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Consumption of picoplankton-size particles by marine ciliates: Effects of physiological state of the ciliate and particle quality

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Abstract

Ingestion of picoplankton-size particles was studied in two marine ciliates, a typical grazer of pico- and nanoplankton, the oligotrich *Strombidium sulcatum,* and a bacteriovorous scuticociliate, *Uronema* sp. In laboratory experiments, both logarithmic- (food-unlimited) and stationary-phase (food-limited) populations were presented with particles of different sizes and surface properties: plain microspheres, protein-adsorbing carboxylate microspheres, fluorescently labelled heterotrophic bacteria, and cyanobacteria. In both log- and stationary-phase populations, *Strombidium* clearance rates varied linearly as function of prey size based on the ingestion of plain microspheres. In contrast, *Uronema* clearance rates were invariant with particle size for log-phase populations but increased with particle size in stationary-phase cells. Discrimination among prey with different surface properties was also dissimilar in the two ciliates. For *Strombidium,* log-phase populations cleared 1-μm-diameter plain microspheres at higher rates than those with carboxylate surfaces. The pattern was repeated by stationary-phase cells for both ~0.5- and 1-μm-diameter microspheres. In *Uronema,* there was no significant difference in clearance rates with surface property in log-phase populations, similar to the findings with regard to particle size. Only in stationary-phase populations of *Uronema* was some selection evident, as 0.97-μm carboxylate microspheres were cleared at rates higher than were 0.95-μm plain microspheres. Overall, selection was higher in stationary-phase ciliates, and *Strombidium* seemed to feed more size-selectively among picoplankton particles than did *Uronema.*

Picoplanktonic organisms, those with a maximum length of 0.2–2 μm, can account for most primary and secondary production; control of these organisms is generally attributed to the grazing activity of flagellates and ciliates (e.g. Rassoulzadegan and Sheldon 1986; Rassoulzadegan et al. 1988). However, picoplankton are a diverse group of heterotrophs, autotrophs, mixotrophs, prokaryotes and eukaryotes, united only by size. The functional and phylogenetic differences of picoplankton are probably reflected in a diversity of grazing losses. For example, in the equatorial Pacific, populations of both heterotrophic bacteria and the autotrophic *Prochlorococcus* are stable over a scale of days in the surface layer growing at rates of ~0.1 and 0.5 d^{-1}, respectively (Kirchman et al. 1995; Vaulot et al. 1995). It thus appears that the two populations must suffer very different removal rates. Because autotrophic picoplankters such as *Synechococcus* and *Prochlorococcus* are generally larger than heterotrophic bacteria, size-related grazing losses are a plausible explanation of differential removal.

Laboratory studies have often shown that large bacteria are ingested preferentially by flagellates (Andersson et al. 1986; Chrzanowski and Simek 1990; Gonzàlez et al. 1990) and ciliates (Turley et al. 1986; Simek et al. 1994). Changes in the size distributions of natural populations of bacteria have been attributed to size-selective grazing by protists (Epstein and Shiaris 1992; Sherr et al. 1992; Pernthaler et al. 1996; Simek and Chrzanowski 1992; Simek et al. 1995, 1997). These studies provided evidence of selective removal of larger picoplankton-size particles. However, the absolute importance of size remains unclear as picoplankton-size particles can differ in other attributes such as surface characteristics, shape, and motility. These attributes can influence ingestion among flagellates (Monger and Landry 1991; Gonzàlez et al. 1993). Among ciliates, the influence of such attributes may change with particle size. For instance, a freshwater bacteriovorous ciliate of the genus *Cyclidium* shows selective ingestion among large particles (0.9 μm in diam.) differing in surface characteristics but no selection among small (0.6 μm diam.) particles (Sanders 1988).

Complicating the prediction of grazing losses is the fact that grazers may show considerable behavioral flexibility. In flagellates, selectivity of ingestion can change with shifts in ambient food concentrations, with selectivity decreasing as food levels decline (Jürgens and DeMott 1995). In bacteriovorous ciliates, behavior can differ with physiological state, i.e. in logarithmic- vs. stationary-phase cells, with food-limited stationary cells displaying lower chemotaxic responses (Snyder 1991). Thus, while selective predation on picoplankton-size particles likely exists, there is uncertainty with regard to the characteristic resulting in differential predation and the role of the physiological state of the grazer.

We were interested in examining the factors governing the consumption of picoplankton-size particles by marine planktonic ciliates. In a set of laboratory experiments we investigated the feeding behavior of *Strombidium sulcatum* and *Uronema* sp. We used *S. sulcatum* as a representative of small marine oligotrich ciliates, forms that can show high rates of bacterial consumption (Sherr and Sherr 1987) and are typical of marine protozooplankton. We used the scuticociliate *Uronema* as a typical bacteriovorous ciliate. We examined ingestion as a function of particle size and surface

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characteristics using fluorescent microspheres as well as fluorescently labeled mini-cells and cyanobacteria.

To examine the role of prey size independent of shape, motility, or surface characteristics, we estimated clearance rates using plain microspheres of different diameters. The effects of surface characteristics were considered in experiments comparing ingestion of plain microspheres with similar-size organic prey analogs or carboxylate microspheres. To examine the role of the physiological state of the grazer, we compared feeding behavior in log-phase and stationary-phase ciliates representing populations unlimited or limited by prey concentration.

Methods

Strombidium sulcatum and *Uronema* sp. originally isolated from the Bay of Villefranche-sur-Mer were maintained on a bacterized wheat-grain media at 17°C. Ciliates for the experiment were transferred into a bacterized yeast-extract media (0.03 g liter^{-1}) and grown at the experimental temperature of 17°C in a temperature-controlled incubator. Prey bacteria were a mixture of naturally occurring strains in Villefranche Bay water. *S. sulcatum* was a clonal culture.

In preliminary experiments, growth curves were generated to establish standard protocols for producing log-phase and stationary-phase ciliate populations (Fig. 1). Particle selection and clearance rates of *S. sulcatum* and *Uronema* sp. were determined in particle-uptake experiments using cells taken from log-phase (between days 4 and 5) and stationary-phase ciliate cultures (between days 6 and 7).

The general experimental protocol consisted of sampling (with time) a solution of ciliate culture to which two or more different fluorescent microspheres or other prey analogs had been added. Microspheres, or prey analogs, were added to yield a final concentration equivalent to 5–10% of the ambient concentration of bacteria in the ciliate culture (Fig. 1). Stock solutions of microspheres or other prey analogs were briefly sonicated before adding to ciliate cultures. Actual final microsphere and bacterial concentrations were determined from time-zero samples. Time-course samples were removed, after gentle mixing, at 10-min intervals for 60 min. Samples were preserved first with alkaline Lugol's solution (2% final concn) and postfixed 2 h later with buffered formaldehyde (2% final concn). Samples were de-stained with 3% sodium thiosulfate immediately preceding sedimentation in Hydrobios settling chambers. Prey particles inside individual ciliates were counted with a Ziess Axiovert 37 inverted epifluorescence microscope. For each time-course sample, the contents of 200 *Strombidium* or 400 *Uronema* were enumerated. Thus, for these experiments more than 19,000 *Strombidium* cells and 28,000 *Uronema* cells were examined. To compare ingestion rates, clearance rates were calculated. Rates were calculated for each time point of the linear portion of the uptake curve; rates were pooled and the average and standard deviation taken as an estimate of ingestion and a measure of variance, respectively. In all cases, the Mann–Whitney test was used to test for differences in clearance rates.

Experimental treatments used are detailed in Table 1 for

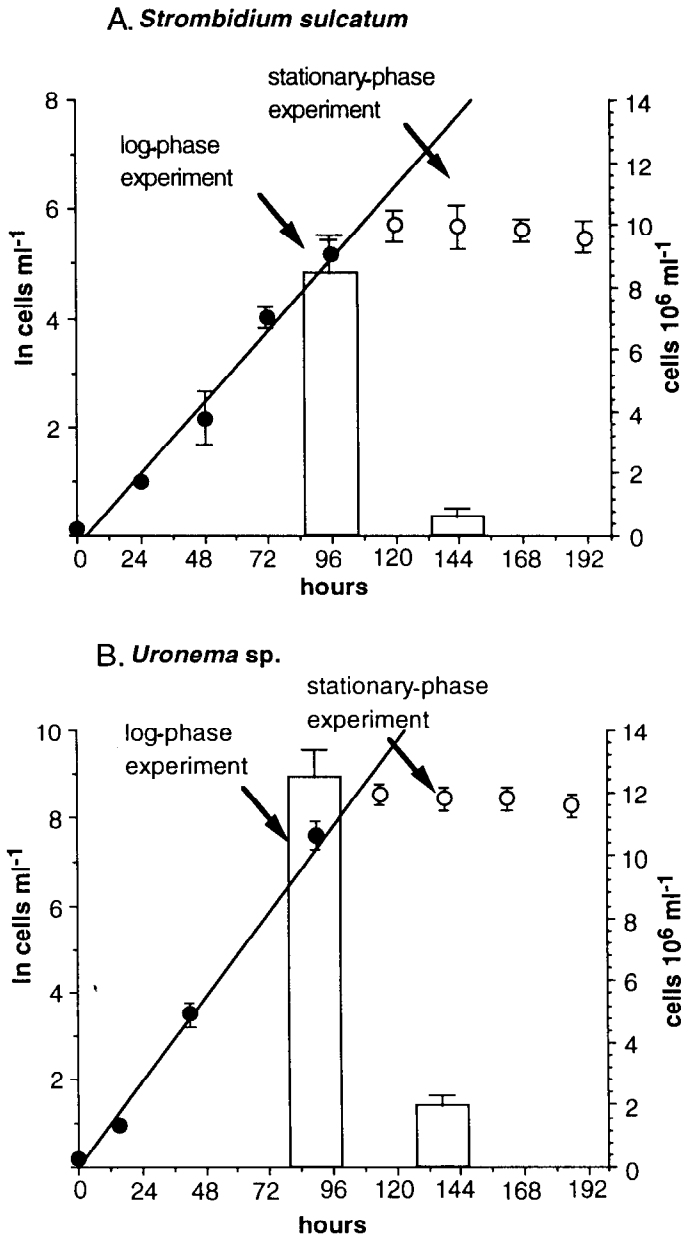


Fig. 1. Growth curves of cultures (A) *Strombidium sulcatum* and (B) *Uronema* sp. on marine bacteria. Bars show bacterial concentrations in 10^6 cells ml^{-1} ciliate and concentrations in ln cells ml^{-1}. Error bars represent SD of three replicate cultures.

S. sulcatum and in Table 2 for *Uronema*. In the first experiments with *Strombidium*, cells were incubated with pairs of plain fluorescent microspheres (pMS) of similar size but different fluorescent properties. Conducted with log-phase (Exp. 1) and then stationary-phase (Exp. 2) ciliates, these experiments served to estimate ingestion as a function of particle size (from 0.49 to 1.0 μm diam.) and determine if very small differences in particle diameters (0.49 vs. 0.52 μm or 0.95 vs. 1.0 μm) gave different ingestion rates. A subsequent experiment (Exp. 3), in which ciliates were offered all the particle sizes simultaneously, was run to check that rates estimated with pairs of particles were similar to

Table 1. Summary of experiments with *Strombidium sulcatum* (pMS, plain fluorescent microspheres; FLC, fluorescently labelled cyanobacteria; FMC, fluorescently labelled *E. coli* mini-cells; cMS, carboxylate microspheres).

Exp.	Culture phase	Prey items (μm in diam.)
1	Log	pMS (0.49, 0.52)
		pMS (0.52, 0.75)
		pMS (0.75, 0.95)
		pMS (0.95, 1.0)
2	Stationary	pMS (0.49, 0.52)
		pMS (0.52, 0.75)
		pMS (0.75, 0.95)
		pMS (0.95, 1.0)
3	Stationary	pMS (0.49, 0.52, 0.75, 1.0)
4	Stationary	pMS (0.95), FLC (0.98)
		pMS (0.75), FMC (0.6)
5	Log	pMS (0.95), FLC (0.98)
6	Log	pMS (0.53), cMS (0.52)
		pMS (0.95), cMS (0.97)
7	Stationary	pMS (0.53), cMS (0.52)
		pMS (0.95), cMS (0.97)

rates estimated when a larger selection of sizes was offered. Because small differences in particle size did not yield detectable differences in ingestion estimates for *Strombidium,* the following experiments were used to examine ingestion of similar-size particles of different types (pairs of ~1 μm or pairs of ~0.7 μm).

In Exp. 4 and 5, *Strombidium* were incubated in the presence of either fluorescently labeled *Synechococcus* cells (0.98 μm) and pMS (0.95 μm) or pMS (0.75 μm) and fluorescently labeled mini-cells of *E. coli* (0.7 μm). The fluorescently labeled *Synechococcus* were prepared following the protocol of Sherr et al. (1987) and were supplied by K. Simek. The fluorescent mini-cells were prepared following the protocol of Pace et al. (1990) and were supplied by C. Marrasé. In Exp. 6 and 7, pairs of similar-size microspheres of different surface properties were offered to *Strombidium* from log- and stationary-phase cultures. Ciliates were incubated with carboxylate microspheres (cMS) and pMS both either ~0.5 in diam. or both ~1.0 μm in diam. Carboxylate microspheres have surface carboxly groups "allowing for both passive adsorption and covalent binding of proteins to the bead surface" (manufacturer info., Polysciences).

Both microsphere types, pMS and cMS, were monodispersed. Examination of microsphere distribution in solutions of ciliate culture revealed very low occurrences of doublets or triplets of either microsphere type. Among 1,000 ~1-μm pMS, 99% were single microspheres, and out of 1,000 ~1 μm cMS, 94% were found as single microspheres.

For *Uronema,* the same experiments were conducted in which pairs of pMS were offered to ciliates from log-phase cultures (Exp. 1) or stationary-phase cultures (Exp. 2). Again, similar to experiments with *Strombidium,* pairs of cMS and pMS of similar sizes were incubated with cells from both log-phase culture (Exp. 3) and using ciliates from a stationary-phase culture (Exp. 4).

Table 2. Summary of experiments with *Uronema* (pMS, plain fluorescent microspheres; cMS, carboxylate microspheres).

Exp.	Culture phase	Prey items
1	Log	pMS (0.49, 0.52)
		pMS (0.52, 0.75)
		pMS (0.75, 0.95)
		pMS (0.95, 1.0)
2	Stationary	pMS (0.49, 0.52)
		pMS (0.52, 0.75)
		pMS (0.75, 0.95)
		pMS (0.95, 1.0)
3	Log	pMS (0.53), cMS (0.52)
		pMS (0.95), cMS (0.97)
4	Stationary	pMS (0.53), cMS (0.52)
		pMS (0.95), cMS (0.97)

Results

The growth curves of *S. sulcatum* and *Uronema* sp. are represented in Fig. 1A and 1B, respectively. The generation time during log growth was 12 h and 9 h for *S. sulcatum* and *Uronema* sp., respectively; the highest ciliate concentration during log phase was between days 4 and 5 for both ciliates. Cell volume was calculated from linear dimensions assuming a geometrical shape described by two ellipsoids. The cell volume of *Uronema* sp. was 540 μm^3 and 830 μm^3 during log and stationary phase respectively, while the cell volume of *S. sulcatum* was 16,000 μm^3 during both growth phases. Bacterial concentrations in cultures of *S. sulcatum* were 8.5 $\pm$ 1.2 and 0.64 $\pm$ 0.28 10^6 ml $^{-1}$ during log and stationary phase, respectively. In the cultures of *Uronema* sp., bacterial concentrations were 12.6 $\pm$ 0.9 and 1.95 $\pm$ 0.36 10^6 ml^{-1} during log and stationary phase. Ingestion of particles was always linear up to at least 50 min for both ciliates. Thus, each clearance rate was calculated on the basis of five time-course measurements.

Experiments designed to examine the effect of particle size revealed both similarities and differences between *Strombidium* and *Uronema.* In both log- and stationary-phase populations of *Strombidium,* clearance rates of pMS increased linearly as function of prey size (Fig. 2A). Rates estimated from Exp. 2, in which pMS were presented in pairs, were virtually identical to rates estimated when the full range of pMS sizes was offered (Exp. 3). In contrast to *Strombidium, Uronema* clearance rates were invariant with pMS size for log-phase populations (Exp. 1), but increased with particle size among stationary phase cells (Fig. 2B, Exp. 2). However, for both *Strombidium* and *Uronema,* clearance rates were significantly higher ($P \leq 0.01$) in cells from log-phase populations relative to stationary-phase cells (Fig. 2A,B; Tables 3, 4).

The clearance rates of *Strombidium* on pMS were not significantly different from their clearance of similar-size organic prey analogs (Fig. 3, Table 3). Log-growth phase ciliates removed from solution fluorescently labeled cyanobacteria at rates slightly lower, but not significantly different from, 0.98-μm pMS. As in tests with pMS alone, *Strombidium* from a stationary-phase culture showed lower clearance rates relative to log-phase cells, and also cleared

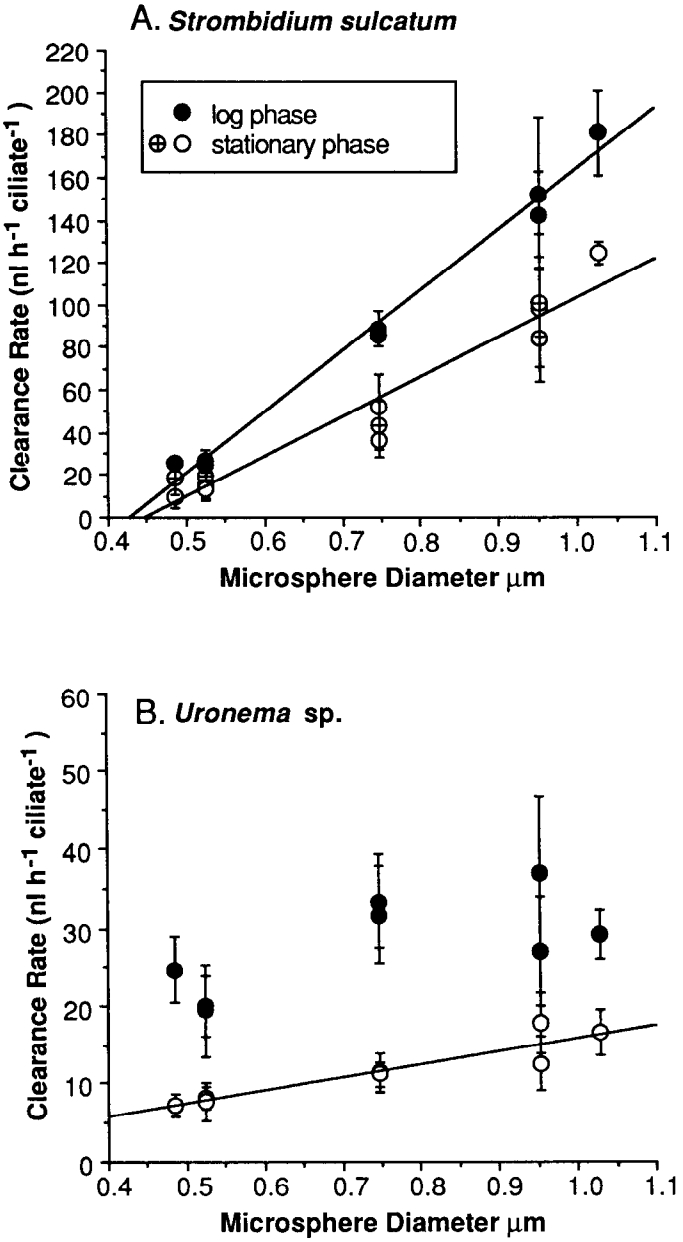


Fig. 2. Clearance rates (nl ciliate^{-1} h^{-1}) of (A) *Strombidium sulcatum* and (B) *Uronema* sp. incubated in the presence of plain fluorescent microspheres (0.487–1.03 µm in size). Error bars represent standard deviation of five sampling times. For *Strombidium*, circles with crosses show clearance rates estimated with the full range of particle sizes offered simultaneously. Regression equations for the line drawn are: for log-phase *Strombidium*, $y = -122.22 + 285.74x$, $r^2 = 0.990$; for stationary-phase *Strombidium*, $y = -83.63 + 186.57x$, $r^2 = 0.935$. The slopes of the lines for *Strombidium* are significantly different ($P < 0.0001$). The regression equation for stationary-phase *Uronema* is $y = -1.149 + 17.11x$, $r^2 = 0.874$.

fluorescently labeled cyanobacteria at rates slightly lower than, but not significantly different from, 0.98-µm pMS. Clearance rates estimated for pMS of 0.75 µm were indistinguishable from those estimated for fluorescently labeled mini-cells (Table 3).

Table 3. Comparison of *Strombidium sulcatum* clearance rates (nl h^{-1} ciliate^{-1}), Mann–Whitney *U*-test (*see* Table 1 for abbreviations).

Exp.	Culture phase	Prey items (µm in diam.)	*P*
1, 2, 3	Log vs. stationary	pMS (0.49)	0.006
		pMS (0.53)	0.0006
		pMS (0.75)	0.0007
		pMS (0.95)	0.005
		pMS (1.0)	0.006
4, 5	Log	pMS (0.95), FLC (0.98)	0.62 (NS)
	Stationary	pMS (0.95), FLC (0.98)	0.06 (NS)
	Stationary	pMS (0.75), FMC (0.6)	0.71 (NS)
6, 7	Log	pMS (0.53), cMS (0.52)	0.07 (NS)
	Stationary	pMS (0.53), cMS (0.52)	0.01
	Log	pMS (0.95), cMS (0.97)	0.003
	Stationary	pMS (0.95), cMS (0.97)	0.001

Experiments with pMS and cMS revealed distinct differences between the feeding behaviors of *Strombidium* and *Uronema* (Fig. 4). *Strombidium* showed a general preference for the plain microspheres, pMS. In log growth-phase cells, *Strombidium* cleared ~1-µm pMS at much higher rates than ~1-µm cMS, but among microspheres of ~0.5 µm, clearance rates were nearly identical. Higher clearance rates on pMS were also shown by stationary-phase *Strombidium*, but for the larger ~1-µm and smaller ~0.5-µm pMS. In contrast, *Uronema* cleared both types of microspheres at similar rates except for stationary-phase cells, which cleared ~1-µm cMS at a higher rate than pMS (Table 4).

Discussion

Among typical marine planktonic ciliates, selective feeding has often been reported when ciliates are offered prey the size of nanoflagellates (e.g. Stoecker et al. 1981, 1986; Stoecker 1988; Verity 1991; Kivi and Setälä 1995). In contrast, there is little consensus concerning selective feeding of ciliates among picoplankton-size particles. Reductions in clearance rates with particle size have been reported and explained by a simple sieving model of feeding in which ciliates filter particles from suspension with reduced efficiency when particle size falls below the distance between membranelles (Jonsson 1986; Fenchel and Jonsson 1988).

Table 4. Comparison of *Uronema* sp. clearance rates (nl h^{-1} ciliate^{-1}), Mann–Whitney *U*-test (*see* Table 1 for abbreviations).

Exp.	Culture phase	Prey items (µm in diam.)	*P*
1, 2, 3	Log vs. stationary	pMS (0.49)	0.006
		pMS (0.53)	0.0002
		pMS (0.75)	0.0001
		pMS (0.95)	0.0005
		pMS (1.0)	0.01
3, 4	Log	pMS (0.53), cMS (0.52)	0.14 (NS)
	Stationary	pMS (0.53), cMS (0.52)	0.36 (NS)
	Log	pMS (0.95), cMS (0.97)	0.51 (NS)
	Stationary	pMS (0.95), cMS (0.97)	0.01

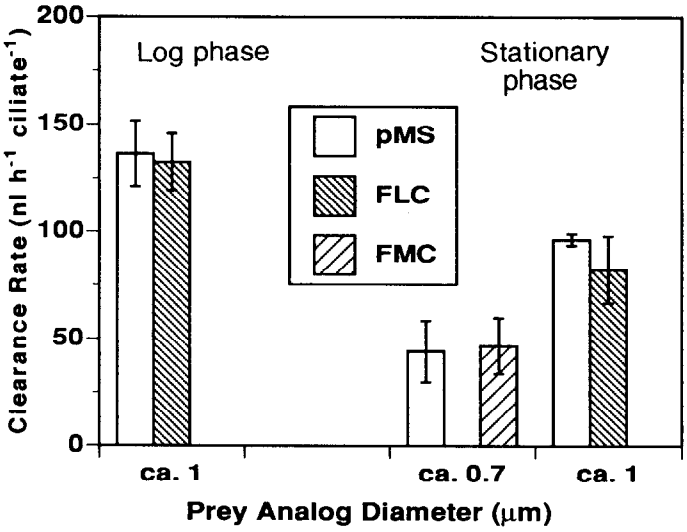
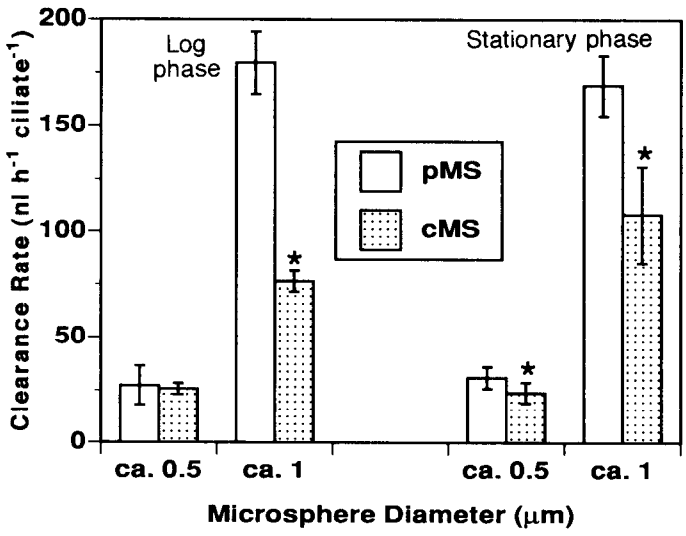


Fig. 3. Clearance rates (nl ciliate^{-1} h^{-1}) of *Strombidium sulcatum* on fluorescently labelled cyanobacteria (FLC) and fluorescent minicells (FMC), as well as 0.97- and 0.75-μm plain fluorescent microspheres (pMS). Error bars represent SD of five time-course estimates of clearance rates. There were no significant differences in clearance rates between FLC and similar-size plain microspheres or between FMC and similar-sized microspheres.



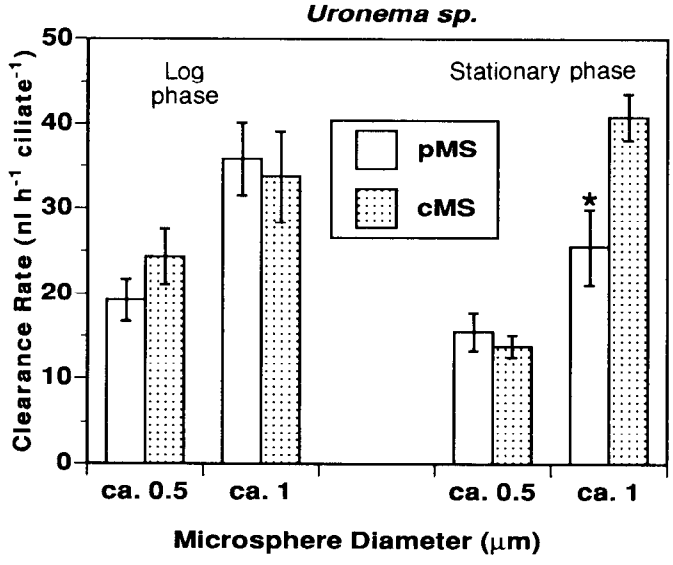


Fig. 4. Clearance rates (nl ciliate^{-1} h^{-1}) of (A) *Strombidium sulcatum* and (B) *Uronema* of plain fluorescent microspheres (pMS) and carboxylate fluorescent microspheres (cMS). Error bars represent SD of five time-course estimates of clearance rates. Significant lower clearance rates ($P < 0.05$) are labeled with a star.

Clearly, such a mechanism cannot be invoked to explain differences in ingestion rates among particles larger than intermembranellar distances or among particles of similar size, shape, and motility. Previous studies conducted with the scuticociliate *Cyclidium* have documented selective feeding among similar-size microspheres (Sanders 1988) as well as considerable variability of size-selective feeding on fluorescently labelled bacteria (Simek et al. 1994). We found that ingestion of picoplankton-size particles in both an oligotrich and a scuticociliate varied with particle size, type, and the physiological state of the ciliates. Note that we considered only two physiological states: cells in exponential growth phase and stationary phase. Among other possible physiological states are lag-phase cells, in an excess of food but not yet dividing, and starving cells, when cell concentrations are declining.

Presented with particles differing only in size (pMS), the clearance rates of *Strombidium* were a linear function of particle size in both log-phase and stationary-phase populations (Fig. 2). However, the slope of the line relating clearance to particle size was significantly greater for log-phase cells, indicating a larger effect of particle size for log-phase cells (Fig. 2). Clearance rates estimated for heat-killed prey analogs, bacterial mini-cells, or cyanobacteria were very similar to rates estimated for pMS of approximately the same size (Fig. 3). However, selective feeding was evident among microspheres with different surface properties (Fig. 4). *Strombidium* cleared ~1.0-μm pMS at much higher rates than did cMS, and such selectivity appeared stronger in stationary-phase ciliates as it extended to pMS of ~0.5 and 1 μm in diameter. Thus, *Strombidium* showed selective ingestion among picoplankton-size particles on a basis other than that of size.

In *Uronema,* neither size selection nor selection according to surface properties was evident in cells from log-phase populations (Figs. 2, 4), in marked contrast to *Strombidium.* Only stationary-phase ciliates ingested larger particles at rates significantly greater than smaller particles and cleared ~1-μm pMS at rates lower than 1-μm cMS. The size selectivity of stationary-phase cells, with minimum clearance rates of ~50% of maximum rates, was less extreme relative to both log- and stationary-phase *Strombidium* in which the minima were ~10% of maxima.

The differences between *Uronema* and *Strombidium* are also evident when clearance rates are considered in terms of volume-specific clearance rates (Table 5)—*Uronema* cleared

Table 5. Volume-specific clearance rates (pMS, plain fluorescent microspheres; rates are given in 10^4 body volumes per hour).

pMS (μm in diam.)	*Strombidium*		*Uronema*	
	Log	Stationary	Log	Stationary
0.49	0.16	0.06	4.2	0.88
0.53	0.16	0.09	4.8	0.95
0.75	0.56	0.28	6.0	1.4
0.95	0.95	0.68	8.4	1.8
1.03	1.2	0.80	5.3	1.4

picoplankton-size particles at volume-specific rates of $\sim 10^4$ body volumes h^{-1} compared to 10^3 body volumes h^{-1} for *Strombidium*. Although prey items between the sizes of 0.5- and 1-μm diameter are probably not the dominant source of nutrition for oligotrichs such as *Strombidium*, its grazing activity could disproportionately affect larger picoplankton cells such as *Synechococcus* or *Prochlorococcoccus* or dividing cells of heterotrophic bacteria. The efficient bacteriovore *Uronema* seemed to be a weakly selective feeder when under food-limited (stationary-phase) conditions and completely nonselective when food is abundant (log-phase cells). For *Uronema*, this suggests that under food-rich conditions, the benefit involved with selective feeding, or the penalty associated with nonselective feeding, does not outweigh the cost (Sierszen and Frost 1992).

For *Strombidium*, our results show that selection can occur among picoplankton-size particles, far smaller than optimum food particle size of ~ 3 μm previously reported for this species (Fenchel and Jonsson 1988; Bernard and Rassoulzadgan 1990). Interestingly, the selection among similar-size microspheres of different surface properties appeared stronger among the food-limited stationary-phase cells as it extended to the 0.5-μm particles. The difference does not seem attributable to differences in average cell sizes, because in our cultures there was no detectable difference in the populations tested in terms of cell volumes.

Our experiments on the ingestion of picoplankton-size prey by planktonic ciliates gave results distinct from recent findings concerning phagotrophic microflagellates. Gonzàlez (1996) reported a close relationship between particle size and clearance rates among flagellates. Although we found such a relationship for *Strombidium*, in *Uronema* the relationship appears weaker relative to *Strombidium* within the range of 0.5–1.10μm diam. particles. In both *Strombidium* and *Uronema*, selectivity was more marked among cells from food-limited conditions, in contrast to a recent report of selectivity decreasing with food concentrations in bacteriovorous flagellates (Jürgens and DeMott 1995). For the ciliates examined, selectivity may not pay when food is plentiful. One possible mechanistic explanation is that the rejection of undesirable particles is much more efficient at the slower swimming speeds characteristic of both ciliates in stationary- vs. log-phase cells.

Our estimates of clearance rates using prey analogs for particles of a given size may not be applicable directly to natural populations. Some ciliate species discriminate against latex microspheres (Pace and Baliff 1987). However, recent work suggests that fluorescent microspheres, natural *Synechococcus*, and heat-killed *Synechococcus* once ingested are treated similarly since all are digested or processed at the same rate in *S. sulcatum* (Dolan and Simek 1997).

More than 20 years ago, Lehman (1976) pointed out that details of feeding behavior in filter-feeding animals become important when such behavior is represented mathematically in ecological models. Our data show quantitatively differences in feeding behaviors with particle sizes and the physiological state of the grazer. In terms of volume-specific clearance rates, the total range of variability was about a factor of 5 (Table 5), perhaps a reasonable factor to use in sensitivity tests of models considering bacteriovory.

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