

## Sequential resuspension of protists by accelerating tidal flow: Implications for community structure in the benthic boundary layer

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### Abstract

We measured resuspension thresholds of protists and bacteria at a subtidal coastal site with in situ flumes and by sampling the benthic boundary layer during tidal accelerations. Heterotrophic nanoflagellates, oligotrich ciliates, the diatom *Navicula distans*, and bacteria resuspended in weak flow (friction velocity  $u_{*crit} = 0.25\text{--}0.80\text{ cm s}^{-1}$ ), likely associated with a surficial fluff layer of sediment. Hypotrich ciliates, scuticociliates, and the diatoms *N. transitans* and *Pleurosigma* sp. resuspended in moderate flow ( $u_{*crit} = 0.82\text{--}1.3\text{ cm s}^{-1}$ ), followed by pigmented nanoflagellates and diatoms of two *Nitzschia* spp. in strong flow ( $u_{*crit} \geq 1.5\text{ cm s}^{-1}$ ). Hypotrichs and scuticociliates resuspended independent of sediment erosion thresholds, whereas most diatoms resuspended with bulk sediment. Differing thresholds may be due to cell size, specific gravity, behavior, or association with particles. As tidal currents accelerated to  $u_* = 1.3\text{ cm s}^{-1}$ , resuspension caused cell concentrations at 5 cm above bottom to increase by 2–16 times, varying among taxa. Community structure shifted accordingly, with total oligotrichs, hypotrichs, and scuticociliates changing from 75% to 96% of the ciliate community and the total diatom taxa listed above changing from 37% to 63% of the pennate cells. Sequential resuspension suggests that the species assemblage entering the water column during a resuspension event depends on the maximal bed shear stress, thus varying with the spring-neap cycle as well as atmospheric forcing and local hydrography. Flow-induced fluctuations of community structure may influence microbial food-web dynamics in the benthic boundary layer and sediment.

Resuspension by currents and waves plays major roles in sediment transport, chemical fluxes to the water column, and biological productivity (Fanning et al. 1982; Hopkinson 1987; Sanford and Maa 2001). Protists can be resuspended and greatly affect water-column and benthic processes. Resuspended microalgae, in particular, can alter phytoplankton community structure, enhance phytoplankton biomass and primary productivity, and serve as food resources for zooplankton as well as benthic suspension feeders (Roman and Tenore 1978; Baillie and Welsh 1980; Shaffer and Sullivan 1988; de Jonge and van Beusekom 1992; Lucas et al. 2001).

In contrast to microalgae, little is known about the role of heterotrophic protists in resuspension or about effects of resuspension on the microbial food web. Only a few studies have addressed the impact of resuspension on distributions or productivity of heterotrophic protists (e.g., Wainright 1987, 1990; Shimeta and Sisson 1999; Garstecki and Wickham 2001).

Resuspension and deposition of protists blur the distinction between planktonic and benthic communities. Protists that regularly or frequently resuspend and deposit constitute a unique guild of benthic-planktonic species. Some species have been identified as benthic-planktonic on the basis of finding them in both plankton and sediment samples (Patterson et al. 1989; Tomas 1997; Arndt et al. 2000; Garstecki et al. 2000). Some heterotrophic protists that are typically considered benthic have also been found on suspended aggregates (Zimmermann-Timm et al. 1998). Direct exchange of such taxa from sediment to the water column has been demonstrated, mostly for microalgae and in a few cases for heterotrophic protists, by flume studies and by time-series field sampling during wind- or tide-induced flow (e.g., Demers et al. 1987; Wainright 1990; Jonsson and Johansson 1997; Shimeta and Sisson 1999; Lucas et al. 2000, 2001).

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There is limited understanding of the unique ecology of benthic-planktonic protists. Key issues include the temporal patterns and influencing factors of the resuspension process and the activities (photosynthesis, feeding, and growth) and fates (dispersal, deposition, and mortality) of cells once they are in the water column.

An important question regarding the resuspension process is whether various benthic-planktonic taxa resuspend simultaneously as a group, characterized by a single threshold level of bed shear stress, or whether taxa resuspend at different levels of bed shear stress. Unique thresholds among taxa or functional groups would create an erosional sequence during flow acceleration, and the particular assemblage of species that exchanges with the water column would depend on the maximal bed stress reached during a resuspension event. Flow variations due to tidal or atmospheric forcing thereby could influence community structure and trophic interactions in both the water column and the sediment. The occurrence of unique thresholds among taxa could be due to differences in cell size, shape, or density; position in the surficial sediment; migratory behavior; or associations with particles. In contrast, simultaneous resuspension at a common threshold of bed stress might occur for taxa with similar physical traits or with similar association to sediment particles that have a single erosion threshold.

There is some evidence for resuspension thresholds differing among sedimentary taxa, particularly microalgae. De Jonge and van den Bergs (1987) found, in flume experiments with estuarine sediment, that benthic diatoms resuspended in two distinct groups of species, likely because of differences in cell size, adhesiveness, and association with the silt or sand fraction. Arfi and Bouvy (1995) found that phototrophs resuspended in two consecutive groups differing in cell size (including cyanobacteria, phytoflagellates, and diatoms) during wind forcing in a 1-m-deep lagoon. Blanchard et al. (1997) found that benthic diatoms eroded before bacteria in flume experiments with intertidal mud, apparently because of the diatoms' association with easily eroded mucus from mud snails. Lucas et al. (2001) found differing resuspension patterns among diatom taxa in both flume experiments and sampling over a tidal flat. To our knowledge, no study elsewhere has addressed the sequential resuspension of protists by tidal currents in a subtidal habitat or the sequential resuspension specifically of heterotrophic protists in any environment.

We investigated sequential resuspension among various heterotrophic and autotrophic protistan groups and bacteria in the subtidal, silty region of a coastal bay under the influence of tidal flow. At this site, tidal resuspension and deposition of heterotrophic flagellates and certain ciliates has been documented elsewhere (Shimeta and Sisson 1999). Two complementary field approaches were applied in our study to investigate resuspension with finer temporal resolution. First, we experimentally eroded undisturbed sediment with *in situ* flumes, which identified a resuspension sequence from the local source contained in the bed. A large-footprint flume was used to resuspend the natural community, and a smaller flume was used to resuspend supplemented populations of individual ciliate isolates to obtain species-specific thresholds. Second, we sampled the benthic boundary layer

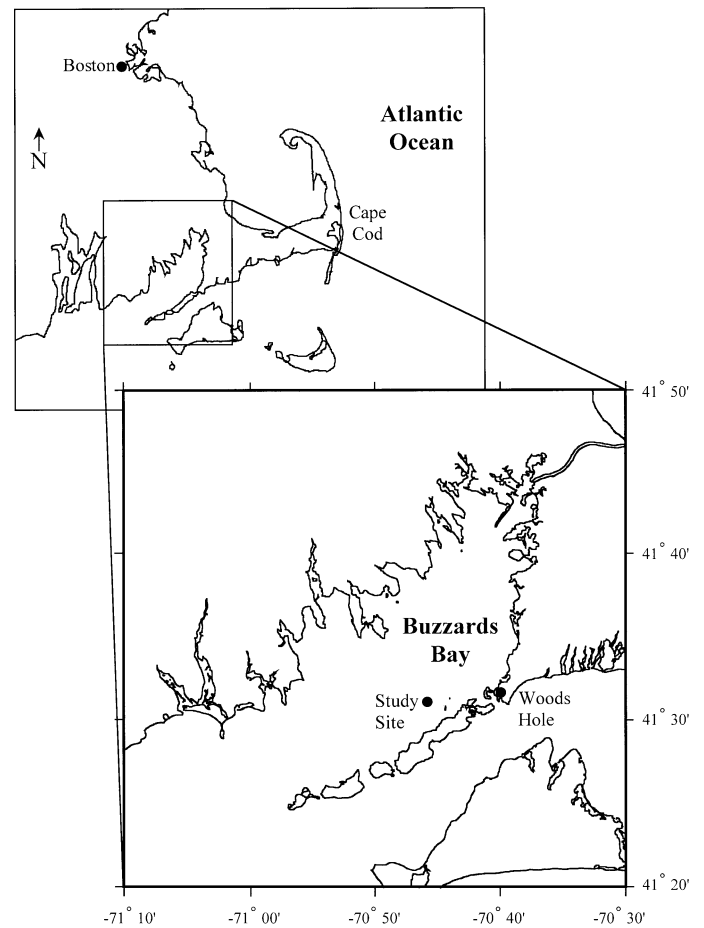


Fig. 1. Study site in Buzzards Bay, Massachusetts, on the north-west Atlantic coast.

with fine-scale temporal resolution during natural tidal accelerations, which confirmed fluctuations of cell concentrations and relative abundances that were consistent with a local resuspension sequence.

## Methods and materials

**Field site and flow measurements**—The 15-m-deep field site (Fig. 1) is in the central silty region of Buzzards Bay, Massachusetts (*see* sediment-distribution map in Moore 1963). Sediment grains  $<25 \mu\text{m}$  constitute  $>50\%$  by mass of the surficial 0.2 cm of the bed (Shimeta and Sisson 1999). Flow at the site is tidally driven and highly rectified on the long axis (northeast–southwest) of the bay (Shimeta and Sisson 1999).

A month-long time series of flow was recorded with an InterOcean S4 current meter mounted on a bottom tripod. During time-series sampling of the benthic boundary layer, flow was measured with a boat-mounted acoustic doppler current profiler (ADCP, RDI 1200 kHz) with 1-m depth averaging. Friction velocity ( $u_*$ ) was estimated as  $u_* = (C_D)^{1/2}u$ , where  $u$  is speed and  $C_D$  is a drag coefficient. Sternberg's (1968) mean  $C_D = 3.1 \times 10^{-3}$  for 1 m above bottom (m.a.b.) in coastal waters was adjusted by use of the Law of the Wall

(Middleton and Southard 1984) to  $2.98 \times 10^{-3}$  for the S4's height of 1.15 m.a.b. and to  $2.12 \times 10^{-3}$  for the midpoint of the ADCP's tenth depth bin (4.5 m.a.b.). Friction velocity relates to bed shear stress ( $\tau_b$ ) as  $u_* = (\tau_b/\rho)^{1/2}$ , where  $\rho$  is the density of seawater.

*Resuspension experiments*—Natural communities of protozoists and bacteria were resuspended with the Sea Carousel, a tethered, in situ annular flume (Amos et al. 1992), during daylight hours on 8 and 10 August 2000. The Sea Carousel is aluminum, with an outer diameter of 2.0 m, a channel width of 15 cm, and a height of 30 cm. Flow is driven by a rotating lid with eight small paddles underneath. Two optical back-scatter (OBS) sensors are positioned inside the channel at 3 and 18 cm above the bed. Three vertically arranged sampling ports are located in the outer channel wall.

The Sea Carousel was lowered gently from the RV *Asterias* onto the bed at slack high water. After allowing disturbed sediment to settle for 30 min, lid rotation began, and the rate was increased incrementally every 5 min. Lid speed was measured with a shaft-end encoder and converted to friction velocity by use of laboratory calibrations as in Amos et al. (1992). Water samples ( $n = 1$  at each time point) were collected immediately before flow initiation and 2 min after each increase in speed. Samples for suspended particulate matter (SPM), particulate organic matter (POM), and chlorophyll *a* were collected from a port at 5 cm above the bed with 0.64 cm inner diameter rubber tubing and a foot pump on deck. Water samples for measuring cell concentrations were collected from a port at 10 cm above the bed with 0.64 cm inner diameter silicone tubing and a peristaltic pump operating at 500 ml min<sup>-1</sup>. (Reynolds number = 1700, thus ensuring laminar flow. Tests involving pumping cultured ciliates at this rate through this tubing revealed no cell losses.) The portion of collected water used for cell counts was preserved with cold glutaraldehyde (1% final). Both tubing lines were flushed before each sample was taken.

During Sea-Carousel deployments, sediment cores (3.8 cm inner diameter) were taken by divers near the flume. Cores were extruded, and the top 0.2 cm were either preserved with cold glutaraldehyde (1% final) for cell counts or frozen for measuring Chl *a* and POM. A sample of surrounding bottom water was taken with a 5-liter Niskin bottle at 1 m.a.b., outside and upstream of the Sea Carousel during the eighth nonzero flow increment on 10 August. Water for cell counts was preserved with cold glutaraldehyde (1% final), and additional water was taken for measuring Chl *a*, SPM, and POM.

The MiniFlume (an autonomous, in situ annular flume; Amos et al. 2000) was used to resuspend cultured ciliates experimentally in the field during daylight hours on 5, 8, and 10 August 2000. The MiniFlume is acrylic, with an outer diameter of 30 cm, a channel width of 4.5 cm, and a height of 30 cm. Flow is driven by a rotating lid with four small paddles underneath. Friction velocity was determined from velocity profiles measured in a laboratory with laser-Doppler velocimetry. One OBS sensor and one sample port are located in the channel wall, both at 12 cm above the bed. The OBS sensor was calibrated in a stirred tank with sediment from the field site. Cultures used in the MiniFlume experi-

ments included the hypotrich ciliate *Euplotes minuta* Yocum and the scuticociliates *Paranophrys magna* Borrer and *Cohnilembus* sp. These species were isolated from surficial sediment and maintained as described in Shimeta et al. (2001). Each species was used in one MiniFlume experiment.

Prior to a MiniFlume experiment, a 1-liter culture of a single species was raised to late exponential phase on 0.005% yeast extract. Two hours before the experiment, the culture was concentrated to 100 ml over a 3- $\mu$ m filter, and it was transported to the field site in two 60-ml syringes. The concentrated cultures contained 136 *E. minuta* ml<sup>-1</sup>, 100 *P. magna* ml<sup>-1</sup>, and 5,430 *Cohnilembus* sp. ml<sup>-1</sup>. The MiniFlume was lowered gently from the RV *Asterias* onto the bed at slack high water. Divers immediately injected the concentrated culture of a single ciliate species into the MiniFlume channel through the sampling port. After allowing 75 min for the ciliates to disperse and enter the sediment, flow was initiated and incrementally increased every 5 min. One water sample was collected at each time point: immediately before flow initiation and 3 min after each increase in speed. Divers collected each sample in a separate syringe through the sampling port. Samples were preserved on deck with cold glutaraldehyde (1% final).

*Time-series sampling of the benthic boundary layer*—Water was sampled at 5 cm above the sediment on 29 and 30 August 2000 with a modified version of the benthic boundary-layer sampler used by Shimeta and Sisson (1999). The aluminum sampler has a 1-m tall, rectangular frame with a 1-m diameter, circular base plate that sits flush on the bed, positioned by divers. The frame held three polycarbonate sample-intake nozzles with circular openings of 0.9 cm inner diameter pointing into the flow, positioned 15 cm behind the leading edge of the base plate and separated from each other by 15 cm in the horizontal plane. Samples from the three replicate intake nozzles were pumped simultaneously through separate lines of 0.64-cm inner diameter silicone tubing by a peristaltic pump on the deck of the RV *Asterias*.

Samples were collected every 15 min, beginning ~1 h before slack high water and continuing until ~1 h past the time of maximal ebbing current. The tubing lines were flushed before each sample was taken. Flow speed and direction were monitored in real time by use of the boat-mounted ADCP. The pumping rate was adjusted between 215 and 500 ml min<sup>-1</sup> so that the velocity of water entering the intake nozzles was roughly isokinetic with the surrounding flow. At each sampling time, three simultaneous replicate samples were taken for cell counts and preserved with cold glutaraldehyde (1% final). One additional sample was taken for measuring Chl *a*, SPM, and POM. At slack high water, divers collected sediment cores near the sampler, and the cores were processed as described above. When the current changed direction to begin ebbing, divers turned the sampler to maintain it facing into the flow.

*Sample and data analyses*—Water samples for measuring Chl *a*, SPM, and POM were filtered onto precombusted filters, and those for SPM and POM were rinsed with reverse-osmosis water. GF/C filters (Whatman, nominal pore size 1.2

$\mu\text{m}$ ) were used for samples from the Sea Carousel and Niskin bottle, whereas GF/F filters (Whatman, nominal pore size  $0.7 \mu\text{m}$ ) were used for time-series samples of the benthic boundary layer. SPM was measured as total dry mass. The percentage of combustible organic matter in water samples and in sediment was determined as the difference between dry weights before and after ashing at  $450^\circ\text{C}$  for 5 h. Chl *a* was measured on a Turner Designs fluorometer after filters or sediment were extracted in 90% acetone (Parsons et al. 1984). Salt corrections were applied to all measurements from sediment.

To count heterotrophic bacteria, samples were sonicated for three 1-min bursts with 0.01% Triton X-100. Sediment samples were diluted 1:5000 with  $0.2\text{-}\mu\text{m}$  membrane-filtered sea water prior to sonication; water samples were undiluted. Cells were filtered onto  $0.2\text{-}\mu\text{m}$  black Nuclepore filters, stained with  $20 \mu\text{g ml}^{-1}$  4,6-damidino-2-phenyl-indole, mounted on microscope slides with immersion oil, and counted at  $1,000\times$  on an epifluorescence microscope under ultraviolet excitation (Porter and Feig 1980). To count nanoflagellates, water samples were filtered onto  $0.8\text{-}\mu\text{m}$  filters, stained, and counted similarly. The presence of photosynthetic pigment was determined by the autofluorescence of chlorophyll under blue excitation. Nanoflagellates were extracted from sediment samples by Percoll-gradient centrifugation (Shimeta and Sisson 1999) prior to filtration and staining. To count ciliates and pennate diatoms, water samples were settled in 100-ml Utermöhl chambers (Utermöhl 1958) for 48 h with 0.004% nigrosin black and examined at  $630\times$  in an inverted compound microscope with phase contrast. Extracted sediment samples were each settled for 5 d after the Percoll supernatant was added from one extraction to an Utermöhl chamber and diluting to 100 ml with deionized water and nigrosin black. Only diatom cells with visible pigment were counted. Diatom frustules from separate samples were cleared (Van der Werff 1955) for identification of predominant taxa.

Threshold values of friction velocity for resuspension ( $u_{*crit}$ ) were calculated from Sea Carousel results by linear regression of concentration against  $\log(u_*)$  in the region in which concentration increased monotonically (Sutherland et al. 1998a). The  $u_*$  at which the regression intercepted the initial sample concentration (prior to flow initiation) was taken as  $u_{*crit}$ . Cumulative numbers of cells resuspended were calculated as the measured increase of cells plus the estimated loss during each flow increment due to leakage from the flume (Amos et al. 1992). Differences in cell concentrations among time-series samples from the benthic boundary layer were deemed significant if 95% confidence intervals around the means failed to overlap.

## Results

**Tidal flow**—Flow measured 1.15 m.a.b. at the site had a strong tidal periodicity (Fig. 2). Peaks of friction velocity ( $u_{*max}$ ) ranged from  $0.4$  to  $1.7 \text{ cm s}^{-1}$ , with ebbing currents typically stronger than flooding currents. Currents during slack water often slowed to  $u_* < 0.1 \text{ cm s}^{-1}$ .

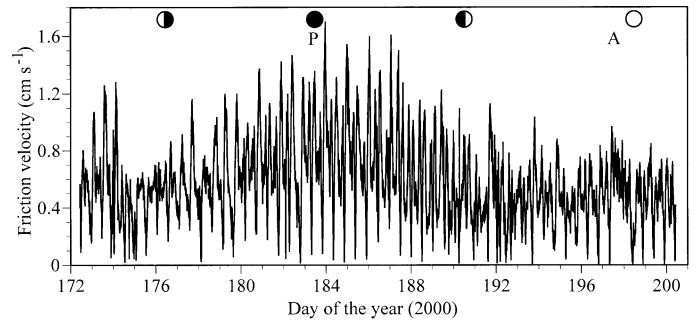


Fig. 2. Month-long time series of friction velocity at the field site. Shaded circles indicate phases of the moon. A, apogee; P, perigee.

**Resuspension experiments**—The two Sea-Carousel deployments yielded similar patterns of resuspension (Figs. 3, 4). The threshold friction velocity ( $u_{*crit}$ ) for sediment erosion, calculated from total particulate matter in water samples (SPM, Fig. 4A), was  $1.55 \text{ cm s}^{-1}$  and agreed well with continuous OBS readings (Fig. 3). The fraction composed of POM, however, displayed an earlier peak at  $u_* = 0.25\text{--}0.34 \text{ cm s}^{-1}$  (Fig. 4A), possibly indicating erosion of organic-rich, low-mass fluff. After this peak, the fraction of POM fell as SPM increased, which indicates a greater mineral component in suspension. Chl *a* (Fig. 4B) resuspended with  $u_{*crit} = 1.57 \text{ cm s}^{-1}$ , similar to that for bulk sediment.

Various protistan groups and bacteria resuspended in the Sea Carousel with differing values of  $u_{*crit}$  (Table 1). Heterotrophic nanoflagellates (HNan, Fig. 4C) and oligotrich ciliates (Fig. 4D) were the most easily resuspended groups ( $u_{*crit} = 0.25$  and  $0.34 \text{ cm s}^{-1}$ , respectively). These thresholds corresponded to the peak of POM (Fig. 4A) that may represent erosion of a fluff layer. After their initial rises in concentration, oligotrichs remained constant, whereas HNan displayed a second resuspension event in stronger flow. Heterotrophic bacteria (Fig. 4E) resuspended after oligotrichs, although the threshold response was weak. Other ciliates displayed thresholds considerably higher than that for oligotrichs. Hypotrich ciliates were virtually absent from the flume channel until they resuspended at  $u_{*crit} = 0.82 \text{ cm s}^{-1}$  (Fig. 4F), and scuticociliates resuspended above the background level soon afterward (Fig. 4G). Both of these ciliate groups continued to resuspend in stronger flow until  $u_* = 2.9 \text{ cm s}^{-1}$ , when decreases in concentration probably resulted from leakage from the flume. Thresholds for benthic diatoms were generally higher than those for ciliates. *Navicula transitans* Heimdal (Fig. 4H) resuspended at  $u_{*crit} = 0.90 \text{ cm s}^{-1}$ , followed in stronger flows by *Pleurosigma* sp. (Fig. 4I), *Navicula distans* Smith (Fig. 4J), and finally two *Nitzschia* species (Fig. 4L). Pigmented nanoflagellates (PNan, Fig. 4K) displayed a very different response from HNan, not resuspending until  $u_{*crit} = 1.47 \text{ cm s}^{-1}$ . The resuspension of SPM, Chl *a*, *Pleurosigma*, *N. distans*, *Nitzschia*, and PNan were roughly concurrent.

Surficial sediment surrounding the Sea Carousel had abundant sources of all organisms that resuspended in the flume (Table 2). Prior to the onset of resuspension, cell concentrations in the Sea Carousel channel (Fig. 4) were similar to

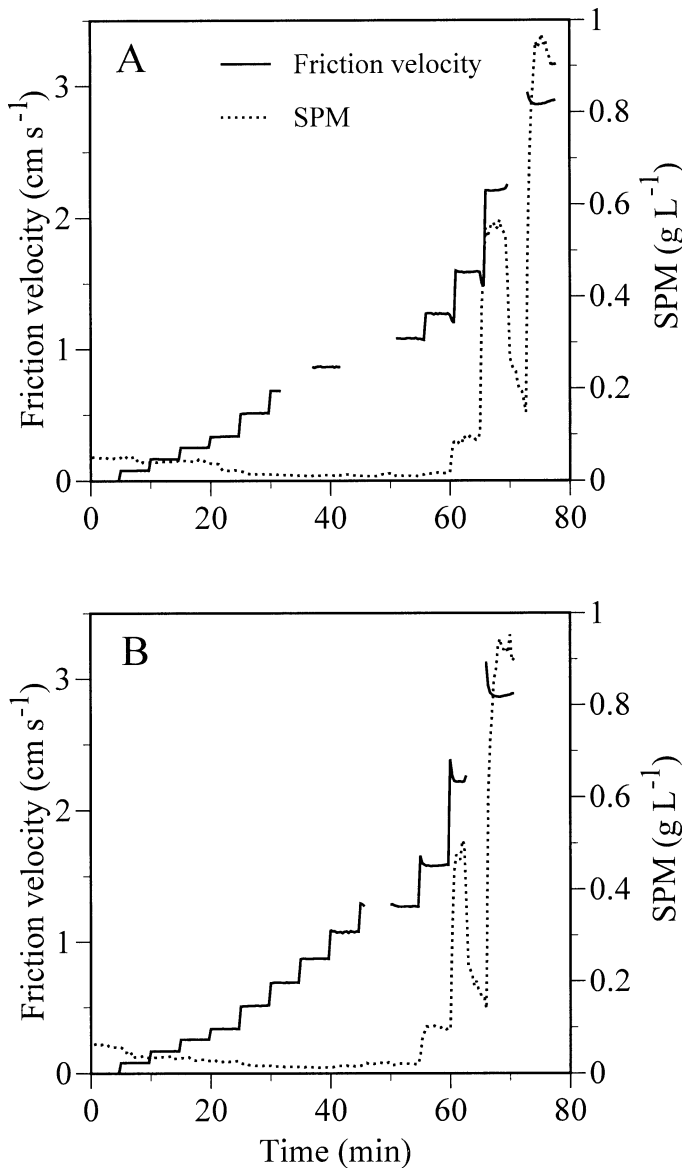


Fig. 3. Friction velocity and SPM (measured from OBS sensors) as functions of time in the Sea Carousel channel during in situ experiments. SPM was corrected for leakage from the flume (Amos et al. 1992). Breaks in the friction-velocity record indicate brief power interruptions. (A) 8 August 2000 and (B) 10 August 2000.

those in the ambient water outside of the flume (measured only on 10 August; Table 2).

Cumulative numbers of cells resuspended in the Sea Carousel were calculated for  $u_* \leq 1.3 \text{ cm s}^{-1}$  (Table 1), which was similar to the maximal  $u_*$  measured during time-series sampling of natural benthic boundary-layer flow (see below). Among the protists, HNan resuspended in the greatest numbers ( $1.4 \times 10^9 \text{ cells m}^{-2}$ ), followed by diatoms ( $9.0 \times 10^5 \text{ cells m}^{-2}$ , dominated by *N. transitans*) and ciliates ( $4.2 \times 10^5 \text{ cells m}^{-2}$ ). Oligotrichs and scuticociliates resuspended in similar numbers, and they greatly exceeded the resuspended hypotrichs, despite the fact that hypotrichs were the most abundant ciliate taxa in the sediment (Table 2).

The three MiniFlume deployments gave similar erosion

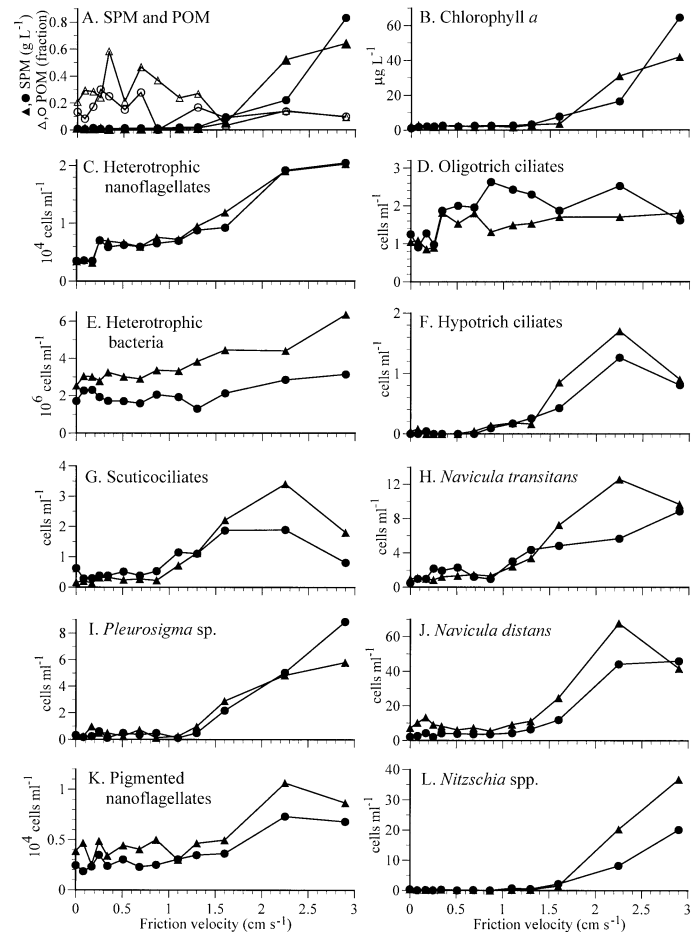


Fig. 4. SPM, fraction composed of POM in SPM, Chl *a*, and organisms in water samples taken from the Sea Carousel at each incremental flow setting during in situ experiments. Taxonomic groups that showed no evidence of resuspension are not included. Organisms (C–L) are in order of increasing threshold for resuspension ( $u_{*crit}$ ; Table 1). *Navicula*, *Pleurosigma*, and *Nitzschia* are diatom genera. Triangles are 8 August 2000; circles are 10 August 2000.

thresholds for particulate matter (mean  $u_{*crit} = 1.89 \text{ cm s}^{-1}$ ; Fig. 5) that were slightly higher than measured in the Sea Carousel. Resuspension thresholds differed among the three cultured ciliates (Fig. 6). The hypotrich *E. minuta* was undetectable in the flume until  $u_* = 1.9 \text{ cm s}^{-1}$ . The scuticociliate *P. magna* showed a sharp rise of concentration at  $u_* = 2.3 \text{ cm s}^{-1}$ . The scuticociliate *Cohnilembus* sp. showed its most evident resuspension at  $u_* = 2.7 \text{ cm s}^{-1}$ .

*Time-series sampling of the benthic boundary layer*—Samples from the two dates yielded similar patterns of flow and particle and cell concentrations. Friction velocity ranged from  $0.25 \text{ cm s}^{-1}$  at slack water to  $1.35 \text{ cm s}^{-1}$  at peak flow (Fig. 7A). Within  $\sim 30 \text{ min}$  after acceleration began ( $u_* = 0.5\text{--}0.6 \text{ cm s}^{-1}$ ), the concentration of SPM rose and the fraction composed of POM fell (Fig. 7B). Chl *a* remained constant throughout sampling (Fig. 7B).

Concentrations of organisms in the benthic boundary layer (at 5 cm above bottom) increased at various times during

Table 1. Resuspension thresholds ( $u_{*crit}$ ) in increasing order and cumulative resuspended cells measured in Sea Carousel experiments (mean of two deployments). Thresholds were calculated by regression analysis as described in the Materials and Methods section, except for oligotrichs and the first HNan threshold (which were step-function increases, assessed visually) and the second HNan threshold (which was regressed to the concentration in the fourth sample); see Fig. 4. Cumulative resuspended cells were calculated for  $u_*$  up to  $1.3 \text{ cm s}^{-1}$  (to allow comparison with benthic boundary-layer sampling), and groups with  $u_{*crit}$  that exceeded this value were therefore excluded (indicated as “NA” for not applicable).

	$u_{*crit}$ ( $\text{cm s}^{-1}$ )	Cumulative resuspension at $u_* = 1.3 \text{ cm s}^{-1}$ ( $\text{cells m}^{-2}$ )
HNan	0.25, 1.14	$1.41 \times 10^9$
Oligotrich ciliates	0.34	$1.91 \times 10^5$
Bacteria	0.72	$1.61 \times 10^{11}$
Hypotrich ciliates	0.82	$4.69 \times 10^4$
Scuticociliates	0.89	$1.81 \times 10^5$
<i>Navicula transitans</i>	0.90	$7.84 \times 10^5$
<i>Pleurosigma</i> sp.	1.23	$1.11 \times 10^5$
<i>Navicula distans</i>	1.41	NA
PNan	1.47	NA
<i>Nitzschia</i> spp.	1.58	NA

HNan, heterotrophic nanoflagellates; PNan, pigmented nanoflagellates; *Navicula*, *Pleurosigma*, and *Nitzschia* are diatom genera.

flow acceleration. Data are presented for those groups that resuspended in the Sea Carousel experiments; no additional groups varied significantly in the benthic boundary-layer samples. The time at which cell concentration began to increase significantly was identified by comparing 95% confidence intervals around mean concentrations between successive time points. HNan began to increase at  $u_* = 0.65 \text{ cm s}^{-1}$ , whereas PNan showed no significant changes throughout sampling (Fig. 7C). Concentrations of heterotrophic bacteria increased during flow acceleration only on 30 August at  $u_* = 0.65 \text{ cm s}^{-1}$  (Fig. 7C). Among ciliates, oligotrichs declined dramatically during slack water and began to increase at  $u_* = 0.3\text{--}0.5 \text{ cm s}^{-1}$ , whereas scuticociliates and hypotrichs did not increase until  $u_* = 1.2\text{--}1.3 \text{ cm s}^{-1}$  (Fig. 7D). Concentrations of *N. distans* declined during slack water and increased at  $u_* = 0.4\text{--}0.8 \text{ cm s}^{-1}$  (Fig. 7E). *N. transitans* showed a strong increase on 30 August beginning at  $u_* = 1.1 \text{ cm s}^{-1}$  and a brief increase on 29 August at  $u_* = 1.25 \text{ cm s}^{-1}$  (Fig. 7E). *Pleurosigma* sp. showed a brief increase only on 30 August at  $u_* = 1.30 \text{ cm s}^{-1}$  (Fig. 7E). *Nitzschia* spp. showed no changes (Fig. 7E). Concentrations of most of these groups declined as tidal flow decelerated, likely because of deposition. All of these organisms were abundant in the surficial sediment on these dates (Table 2).

Tidal variations in cell concentrations altered the community structure (relative abundances) in the benthic boundary layer. As flow accelerated, concentrations of various groups increased by factors ranging from 2 to 16 (i.e., the ratio of maximal to minimal concentration, Table 3). The percentage of oligotrich individuals in the ciliate community was relatively low during slack water and during peak flow (Fig. 8A), the former because of low absolute concentrations

of oligotrichs and the latter because of the addition of scuticociliates and hypotrichs. Oligotrichs varied from 40% to 78% of the ciliate community, scuticociliates varied from 10% to 41%, and hypotrichs varied from 0% to 6.5%. Of the pennate diatoms in the benthic boundary layer, the four groups shown in Fig. 8B (which had resuspended in the Sea Carousel experiments) were a relatively low percentage of total individuals during slack water (37%–42%) but were higher during peak flow (59%–63%). Most of the variation was due to the two *Navicula* species.

## Discussion

*Sequential resuspension of sediment and organisms*—Sediment displayed Type I erosion in the flumes—that is, incremental increases in bed stress produced discrete amounts of erosion, rather than continuous erosion over time (Figs. 3, 5). Type I erosion has been observed in many coastal and shelf environments, and it is explained by a direct relationship between bed shear strength and depth in the sediment (e.g., Amos et al. 1992; Thomsen and Gust 2000). The first layer to erode in some cases is loose, flocculent material (a fluff layer) at the sediment-water interface (e.g., Jago and Jones 1998; Maa et al. 1998). At our site, the peak percentage of POM that preceded the increase of total SPM in the Sea Carousel (Fig. 4A) may have been due to resuspension of such a surficial fluff layer of organic-rich material, too low in mass to be detected in the SPM measurements. The subsequent decline in percentage of POM when total SPM increased was likely due to the increased mineral mass in suspension, but there may also have been some leakage of fluff material from the flume. During time-series sampling of benthic boundary-layer flow, in contrast, SPM increased at the onset of current acceleration without a peak in percentage of POM (Fig. 7B); in fact, the percentage of POM declined, which indicates more mineral material in suspension. We cannot exclude, however, that a surficial fluff layer was the first material to erode and that the organic-rich component was mixed above our sampling height of 5 cm above bottom. The clear signal of this organic-rich material in the Sea Carousel may have been enhanced by confinement within the flume channel.

As flow accelerated, various groups of protists and bacteria resuspended in sequence, rather than simultaneously, both in the in situ flume experiments and during natural tidal flow in the bay. The first groups to resuspend were HNan and oligotrich ciliates, with  $u_{*crit}$  in the range of 0.25–0.65  $\text{cm s}^{-1}$ . Their low resuspension thresholds may be due to loose association with sediment or to attachment to an easily eroded fluff layer. HNan are abundant on sinking, organic-rich aggregates (Novitsky 1990; Caron 1991; Zimmermann-Timm et al. 1998), and they are highly concentrated at the sediment-water interface (Bak and Nieuwland 1989; Shimeta and Sisson 1999), which may make them easily erodable. Benthic oligotrichs commonly live interstitially in sands (Fenchel 1969), but their depth distribution in silty sediment has not been well documented. Some oligotrichs have been described as epibenthic (Fenchel and Jonsson 1988). Therefore, it is possible that oligotrichs were only loosely asso-

Table 2. Measurements from sediment cores (top 0.2 cm) and a bottom-water sample (1 m.a.b.). Samples on 8 and 10 Aug were taken during Sea Carousel deployments; samples on 29 and 30 Aug were taken during time-series sampling of the benthic boundary layer. Where shown, error estimates are  $\pm 1$  standard error ( $n = 3$ ); otherwise,  $n = 1$ .

	8 Aug sediment	10 Aug sediment	10 Aug bottom water	29 Aug sediment	30 Aug sediment
SPM (g L <sup>-1</sup> )	NA	NA	0.007	NA	NA
POM (mass fraction)	0.10 ( $\pm 0.01$ )	0.072	0.36	0.15 ( $\pm 0.05$ )	0.088 ( $\pm 0.009$ )
Chl <i>a</i> ( $\mu\text{g}$ [g sediment] <sup>-1</sup> ) or ( $\mu\text{g}$ [L water] <sup>-1</sup> )	36.6 ( $\pm 4.0$ )	110 ( $\pm 2$ )	2.91	81.5 ( $\pm 6.5$ )	56.1 ( $\pm 5.0$ )
Bacteria (cells [g sediment] <sup>-1</sup> ) or (cells [ml water] <sup>-1</sup> )	8.06 ( $\pm 1.77$ ) $\times 10^9$	6.66 ( $\pm 1.16$ ) $\times 10^9$	$2.36 \times 10^6$	12.62 ( $\pm 2.89$ ) $\times 10^9$	9.50 ( $\pm 2.01$ ) $\times 10^9$
HNan (cells ml <sup>-1</sup> )	5.97 ( $\pm 0.64$ ) $\times 10^5$	7.82 ( $\pm 0.88$ ) $\times 10^5$	$5.61 \times 10^3$	1.43 ( $\pm 0.17$ ) $\times 10^6$	1.05 ( $\pm 0.17$ ) $\times 10^6$
PNan (cells ml <sup>-1</sup> )	2.27 ( $\pm 0.27$ ) $\times 10^5$	2.46 ( $\pm 0.26$ ) $\times 10^5$	$3.58 \times 10^3$	6.21 ( $\pm 0.59$ ) $\times 10^5$	5.18 ( $\pm 1.15$ ) $\times 10^5$
Hypotrich ciliates (cells ml <sup>-1</sup> )	1.51 ( $\pm 0.75$ ) $\times 10^3$	1.67 ( $\pm 0.33$ ) $\times 10^3$	0.045	2.43 ( $\pm 0.21$ ) $\times 10^3$	397 ( $\pm 52$ )
Oligotrich ciliates (cells ml <sup>-1</sup> )	71 ( $\pm 48$ )	125 ( $\pm 37$ )	1.48	162 ( $\pm 47$ )	39 ( $\pm 20$ )
Scuticociliates (cells ml <sup>-1</sup> )	734 ( $\pm 334$ )	616 ( $\pm 169$ )	0.36	594 ( $\pm 195$ )	514 ( $\pm 106$ )
<i>Navicula distans</i> (cells ml <sup>-1</sup> )	5.20 ( $\pm 3.46$ ) $\times 10^3$	2.86 ( $\pm 0.67$ ) $\times 10^3$	3.62	2.10 ( $\pm 0.36$ ) $\times 10^3$	1.56 ( $\pm 0.50$ ) $\times 10^3$
<i>Navicula transitans</i> (cells ml <sup>-1</sup> )	4.72 ( $\pm 2.38$ ) $\times 10^3$	5.31 ( $\pm 1.23$ ) $\times 10^3$	0.36	3.51 ( $\pm 0.47$ ) $\times 10^3$	4.28 ( $\pm 1.23$ ) $\times 10^3$
<i>Nitzschia</i> spp. (cells ml <sup>-1</sup> )	6.37 ( $\pm 3.52$ ) $\times 10^3$	1.50 ( $\pm 0.32$ ) $\times 10^4$	0.12	6.76 ( $\pm 1.08$ ) $\times 10^3$	4.57 ( $\pm 0.70$ ) $\times 10^3$
<i>Pleurosigma</i> sp. (cells ml <sup>-1</sup> )	2.48 ( $\pm 0.75$ ) $\times 10^3$	7.54 ( $\pm 0.95$ ) $\times 10^3$	0.24	2.82 ( $\pm 0.32$ ) $\times 10^3$	1.18 ( $\pm 0.21$ ) $\times 10^3$

NA, not applicable.

ciated with the sediment-water interface at our site, thus accounting for their resuspension in weak flow. Swimming behavior, cued to boundary-layer flow, could also be involved, which would explain the precipitous drop in concentration at slack water (if cells swam to the bed) as well as the resuspension in weak flow. The second, higher resuspension threshold for HNan in the Sea Carousel could correspond to a separate taxonomic or functional group of flagellates residing beneath the surficial fluff layer. Curiously, PNan differed from HNan in showing no evidence of resuspension during benthic boundary-layer sampling and a very high threshold in the Sea Carousel experiments ( $u_{*crit} = 1.47$  cm s<sup>-1</sup>) that corresponded roughly to the erosion of bulk sediment. This difference could be due to position in the sediment and/or migratory behavior in response to overlying flow. For example, Berninger and Huettel (1997) suggested that some benthic microalgae migrate downward as flow increases, thus avoiding resuspension.

Hypotrich ciliates and scuticociliates resuspended in stronger flow ( $u_{*crit} = 0.82$ – $1.3$  cm s<sup>-1</sup>) than oligotrichs, possibly because of more thigmotactic and interstitial lifestyles (Patterson et al. 1989) and/or avoidance of the water column. The isolated species were strongly thigmotactic when observed in culture dishes, swimming rapidly to the bottom surface after being stirred. This does not, however, exclude

active emergence cued to flow (e.g., Jonsson and Johansson 1997). Hypotrichs and scuticociliates resuspended separately from sediment in all cases, and this lack of coupling with sediment erosion also suggests possible behavioral control of resuspension. The MiniFlume experiments revealed species-specific resuspension thresholds for ciliates in these groups, although confidence in these results is limited by lack of replication. *E. minuta*, *P. magna*, and *Cohnilembus* sp. each displayed an apparently unique resuspension threshold, possibly because of behavioral differences at the species level. The hypotrich resuspended before the two scuticociliates, consistent with the results of Sea Carousel experiments, yet in the benthic boundary-layer samples the resuspension patterns of hypotrichs and scuticociliates were indistinguishable. Resolution to species level is important to distinguish differences in the autecology of various taxa.

Diatom taxa also resuspended in sequence. A striking discrepancy, though, between results of the Sea Carousel experiments and benthic boundary-layer sampling was that *N. distans* showed a much higher resuspension threshold in the flume. Diatoms in this genus migrate vertically in response to changes in light (Round and Palmer 1966), so it may be that the darkness created by the presence of the Sea Carousel induced downward migration in the sediment and a correspondingly elevated resuspension threshold. During benthic

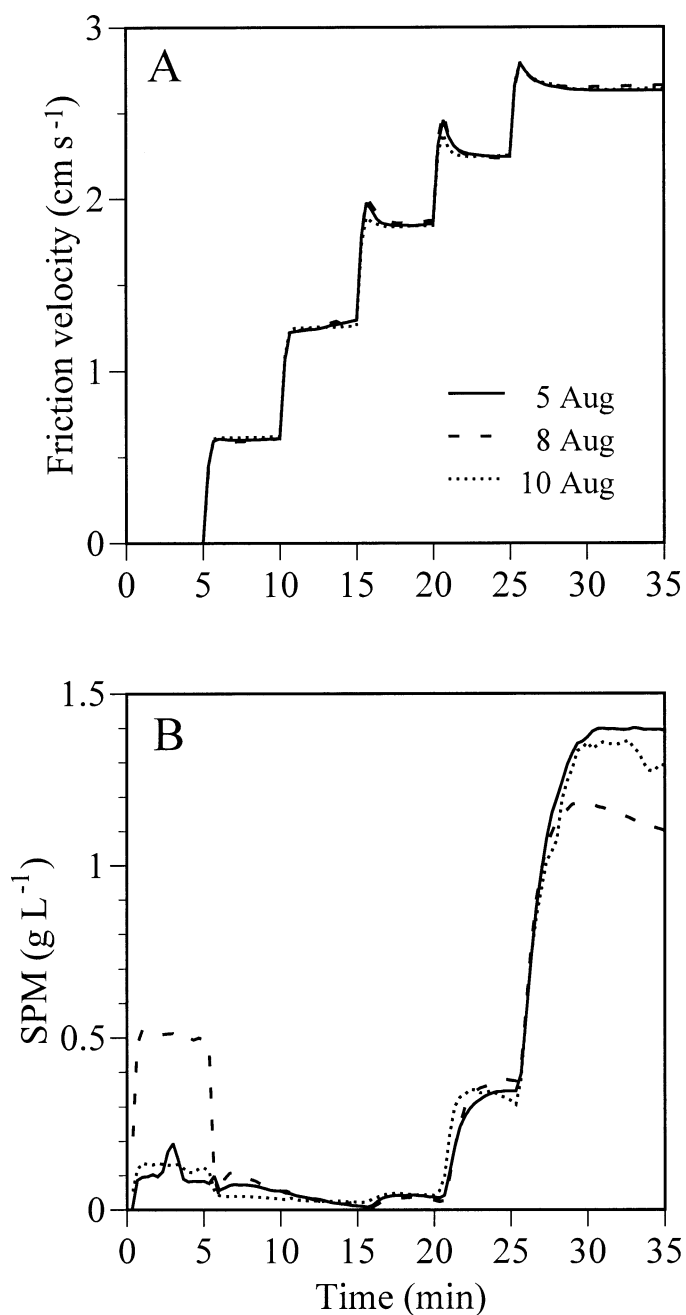


Fig. 5. Friction velocity and SPM as functions of time in the MiniFlume during in situ experiments. SPM was measured by an OBS sensor in the channel wall. Elevated levels of SPM during the first 5 min were likely remnant from sediment disturbance during deployment.

boundary-layer sampling, concentrations of *N. distans* increased roughly concurrent with those of HNan and oligotrichs, which suggests that *N. distans* may naturally resuspend with the surficial fluff layer. These conflicting results suggest, though, that *N. distans* may only resuspend with the fluff during daylight hours and not at night. Considering both the flume experiments and benthic boundary-layer sampling (but disregarding the Sea Carousel results for *N. distans*), we can construct the following resuspension sequence and

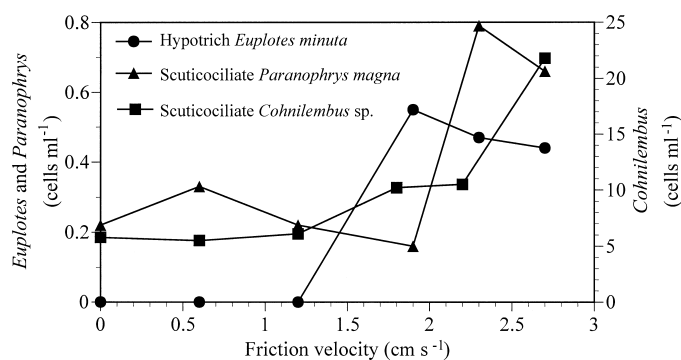


Fig. 6. Concentrations of ciliates in water samples taken from the MiniFlume at each incremental flow setting during in situ experiments. *P. magna* was run on 5 August, *E. minuta* on 8 August, and *Cohnilembus* sp. on 10 August.

$u_{*crit}$  ranges for diatoms: *N. distans* (0.40–0.80 cm s<sup>-1</sup>), *N. transitans* (0.90–1.25 cm s<sup>-1</sup>), *Pleurosigma* sp. (1.23–1.30 cm s<sup>-1</sup>), and the two *Nitzschia* species (1.58 cm s<sup>-1</sup>). Species specificity of thresholds could be due to cell size (the *Navicula* spp. are smaller than the others), position in the sediment, and/or mucus production (as suggested by de Jonge and van der Bergs 1987). Resuspension of most diatom taxa was generally concurrent with the erosion of bulk sediment in the Sea Carousel experiments, although such coupling was not as evident in the benthic boundary-layer sampling.

Resuspension thresholds were generally consistent at this site between sampling dates and between the two field methods (flume experiments and boundary-layer sampling), but they might vary over space and time. For particle-attached protists, the sediment grain-size distribution and degree of flocculation, pelletization, and mucus-binding of sediments could influence resuspension thresholds. Macrofaunal and protistan communities themselves influence sediment resuspension thresholds through bioturbation and production of mucopolysaccharides (Blanchard et al. 1997; Sutherland et al. 1998b). It is also possible that sediment fabric influences the vertical distributions of protists within sediment and hence their exposure to flow forces. Sediment properties may change seasonally as organic content and pelletization fluctuate, particularly in the surficial fluff layer. Vertical distributions of cells within sediment likely fluctuate on shorter timescales as well, particularly for migrating diatoms (e.g., Round and Palmer 1966 and as suggested by our results with *N. distans*), which may induce diel variation in resuspension dynamics.

The vertical extent of cell exchange between the sediment and water column during natural tidal flow was likely limited to a narrow zone around the sediment-water interface. The erosion depth can be calculated by dividing the cumulative numbers of resuspended cells in the Sea Carousel (at  $u_* = 1.3$  cm s<sup>-1</sup>, Table 1) by the average cell concentrations in the sediment on 8 and 10 August (Table 2). A consistent erosion depth of 0.2 cm was obtained for HNan, oligotrichs, scuticociliates, and *N. transitans*. Interesting exceptions to these calculations were hypotrichs and *Pleurosigma* sp., which gave erosion depths of only 0.002 cm. Thus, relative to their population size in the sediments, these taxa resus-

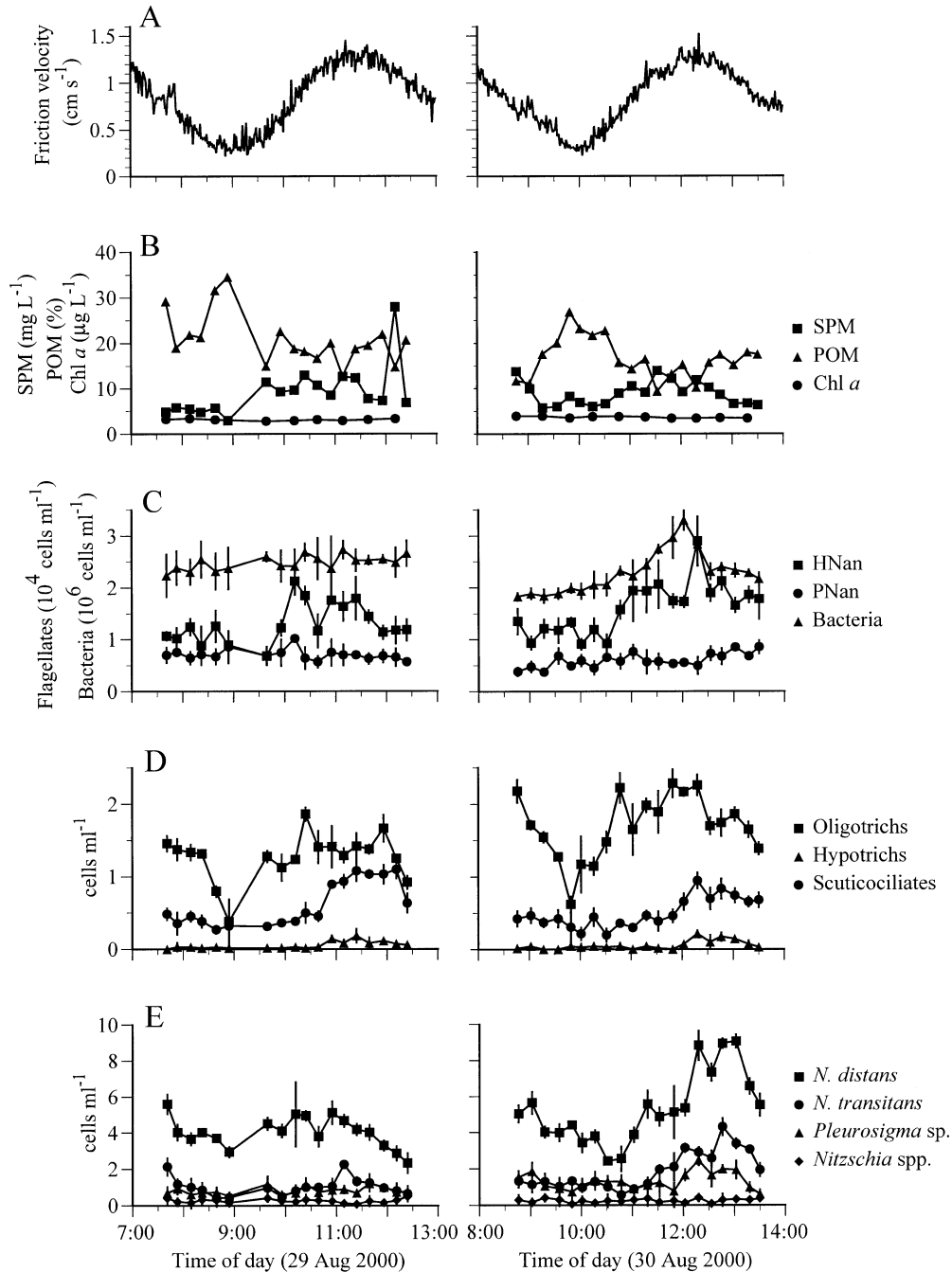


Fig. 7. Results from time-series sampling of the benthic boundary layer at 5 cm above bottom. Left panels are 29 August 2000 (samples at 0900 and 0915 h were lost); right panels are 30 August 2000. (A) Friction velocity. (B) SPM, percentage of POM in SPM, and Chl *a*. (C–E) Organisms: symbols are the mean ( $n = 3$ ) and bars are 95% confidence limits. All groups that had resuspended in Sea Carousel experiments are shown. (C) Nanoflagellates (HNan, heterotrophic nanoflagellates; PNan, pigmented nanoflagellates) and bacteria. (D) Ciliates. (E) Pennate diatoms.

pended far less than the others, which perhaps reflects a behavioral resistance to erosion. The extent of upward mixing into the water column can be estimated by comparing the cumulative numbers of cells resuspended in the Sea Carousel (Table 1) with the increases of cell concentrations measured at 5 cm above bottom in natural tidal flow of similar strength ( $u_{*max} = 1.3 \text{ cm s}^{-1}$ , Table 3). Mixing of the resuspended

cells to  $\sim 50$  cm above bottom with a uniform concentration profile would have produced the observed concentrations at 5 cm. In reality, a vertical gradient of resuspended cell concentration should result in the benthic boundary layer, thus extending the estimated resuspension zone above 50 cm. Vertical profiles measured by Shimeta and Sisson (1999) in the boundary layer showed enhanced concentrations during

Table 3. Relative increases of mean cell concentrations at 5 cm above bottom while tidal currents accelerated. Values are the ratio of the maximal concentration during ebbing flow to the minimal concentration during the preceding slack water, from data in Fig. 7. Included are only those groups whose concentrations showed significant temporal change (i.e., nonoverlap of 95% confidence intervals around mean values). Calculations for hypotrichs used the minimal nonzero concentration.

	29 Aug	30 Aug
Bacteria	NS	1.8
HNan	3.1	3.2
Hypotrich ciliates	13.6	15.8
Oligotrich ciliates	4.9	3.7
Scuticociliates	4.1	4.8
<i>Navicula distans</i>	1.7	3.8
<i>Navicula transitans</i>	5.6	7.6
<i>Pleurosigma</i> sp.	NS	3.4

NS, no significant change on this day.

tidal exchange extending to  $\sim 1$  m.a.b. The zone of exchange between the sediment and water column is therefore from  $\sim 0.2$  cm in the sediment to  $\sim 1$  m.a.b.

Resuspension appears to be followed by deposition during the ensuing slack water period, likely facilitated by the limited height to which cells are mixed above the bottom. For most groups of protists, concentrations measured in the benthic boundary layer decreased during flow deceleration (Fig. 7). Shimeta and Sisson (1999) also found evidence for deposition: during slack water, concentrations of cells in the boundary layer were reduced, and concentrations in the surficial sediment were enhanced by corresponding amounts.

Advection cannot be excluded as a process that influenced concentrations of cells during the time-series sampling of benthic boundary-layer flow. We infer, however, that resuspension dominated over advection because Sea Carousel experiments demonstrated local resuspension at thresholds generally similar to those apparent in the natural time series. Shimeta and Sisson (1999) also concluded that resuspension was the predominant process at this site on the basis of vertical profiles and time series of turbidity.

*Tidal and spring-neap variations in community structure*—Sequential resuspension of taxa suggests a spring-neap periodicity in community structure within the benthic boundary layer. Stronger tidal currents (during spring tides) should resuspend more groups of microbes and have a different effect on relative abundances than weaker tidal currents (during neap tides). To illustrate this point, we used the month-long record of  $u_*$  (Fig. 2) to identify three regimes of tidal-current strength at the site (Table 4). The strongest currents occurred during the coincidence of spring tides and perigee (days 182–187), when  $u_{*max}$  was  $>1.3$  cm  $s^{-1}$  (thus greater than occurred during our benthic boundary-layer sampling) for most of the tidal currents. The upper limit of  $u_{*max}$  at the site is at least 2.2 cm  $s^{-1}$ , measured during spring tides by Shimeta and Sisson (1999). The weakest currents occurred during neap tides (days 175–178 and 190–194), when  $u_{*max}$  was  $<0.8$  cm  $s^{-1}$  for most of the tidal currents. Finally, moderate currents are identified as having

Table 4. Cells predicted to resuspend in each of three ranges of tidal-current strength, as inferred from the results of this study.

Weakest currents ( $u_{*max} < 0.8$ cm $s^{-1}$ )	Moderate currents ( $u_{*max} = 0.8$ – $1.3$ cm $s^{-1}$ )	Strongest currents ( $u_{*max} > 1.3$ cm $s^{-1}$ )
<b>Heterotrophs</b>		
Bacteria	Bacteria	Bacteria
HNan	HNan	HNan
Oligotrich ciliates	Oligotrich ciliates	Oligotrich ciliates
	Hypotrich ciliates	Hypotrich ciliates
	Scuticociliates	Scuticociliates
<b>Autotrophs</b>		
<i>Navicula distans</i>	<i>Navicula distans</i>	<i>Navicula distans</i>
	<i>Navicula transitans</i>	<i>Navicula transitans</i>
	<i>Pleurosigma</i> sp.	<i>Pleurosigma</i> sp.
		<i>Nitzschia</i> spp.
		PNan

an intermediate  $u_{*max}$  ranging from 0.8 to 1.3 cm  $s^{-1}$ . The three regimes of tidal-current strength should induce different assemblages of species to exchange between the benthos and water column (Table 4). The weak currents during neap tides should resuspend only heterotrophic bacteria, HNan, oligotrichs, and the diatom *N. distans*. Moderate currents should additionally resuspend hypotrichs, scuticociliates, *N. transitans*, and *Pleurosigma*. The strong currents during spring tides should resuspend the entire assemblage of microbes that we identified as erodable. Thus, community structure and the associated population and food-web dynamics should vary on lunar as well as daily tidal cycles. Spring-neap cycles of resuspension have been documented elsewhere for bulk particulate matter (e.g., Fettweis et al. 1998) but not for protists. The species composition of resuspended assemblages also may be influenced by atmospheric forcing of currents and by spatial variations in hydrography.

*Implications for microbial food-web dynamics*—The benthic boundary layer and sediment-water interface are physically and ecologically dynamic zones where benthic-pelagic coupling, nutrient cycling, and high levels of biological activity occur (Boudreau and Jørgensen 2001). The resuspension documented here transferred a 0.2-cm veneer of the sedimentary protistan community to the water column, causing dramatic fluctuations of boundary-layer cell concentrations (up to a factor of 16) during the tidal cycle. These fluctuations altered the relative abundances in both the ciliate and pennate diatom assemblages. Flagellate community structure likely changed as well, because of the resuspension of heterotrophic forms, although we did not distinguish among taxa of HNan in this study. Resuspension and alteration of community structure may affect protistan ecology in several ways. Resuspension causes cells to be exposed to different types and concentrations of competitors, predators, and prey, as well as to gradients in physical and chemical conditions such as flow and oxygen concentration. Tidal resuspension therefore might cause cyclical patterns in food-web interactions and feeding rates, as well as cumulative

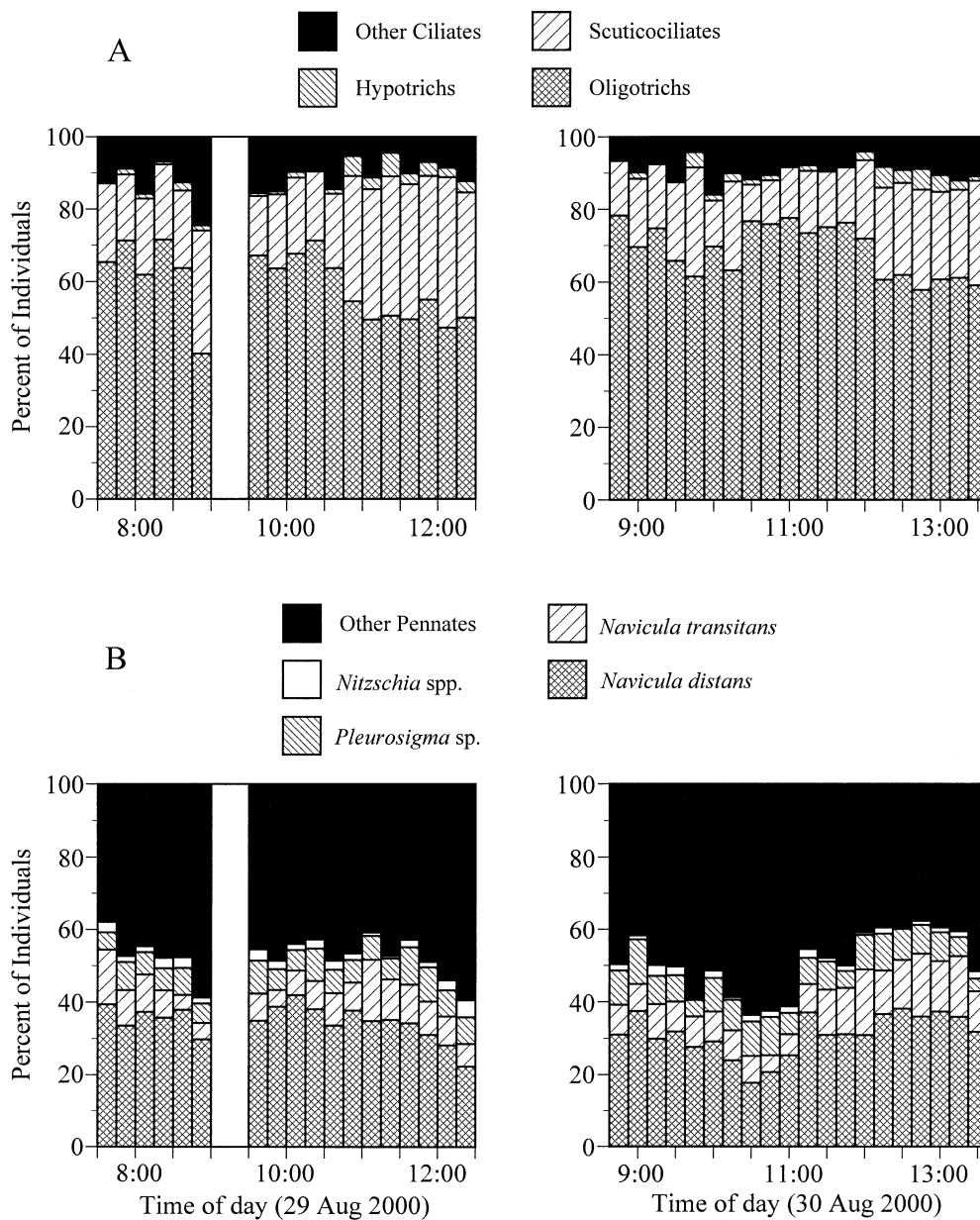


Fig. 8. Relative abundances of cells in the benthic boundary layer at 5 cm above bottom. Left panels are 29 August 2000 (samples at 0900 and 0915 h were lost); right panels are 30 August 2000. Refer to Fig. 7A for the corresponding friction velocities. (A) Ciliates. (B) Pennate diatoms.

effects on growth and death rates. For example, flow strength at the sediment-water interface and in the water column strongly influences the feeding rates of some heterotrophic protists (Shimeta et al. 1995, 2001). Also, resuspension has been shown by Garstecki and Wickham (2001) to enhance trophic interactions and population growth rates in a simple benthic microbial food web of bacteria and protists. Furthermore, although resuspension may be beneficial to some taxa, it might be detrimental to others. Resuspension of the sedimentary fluff layer may also seed the water column with surface-associated protists that colonize suspended aggregates (Caron 1991; Zimmermann-Timm et al. 1998) and influence particulate transformations and remineralization rates

in the water column (Lochte 1991). Exposure of resuspended diatoms to altered levels of light and nutrients, as well as consumers, may affect their productivity and population growth rates (see Carrick et al. 1993; MacIntyre and Cullen 1996). Cyclical resuspension and deposition of a benthic-planktonic microbial community thereby may affect food-web dynamics, biological productivity, and biogeochemical activity in the benthic boundary layer and in sediments. These effects may be widespread in shallow-water systems with fine sediment and tidal or wind-driven currents in both marine and freshwater environments.

Benthic-planktonic protists such as flagellates, ciliates, and diatoms form a unique guild that links the traditionally

recognized water-column and sedimentary communities. Within this guild are species-specific resuspension dynamics characterized by unique values of  $u_{*crit}$  among taxa. Those species with low thresholds should resuspend more frequently and spend a greater percentage of time in the water column compared with species with higher thresholds. These dynamics may link a variety of aspects of their ecology to temporal and spatial variations in benthic boundary-layer flow.

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