Limnol. Oceanogr., 46(7), 2001, 1709–1719
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Influences of benthic boundary-layer flow on feeding rates of ciliates and flagellates at the sediment-water interface

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Abstract

Heterotrophic protists are integral to sedimentary food webs, but influences on their activities are poorly understood, especially the role of benthic boundary-layer flow. Effects of flow on ingestion rates were measured for bacterivorous protists at the sediment surface in a flume. Results from four common, benthic suspension-feeding ciliates were species specific. Mean clearance rates of the scuticociliates *Cohnilembus* sp. and *Paranophrys magna* and the hypotrich *Euplotes minuta* increased by factors of two to three as friction velocity (u_*) increased from 0 to 1.0 cm s^{-1}. Above $u_* = 1.0$ cm s^{-1}, clearance rates of *Cohnilembus* sp. and *P. magna* were constant, whereas the clearance rate of *E. minuta* was reduced by 40% at $u_* = 1.5$ cm s^{-1}. *E. minuta* thus revealed an optimal flow regime for feeding. In contrast, the mean clearance rate of the scuticociliate, *Cyclidium* sp., was unrelated to u_*. In experiments with sediment cores from a subtidal, silty sand site, the mean clearance rate of the bacterivorous ciliate community of the sediment-water interface increased by a factor of five between $u_* = 0$ and 0.9 cm s^{-1}. The effects of flow were likely due to enhanced advection of prey to the ciliates. In contrast, the clearance rate of the nanoflagellate community in sediment cores was unrelated to u_*. Tidal currents at the field site were estimated to increase the ciliate community's daily integrated feeding by a factor of 3.2 compared to still water. Epibenthic ciliates create a dynamic link between planktonic and benthic food webs, mediated strongly by benthic boundary-layer flow.

Heterotrophic protists play important roles in marine sedimentary food webs as consumers, facilitators of organic-matter decomposition, and as links to higher trophic levels (Fenchel 1987; Patterson et al. 1989; Epstein 1997*a,b*). An understanding of the factors that influence feeding rates, growth rates, and trophic interactions of benthic heterotrophic protists, however, is at an early stage of development, especially when compared to knowledge of planktonic protistan ecology (Fenchel 1987; Caron and Finlay 1994). Some of the clearest influences on distributions and activities of sedimentary protists are those of physical factors, including temperature, salinity, O_2 concentration, grain size, and organic-matter input (e.g., Fenchel 1987, 1996; Patterson et al. 1989; Bak et al. 1995; Berninger and Epstein 1995).

Benthic boundary-layer flow is a ubiquitous phenomenon with strong and pervasive effects on sedimentary biogeochemistry and metazoan ecology (e.g., Jumars and Nowell 1984; Butman 1987; Gundersen and Jørgensen 1990). Yet only recently have influences of flow on the ecology of benthic heterotrophic protists been studied. For example, sediment resuspension affects the abundance and population growth of heterotrophic protists in near-bottom water (Wainright 1987; Shimeta and Sisson 1999; Garstecki et al. 2000). The regime of hydrodynamic disturbance correlates with the community structure of interstitial ciliates in sand (Lucchesi and Santangelo 1997). Near-bottom flow also affects the crawling, swimming, and dispersal of some epibenthic, hypotrich ciliates (Jonsson and Johansson 1997; Ricci et al. 1999).

Previously unstudied is the influence of flow on feeding rates of benthic protists. Numerous studies of planktonic protists have shown that small-scale flow, specifically that driven by turbulence, affects rates of feeding, growth, and nutrient uptake (reviews by Karp-Boss et al. 1996; Thomas et al. 1997; Peters and Marrasé 2000). In many cases, these

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Acknowledgments

We thank N. Trowbridge, J. Sisson, and M. Gould for help in the field and/or lab; the director of the Rinehart Coastal Research Center (WHOI) for use of facilities; W. McGillis and J. S. Fries for assisting with particle-imaging velocimetry; J. Grant for advice on calibrating the hot film; D. Caron for providing a culture of *H. halodurans*; and two anonymous reviewers for comments that improved the manuscript. Supported by NSF grant OCE-9711441 and a grant from the Rinehart Coastal Research Center (J.S.), a Hackman fellowship from Franklin and Marshall College (O.M.A.), and NSF grants OCE-8812651 and OCE-9729972 (C.A.Z.). WHOI contribution 10402.

results are due to a mass-transfer effect of small-scale laminar shear around cells. Shimeta et al. (1995) found species-specific effects of shear on ingestion rates among a variety of planktonic flagellates and ciliates, including enhancement or depression of feeding rate for some species in strong shear. Shimeta and Sisson (1999) suggested that such effects of shear may be stronger for protists at the sediment-water interface because the shear rate of laminar flow in the viscous sublayer can greatly exceed typical values in the water column and because benthic protists remain relatively stationary against the substratum rather than moving with the flow.

We investigated whether boundary-layer flow strength influences feeding rates of benthic protists by measuring ingestion rates of bacterivorous ciliates and flagellates at the sediment-water interface of a flume. Feeding rates were measured by the uptake of fluorescently labeled bacteria during short-term incubations, thus isolating the effects of flow on feeding mechanics and behavior from longer term effects such as physiological responses and population growth. Measurements at the sediment-water interface were facilitated by adding cultured protists to a thin layer of cleaned sediment with manipulated bacterial concentrations, thereby preventing a subsurface refuge from flow and allowing control of the type and distribution of food resources. Four species of benthic suspension-feeding ciliates were tested in this fashion, including several scuticociliates and a hypotrich, which are common taxa in fine sediments (Fenchel 1987; Shimeta and Sisson 1999; Garstecki et al. 2000). To corroborate the results, separate experiments were run with freshly collected sediment cores to measure feeding by uncultivated protists in natural positions within unaltered sediment, as well as to look for community-level effects of flow on natural assemblages of ciliates and nanoflagellates. Flow data from the field site were used to extrapolate the laboratory results to predict the effects of tidal flow on feeding rates in nature.

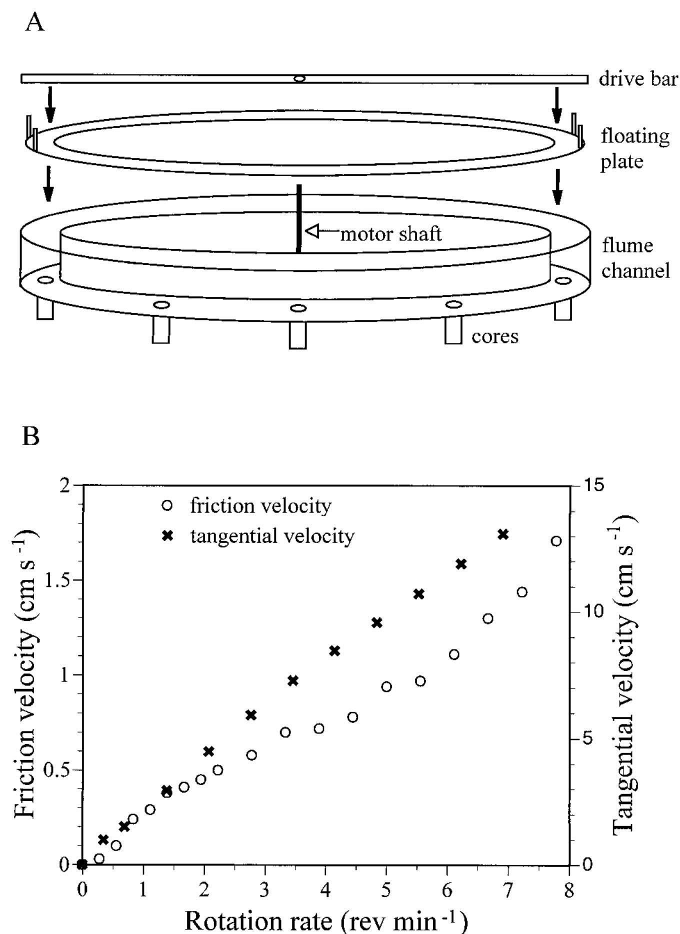

Fig. 1. Annular flume. (A) Main components of the flume (dimensions given in text). The flume is assembled as shown by arrows. (B) Flow characteristics at the center line of the cores as functions of rotation rate for a 5-cm deep water column and smooth bed. Friction velocity at the bed was measured with a flush-mounted hot film. Tangential velocity was measured with particle-imaging velocimetry at 2.5 cm above bottom.

Methods and materials

Field site, sediments, and protists—Sediment and protists were collected from a 15-m deep, silty sand site in Buzzards Bay, on the Northwest Atlantic coast (41°31.96′ N, 70°54.17′ W). For grain-size analysis, SCUBA divers collected sediment with acrylic cores (3.8 cm inner diameter); sediment was extruded and the top 0.2 cm was wet-sieved into size fractions, dried on filters, and weighed (Fuller and Butman 1988). Sediment for ciliate isolation and for use in experiments with ciliate cultures was collected from the top 1 cm of Van Veen grabs. Ciliates were isolated after several days from yeast-extract enriched sediment slurries, and monoclonal cultures were established using the bacterium *Halomonas halodurans* as the sole food source. Cultures were maintained at 20°C and transferred every 3 weeks in tissue-culture flasks with 20 ml of 0.45-μm filtered and sterilized seawater, a drop of 10% yeast extract, and a sterile rice grain. Ciliates were identified from live and protargol-stained (Skibbe 1994) specimens using keys in Small and Lynn (1985), Carey (1992), and references therein. Sediment for use in flume experiments with ciliate cultures was combusted at 500°C for 4 h to destroy all organisms and organic matter, and it was sieved to remove the size fraction <25 μm, which otherwise eroded too easily in the flume because combustion rendered it noncohesive. Fresh sediment for experiments with natural communities of nanoflagellates and ciliates was collected by SCUBA divers in acrylic cores (3.18 cm inner diameter) that fit directly into the flume. Intact cores were transported to the lab in a cooler and used within 10 h.

Velocity (u) at the field site was measured with an InterOcean S4 current meter mounted on a tripod at 1.15 m above bottom. Friction velocity (u_*) was calculated as $C_D^{1/2}u$, with a drag coefficient $C_D = 2.98 \times 10^{-3}$ (Sternberg 1968).

Flume—Experiments were run at 20°C in a polycarbonate, 1.5-m diameter annular flume having a 10-cm channel width and 5-cm water depth (Fig. 1). The flow is driven by friction from an annular plate floating on the water and turned by a DC motor attached by an aluminum bar from the center of

the flume. The flume bed has 10 circular holes with removable plugs through which sediment cores (3.18 cm inner diameter) can be inserted from below. Sediment is raised flush with the flume bed using a threaded piston secured underneath each core. The core holes are centered 4.1 cm from the inner wall, and they are equally spaced along the circumference of the channel.

Bed shear stress at the centerline of the core holes was measured while the bed was smooth using a flush-mounted hot-film shear probe (TSI model 1237W) and TSI Flowpoint anemometer. The probe was calibrated in pipe flow, with wall shear stress calculated from the pressure drop and from the volume-discharge rate following Schlichting (1979). Friction velocity in the flume was calculated as $u_* = (\tau_b/\rho)^{1/2}$, where τ_b is the bed shear stress and ρ is the density of seawater (Nowell and Jumars 1984). Owing to secondary flow, bed shear stress in annular flumes varies across the width of the channel (Graham et al. 1992). Measurements in our flume with particle-imaging velocimetry showed that the tangential component of flow at 0.4 cm above bottom varied across the width of the core holes by $\leq$25% of the midline value, and bed shear stress presumably varied by a similar amount. The variation of u_* across the cores at a single flume setting was therefore less than the differences among the experimental treatments.

Experiments with cultured ciliates—Fluorescently labeled bacteria (FLB) were prepared by heat-killing and staining early stationary-phase cultures of *H. halodurans* with DTAF, following Sherr and Sherr (1993). FLB were spherical to slightly rod-shaped, 1.5 μm diameter.

Experiments were conducted separately for each ciliate species and followed a Latin Square design (Fleiss 1986) with three factors: flow treatment, culture batch, and treatment order. On a single day, feeding rate was measured at four u_* values using aliquots from a single batch culture of one species in exponential growth phase. This experiment was replicated on 4 d, using different batch cultures that had reached the same age, and the order of the u_* treatments was varied among days. A newly randomized Latin Square was used for each ciliate species.

In each flume run at a single u_*, ciliates occupied four cores of uniformly 0.1-cm deep, combusted sediment. An unused core hole (plugged flush) was located between adjacent cores in the flume. The sediment layer was thin in order to maximize the exposure of ciliates to the overlying flow and to ensure that advection through the pore space would maintain bacterial concentrations in equilibrium with the water column. The water column and the sedimentary pore water each contained roughly 1.4×10^6 cells ml^{-1} of live, unstained *H. halodurans* and 0.8×10^6 FLB ml^{-1}. These pore-water concentrations were achieved by adding unstained bacteria (as part of the ciliate culture) and FLB to sediment in initial concentrations that exceeded those desired by factors of 12.5 and 20, respectively, to account for adhesion onto grains as indicated from preliminary experiments. At the beginning of a day, the ciliate culture was diluted to the appropriate bacterial concentration, and the ciliates were then concentrated over a 3-μm filter. Ciliate densities in these concentrated cultures averaged 2.2×10^4 cells ml^{-1} for *Cohnilembus* sp., 1.6×10^3 cells ml^{-1} for *Paranophrys magna,* 3.0×10^2 cells ml^{-1} for *Euplotes minuta,* and 1.4×10^4 cells ml^{-1} for *Cyclidium* sp. Prior to a flume run, 3.5 ml of ciliate culture was added to each core and allowed to acclimate undisturbed for 30 min. The flume was filled with 0.2-μm filtered seawater containing added unstained *H. halodurans* and FLB. The feeding-measurement period began by stirring FLB into the sediment cores. Cores were immediately placed in the flume and raised flush with the floor, the annular plate was lowered, and the flume speed was set. After the flume was stopped, cores were quickly removed; the contents of three cores were rinsed out with 0.2-μm filtered seawater; and they were preserved with cold glutaraldehyde (1% final) to end the feeding-measurement period. At the end of each flume run, a 4.5-ml sample of the water was preserved with 1% final glutaraldehyde for later enumeration of bacteria.

The mean length of the feeding-measurement period until fixation of ciliates was 34 ($\pm$1) min, and the mean time during which cells were exposed to flow was 25 ($\pm$1) min. The remaining 9 min was the handling time required to set up the flume with cores and to break down the flume and retrieve sediment from cores. A still-water flume treatment ($u_* = 0$, in which the cores were handled identically as above) served as a control for any effects caused by handling. It also served as a baseline measurement of feeding rates in zero-flow conditions, for comparison with feeding rates in flow.

Clearance rates of two ciliate species (*Euplotes minuta* and *Cyclidium* sp.) were also measured in still water within polycarbonate flasks, in the absence of sediment, in order to compare with the still-water flume treatments. Cultures were prepared by the same methods as in flume experiments; concentrations of FLB and unlabeled bacteria matched those in the water column of the flume experiments; and the incubation period was the same length. These measurements involved no physical disturbances due to core handling, and ciliates were sampled gently by pipet at the end of the incubation period.

Bacterial concentrations in the sediment were measured from the fourth core in each flume run. Overlying water was withdrawn from the core and discarded. Pore-water bacteria were separated from grain-attached bacteria by inverting and submerging the core gently into a filtration funnel containing 0.2-μm filtered seawater over a 10-μm membrane filter, so that the sediment could sink gently onto the filter. The funnel was then drained by gravity. The filtrate (containing pore-water bacteria) and the sediment (which was rinsed off of the filter) were each preserved in 1% final glutaraldehyde. The pore-water volume was determined by drying and weighing additional samples of this sediment.

Velocities of feeding currents were measured from videotapes of the trajectories of bacteria entrained toward the cytostome of stationary, feeding ciliates in a petri dish on a Leica DMIRB inverted microscope.

Experiments with natural communities of protists—Experiments followed a Latin Square design with factors of flow treatment, day, and treatment order. On a single day, feeding rates were measured at four u_* values using cores

collected that day. Each core was used for one u_* setting. This experiment was replicated on 4 d, and the order of u_* treatments was varied among days.

In each flume run at a single u_*, four cores of ca. 10 cm depth were used, with plugged core holes located between them in the flume, as described above. Almost all of the overlying water from the field was removed from the cores before inserting them into the flume. The flume was filled with 0.2-μm filtered seawater containing added FLB at roughly 5×10^6 cells ml^{-1}. The feeding-measurement period began by exposing the cores to the water column and raising them flush with the flume floor, after which the annular plate was lowered and the flume speed was set. After the flume was stopped, cores were quickly removed; a small amount of flocculent material (ca. 0.15 g) was removed from the sediment-water interface of three cores via Pasteur pipet; and it was preserved with cold glutaraldehyde (1% final) to end the feeding-measurement period. The water column was sampled for bacteria at the end of each flume run, as described above. The mean length of the feeding-measurement period until fixation was 56 ($\pm$4) min, and the mean time during which cells were exposed to flow was 40 ($\pm$3) min. A still-water flume treatment served as a control as described above.

FLB concentrations in the sediment were measured from the fourth core in each flume run. Overlying water was withdrawn and replaced with 0.2-μm filtered seawater. Flocculent material was then removed from the sediment-water interface and preserved as described above.

Sample analyses—Cultured ciliates were extracted from preserved sediment by gently resuspending, allowing the sediment to settle for 1 min, then decanting. Natural communities of nanoflagellates and ciliates were extracted by centrifugation on Percoll density gradients following the protocol in Shimeta and Sisson (1999) without dilution. Attached, unstained bacteria and FLB were removed from sediment by sonicating for three 1-min bursts with 0.01% Triton X-100; field sediment was diluted 1 : 5,000 prior to sonication. Cells were filtered onto black Nuclepore filters (0.8 μm for protists, 0.2 μm for bacteria), stained with 20 μg ml^{-1} DAPI, and mounted on microscope slides with immersion oil. Cells and ingested FLB were counted on a Leica DMRB epifluorescence microscope using UV excitation for DAPI visualization and blue excitation for FLB. In each sample of cultured ciliates, 50–100 ciliates were examined for FLB depending on the number retrieved from the sediment. On rare occasion a small and elongate *Euplotes* cell was seen in samples; these cells were not counted in case they were slow-feeding swimmers that had metamorphosed in response to reduced food densities (cf. Fenchel 1990). In each sample of natural communities, protists were examined until 50 nanoflagellates and 25 ciliates that contained FLB were found. Cells without FLB were not counted in the natural communities because we could not assume that such cells had been at the sediment surface with access to FLB; they might have been sampled from too far beneath the sediment-water interface. Apparent mixotrophs were included.

The clearance rates of cultured ciliates were calculated by dividing the average number of ingested FLB per ciliate by the length of the feeding-measurement period and by the water-column FLB concentration. The clearance rates of natural communities of protists were calculated by two methods. First, the clearance rate among only cells that had ingested $\geq$1 FLB was calculated by dividing the average number of ingested FLB by the length of the feeding-measurement period and by the water-column FLB concentration. Second, the clearance rate of the entire community of bacterivorous cells feeding at the sediment-water interface (accounting for cells that were feeding but failed to ingest any FLB during the flume run) was calculated as follows. The frequency distribution of cells that ingested $\geq$1 FLB was fit by iteration to a truncated Poisson distribution (i.e., lacking occurrences of zero ingested FLB), and the corresponding full Poisson distribution (i.e., including assumed occurrences of zero ingested FLB) was computed, following equations in Bratvold et al. (2000). The occurrences of zero ingested FLB were then added to the data of $\geq$1 ingested FLB, and the average number of ingested FLB was recalculated and converted to clearance rate.

Analysis of variance was performed on Systat v5.2.1 for the Macintosh with the following model: *clearance rate* = *flow treatment* + *culture batch* or *core collection day* + *treatment order* + *constant.* The experimental design did not allow testing of interactions between factors. The three cores in a single flume run were averaged to give a single clearance rate. *Culture batch* or *core collection day* was a blocking factor representing the four replicate days that each experiment was run with a different culture or with a different collection of fresh sediment cores. When appropriate, data were transformed to reduce heterogeneity of variances (Table 1). When an ANOVA factor was significant, the Tukey-Kramer HSD test was used to determine which pairs of means differed. The same three-factor ANOVA design was used to test bacterial concentrations as the dependent variable.

Results

Sediment at the field site was poorly sorted, silty sand. Fine and medium sand (125–499 μm) comprised 76.5% of the mass; very fine sand (63–124 μm) and silt (<25 μm) were each 7% of the mass; but sediment between 25 and 62 μm was <4%. After combustion and removal of silt, the sediment used in experiments with cultured ciliates was a noncohesive sand that was much more permeable than the unaltered field sediment.

The clearance rates of three cultured ciliate species were significantly affected by friction velocity (Fig. 2, Table 1). The mean clearance rate of the scuticociliate *Cohnilembus* sp. increased by a factor of 2.1 between $u_* = 0$ and 1.0 cm s^{-1}, but it remained constant between $u_* = 1.0$ and 1.5 cm s^{-1}. A similar pattern occurred for the scuticociliate *Paranophrys magna,* with the mean clearance rate increased by a factor of 1.8 between $u_* = 0$ and 1.0 cm s^{-1} and a plateau in stronger flow. The mean clearance rate of the hypotrich ciliate, *Euplotes minuta,* increased by a factor of 2.8 between $u_* = 0$ and 1.0 cm s^{-1}, but it showed a different response in stronger flow, with a statistically significant reduction by

Table 1. ANOVA results from clearance rates measured in flume experiments (data shown in Figs. 2, 3). Heterogeneity of variances was reduced with the following transformations: log (x) for *P. magna, E. minuta,* and *Cyclidium;* $x^{1/2}$ for the ciliate community; and $-1/x$ for *Cohnilembus.* Results for the natural communities include inferred numbers of feeding cells that ingested no FLB (Fig. 3, filled circles).

Source of variation	Sum of squares	d.f.	Mean square	F	P
Cohnilembus sp.					
Flow	3.83	3	1.28	98.17	<0.001
Batch	0.48	3	0.16	12.18	0.006
Order	0.26	3	0.09	6.72	0.024
Error	0.08	6	0.01		
Paranophrys magna					
Flow	0.20	3	0.07	5.88	0.032
Batch	0.25	3	0.08	7.50	0.019
Order	0.01	3	<0.01	0.38	0.769
Error	0.07	6	0.01		
Euplotes minuta					
Flow	0.38	3	0.13	75.73	<0.001
Batch	0.36	3	0.12	70.52	<0.001
Order	0.04	3	0.01	7.96	0.016
Error	0.01	6	<0.01		
Cyclidium sp.					
Flow	0.09	3	0.03	2.35	0.172
Batch	0.10	3	0.03	2.66	0.142
Order	0.04	3	0.01	0.93	0.483
Error	0.08	6	0.01		
Natural nanoflagellate community					
Flow	0.01	3	<0.01	2.53	0.153
Day	0.01	3	<0.01	2.82	0.130
Order	<0.01	3	<0.01	1.24	0.375
Error	0.01	6			
Natural ciliate community					
Flow	0.80	3	0.27	211.07	<0.001
Day	0.02	3	0.01	5.30	0.040
Order	0.02	3	0.01	4.94	0.046
Error	0.01	6	<0.01		

40% at $u_* = 1.5$ cm s^{-1}. In contrast to these three species, the clearance rate of the scuticociliate *Cyclidium* sp. was unrelated to u_*.

The mean (±standard error [SE]) clearance rate of *E. minuta* among three still-water flasks was 1.02 (±0.10) nl h^{-1}, and that of *Cyclidium* sp. was 0.37 (±0.03) nl h^{-1}. These rates were similar to the mean rates measured in the flume at $u_* = 0$ cm s^{-1} (Fig. 2).

Three of the four species yielded clearance rates that differed significantly among culture batches (Table 1; compare lines through data in Fig. 2). Some batches had generally higher or lower clearance rates than others, likely due to differences in physiological state. The order of flow treatments was a significant effect for two species (Table 1). For *Cohnilembus* sp. some of the highest clearance rates occurred in the last two treatments of the day, and for *E. minuta* they occurred in the middle two treatments of the day. For both of these species, the flow effect was more significant than the treatment-order effect.

Concentrations of suspended bacteria in the flume (Table 2) were similar to those in near-bottom water at the field site (Shimeta, unpubl. data), and there were no differences between water-column and pore-water concentrations of either total bacteria or FLB (Tables 2, 3). Concentrations of grain-attached bacteria were lower in combusted sediment than in natural sediment (Table 2). None of the measurements of bacterial concentrations (total bacteria or FLB in the water column, pore water, or attached to grains) showed significant differences among flow treatments (Table 3).

Cohnilembus sp. had a considerably smaller cell size than the other three ciliates, which were relatively similar (Table 4). *E. minuta,* however, had the weakest feeding current, and *Cyclidium* sp. had the strongest.

Experiments with field sediment cores were run only up to $u_* = 0.9$ cm s^{-1} because bedload transport began above this point. The clearance rate of the natural nanoflagellate community was unrelated to u_*, whereas the natural ciliate community was strongly affected by flow (Fig. 3, Table 1). The mean clearance rate of the bacterivorous ciliate community (extrapolated data that included feeding cells that ingested no FLB; Fig. 3, filled circles) increased monotonically by a factor of 5.1 between $u_* = 0$ and 0.9 cm s^{-1}. The clearance rates also differed significantly among replicate days (compare lines through data in Fig. 3), and the order of flow treatments was significant, possibly due to physiological state or handling effects. The second flume run of the day had some of the lowest clearance rates. As for the cultured ciliates, flow had a more significant effect on clearance rates than did treatment order. Similar statistical results (not shown) were obtained when clearance rates of ciliates

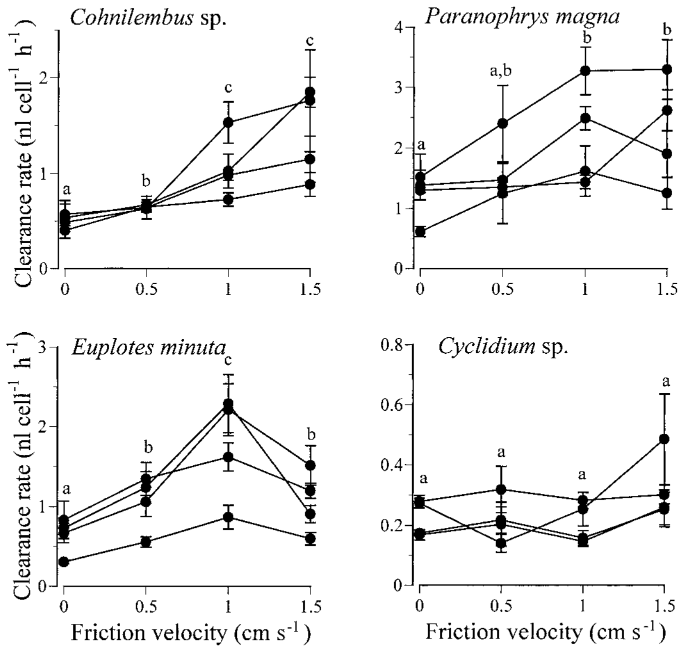

Fig. 2. Clearance rates of cultured ciliates as a function of friction velocity (u_*) in the flume. Each point is the mean ± s.e. of three cores in a single flume run. Lines connect measurements made on the same replicate day using aliquots from a single batch culture. Clearance rates at u_* values with matching letters above the data are not significantly different at $\alpha = 0.05$.

that ingested ≥1 FLB (Fig. 3, open circles) were analyzed. Most of the ciliates that ingested FLB in the natural community appeared under epifluorescence microscopy to be scuticociliates and hypotrichs. Examination of additional preserved field samples under phase-contrast microscopy (method of Shimeta and Sisson 1999) revealed that 33% of individuals in the ciliate community were scuticociliates, 35% were hypotrichs, and the remainder were mostly from the orders Karyorelictida, Hymenostomatida, and Oligotrichida.

FLB that entered the natural sediment cores were present at very low levels compared to resident bacteria from the field (Table 2). Neither the total sedimentary bacterial concentration, the sedimentary FLB concentration, nor the water-column FLB concentration differed among flow treatments (Table 3).

Friction velocity in the field displayed a strong tidal periodicity, ranging from 0.02 to 2.4 cm s^{-1} (Fig. 4). The levels of u_* used in flume experiments occurred commonly at the field site. On average over the six full days of data in Fig. 4, u_* in the field was ≤1.5 cm s^{-1} (matching the range in the experiments with cultured ciliates) for 93% of the day and ≤0.9 cm s^{-1} (matching the experiments with natural communities) for 71% of the day.

Discussion

Influences of flow on cultured ciliates—Three of the four ciliate species showed a direct relationship between clearance rate and u_* in the range of 0–1.0 cm s^{-1}. The mechanism explaining these results is most likely that boundary-layer flow enhanced the advection of suspended bacteria to the ciliates.

All four species are suspension feeders, as is typical of hypotrichs and scuticociliates (Fenchel 1986). A suspension-feeding mode is further evident from the similarity of clearance rates in still-water flasks and in the flume at $u_* = 0$ cm s^{-1} because if ciliates fed on attached bacteria the rates would have been higher in the flume due to abundant bacteria on sediment grains. The hypothesis that boundary-layer flow enhanced the advection of suspended bacteria to these suspension-feeding ciliates is supported by comparisons of near-bottom flow speed with the measured velocities of ciliate feeding currents. Owing to their small size, ciliates at the sediment-water interface were contained within the viscous sublayer, a region of predominantly laminar flow extending at least 0.07 cm above the bed, given the u_* values in our experiments (sublayer thickness = $10\nu u_*^{-1}$ in hydraulically smooth, turbulent flow; Nowell and Jumars 1984). In the viscous sublayer, velocity is linearly related to height above the bed (z): $u = u_*^2 z \nu^{-1}$ (Middleton and Southard

Table 2. Bacterial concentrations in flume experiments; mean (±s.d.) of 4 replicate days. FLB = fluorescently labeled bacteria; total bacteria includes live unstained cells and FLB; n/a = not applicable.

Experiment	Water column total bacteria (10^6 cells ml^{-1})	Water column FLB (10^6 cells (ml^{-1})	Pore water total bacteria (10^6 cells ml^{-1})	Pore water FLB (10^6 cells ml^{-1})	Grain-attached total bacteria (10^7 cells g^{-1})	Grain-attached FLB (10^7 cells g^{-1})	Natural sediment total bacteria (10^9 cells g^{-1})	Natural sediment FLB (10^9 cells g^{-1})
Cohnilembus sp.	2.20 (±0.33)	0.81 (±0.06)	2.28 (±0.33)	0.79 (±0.04)	1.17 (±0.12)	0.33 (±0.15)	n/a	n/a
Paranophrys magna	2.06 (±0.24)	0.69 (±0.13)	1.96 (±0.24)	0.71 (±0.02)	1.21 (±0.13)	0.34 (±0.01)	n/a	n/a
Euplotes minuta	2.20 (±0.21)	0.79 (±0.17)	2.38 (±0.66)	0.68 (±0.08)	1.36 (±0.30)	0.30 (±0.04)	n/a	n/a
Cyclidium sp.	2.34 (±0.26)	0.83 (±0.15)	2.02 (±0.47)	0.77 (±0.09)	1.28 (±0.42)	0.30 (±0.05)	n/a	n/a
Natural community	4.69 (±0.34)	4.69 (±0.34)	n/a	n/a	n/a	n/a	3.36 (±0.58)	0.02 (±0.01)

Table 3. *P* values from statistical tests involving bacterial concentrations in flume experiments. The first two columns are paired *t*-tests; all other columns are three-factor ANOVA (*see Methods*) showing only the result for flow treatment. FLB = fluorescently labeled bacteria; total bacteria includes live unstained cells and FLB; n/a = not applicable.

Experiment	Total bacteria in water column vs. pore water	FLB in water column vs. pore water	Water column total bacteria vs. u_*	Water column FLB vs. u_*	Pore water total bacteria vs. u_*	Pore water FLB vs. u_*	Grain-attached total bacteria vs. u_*	Grain-attached FLB vs. u_*	Natural sediment total bacteria vs. u_*	Natural sediment FLB vs. u_*
Cohnilembus sp.	0.86	0.83	0.22	0.72	0.40	0.48	0.67	0.46	n/a	n/a
Paranophrys magna	0.51	0.66	0.27	0.66	0.65	0.41	0.47	0.59	n/a	n/a
Euplotes minuta	0.66	0.14	0.16	0.72	0.81	0.94	0.23	0.23	n/a	n/a
Cyclidium sp.	0.20	0.42	0.55	0.60	0.76	0.34	0.64	0.37	n/a	n/a
Natural community	n/a	n/a	0.20	0.20	n/a	n/a	n/a	n/a	0.93	0.96

1984). By this relationship, u_* values in the range of 0.25–0.52 cm s^{-1} were required for the ambient velocity at one ciliate body width above the bed to match each ciliate's feeding-current velocity (Table 4). These calculations are consistent with the results that u_* values $\geq$0.5 cm s^{-1} resulted in enhanced feeding rates compared to still water, which suggests that ambient flow increased the advection of bacteria to the ciliates once it exceeded the feeding-current velocity. These calculations are, however, strongly dependent on the ciliate's position in the viscous sublayer and they do not apply to ciliates that are located in interstices.

Several alternative explanations for the direct relationships between u_* and clearance rate can be excluded. First, changes in prey density within the sediment or water column cannot explain the relationships because none of the measured bacterial concentrations was affected by u_*. Second, any flow-induced movement of ciliates between the interstitial space and the sediment-water interface could not have affected feeding by exposing cells to differing food concentrations because neither the total bacterial nor FLB concentrations differed between the water column and the pore water. Third, if local depletion of the suspended bacterial concentration in still water were to explain the results, then *Cyclidium* sp. (which was unaffected by flow) should have had the lowest population feeding rate. In contrast, the population of *Cyclidium* sp. in each core consumed 2.5×10^4 bacteria h^{-1} in still water (based on culture density and mean clearance rate), which was greater than both *Paranophrys magna* (1.4×10^4 bacteria h^{-1}) and *Euplotes minuta* (1.5×10^3 bacteria h^{-1}). Fourth, flow-dependent selection among food types (due to behavioral choice or to the dynamics of particle motions in flow) can also be excluded because only the bacterium *Halomonas halodurans* was present. Fifth, protists are known to select behaviorally against FLB in favor of live bacteria (Landry et al. 1991), but there is no reason to suspect that the degree of this selection is flow dependent. Furthermore, the following analysis indicates that the results cannot be explained by a disproportionate increase in the number of ciliates actively feeding on FLB as flow increased. The Poisson distribution predicts that the percentage of cells containing FLB increases along with the mean number of ingested FLB (Gonzalez 1999). As flow increased, our measured percentages of cells containing FLB increased no more than expected from Poisson distributions calculated from the numbers of ingested FLB (calculated with equations in Bratvold et al. 2000), and deviations from expectation were unrelated to u_* (*P* values from three-factor ANOVA ranged from 0.21 to 0.61 among species).

Table 4. Cell dimensions and feeding currents (mean ± s.e., *n* = 10). Cell width for *Euplotes minuta* was measured along the dorso-ventral axis, representing its height above the substratum. Critical u_* is the friction velocity that produces a velocity in the viscous sublayer at one body width above the bed that is equal to the feeding current.

Species	Cell length (μm)	Cell width (μm)	Feeding current velocity (μm s^{-1})	Critical u_* (cm s^{-1})
Cohnilembus sp.	25 (±1)	6 (±<1)	148 (±13)	0.52
Paranophrys magna	44 (±1)	23 (±1)	184 (±10)	0.29
Euplotes minuta	42 (±1)	20 (±1)	122 (±8)	0.25
Cyclidium sp.	35 (±1)	17 (±1)	217 (±21)	0.37

The clearance rates reported here (of order nl h^{-1} or less) are low compared to other measurements among bacterivorous scuticociliates and hypotrichs (e.g., Fenchel 1986). It is possible that ciliates fed on fluorescent *H. halodurans* at low rates because of the rather large bacterial cell size (1.5 μm) or the chemical nature of the FLB. For example, Fenchel (1980*a,* his fig. 6) indicated that *Cyclidium glaucoma* cannot feed on bacteria much larger than 1.1 μm. Nonetheless, clearance rates similar to ours have been reported previously. Tso and Taghon (1999) obtained clearance rates on smaller FLB as low as 0.03 nl h^{-1} for *Cyclidium* and 1.5 nl h^{-1} for *Euplotes.* Also, Fenchel (1986) calculated a maximal clearance rate of 3.6 nl h^{-1} for *Cyclidium* feeding on 0.36 μm beads, and Fenchel (1980*a,* his fig. 5) showed that clearance rate decreased from that value as particle size increased. The fact that clearance rates measured in the flume at $u_* = 0$ cm s^{-1} were similar to those in still-water flasks indicates that low clearance rates were not an artifact of flume methodology.

The effects of flow strength on ciliate feeding rate were species specific, including three types: (1) no effect of flow; (2) a direct relationship with a plateau of feeding rate in

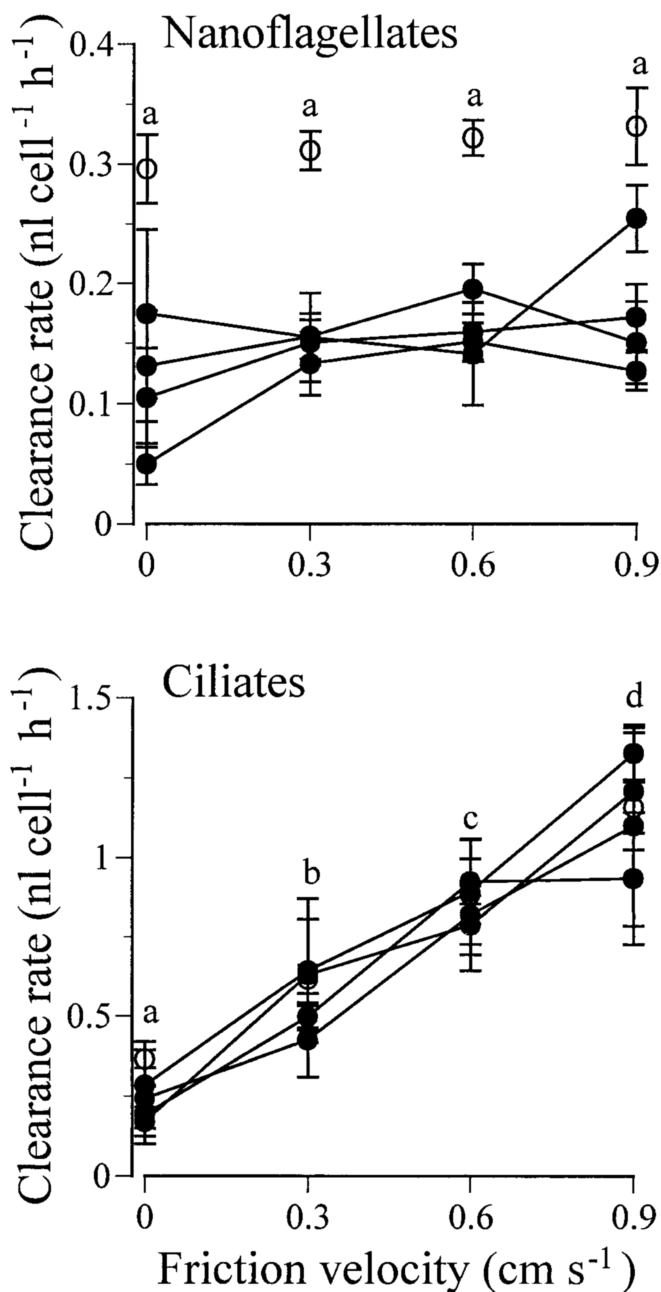

Fig. 3. Clearance rates of natural communities of protists as a function of friction velocity (u_*) in the flume. Open circles (mean ±SE of four replicate days of experiments) include only protists that ingested ≥ 1 FLB (replicates are not shown for the sake of clarity). Filled circles (mean ±SE of three cores in a single flume run) include feeding protists that did not ingest FLB, as estimated from Poisson distributions calculated from the data used for the open circles. Lines connect measurements made using sediment cores collected on a single replicate day. Clearance rates at u_* values with matching letters above the data are not significantly different at $\alpha = 0.05$ (results were similar for open and filled circles).

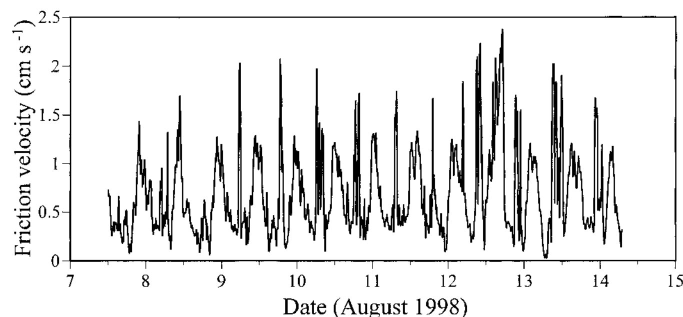

Fig. 4. Friction velocity at the field site calculated from the speed measured by a current meter mounted 1.15 m above bottom.

strong flow; and (3) a parabolic response indicating an optimal flow strength for maximal feeding rate. The species specificity is consistent with the results of Shimeta et al. (1995) for the effect of laminar shear on feeding by planktonic protists. They postulated that ingestion rate is independent of ambient flow below a critical level required to match the feeding current; above the critical level, ingestion rate is directly related to ambient flow strength; and at some strong level of flow either the ingestion rate becomes saturated or there can be feeding inhibition caused by an interference with particle-capture mechanisms or a behavioral avoidance. Thus, the plateau in clearance rates for *Cohnilembus* sp. and *Paranophrys magna* at $u_* \geq 1.0$ cm s^{-1}, as well as the decreased rates for *Euplotes minuta* at $u_* = 1.5$ cm s^{-1}, may have been caused by reduced prey retention or reduced feeding activity. Feeding-rate saturation is a less likely explanation because the clearance rates were still rather low. An alternative explanation is that in strong flow some ciliates could have entered the water column, where their feeding rates may have been temporarily reduced, and immigration back into a sediment core would have lowered our measured clearance rates. *Cyclidium* sp. had the strongest feeding current of the four ciliates, which may explain its lack of response to ambient flow. Although *Cyclidium* sp. did not have the smallest calculated critical u_* (Table 4), the meaningfulness of comparing these values among species is strongly dependent on knowing the positioning of cells within the viscous sublayer or interstitially while feeding in the flume, which was not measured. Thus, *Cyclidium*'s strong feeding current alone may be the best explanation for its constant feeding rate.

Influences of flow on natural communities of protists—Results from the natural community of ciliates indicated that, although flow effects are species specific, there are enough species and individuals present in the field that are strongly influenced by flow to cause a community-level effect of u_* on bacterivory rates. The effect was stronger on the entire community than on any one of the cultured species, which suggests that the isolated species were not the most strongly affected by flow or the most common members of the community. As in the experiments with isolates, the results with the natural community may have been caused by an enhanced advection of prey to the ciliates, particularly because

bacterial concentrations were unrelated to u_* levels. Because FLB were not mixed into the field sediment cores, however, it is possible that elevated clearance rates resulted from flow-induced movement of ciliates from interstitial space to the sediment surface, where FLB were more available. Such a behavioral response could explain why the effect of flow on feeding rates was greater than it was in experiments with cultured ciliates. Clearance rates of the ciliate community were slightly lower than the clearance rates measured for most of the cultured ciliates. As discussed above, FLB might have been discriminated against, and they might have been rather large for some bacterivorous ciliates to ingest. Our measurements therefore may not have included the entire community of bacterivorous ciliates. It is also possible that low concentrations of FLB at depth in the sediment caused the feeding rates of ciliates beneath the sediment-water interface to be underestimated.

There was no detectable community-level influence of flow on feeding rates of nanoflagellates, although it is possible that flow affects some species of suspension feeders that were a minority in the community or that discriminated against the FLB. Many sedimentary flagellates feed from particle surfaces rather than from suspension (Fenchel 1987; Patterson et al. 1989), and in the flume these species would have had access to FLB that entered the sediment at low concentrations, mostly attached to fine grains. If these flagellates ingested FLB from sediment grains, they were included in the data, but since sedimentary FLB concentrations were unrelated to u_*, the feeding rates of these cells would not likely have been influenced by flow.

Implications for ciliates and the microbial food web—This is the first demonstration of flow influencing the feeding rates of benthic ciliates. The results are for bacterivory, but the effect may also occur for suspension feeding on algal cells. Fenchel (1986) suggested that suspension-feeding protists benefit from attaching to a surface because they can create a stronger feeding current while attached than while swimming. The results here indicate that being on a stationary surface furthermore allows cells to take advantage of ambient flow, which gives them a greater feeding rate than possible from their feeding current alone. Flow may be an important selective force in the evolution of benthic protistan traits, as suggested especially by the flow optimum observed for *Euplotes minuta.* Not only does flow influence *Euplotes*'s feeding rate, but Jonsson and Johansson (1997) concluded that a *Euplotes* sp. is rheotactic and actively uses benthic boundary-layer flow for dispersal. Görtz (1982) suggested that the dorsal cilia of *Euplotes minuta* act as sensory structures for detecting flow.

The results from flume experiments can be applied to the field data of flow to estimate the integrated effect on feeding under a natural tidal regime. The time series (Fig. 4) was divided into segments in which u_* was bounded by the midpoints between flume treatments (i.e., $u_* \leq 0.25$, $0.25 < u_* \leq 0.75$, $0.75 < u_* \leq 1.25$, and $1.25 < u_* \leq 1.5$ cm s^{-1} corresponding to experiments with cultured ciliates; and $u_* \leq 0.15$, $0.15 < u_* \leq 0.45$, $0.45 < u_* \leq 0.75$, and $0.75 < u_* \leq 0.9$ cm s^{-1} corresponding to experiments with natural communities). Mean clearance rates measured in the flume were applied to the corresponding segments of the time series, and the integrated volume of water cleared by the cells was calculated (Table 5). The values represent the daily average clearance during the portion of the day that u_* did not exceed the maximal value tested in the flume (i.e., a 22.4-h day for data from cultured ciliates and a 17.0-h day for data from the natural community). Comparison of these calculations to the integrated clearance in the absence of flow (based on clearance rates in still water) suggests that natural tidal flow causes up to an 89% increase in the daily feeding of the ciliate isolates and a 216% increase in the daily feeding of the ciliate community (Table 5). These values may be conservative because the effects of flow measured in the flume were likely underestimated (protists were exposed to flow for only part of the time that they fed on FLB); on the other hand, the effects of flow exceeding the maximal u_* tested in the flume are unknown.

Table 5. Estimates of the integrated volume cleared per cell per day in the field, calculated by applying the mean feeding rates in flume experiments (Figs. 2, 3) to the time series of friction velocity (u_*) measured in the field (Fig. 4). Calculations for cultured ciliates include only the 22.4-h period (a daily average) during which $u_* \leq 1.5$ cm s^{-1}. Calculations for natural communities include only the 17.0-h period (a daily average) during which $u_* \leq 0.9$ cm s^{-1}. Volume cleared without flow effect was calculated from the mean clearance rates in still water.

Species	Volume cleared without flow effect (nl cell^{-1})	Volume cleared with flow effect (nl cell^{-1})	Increase due to flow (%)
Cohnilembus sp.	11.2	18.4	64.9
Paranophrys magna	31.6	40.1	26.8
Euplotes minuta	14.2	26.8	88.7
Cyclidium sp.	5.48	5.48	0
Natural nanoflagellate community	2.55	2.55	0
Natural ciliate community	3.77	11.9	216

Above a critical level of friction velocity, benthic protists can be resuspended into the water column. Sampling at a subtidal silty site in Buzzards Bay, Shimeta and Sisson (1999) found that concentrations of *Euplotes* spp. and scuticociliates in the benthic boundary layer were greater when u_* was 1.3 cm s^{-1} than they were during slack water. Experiments at that site with an in situ flume revealed that the erosion threshold specifically for *Euplotes minuta* was between u_* of 1.2 and 1.9 cm s^{-1}, and the thresholds for *Cohnilembus* sp. and *Paranophrys magna* were between 1.9 and 2.7 cm s^{-1} (Shimeta et al. pers. comm.). These u_* values are roughly similar to or greater than the maximal values used in the flume experiments; thus, we expect ciliates in the field to be present at the sediment-water interface at $u_* \leq 1.5$ cm s^{-1} and susceptible to the flow effects measured here. Once eroded, suspension-feeding protists may still be affected by flow, as shown by Shimeta et al. (1995) for certain planktonic ciliates and flagellates.

Variation of benthic boundary-layer flow in the field has potentially strong impacts on sedimentary microbial food

webs. In areas with strong tidal currents, feeding rates of certain suspension-feeding protists should have a tidal periodicity, as well as a lunar periodicity with the spring-neap cycle. Furthermore, assuming that differences in feeding rates translate into differences in growth rates, productivity of the protistan community may differ among habitats according to flow regime. The species specificity of our results, as well as the finding of a flow optimum for one species, suggests that the flow regime might influence the competitive balance among species and help to explain differences in community structure among habitats (e.g., Lucchesi and Santangelo 1997). In high-energy environments, species with feeding rates that have a strong direct relationship to friction velocity may experience a competitive advantage over other species.

There is uncertainty about the importance of ciliate bacterivory in the transfer of material and energy within sedimentary microbial food webs. This uncertainty is caused by differing results from comparisons of grazing rates of interstitial ciliates with productivity of sedimentary bacteria, differences among measurement methods, and the fact that the best studied habitats are sands, in which bacterivory is not always a common trophic mode among the resident ciliates (Fenchel 1969, 1980*b;* Kemp 1988; Epstein et al. 1992; Epstein 1997*a,b*). However, the marine benthos is dominated by fine sediment where bacterivorous ciliates are common, and many of them are suspension feeders (Fenchel 1987; Shimeta and Sisson 1999; Garstecki et al. 2000; this study). The importance of their activities in transferring water-column bacterial productivity to the sediments and to higher trophic levels is understudied. These ciliates may play a significant role in sedimentary microbial food webs, where they create a dynamic link between planktonic and benthic productivity, mediated strongly by benthic boundary-layer flow.

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Received: 31 January 2001
Accepted: 23 July 2001
Amended: 25 July 2001