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Taxon-specific tidal resuspension of protists into the subtidal benthic boundary layer of a coastal embayment

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ABSTRACT: Sediment resuspension has widespread effects on microbial processes, primary and secondary production, and nutrient cycles, but its influence on protists other than microalgae is largely unknown. Distributions and abundances of protists in subtidal benthic boundary layers (BBL), in particular, are poorly known. We measured vertical profiles of protists in the BBL and underlying sediment at a subtidal silty site in Buzzards Bay, Massachusetts, USA, to determine cell-resuspension patterns. Tidal flow produced maximal bottom shear velocities of 1.4 to 2.2 cm s^{-1}. Near-bottom turbidity increased during each slack tide, when the suspended load settled, and it decreased during tidal exchange, presumably after a thin veneer of sediment resuspended from the sediment-water interface (SWI) and mixed into the upper water column. Tidal periodicities in protistan vertical profiles were taxon- and functional-group specific. Heterotrophic nanoflagellates (HNan) and ciliates, including scuticociliates, oligotrichs, and hypotrichs of the genera *Euplotes* and *Urostrongylum*, showed periodicities in distribution consistent with cycles of resuspension and deposition. BBL concentrations of HNan and scuticociliates were elevated during tidal exchange by factors of ≤2.1 and 4.6, respectively, within 5 cm of the SWI; oligotrichs were found consistently in the BBL but were in the sediment only during slack tide; *Euplotes* was present consistently in the sediment but was in the BBL only during tidal exchange. Total resuspended cells in the bottom 1 m were of the order 10^8 to 10^9 HNan m^{-2} and 10^5 to 10^6 ciliates m^{-2}, and in some cases the measured cell disappearance from surficial sediment during tidal exchange balanced the increase in the BBL. In contrast, pigmented nanoflagellates, pennate diatoms, and ciliates, including karyorelictids and other hypotrichs, maintained constant profiles throughout tidal cycles. Specificity of results among protistan groups might be due to behavioral adaptations such as depth zonation in the sediment, associations with particles, and vertical migration. We know of no other documentation in the field of cyclical emergence of heterotrophic protists and re-entry into sediment. Our data suggest complex taxon-specific linkages between sedimentary and water-column protistan communities that may be controlled by flow in the BBL, potentially influencing food-web dynamics.

KEY WORDS: Protists · Benthic boundary layer · Resuspension · Benthic-pelagic coupling · Buzzards Bay

INTRODUCTION

Resuspension of sedimentary material plays an integral role in coupling the benthos and plankton by transferring nutrients, detritus, and organisms to the water column. Resuspended microalgae can contribute greatly to phytoplankton stocks and primary productivity in estuaries, and resuspended cells and detritus can augment secondary productivity of suspension feeders (Roman & Tenore 1978, Baillie & Welsh 1980, de Jonge & van Beusekom 1992). The subtidal benthic boundary layer (BBL) is most directly influenced by resuspension, and in this zone there is an active food web, particularly involving microbes (Townsend et al. 1992, Ritzrau et al. 1997). Boundary-layer flow and resuspension may have large effects on the BBL microbial community and its

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activities, e.g. by increasing bacterial concentrations, cell sizes, and growth rates (Wainright 1987, 1990, Ritzrau & Graf 1992, Ritzrau 1996).

Influences of resuspension on protistan communities, other than microalgae, are largely unknown. The issue was addressed only by Wainright (1987, 1990), who reported increases in the biovolume of total suspended heterotrophic protists after eroding box cores of sediment in a laboratory flume.

Field sampling of protists, especially heterotrophs, has been rare in subtidal near-bottom water (Novitsky 1990, Townsend et al. 1992), and studies of heterotrophs other than forams and amoebae in subtidal sediments are few (e.g. Bak & Nieuwland 1989, Alongi 1990, Hondeveld et al. 1994). Abundances and activities of protists in the BBL, and their distinctiveness from or linkages with the sedimentary community, are largely uncharacterized.

We measured vertical distributions of protists in the subtidal BBL and sediment of Buzzards Bay, Massachusetts, USA, where material resuspension has been demonstrated previously (Rhoads 1973, Roman & Tenore 1978). Samples taken repeatedly throughout tidal cycles, with resolution in the BBL to within 1 cm of the sediment-water interface (SWI), revealed periodicities in vertical cell profiles consistent with a cycle of resuspension and deposition, and the effects were specific to certain protistan taxa and functional groups.

METHODS

We collected samples during spring tides at the 15 m deep Weepecket Island site (41° 31.25' N, 70° 45.7' W) in Buzzards Bay, a nonestuarine embayment (see maps in Banta et al. 1995). This position is within the central silty region of the bay (Moore 1963), and it is at or very near sites of previous studies of tidal resuspension and benthic-pelagic coupling (Rhoads et al. 1975, Roman 1978, 1980, Roman & Tenore 1978) as well as sediment biogeochemistry (Rowe & McNichol 1991, Banta et al. 1995).

An InterOcean Systems S4 current meter and a SeaTech transmissometer (5 cm path length, with a coupled ParoScientific pressure sensor and TattleTale data logger) were each moored 1 m above bottom (m.a.b.), ca 80 m from the Weepecket site coordinates. Moorings were positioned so they were never directly upstream or downstream of the site coordinates at the times of water and sediment collection. On days that we collected samples throughout the tidal cycle, we took vertical profile casts with another SeaTech transmissometer (25 cm path length).

We collected water samples throughout tidal cycles on 30 July and 26 September, 1996, with a benthic boundary-layer sampler (Fig. 1) consisting of a vertical rack of intakes attached by silicone tubing (0.6 cm inner diameter) to a peristaltic pump aboard ship. Before each sampling, SCUBA divers positioned the 1 m diameter aluminum base plate flush with the SWI to prevent artifactual resuspension underneath the intakes, which faced directly into the ambient flow. The lower intakes were flat polycarbonate funnels with 0.5 cm vertical openings, positioned 15 cm behind the leading edge of the base plate, and centered at 0.75, 5, 10, and 20 cm above bottom. All intakes were pumped simultaneously to collect 1 l of sample at 400 ml min^{-1} (tubing Re ≈ 1400, thus laminar flow). Face velocities differed depending on the widths of the intakes, which were constructed individually to create a logarithmic profile of sampling velocities (as low as 0.25 cm s^{-1} at 0.75 cm). Three sets of intake funnels of different widths were interchanged depending on the ambient flow speeds at the time of sampling (monitored from the surface with an acoustic Doppler current profiler), so that intake velocities were ca 20 to 50% below ambient to avoid entraining fluid from outside the target depth interval. Centered at 50 and 100 cm above bottom were 9.5 cm diameter polycarbonate pipes that were capped manually on both ends by divers to enclose water samples. On 26 September, however, strong swell prevented tethering the sampler to the ship by the intake tubing, so a third set of manually capped pipes (3.8 cm diameter) was attached to the sampler, centered at 8.5 cm above bottom. Samples for protistan counts were preserved with 1% glutaraldehyde.

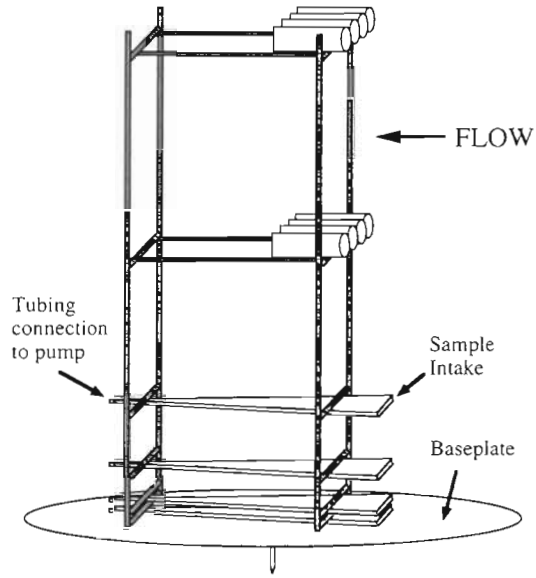

Fig. 1. Benthic boundary-layer water sampler. See text for description

Sediment cores (3.8 cm diameter) were taken manually by divers 8 m from the water sampler in a direction

normal to the flow while the sampler was deployed. Cores were transported gently to the surface while being maintained in a vertical orientation. Overlying water was carefully removed with a Pasteur pipet to <0.1 cm of the sediment surface, with great care taken not to resuspend any material. Only cores with level surfaces that appeared undisturbed throughout all steps of handling were subsequently used for samples. Using a calibrated piston device (Fuller & Butman 1988), the sediment was raised flush by eye with the core tube to identify the sediment-water interface, from which it was extruded (with accuracy ≈ 0.01 cm) and sliced into depth sections of 0–0.2, 0.5–1.0, 1.5–2.0, 4.5–5.0, and 9.5–10 cm. Sections were sliced with a stiff plastic card and rinsed with 0.2 µm filtered sea water into a funnel over sample containers, then preserved for protistan counts with 1% glutaraldehyde by volume.

Characterization of deposited and suspended sediment was made from unpreserved samples. Total suspended mass was measured from portions of water samples that were filtered onto preweighed GF/F filters, rinsed with distilled water, dried, and reweighed. Sediment grain size was determined by wet sieving into size fractions and weighing dry (Wheatcroft & Butman 1997). Sediment porosity was determined by weighing depth sections before and after drying to determine percent water content (converted to volume fraction).

We extracted protists from sediment samples by modified protocols from Starink et al. (1994) and Epstein (1995). Density gradients were formed in 16 ml centrifuge tubes, using 9 ml of 50% Percoll in double-salinity sea water, centrifuged at 38 800 × g for 30 min. The sample was diluted to 0.05 cm^3 sediment ml^{-1}, vortexed at medium strength for 10 s, and allowed to settle for 15 s before loading 2 ml onto the Percoll gradient. The sample was extracted once by centrifuging at 4300 × g for 15 min in a swinging-bucket rotor, and the supernatant was retained for microscopy.

To count nanoflagellates and diatoms, water samples and extracted sediment samples were stained with 50 µg ml^{-1} DAPI and observed on 0.8 µm pore size Nuclepore filters by epifluorescence microscopy under UV excitation (Porter & Feig 1980), switching to blue excitation to identify pigmented cells by chlorophyll fluorescence. To count ciliates, water samples were settled in 100 ml Utermohl chambers overnight with 0.004% Nigrosin Black and examined in an inverted compound microscope with phase contrast. Sediment samples were each settled for 5 d after adding the Percoll supernatant from one centrifuge-tube extraction to an Utermohl chamber and diluting to 100 ml with deionized water and Nigrosin Black. Sedimentary ciliates were tentatively identified only by gross morphology according to drawings in Carey (1992). Samples from 30 July at 5 cm above bottom were only examined for nanoflagellates and diatoms, and those from 10 cm above bottom were not examined.

Vertical profiles of cell concentrations in the BBL and the sediment were tested separately by ANOVA (Systat 5.2.1) to determine differences among depths and among tidal stages. Sediment data were analyzed by 2-way repeated measures ANOVA (individual cores as replicates with depth as the repeated variable). In cases with significant differences among tidal stages or significant tidal stage × depth interactions, Bonferroni-adjusted pairwise comparisons were also made. Because the water sampler took only 1 sample at each depth during each deployment, we analyzed BBL profiles from 30 July by randomized block ANOVA without replicates and no pairwise comparisons, while profiles from 26 September were merely assessed visually because of missing blocks.

RESULTS

Sediment at the site was predominantly silt. The total sediment mass residing in the <25 µm fraction was >50% (Table 1). The surficial sediment (top 0.2 cm) had a porosity ≥90% and appeared highly unstable to divers, being easily eroded by nearby movements or slight contact.

Current velocity measured at 1 m.a.b. was strongly dominated by tidal forcing and highly rectified along the long axis of the bay running NE-SW, turning counter-clockwise during the tidal cycle (Fig. 2). Maximal resultant speeds during tidal exchange ranged from 25 to 40 cm s^{-1}, corresponding to shear velocities (u_*) of 1.4 to 2.2 cm s^{-1} (assuming a bottom drag coefficient of 3×10^{-3}, Sternberg 1968).

Light transmittance measured over a several-day period at 1 m.a.b. fell toward the end of each slack tide and increased during the ensuing tidal exchange (Fig. 2). This pattern was consistent with a turbidity cloud settling during slack tide, then mixing higher

Table 1 Disaggregated grain size distribution (mass fraction) in the top 2 depth sections of sediment

Size class (µm)	0.0–0.2 cm depth section (±SD, n = 8)	0.5–1.0 cm depth section (±SD, n = 4)
≥250	0.040 (± 0.033)	0.012 (± 0.0078)
125–249	0.027 (± 0.014)	0.0075 (± 0.0042)
63–124	0.14 (± 0.020)	0.13 (± 0.015)
38–62	0.17 (± 0.018)	0.18 (± 0.025)
25–37	0.11 (± 0.020)	0.11 (± 0.010)
<25	0.52 (± 0.027)	0.56 (± 0.048)

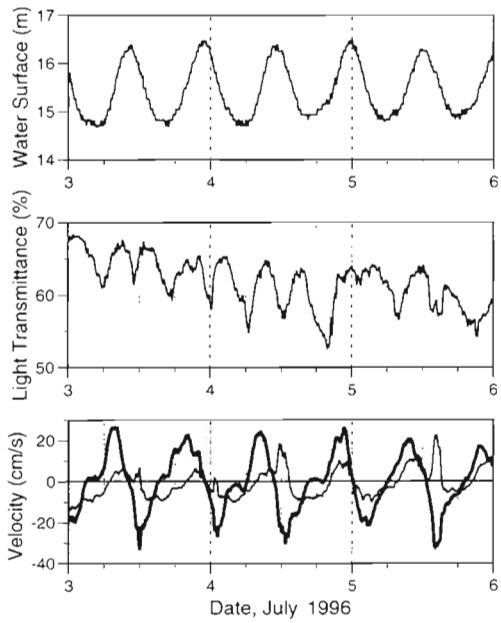

Fig. 2. Record of tide level (water surface height), light transmittance (1 m.a.b.) and velocity (1 m.a.b.) over 3 d. Transmittance dropped at the end of each slack-tide period. The major-axis component of flow variation (thick line) was on 20.0°; minor-axis component (thin line) was on 290.0°

into the water column as flow speed increased, thereby rendering the BBL clearer despite any addition of material resuspended from the bed. Of the 2 dates on which we sampled protists repeatedly throughout the tidal cycle, this turbidity pattern was most consistent on 30 July (Fig. 3). On both of these dates, nonetheless, water-column profiles of light transmittance (Fig. 4) were consistent with a cycle of settling and upward mixing. Profiles showed that turbidity consistently increased toward the bed, but during slack tide the near-bottom turbidity layer was confined closer to the bottom (i.e. the lutocline was lowest at slack tide). Filtered seston collected on 26 September was elevated to 55 mg l^{-1} during slack tide at 8.5 cm above the bed (Fig. 5). Surface temperature was 21 and 18°C on 30 July and 26 September, respectively, and on both dates a thermocline was present at 5 m depth.

The tidally periodic changes in near-bottom turbidity were the result of local processes of alternating settling and re-entrainment into the upper water column, as opposed to advection of differing water masses past the site. Light transmittance was strongly correlated with flow speed during the acceleration phase, and it did not fall until the end of the deceleration phase (Fig. 6), suggesting a local settling event at slack tide as opposed to predominant advection. The suspended material and cells that we collected in the BBL were certainly undergoing some advection and, if recently resuspended, they derived from somewhere upstream of our site. Nonetheless, using the velocity records at 1 m.a.b. and assuming a spatially uniform flow field, reconstructions of the flow path leading to our site suggested that the water we sampled had been restricted to the central silty region of the bay throughout the day (Fig. 7). We assumed that the bottom sediments and protistan communities were homogeneous horizontally throughout the center of the bay (cf. Moore 1963) and

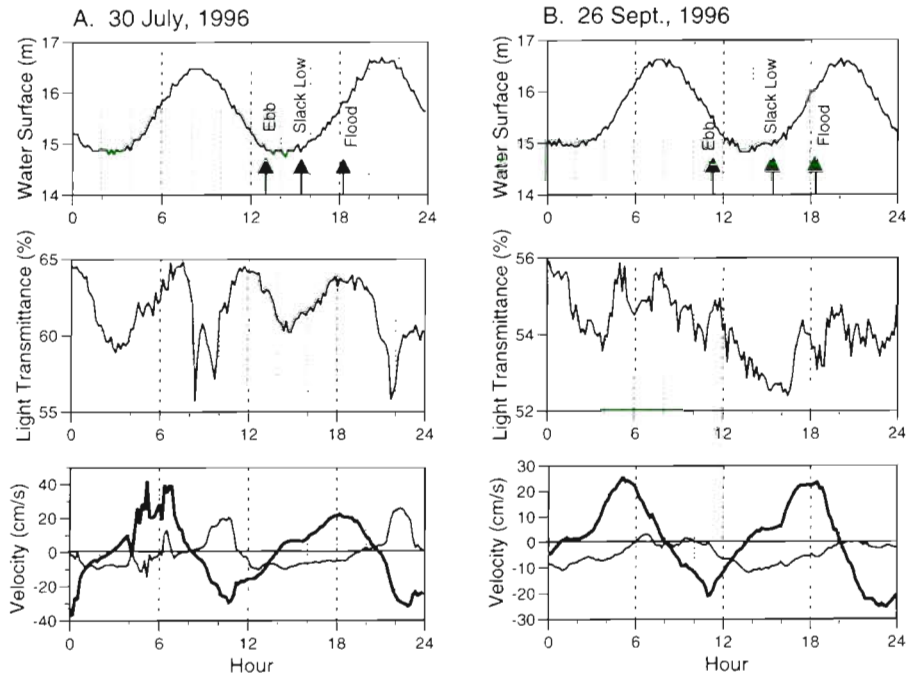

Fig. 3. Tide level (water surface height), light transmittance (1 m.a.b.) and velocity (1 m.a.b.) on 2 dates during which the benthic boundary layer and sediment were sampled for protists repeatedly throughout the tidal cycle. Arrows in top panels identify the sample times labeled 'Ebb', 'Slack Low', and 'Flood' in subsequent figures and tables. On 30 July and 26 September, respectively, the major axis of flow (thick line) was on 45.3° and 41.8°, the minor axis (thin line) was on 315.3° and 311.8°

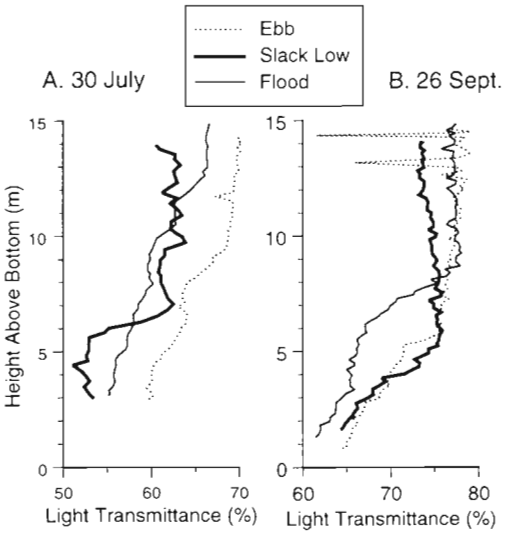

Fig. 4. Transmissometer casts corresponding to the sampling times indicated in Fig. 3

therefore that the suspension we sampled at the study site was the result of processes identical to those occurring at the site. There was significant flow normal to the principle axis of tidal exchange, especially the net advection to the southeast on 26 September (Fig. 7), so we had not merely resampled the same water as it oscillated back and forth.

The turbidity dynamics observed in Fig. 2 were used to schedule times for sampling protists during the expected maximal and minimal near-bottom turbidity (labeled roughly as 'ebb', 'slack low', and 'flood' on Fig. 3). On the 2 dates that we sampled protists, tidal periodicity of cell profiles differed among taxonomic

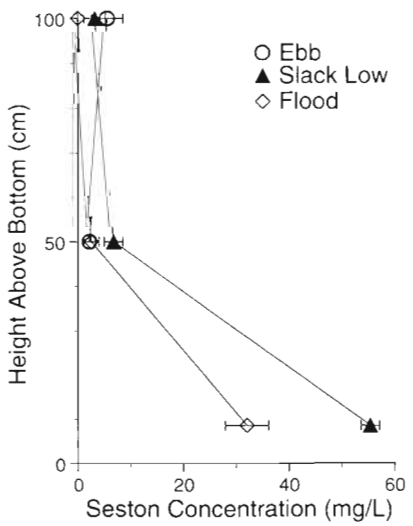

Fig. 5. Profiles of seston (total GF/F-filtered particulates) on 26 September, with sampling times corresponding to those shown in Fig. 3B

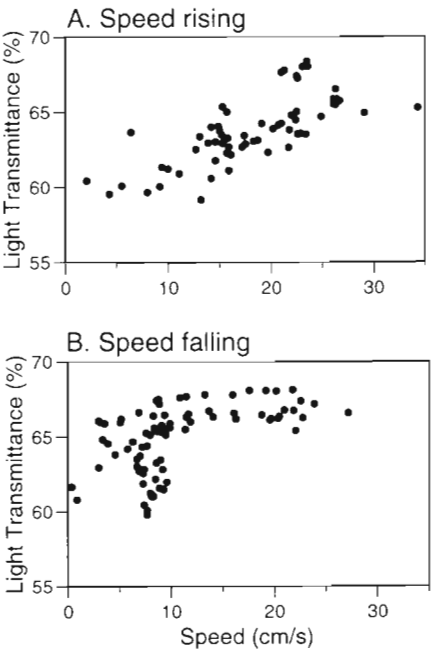

Fig. 6. Light transmittance (1 m.a.b.) as a function of flow speed on 3 July (data from Fig. 2). (A) Accelerational phases of the tidal cycle (Pearson correlation coefficient = 0.73, $p < 0.001$). (B) Decelerational phases and ensuing slack tide periods combined

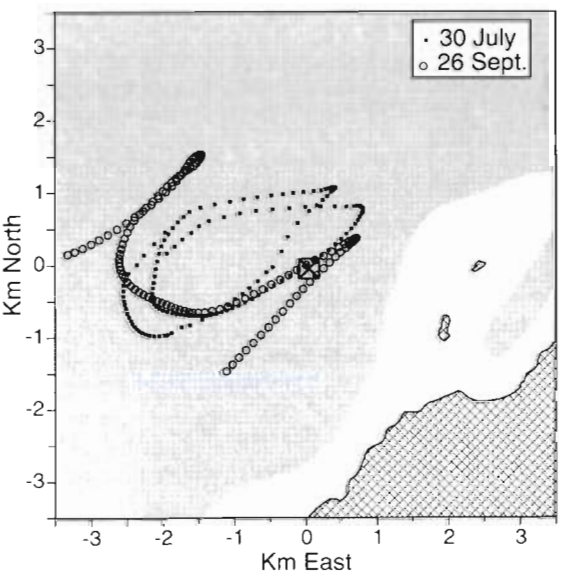

Fig. 7. Pathlines of flow at 1 m.a.b. in Buzzards Bay (MA, USA), reconstructed from the velocity data in Fig. 3 and assuming a uniform flow field. Paths for 30 July and 26 September begin at 00:00 and 04:00 h, respectively, and both paths pass the field site (marked X) at the time of final sampling (see 'Flood' tide sampling times on Fig. 3). Gray area indicates the central silty region of the bay, after Moore (1963). The 2 small Weepecket Islands, as well as a portion of Naushon Island marking the eastern boundary of the bay, are in the lower right corner

and functional groups, with generally consistent results between days (Figs. 8 & 9). All groups showed significant vertical gradients of concentration in the sediment, but most yielded statistically uniform profiles in the water column (with the exception on 30 July of heterotrophic nanoflagellates [HNan] and a nonsignificant trend in scuticociliates, Table 2). Cell concentrations were generally higher on 30 July, when water temperature was greater.

Profiles of HNan in both the sediment and BBL showed significant differences among tidal stages on 30 July (Fig. 8A, Tables 2 & 3). Compared to slack tide, concentrations during tidal exchange were elevated by as much as 112% in the bottom 5 cm of the BBL and reduced by as much as 39% in the top 0.2 cm of sediment. Surficial sediment on 26 September also showed a significant difference of 40% between flood and slack low tide (Fig. 9A, Tables 2 & 3). These patterns are consistent with cells having resuspended from surficial sediment to a narrow zone above the SWI during tidal exchange.

In contrast to HNan, profiles of pigmented nanoflagellates (PNan) and of pennate diatoms were not significantly different among tidal stages in either the BBL or the sediment (Figs. 8B,C & 9B,C, Table 2). On 30 July, however, there were nonsignificant trends of differences among tidal stages for PNan in the BBL and of a tidal stage × depth interaction for diatoms in the sediment (Table 2).

Profiles of scuticociliates (mostly *Uronema*) showed patterns similar to those of HNan, with significant differences among tidal stages in both the sediment and BBL for both sampling dates (Figs. 8D & 9D, Tables 2 & 3). Compared to slack tide, concentrations during tidal exchange were elevated by as much as 356% at 1 cm above the bed (and present at higher elevations where no scuticociliates were found during slack tide) and reduced by as much as 63% in the top 0.2 cm of sediment. These data are also consistent with cells having resuspended from surficial sediment to the BBL during tidal exchange.

Other ciliate taxa yielded differing results. Oligotrichs on both dates were found consistently in the BBL, with no differences among tidal stages, but only during slack tide were they in the sediment (Figs. 8E & 9E, Tables 2 & 3). (Grouped into our category of

Table 3. Bonferroni-adjusted p-values of pairwise multiple comparisons following ANOVA analyses of sedimentary data in Table 2. All pairwise comparisons (tidal stage by depth) were calculated simultaneously, but results are shown only comparing among tidal stages in the 0.0–0.2 cm sections. Within no other depth section was there a significant pairwise difference among tidal stages. *Statistically significant at an overall $\alpha = 0.05$

	30 July		26 September	
	Ebb	Slack Low	Ebb	Slack Low
HNan				
Slack Low	0.023*		0.266	
Flood	1.000	<0.001*	1.000	0.024*
Scuticociliates				
Slack Low	<0.001*		1.000	
Flood	1.000	<0.001*	0.451	0.017*
Oligotrichs				
Slack Low	0.008*		<0.001*	
Flood	1.000	0.008*	1.000	<0.001*
Euplotes				
Slack Low	0.283			
Flood	0.008*	1.000		
Urostrongylum			0.004*	
			1.000	0.002*

Table 2. p-values from ANOVA analyses on protistan concentration profiles (Figs. 8 & 9). Sedimentary data were run as 2-way repeated measures ANOVA with depth as the repeated variable in each of 3 replicate cores. Boundary-layer data were run as 2-way randomized block ANOVA using the means shown in Fig. 8. *Statistically significant at $\alpha = 0.05$. HNan: heterotrophic nanoflagellates; PNan: pigmented nanoflagellates

	Flagellates		Diatoms	Ciliates					
	HNan	PNan	Pennate	Scutico-ciliates	Oligo-trichs	*Euplotes*	*Urostron-gylum*	*Sticho-tricha*	Karyo-relictids
30 July sediment									
Tidal Stage	0.016*	0.536	0.337	0.006*	0.079	0.118	0.559	0.422	0.430
Depth	<0.001*	<0.001*	<0.001*	<0.001*	0.024*	<0.001*	<0.001*	0.415	<0.001*
Tidal Stage × Depth	0.002*	0.843	0.057	<0.001*	0.010*	0.029*	0.696	0.455	0.496
30 July boundary layer									
Tidal Stage	0.028*	0.053	0.102	0.015*	0.164	0.132			
Height	0.081	0.939	0.110	0.041*	0.819	0.455			
26 September sediment									
Tidal Stage	0.809	0.141	0.729	0.033*	0.027*	0.506	0.028*	0.824	0.912
Depth	<0.001*	<0.001*	<0.001*	<0.001*	0.003*	<0.001*	<0.001*	<0.001*	<0.001*
Tidal Stage × Depth	0.009*	0.281	0.956	0.059	0.001*	0.673	0.005*	0.972	0.968

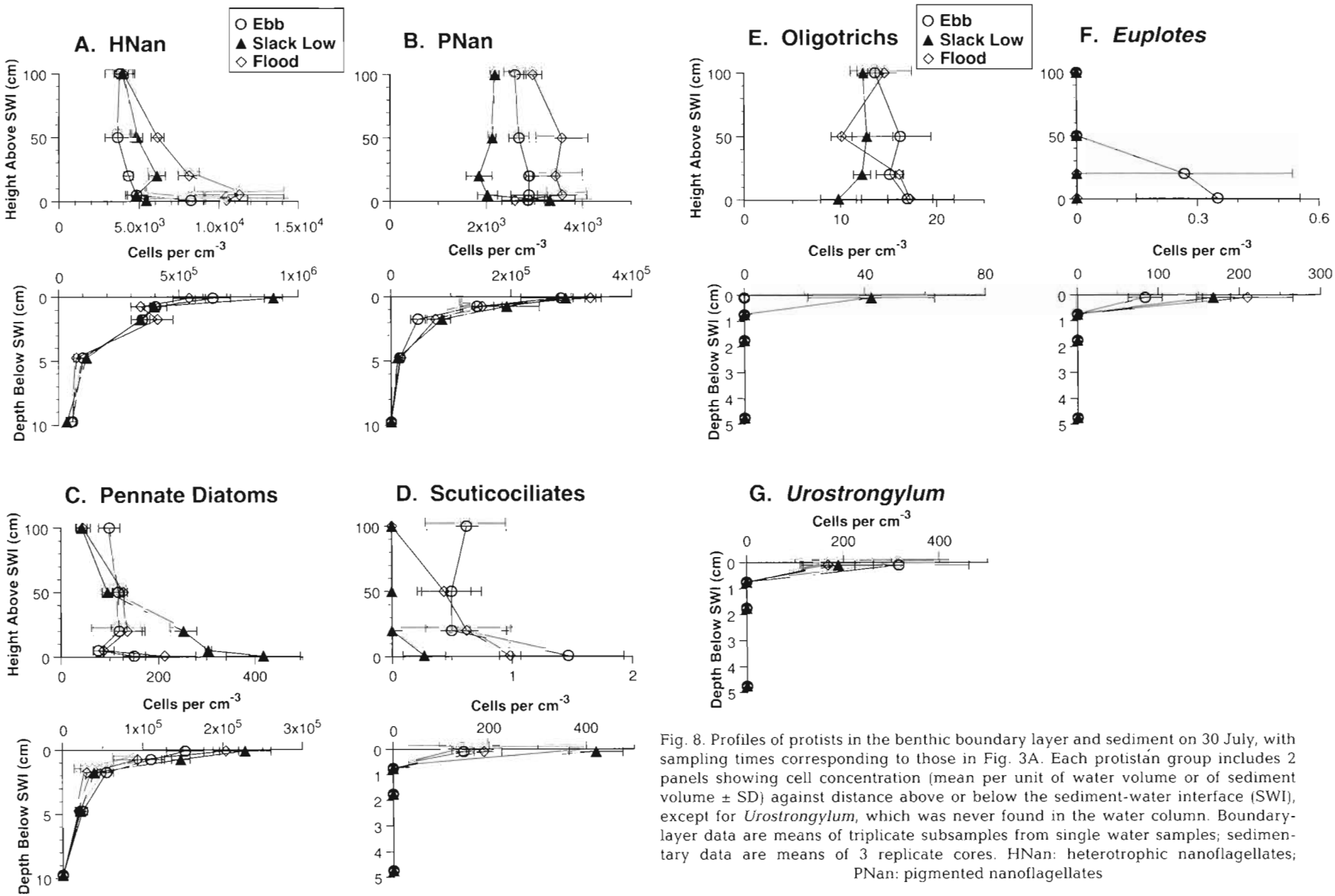

Fig. 8. Profiles of protists in the benthic boundary layer and sediment on 30 July, with sampling times corresponding to those in Fig. 3A. Each protistan group includes 2 panels showing cell concentration (mean per unit of water volume or of sediment volume ± SD) against distance above or below the sediment-water interface (SWI), except for *Urostrongylum*, which was never found in the water column. Boundary-layer data are means of triplicate subsamples from single water samples; sedimentary data are means of 3 replicate cores. HNan: heterotrophic nanoflagellates; PNan: pigmented nanoflagellates

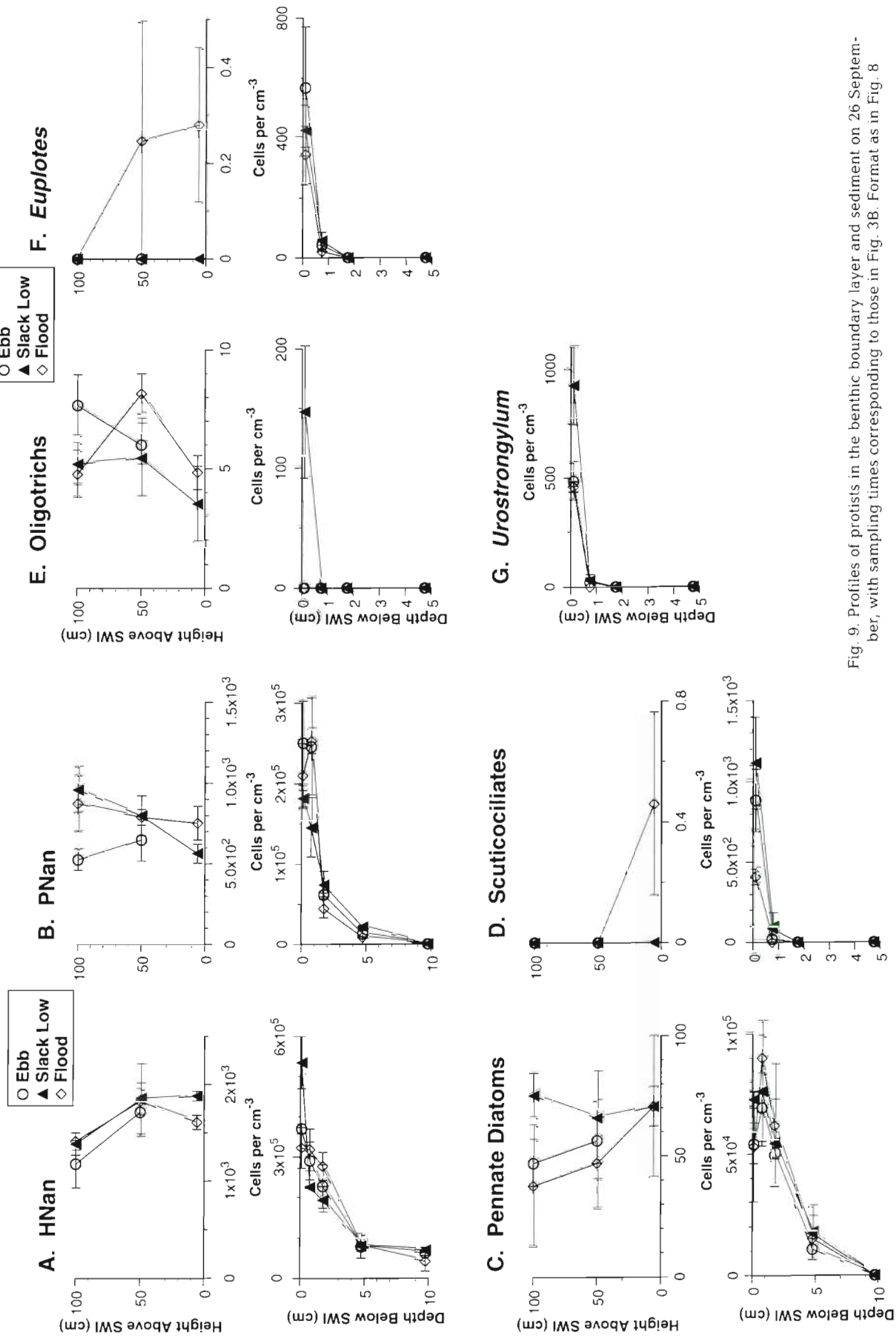

Fig. 9. Profiles of protists in the benthic boundary layer and sediment on 26 September, with sampling times corresponding to those in Fig. 3B. Format as in Fig. 8

oligotrichs were at least 4 species of Oligotrichina and a *Tintinnopsis*; at least 2 of these species of Oligotrichina were found in the sediment.) The hypotrich *Euplotes* showed the opposite pattern: consistent presence in surficial sediment, but presence in the BBL only during some periods of tidal exchange (Figs. 8F & 9F, Tables 2 & 3). Other abundant ciliates, such as karyorelictids and other hypotrichs including *Urostrongylum* and *Stichotricha*, were found exclusively in the sediment at all times, with concentrations in the top 0.2 cm up to 315 cells cm^{-3}, 925 cells cm^{-3}, and 63 cells cm^{-3}, respectively. Of these latter taxa, only *Urostrongylum* on 26 September showed significant differences among tidal stages, with concentrations in the top 0.2 cm of sediment during tidal exchange reduced by as much as 50% compared to slack low tide (Figs. 8G & 9G, Tables 2 & 3). (Data for karyorelictids and *Stichotricha* are not shown.)

The total number of cells and amount of particulate material resuspended was estimated by several different methods (Table 4). The measured depletion of cells in the top 0.2 cm of sediment during tidal exchange suggested that order 10^8 flagellates m^{-2} and 10^5 to 10^6 ciliates m^{-2} were resuspended. Estimates of cell resuspension by integrating BBL profiles were less reliable because of the lack of true replicates, but for HNan and scuticociliates the 2 methods gave roughly similar values (within a factor of 1 to 3, Table 4), suggesting that the disappearance of cells from surficial sediment was approximately accounted for by their appearance in the BBL. A notable exception to this balance was *Urostrongylum*, which was reduced in the surficial sediment during tidal exchange on 26 September but was not found in elevated abundances either elsewhere in the sediment or in the BBL.

Assuming that cells were uniformly distributed throughout the top 0.2 cm of sediment, the changes in cell concentrations between tidal stages indicated that sediment was resuspended to a depth of 0.079 to 0.2 cm. Using the mass of sediment measured in the top 0.2 cm from porosity samples, this erosion depth suggests that 131 to 333 g sediment m^{-2} was eroded.

Table 4. Numbers of cells resuspended, calculated from both sedimentary and boundary-layer profiles. Sedimentary calculations were made only for those protists with significant pairwise differences between slack tide and tidal exchange (Table 3), and used only data from the 0.0–0.2 cm depth sections. Boundary-layer calculations were made only for those protists with a significant difference among tidal stages on 30 July (Table 2), except for *Euplotes*, which was only found in the boundary layer during tidal exchange. Boundary-layer calculations were integrated over the bottom 100 cm (see Figs. 8 & 9), and in the case of HNan only comparing flood vs low tides

	Resuspension calculated from sedimentary profiles (cells m^{-2})	Observed addition to boundary layer during tidal exchange (cells m^{-2})
HNan		
30 Jul	$5.1 \times 10^8 - 7.1 \times 10^8$	1.7×10^9
26 Sep	4.2×10^8	
Scuticociliates		
30 Jul	$4.6 \times 10^5 - 5.5 \times 10^5$	$2.7 \times 10^5 - 5.5 \times 10^5$
26 Sep	1.4×10^6	
Oligotrichs		
30 Jul	8.4×10^4	
26 Sep	2.9×10^5	
Euplotes		
30 Jul		6.2×10^4
26 Sep		1.3×10^5
Urostrongylum		
26 Sep	$8.8 \times 10^5 - 9.3 \times 10^5$	

DISCUSSION

Material resuspension

The tidal periodicity in turbidity is consistent with previous studies of material resuspension in Buzzards Bay (Rhoads 1973, Rhoads et al. 1975, Roman & Tenore 1978). Rhoads (1973) described a turbid layer extending 3 m or more above bottom where suspended solids reached a maximum of 10 to 35 mg l^{-1} (cf. Figs. 4 & 5). He also found that near-bottom turbidity peaked around slack tide, due to sinking of the resuspended load (cf. Figs. 2, 3), as did Eisma et al. (1994) in the Elbe estuary (Germany) . For near-bottom water to become clearer during tidal exchange, erosion must be limited to a thin veneer of quickly eroded flocculent material at the SWI that overlies more erosion-resistant sediment; otherwise, continual resuspension during tidal exchange would cause maximal near-bottom turbidity to occur during peak flow. Such floc erosion, or 'Type I' erosion, has been well described and modeled with an exponentially decreasing erosion rate during constant flow and a direct relationship between depth and bed shear strength (Amos et al. 1992). The changes we measured in sedimentary cell concentrations suggested that ≤0.2 cm of sediment was likely to have eroded.

Our calculated mass erosion of 131 to 333 g sediment m^{-2} is higher than the resuspension in Buzzards Bay reported by Roman & Tenore (1978; 80 g m^{-2}, calculated from their POC resuspension and assuming 2.5% POC content in the sediment, Banta et al. 1995). However, our erosion depth calculated from cell profiles would be an overestimate if cells were concentrated at the SWI rather than uniformly distributed in the top 0.2 cm of sediment.

Specificity of protistan resuspension

The protistan communities of the BBL and surficial sediment displayed taxon-specific and functional group-specific responses to material resuspension. HNan, scuticociliates, oligotrichs, *Euplotes*, and *Urotrongylum* showed significant periodicities in their vertical distributions consistent with a cycle of resuspension and deposition. In contrast, PNan, pennate diatoms, karyorelictids, and *Stichotricha* maintained constant vertical profiles throughout tidal cycles.

Among those groups displaying periodicities, there was no direct evidence that they left the surficial sediment during tidal exchange by migrating downward, and in the cases of HNan and scuticociliates the disappearance of cells from surficial sediment was roughly balanced by increases in the BBL. Oligotrichs, *Euplotes*, and *Urostrongylum* only showed a significant flux out of either the sediment or the BBL (Table 4), with no corresponding change in the profile on the other side of the SWI. This discrepancy can be easily explained for oligotrichs and *Euplotes* because the expected increases in concentration on the other side of the interface would have been similar to or much less than the standard deviations of measured concentrations there, rendering them undetectable. In contrast, resuspended *Urostrongylum* should have been detectable in the BBL during tidal exchange, unless they instead migrated slightly downward in the sediment and were hidden from our sampling by being in the 0.2 to 0.5 cm depth range.

Taxon- and functional-group-specific resuspension can be further understood by considering behavioral adaptations. Flagellates and ciliates can be classified as tectic (those that crawl or glide on particle surfaces and may attach, particularly for feeding) or free swimmers in the water column or interstices of sediment (Patterson et al. 1989).

Tectic flagellate taxa tend to be predominantly heterotrophic (Patterson et al. 1989). If HNan are more commonly or more strongly associated with particles at the SWI than are PNan, this might partially explain why only HNan resuspended and deposited along with particulate matter. Although both HNan and PNan are abundant on marine snow in surface water (Caron et al. 1986), their relative numbers on resuspended BBL particles have not been measured. However, even if predominantly in pore water, the failure of PNan to resuspend as the SWI was eroded implies that they either live sufficiently below the erosional layer (i.e. > 0.1 cm deep) or migrate downward to this depth during tidal exchange.

Hypotrichs, generally (including *Euplotes*, *Urostrongylum*, and *Stichotricha*), and karyorelictids are tectic (Patterson et al. 1989). Many hypotrichs are epibenthic, both swimming and using their cirri to crawl on sedimentary particles. Jonsson & Johansson (1997) documented *Euplotes* moving between the SWI and BBL in a flume, and they suggested that cells use flow for dispersal and location of food patches. Our data on *Euplotes* and *Urostrongylum* might represent this behavior in the field, correlating with the periodicity of tidal currents, and perhaps it should be considered active emergence from the SWI. Karyorelictids are vermiform, a shape that might aid retention in the sediment, and these ciliates have not been reported in water samples (Patterson et al. 1989).

Scuticociliates are primarily swimmers, but they can rest on surfaces to suspension feed (Patterson et al. 1989). If loosely associated with the SWI, they might readily resuspend merely due to the shear stress of the flow. However, Burkovsky et al. (1983) found a scuticociliate to behaviorally migrate vertically through sands on a diel cycle. We can only speculate as to whether the emergence of scuticociliates from the sediment is partially behavioral. Because they are unassociated with particles in the water column, however, scuticociliates would be slow to deposit at slack tide unless they swim toward the sediment.

Oligotrichs are swimmers. Certain species have been found in both the plankton and benthos and are considered epibenthic (Fenchel & Jonsson 1988), but we have found no direct evidence in the literature that any oligotrich migrates between the sediment and water column. Because they are not associated with particles, deposition into the sediment must be by downward swimming.

Groups that did not resuspend must either live below the erosional surface of the SWI, migrate to that depth during tidal exchange, or adhere to particles large enough to resist resuspension. The nonsignificant results for pennate diatoms contrast with numerous studies of benthic diatom resuspension (e.g. Baillie & Welsh 1980, de Jonge & van Beusekom 1995), although some benthic microalgae have been found to migrate a few mm downward from the SWI as flow speed increases, thus avoiding resuspension (Berninger & Huettel 1997). Benthic diatoms and PNan at the Weepecket site might have similarly found a refuge from resuspension below the erosional depth.

Ecological implications

Our data reveal taxon-specific migratory links between the sedimentary and water column communities of heterotrophic protists. Movement of epibenthic cells between the sediment and water column has been documented previously in laboratory observations of ciliates (Jonsson & Johansson 1997), and

planktonic heterotrophic flagellates are known to deposit on the bed with sinking particles (Novitsky 1990, Caron 1991), but we know of no prior documentation of cyclical emergence and re-entry into sediment in the field. Those heterotrophic protists that regularly resuspend and deposit represent a functional group that is both planktonic and benthic, although we do not know if they are equally active in both habitats. Meiofauna enter the BBL, by both passive and active means, where they may feed (Suderman & Thistle 1998) and benefit from advection for dispersal (Palmer 1988). Jonsson & Johansson (1997) concluded from flume studies that *Euplotes* may also use the BBL for dispersal, and our data suggest that this phenomenon could be common for a variety of heterotrophic protists in the field.

The dynamics of heterotrophic-protistan resuspension might be complex, as is known for benthic diatom resuspension (de Jonge & van den Bergs 1987, Blanchard et al. 1997). The taxonomic and functional-group specificity of resuspension that we observed might have been caused by differing threshold levels of bed shear stress for erosion, similar to the findings of Arfi & Bouvy (1995) and Blanchard et al. (1997) for phytobenthos and bacteria. Different groups therefore could resuspend in succession as flow speed increases, and deposit in a different sequence (perhaps reversed) as flow decelerates. The total number of taxa that exchanges between the benthic and planktonic communities could therefore vary with maximal flow speed during the lunar cycle (e.g. spring tides vs neap tides), as well as varying among habitats that differ in flow regime, sedimentary grain-size distribution or cohesiveness.

Periodic resuspension might alter not only the community structures of the plankton and benthos but also trophic interactions, feeding rates, and growth rates. We have documented heterotrophic protists as being abundant near the bed in a subtidal BBL, and they are likely integral to the food-web structure there. The BBL is a region of distinctly high bacterial abundances and growth rates compared to other water-column depths, and resuspension enhances bacterial cell size and possibly growth rates (Wainright 1987, Ritzrau & Graf 1992, Ritzrau et al. 1997). Resuspended flagellates and ciliates are therefore exposed to an abundant and actively growing food resource. Concentrations of bacteria and microalgae may be lower in the BBL than in surficial sediment, as we found here, which could result in lowered feeding rates, but resuspended protists might benefit from exposure to a different community assemblage of prey species. However, resuspension also exposes protists to zooplankton predators. Periodic alterations of trophic interactions may thus be complex.

Feeding rates might also be influenced by resuspension and near-bottom flow via the direct effects of fluid shear on feeding mechanics (Shimeta et al. 1995). As cells are resuspended or deposited, they pass through regions with differing flow characteristics. Flow within sedimentary pore space is greatly restricted, whereas at the SWI cells experience strong shear in the viscous sublayer (with shear rate = $u_*^2/0.01$, Caldwell & Chriss 1979). Maximal shear rates in the viscous sublayer at our site therefore reached order 10^2 s^{-1}, assuming that a sublayer was maintained. Cells suspended in the turbulent BBL experience a vertical gradient of shear rate; calculated maximal values at our site ranged from 2 s^{-1} at 1 m.a.b. to 19 s^{-1} at 1 cm (following equations in Shimeta & Jumars 1991, Shimeta et al. 1995). For comparison, Shimeta et al. (1995) found that shear rates of only 0.1 to 10 s^{-1} were required to significantly enhance or suppress feeding rates of certain heterotrophic protists compared to feeding rates in still water. Therefore, feeding rates could be accelerated or reduced as cells move among the sedimentary and BBL habitats, and the division of time spent among the different habitats might impact growth rates. Taxa that benefit from ambient shear might experience the greatest feeding rates at the SWI, although they could be most susceptible to periodic erosion.

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