produce more EPS than *S. costatum* (Hoagland et al. 1993), and Kiorboe and Hansen (1993) reported cell–cell sticking in *S. costatum* versus cell–TEP–cell sticking in *C. affinis*. Stickiness of phytoplankton, usually determined empirically in a Couette device (e.g., Dam and Drapeau 1995), is a difficult parameter to quantify. Differences in the mucous matrix responsible for stickiness of phytodetritus require further study (as detailed below).

The detrital matrix changed as phytodetritus decomposed, leading to changes in τ_{ocrit} with age of phytodetritus. Results of this study were consistent with the suggestion that phytodetritus can be resuspended “only if the detrital aggregates have degraded somewhat” (Lampitt 1985). The *S. costatum* detritus used in the flume experiments closely followed the schematic of phytodetritus decomposition presented by Bidanda and Pomeroy (1988), in which bacterial colonization occurs by day 1 and detritus aggregation by day 3 and disaggregation and dissolution of phytodetritus starts by day 9. As for the phytoplankton (mainly *Chaetoceros* spp.) collected in February 2000 and kept at a much lower temperature, the detritus had little change in appearance under the microscope and no change in chlorophyll content over 11 d. Although the February 2000 phytodetritus did not appear to have degraded, there were two major changes in the detrital matrix: more bacteria colonized the 5- and 11-d samples and bumps developed in the 5-d (and some 11-d) phytodetrital layers upon exposure to the flow.

Qualitative observations suggested that the change in τ_{ocrit} likely was influenced by changes in stickiness of the detrital matrix with age. Dam and Drapeau (1995) determined that stickiness of live planktonic diatoms was correlated with chlorophyll weight-specific carbohydrate concentration, considered a measure of “organic glue.” Sutherland et al. (1998), studying benthic diatoms, found a negative correlation between erosion rate and bulk carbohydrate-to-chlorophyll ratio. However, the bulk carbohydrate-to-chlorophyll ratio was not correlated with the u_{*crit} for *S. costatum* detritus and, apparently, was not a useful biochemical proxy for stickiness. Although polysaccharides are the primary component of diatom EPS (Hoagland et al. 1993), the phenol-sulfuric acid assay for bulk carbohydrates was not specific for extracellular carbohydrates. Perhaps an assay specific for extracellular carbohydrates, such as TEP, would be more appropriate for generating information on detrital stickiness. In addition, mucus deriving from bacterial EPS, reported to influence the structure of marine snow (Heissenberger et al. 1996), may have increased the stickiness of phytodetritus.

Implications for resuspension of phytodetritus in the field—Most estimates of u_{*crit} for resuspension of phytodetritus in the field were indirect, depending on associating an

Table 2. Comprehensive list of critical shear velocities for resuspension of phytodetrital (and other) fluff layers. A quadratic drag coefficient ($C_D = 0.0025$) was assumed for those studies that reported only a horizontal flow speed. a.b., above bottom; n.d., not determined; n/a, not applicable.

| Composition of fluff layer | Locale | Method | u_{*crit} (cm s ⁻¹) | Citation |
|--|-----------------------------|---|-----------------------------------|--------------------------------|
| <i>Phaeocystis</i> sp. | North Sea, 29 m | Photographs of the sea floor; transmissometer and flow at 1 m a.b. | 0.3* | Williams et al. (1998) |
| n.d. | Loch Ewe, Scotland, 30 m | In situ annular chamber | 0.3–0.35† | Davies (1975) |
| n.d. | NE Atlantic, 4,025 m | Photographs of the sea floor; flow at 1 m a.b. | 0.35 | Lampitt (1985) |
| Organic-rich aggregates deriving mainly from phytoplankton | Western Baltic Sea, 16–47 m | Water samples, video, and flow at 40 cm a.b. | 0.4–0.5 | Leipe et al. (2000) |
| Mainly <i>Chaetoceros</i> spp. | n/a | Laboratory flume | 0.4–0.6 | This paper |
| Diatoms and radiolarians | NE Pacific, 4,100 m | Turbidity in near-bottom photographs; flow at 2.5 m a.b. | 0.4–0.7 | Beaulieu and Baldwin (1998) |
| Particles >100 μ m with organic content up to 75% and C:N >8 | NE Atlantic, 212–4,940 m | Core-top erosion chamber | 0.4–1.2 | Thomsen and Gust (2000) |
| Discrete phytodetrital aggregates | NE Atlantic, 4700 m | Photographs of the sea floor; nephelometer at 1 m a.b.; flow at 10 m a.b. | 0.45 | Auffret et al. (1994) |
| Organic-rich aggregates deriving mainly from phytoplankton | North Sea, 110 m | Transmissometers at 1.5 and 10 m a.b.; flow at 0.3 and 0.6 m a.b. | 0.45–0.55‡ | Jago et al. (2002) |
| <i>Skeletonema costatum</i> | n/a | Laboratory flume | 0.5–0.8 | This paper |
| Diatoms, silt, and amorphous matter | Rockall Trough, 2,285 m | Water samples and flow at 10–40 cm a.b. | 0.6 | Thomsen and McCave (2000) |
| n.d. | Chesapeake Bay, 6 m | In situ benthic flume | 0.7§ | Maa et al. (1998) |
| Diatoms and fine-grained sediment; enriched in organic carbon | North Sea, 45 m | Sediment trap at 3 m a.b.; turbidity at 4.5 m a.b.; flow at 1.5 m a.b. | 0.8 | Van Raaphorst et al. (1998) |
| Sediment/phytodetritus mixture | NE Atlantic, 670 m | Cores inserted into laboratory flume | 0.9–1.2 | Thomsen and van Weering (1998) |

* However, maximum suspended matter occurred when flow was 13 cm s⁻¹, corresponding to $u^* \sim 0.65$ cm s⁻¹ (fig. 14 in Jago and Jones 1998).

† Flow 6–7 cm s⁻¹ in chamber 5 cm high. Fluff layer enriched in organic content but not necessarily phytodetritus.

‡ Assumed fluid density $\rho = 1$ for reported values of τ_{0crit} (0.02–0.03 Pa).

§ Some resuspension occurred at lower bed stress, and Sanford and Maa (2001) assumed $u_{*crit} \sim 0.3$ cm s⁻¹. A dinoflagellate bloom might have contributed to the fluff layer (L. Sanford pers. comm.).

increase in water-column turbidity with an increase in mean flow speed (Table 2). A major objective of this study was to obtain more controlled estimates of the threshold for entrainment of a phytodetrital “fluff” layer into the water column. Although these experiments simulated the resuspension of flocs in a turbulent benthic boundary layer, the initial settling and deposition of the flocs occurred in a relatively still and clear water column. Flocs settling in the field would be exposed to turbulence as well as scavenge suspended particulate matter. These factors would have to be considered before laboratory results could be applied directly to ecological models. Nevertheless, the measurements obtained in this study validate the u_{*crit} estimates from field studies, which ranged from 0.3 to 1.2 cm s⁻¹ (Table 2). These u_{*crit} values for phytodetritus and organic aggregates are much lower than for benthic diatoms (u_{*crit} up to 2.7 cm s⁻¹; Sutherland et al. 1998). However, this study demonstrates that, when planktonic diatoms accumulate as a phytodetrital layer on the sea floor, it is not true that “sedimented planktonic algae

are resuspended by even the slightest boundary flow” (Huetel and Rusch 2000). Given the results of this laboratory study and assuming a drag coefficient ($C_D = u_{*crit}^2 \bar{u}^{-2} = 0.0025$) for flow above the bottom boundary layer, resuspension of planktonic diatom-derived detritus in the field would be initiated at flow speeds of ~ 8 –16 cm s⁻¹.

Settling velocity of the resuspended flocs of phytodetritus was not measured during the flume experiments. However, resuspension would be expected when the settling velocity (w_s) of the flocs scales to critical shear velocity, on the order of 0.5 cm s⁻¹. This estimate, which corresponds to 432 m d⁻¹, is greater than the settling velocity usually suggested for marine snow (100–200 m d⁻¹). However, this estimate matches direct measurements of w_s for phytodetritus collected from multiple core samples (300–1,020 m d⁻¹, Lampitt 1985; 0.5 cm s⁻¹, Thomsen and van Weering 1998) and indirect estimates from field studies (e.g., 0.5 cm s⁻¹, Jago et al. 1993; up to 0.57 cm s⁻¹, Jago et al. 2002). This higher settling velocity may be responsible for the “bottom-heavy”

concentration profile of organic aggregates transported in the benthic boundary layer (assumed to be phytodetritus based on concentration profiles of phaeopigments; Thomsen and van Weering 1998; Leipe et al. 2000). However, as observed in some of the flume runs, the bed shear stress sometimes pulled very small particles off the tops of bumps that developed in the fluid phytodetrital layer. This observation was consistent with a suggestion that fine particles in the benthic boundary layer can derive from "the destruction of the large flocculent [particles] on the seabed and by upward diffusion of disintegrated particles" (Kajihara et al. 1974).

Resuspension of phytodetritus and lateral transport of the organic particles can be important to consider when constructing a carbon budget for some aquatic systems. The erosion of a fluff layer may be described by Type I erosion, or erosion of a finite supply of sediment overlying a more consolidated bed (Sanford and Maa 2001). Thomsen and Gust (2000) detailed such a two-layer concept of the sediment interface and suggested that organic aggregates are transported in resuspension-deposition loops over long distances. A model for the transport of phytodetritus (and other types of organic particles) would have to include transport parameters (mean and/or tidal flow, wave boundary layer, u_{*crit}) and loss terms (burial, consumption, decomposition, dissolution). Type I erosion and advection of organic fluff in the North Sea was described in a simple model by Van Raaphorst et al. (1998), which assumed $u_{*crit} = 0.8 \text{ cm s}^{-1}$. Also for the North Sea, Type I erosion of *Phaeocystis* sp. fluff was described in a more complex model by Jones et al. (1996) that included both fresh and degraded phytodetritus. However, these models did not incorporate wave/current interaction, changes in particle characteristics over time, or loss terms due to biological processes. Instead of defining u_{*crit} for phytodetritus, Jones et al. (1996) parameterized entrainment (erosion) rate as a function of bed shear stress (e.g., Lavelle and Mofjeld 1987). The flume experiments in this study were not designed to measure the erosion rate of phytodetritus; however, crude estimates can be made by dividing the volume of eroded detritus by the area of the test bed and by the elapsed time. Conservative estimates for the erosion rate of *S. costatum* detritus at τ_{ocrit} for resuspension were $2\text{--}5 \times 10^{-5} \text{ cm s}^{-1}$. Estimates for phytodetritus from the natural assemblage collected in February 2000 were $6\text{--}8 \times 10^{-4} \text{ cm s}^{-1}$. These erosion rate estimates may be converted to milligrams dry weight (or no. cells) $\text{cm}^{-2} \text{ s}^{-1}$ by multiplying by 5 mg cm^{-3} (or $5 \times 10^6 \text{ cells cm}^{-3}$). In addition to models of transport, a model such as that proposed by Sanford (1992) could be modified to derive the probability of organic carbon burial given a certain phytodetrital sedimentation rate. Sanford (1992) incorporated a critical shear stress for resuspension in a model for the probability of burial as a function of time after initial deposition of a sediment particle.

In this study, total bed shear stress was calculated as the sum of mean and wave-induced shear stress. Other laboratory investigations have confirmed that long-period (12–15 s) waves interact with unidirectional currents to produce a "fully combined" flow near the bed, thus requiring lower mean current speeds to initiate sediment transport (Paphitis et al. 2001). Such wave-forced sediment resuspension is con-

sidered important in many lake and coastal marine environments (e.g., Sanford 1994). In the North Sea, resuspension of phytodetritus increased during wave enhancement of bed stress (Jago et al. 1993; Williams et al. 1998). Indeed, Gons (1991) suggested wind-generated surface waves as the main cause of resuspension of settled diatom cells in shallow lakes. In the Baltic Sea, resuspension events in shallow areas were driven mainly by wind-forced waves, decreasing the residence time of fluff layers on the bottom as compared with deeper areas (Leipe et al. 2000). In addition to applying shear stress on the bed, wave forcing may affect the physical consistency of the uppermost sediments. For example, Sanford (1994) suggested that recently deposited sediments in Chesapeake Bay were susceptible to resuspension in part because wave forcing loosened the sediment grains by "partial fluidization," effectively increasing porosity and decreasing τ_{ocrit} (Sanford and Maa 2001). This wave-forced agitation was suggested as a means of hydrodynamic coupling between a fluff layer and the overlying water column that enhanced deposition of fine particles to the bed (Stolzenbach et al. 1992). In these flume experiments, wave forcing also appeared to interact with the stickiness of the phytodetrital layers, with the reversal in direction of flow in the wave boundary layer causing the formation of bumps that projected into the flow. Stolzenbach et al. (1992) suggested that shear induced by near-bottom wave motion can be sufficient to entrain overlying fluid into a porous interfacial layer. Thus, in the field, in addition to enhancing resuspension, oscillatory forcing may enhance advective flushing of fluff layers, promoting aerobic decomposition of organic particles that accumulate on the sediment surface.

In summary, these laboratory experiments confirmed the indirect estimates of τ_{ocrit} for resuspension of phytodetritus in the field and pointed to factors that would contribute to variability in the entrainment threshold. Ideally, further laboratory studies of the resuspension of organic flocs should incorporate waves, turbulence, suspended inorganic particulate matter, and the measurement of size spectra and settling velocity of flocs during settling and resuspension. The processes involved in the selective entrainment of organic particles from an inorganic bed deserve much future study.

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