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Bacterivory by pelagic choreotrichous ciliates in coastal waters of the NW Mediterranean Sea

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ABSTRACT: Ability of natural assemblages of pelagic ciliates to ingest bacteria was tested using fluorescently labeled bacteria (FLB) prepared from in situ bacterioplankton. Ciliate bacterivory was analysed both in freshly collected samples from the mouth of Villefranche Bay, NW Mediterranean Sea, and in 50 µm screened water held in 20 l plastic carboys in the laboratory. In various experiments, from 23 to 97 % of the choreotrich assemblage ingested FLB added in tracer amounts (2 to 4×10^5 FLB ml^{-1}), with average clearance rates ranging from 14 to 308 nl $cell^{-1}$ h^{-1}. Very little ingestion of FLB was observed for other types of ciliates, e.g. didinids and hypotrichs, seen in the samples. Specific clearance rates (on the basis of FLB ingested) of individual morphological types of ciliates was on the order of 0.6 to 4×10^4 body volumes h^{-1} for larger choreotrichs, and up to 2×10^5 body volumes h^{-1} for the smallest choreotrichs. We estimated that it would be possible for choreotrichs < 15 µm in size to grow at a rate of about 0.5 d^{-1} on an exclusive diet of bacteria at a concentration of 10^6 bacteria ml^{-1}, but that the larger ciliates were obtaining less than 15 % of their food rations as bacteria. These data are the first direct evidence that some pelagic ciliates can be consumers of heterotrophic bacterioplankton in meso- to oligotrophic seawater.

INTRODUCTION

Pelagic ciliates, the majority of which are in Class Spirotrichea, Subclass Choreotrichia (Small & Lynn 1985), have long been recognized as a major component of microzooplankton in both marine and freshwaters (see reviews by Sorokin 1981, Porter et al. 1985, Sherr et al. 1986). However, their trophic status remains poorly known. The grazing of > 20 µm ciliates, particularly tintinnids, on nanoplanktonic (2 to 20 µm) phytoplankton has been established as a significant pathway in aquatic food webs (e.g. Rassoulzadegan 1977, Rassoulzadegan & Etienne 1981, Capriulo & Carpenter 1983, Verity 1986a, b). Many algivorous ciliates apparently sequester functional chloroplasts from their prey (Blackbourn et al. 1973, McManus & Fuhrman 1986, Jonsson 1987, Stoecker et al. 1987, Laval-Peuto & Rassoulzadegan 1988). In addition, recent studies suggest that pelagic ciliates also can consume and grow on picoplanktonic (< 2 µm in size) cells, i.e. tiny eukaryotic algae, cyanobacteria, and bacteria (Johnson et al. 1982, Rivier et al. 1985, Iturriaga & Mitchell 1986, Sherr & Sherr 1987, Rassoulzadegan et al. 1988).

Ingestion of bacterioplankton by pelagic choreotrichous ciliates is at present controversial. Most tested choreotrichs have been shown to clear < 2 µm particles with much lower efficiency than they do larger particles (Fenchel 1980a, Rassoulzadegan 1982, Børsheim 1984, Jonsson 1986), due to > 2 µm intermembranelle distances (sieve spacing) (Fenchel 1980b, c, Jonsson 1986). However, bacteria have been observed in food vacuoles of field-collected choreotrichs (Gast 1985, Sherr et al. 1986, Rassoulzadegan et al. 1988), and incorporation of radiolabeled bacteria into open ocean pelagic ciliates has been demonstrated (Lessard & Swift 1985).

Here we present results of a study of the ability of pelagic choreotrichous ciliates from the coastal waters of the NW Mediterranean Sea to ingest bacterioplankton. To do this, we analyzed rates of uptake of fluorescently labeled bacteria (FLB), prepared from natural communities of suspended bacteria, by assemblages of ciliates present in surface water. Initial work using FLB showed that choreotrichous ciliates ingest FLB at higher rates than they do plastic microspheres (Sherr et al. 1987), and that some choreotrichs have much higher clearance rates for bacteria than was previously reported (Sherr & Sherr 1987).

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MATERIALS AND METHODS

Surface seawater was collected from Point B, a standard oceanographic station at the mouth of the Bay of Villefranche, France (43° 41' 10" N, 7° 19' 0" E). Point B water can be considered as oligo-mesotrophic according to classifications in the literature (see Sorokin 1981 for review). Although Sheldon & Rassoulzadegan (1987) found that for the period March–April, primary production at this site can reach 180 µg C l^{-1} d^{-1}, the Bay's average production varies between 5 and 10 µg C l^{-1} d^{-1}. The water was collected in 20 l polyethylene carboys and transported directly to the laboratory.

Two types of experiments were carried out: (1) assays of bacterivory for the natural assemblage of pelagic ciliates in subsamples of whole water incubated at in situ temperature (16 to 19 °C) within 2 to 3 h of sample collection, and (2) assays of bacterivory for ciliates in 50 µm screened seawater held in 1 l glass bottles or in a 20 l polyethylene carboy in the laboratory at room temperature (19 to 20 °C) for periods of 2 to 6 d.

FLB were prepared as described by Sherr et al. (1987), using natural assemblages of bacterioplankton (about 10^6 ml^{-1}, average cell biovolume of 0.06 μm^3) present in freshly collected surface seawater prescreened through 0.8 µm Nuclepore filters. The bacteria were concentrated using an Amicon ultrafiltration system, Model CH2, with hollow fiber filters of 0.1 µm pore size. FLB were stored frozen, and thawed and briefly sonicated immediately prior to use.

Experiments were conducted in 400 ml Whirl-pak bags, presoaked in 10 % HCl and copiously rinsed. Seawater sample (200 ml) was added to the bags, which were incubated in a water bath either at in situ temperature (fresh Point B samples) or at room temperature (bottle or carboy samples). A separate 50 ml sample was taken for each experiment and preserved with 2 % final volume alkaline Lugol solution for enumeration of ciliates via the Utermöhl technique. In each experiment, FLB were added to yield concentrations of 2 to 4 × 10^5 FLB ml^{-1}, or about 20 to 40 % of the in situ bacterioplankton concentration. Subsamples of 50 ml were taken 10, 20, and 30 min after addition of FLB and fixed with 0.5 % final volume alkaline Lugol solution, to which 3 % final volume borate-buffered formalin was immediately added to decolorize the Lugol stain so that FLB could be visualized within the ciliates. This treatment greatly reduces dissolution of naked ciliates in the formalin (F. Rassoulzadegan unpubl.). Samples of 5 ml taken at the end of the experiment were preserved only with formalin for enumeration of total bacteria and of FLB.

Preserved samples were stained with diamidinophenylindole (DAPI) (Porter & Feig 1980) and filtered onto 0.8 µm Nuclepore-black membrane filters. Filters were mounted onto slides with immersion oil and inspected via epifluorescence microscopy using a Zeiss photomicroscope outfitted with a 50 W mercury lamp. DAPI-stained ciliates were located using Zeiss filter set 47 77 02 at 100 ×, and then Zeiss filter set 47 77 09 was used to look for and enumerate FLB within the ciliates at a magnification of 1250 × (Sherr et al. 1987). From 20 to 80 ciliates were inspected in each sample. The linear dimensions of the body of each ciliate were used to compute cell biovolume using equations for a sphere, prolate spheroid, or cone, depending on cell shape.

For those ciliates with ingested FLB, the rate of increase of the average number of FLB $ciliate^{-1}$ was determined from the uptake curve, which was linear during the 30 min incubations (Sherr et al. 1988) and extrapolated to an hourly rate. The FLB ingestion rate was used to derive an average clearance rate of bacteria (nl $ciliate^{-1}$ h^{-1}) for the portion of the choreotrichous ciliate assemblage with ingested FLB, using the equation: C = I/FLB, where C = clearance rate, I = FLB ingested $ciliate^{-1}$ h^{-1}, and FLB = concentration of FLB nl^{-1}. In addition, in several experiments we calculated specific clearance rates (body volumes $ciliate^{-1}$ h^{-1}) for individual morphological types of choreotrichs (based on cell size, shape, and ciliature, and number and shape of nuclei).

Samples for enumeration of bacteria were stained with DAPI (Porter & Feig 1980), filtered onto 0.2 µm Nuclepore black filters, and counted by epifluorescence microscopy at 1250 × as described above.

RESULTS

Naked choreotrichs composed between 80 and 100 % of the total ciliate assemblage during our study. The smallest cells were about 8 × 12 µm and the largest, 30 × 60 µm. Although we were not able to make precise taxonomic identifications, we did find species of *Strombidium, Strombilidium, Lohmanniella,* and *Laboea* in samples (see Rassoulzadegan 1977, Rassoulzadegan & Sheldon 1986). Total ciliate abundance ranged between 1 and 23 ciliates ml^{-1}.

In the experiments with fresh Point B water, bacterioplankton standing stocks were 0.4 to 1.2 × 10^6 cells ml^{-1}; in the bottle and carbon experiments, bacterial standing stocks ranged from 0.6 to 3.5 × 10^6 cells ml^{-1} (Table 1). Average ciliate clearance rates ranged from 14 to 308 nl $ciliate^{-1}$ h^{-1}, and were generally higher in the carboy experiments (Table 1), perhaps because the species composition of choreotrichs shifted in favor of bacterivores during incubation in the laboratory. Since protozoan grazing rates are negatively related to prey concentration (Fenchel 1980a, Jonsson 1986), the increase of bacterial abundance by addition of FLB

Table 1. Summary of data on bacterivory by assemblages of naked choreotrichous ciliates in NW Mediterranean coastal waters

Date (1987)	Bacterioplankton (10^6 ml^{-1})	Choreotrichs (no. ml^{-1})	Estimated choreotrich bacterivory (nl cell^{-1} h^{-1})	(bacteria cell^{-1} h^{-1})	% of choreotrichs with ingested FLB
(A) Bottle/carboy experiments					
22 Apr	3.5	–	180	630	94
23–24 Apr	2.0	2.4	285	571	88
27–28 Apr	1.4	0.2	211	295	100
29 Apr	0.6	1.4	228	137	97
12 Jun	1.2	12	130	155	89
13 Jun	1.0	14	128	128	100
14 Jun	1.0	5	125	125	94
15 Jun	0.9	3	198	178	97
16 Jun	0.8	4	136	109	100
(B) Point B water experiments					
1 Jun	0.8	0.9	308	246	88
2 Jun	0.6	1.0	70	46	94
9 Jun	0.4	4.3	14	6	26
10 Jun	1.0	20	82	82	71
11 Jun	1.2	4	127	152	49
12 Jun	1.0	2.5	92	92	86
15 Jun	1.0	8.5	83	83	70

may have resulted in a slight underestimation of the clearance rates. From the clearance rates, we calculated total bacterial ingestion rates of 6 to 630 bacteria ciliate^{-1} h^{-1}. In all but 2 experiments, > 50 % of naked choreotrichous ciliates ingested FLB. Other types of ciliates seen in the samples, e.g. didinids and hypotrichs, were rarely observed with ingested FLB. These cells were not included in our calculations.

Specific clearance rates were calculated for 22 separate morphological types of ciliates for those experiments in which bacterial standing stocks were about 1×10^6 ml^{-1}. Usually there were from 2 to 5 individual ciliates represented for each morphological type, for which an average biovolume and rate of clearance was calculated. Undoubtedly the 22 morphological types selected represent a lesser number of ciliate species, however we could not be sure that identical species occurred in separate water samples. Body volume for individual morphological types varied from 425 μm^3 to 14 200 μm^3. It is possible that fixation may have caused some shrinkage of cell size, as has been reported for heterotrophic flagellates (Børsheim & Bratbak 1987). However, the proportional amount of shrinkage would be expected to be similar across the spectrum of sizes of naked choreotrichs, and this should not seriously affect the relationship between cell size and clearance rate. A logarithmic plot of specific clearance vs body volume (Fig. 1) showed a general negative relationship between the two. The highest specific clearance rates, 1.2 to 2.4 × 10^5 body volumes h^{-1}, were found for ciliates with cell volumes of less than 1800 μm^3.

Based on the specific clearance rates of choreotrichous ciliates at the in situ bacterioplankton abundance of 1×10^6 bacteria ml^{-1}, we estimated the bacterial ingestion of individual ciliate types in terms of food requirements for growth. We made the following assumptions: a ciliate growth efficiency of 40 % (Jonsson 1986, Verity 1986a); a ciliate carbon content of 0.1 pg C μm^{-3} (Sherr et al. 1986); an average size for in situ bacterioplankton of 0.06 μm^3 (Rassoulzadegan unpubl.); and an average carbon content of bacterioplankton of 0.35 pg C μm^{-3} (Bjørnsen 1986, Lee &

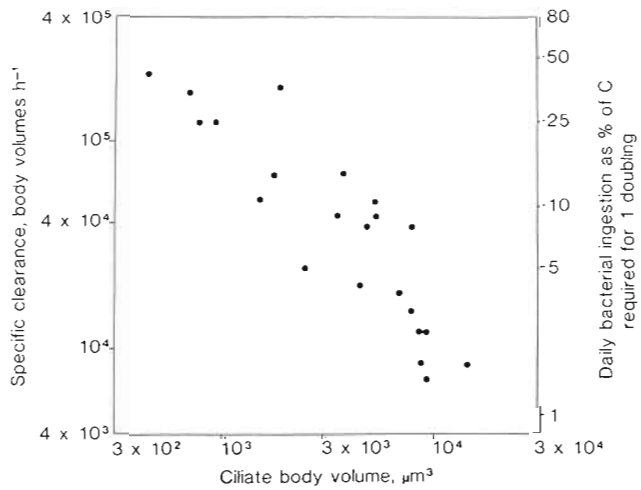

Fig. 1. Logarithmic plot of cell-specific clearance rates as a function of ciliate body volume determined via uptake of FLB by discrete morphological forms within choreotrichous ciliate assemblages in surface waters of the NW Mediterranean Sea. Estimated daily ingestion of bacteria as the percent of calculated carbon required for one cell doubling, at a bacterial concentration of 1×10^6 cells ml^{-1}, is shown on the right vertical axis

Fuhrman 1987). Using these assumptions, the specific clearance values were converted to daily bacterial ingestion as percent of the total carbon required for one cell doubling (right vertical axis in Fig. 1). For ciliates with specific clearance rates greater than 10^5 h^{-1}, daily bacterial ingestion could provide from 25 to 50% of their food requirements for one doubling. For the other ciliates analysed, daily bacterial uptake would provide less than 15% of food requirements for growth (Fig. 1).

DISCUSSION

The current theory of protozoan bacterivory in the sea holds that pelagic ciliates cannot be primarily bacterivorous except under special circumstances: dense patches of bacteria or very rich estuarine water (Fenchel 1984, Sieburth 1984). Experimental studies carried out with pelagic ciliates have generally supported this idea (e.g. Fenchel 1980b, Rassoulzadegan 1982, Børsheim 1984, Gast 1985, Jonsson 1986). However, contrary evidence has been presented that (1) a 20 to 30 µm choreotrich, *Strombidium sulcatum,* could be grown on bacteria at concentrations less than 10^6 bacteria ml^{-1} (Rivier et al. 1985), and (2) based on FLB uptake, pelagic ciliates in waters of a salt marsh estuary grazed in situ bacteria at rates of 140 to 270 nl h^{-1}, corresponding to cell-specific clearance rates of 4×10^4 h^{-1} to 6.8×10^5 h^{-1} (Sherr & Sherr 1987).

These data are likely not in conflict. An important factor is choice of experimental organisms. In the earlier studies, the investigators experimented with either hymenostome ciliates such as *Uronema,* or medium to large polyhymenophoran ciliates which were primarily algivorous. The latter 2 studies, however, addressed the physiological capabilities of in situ pelagic ciliates < 20 to 30 µm in size (Sherr & Sherr 1987) and of a choreotrich, *Strombidium sulcatum,* which could be cultured on bacteria alone (Rivier et al. 1985).

Ciliates capable of filtering bacterial-sized particles are characterized by very small (< 2 µm) intermembranelle distances within the oral ciliature, which, based on hydrodynamic considerations, leads to absolute clearance rates for bacterivorous ciliates which are much lower than those found for ciliates adapted to grazing on phytoplankton (Fenchel 1980a, c). Herbivorous ciliates typically filter algal cells at rates of 2000 to 26000 nl h^{-1} (summarized by Jonsson 1986), while rates for ciliate bacterivory are on the order of 40 to 300 nl h^{-1} (Fenchel 1980b, Børsheim 1984, Sherr & Sherr 1987).

In the present study, we found rates of bacterivory to be similar for choreotrichs over a wide range of size. We suspect that for small ciliates, low filtering rates are due to their closely spaced membranelles, while the coarser filtering apparatus of medium to large ciliates makes them rather inefficient bacterivores. For larger, mainly algivorous choreotrichs, the apparent clearance rate based on bacterial ingestion should thus be much lower than the actual filtration rate. It is likely that bacterivory in the algivorous species was a by-product of their grazing on phytoplankton.

Ciliates other than choreotrichs found in the samples were rarely seen with ingested FLB. The feeding habits of such species may have precluded significant uptake of freely suspended picoplankton. For example, *Didinium* spp. usually prey on other ciliates (Antipa et al. 1983) and *Euplotes* spp. are specialized for grazing on particle surfaces (Albright et al. 1987).

Bacterivorous ciliates are not necessarily excluded from a pelagic existence because of low absolute filtering rates. A 15 µm ciliate grazing bacteria at 300 nl h^{-1} will have a specific clearance rate of 1.7×10^5 body volumes h^{-1}, comparable to the specific clearance rates of larger ciliates grazing algae (Jonsson 1986). In addition, it appears that bacteria are more carbon-rich per unit biovolume than previously thought. Recent estimates of carbon content of in situ marine bacterioplankton have suggested values of 0.35 and 0.38 pg C μm^{-3} of bacterial biovolume (Bjørnsen 1986, Lee & Fuhrman 1987). We used a value of 0.35 pg C μm^{-3} for bacterial carbon content in our calculations, based on the 2 papers cited above and on the fact that this is a median value for various recent estimates which range from 0.11 pg C μm^{-3} (Heldal et al. 1985, Nagata 1986) to 0.56 pg C μm^{-3} (Bratbak 1985). If in situ bacterioplankton are several-fold richer in carbon than are their ciliate predators, ciliates would need to graze concommitantly less bacterial biovolume to meet their food requirements.

A secondary factor may also in part explain discrepancies between our bacterial grazing rates and those measured using uptake of latex particles (Børsheim 1984, Jonsson 1986, Stoecker 1988). Emerging natural history information about filter-feeding ciliates indicates that these phagotrophic protozoa are not simple mechanistic feeders as previously supposed. Filter-feeding ciliates may be chemosensory to their prey (Antipa et al. 1983, Capriulo et al. 1986, Verity 1988), show active selection and rejection of potential food items (Stoecker et al. 1981, Stoecker 1988, Taniguchi & Takeda 1988), and are capable of differential selective uptake of free or particle-attached bacteria (Albright et al. 1987). We have found experimentally that both estuarine choreotrichous ciliates (Sherr et al. 1987) and *Strombidium sulcatum* (E. Sherr unpubl.) ingest FLB at rates several-fold higher than they do latex microspheres of equivalent size. Thus rates of bacterivory obtained using inert latex particles may be underestimates of the true grazing rate on bacteria.

The question of whether ciliates also show discrimination for or against FLB compared to untreated bacteria is another matter. We have recently carried out a series of experiments designed to compare relative uptake of FLB and live bacteria, using mixed species cultures of bacterivorous flagellates and an isolated pelagic choreotrich, *Strobilidium conicum*. In these experiments, we found no significant differences in long-term (18 to 24 h) percent decrease of FLB or of live bacteria which were prevented from dividing by addition of prokaryotic inhibitor, when grazed by a mixture of flagellates and *S. conicum* (Sherr et al. 1989).

In the present study, we have demonstrated bacterial ingestion by a large fraction of the assemblage of pelagic choreotrichous ciliates present in surface coastal waters of the NW Mediterranean. In most of our experiments, the total abundance of bacterioplankton was equal to, or less than, 10^6 cells ml^{-1}. Only during the end of the spring phytoplankton bloom, in May, were bacterial abundances much above this value (Table 1). For the smallest ciliates in our samples, daily bacterial ingestion at 10^6 bacteria ml^{-1} could satisfy up to 50% of food requirements for 1 doubling (Fig. 1). These ciliates could either be growing in bacteria at a rate of $0.5\,d^{-1}$, or supplementing their diet with other picoplanktonic and small nanoplanktonic cells (Rassoulzadegan et al. 1988) to sustain higher growth rates. Bacteria were of lesser importance in the diet of larger ciliates in our study, as suggested previously by Rassoulzadegan et al. (1988). However, if they were to encounter denser concentrations of bacteria, some of the pelagic choreotrichs might be able to support reasonable rates of growth on a solely bacterial diet, as has already been shown for *Strombidium sulcatum* in laboratory culture (Rivier et al. 1985).

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