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Ciliate bacterivory in epilimnetic waters

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ABSTRACT: Simultanous measurements of bacterial production (^{3}H-thymidine incorporation) and ciliate bacterivory (uptake of fluorescently labeled bacteria, FLB) were carried out on samples from the epilimnion of 17 lakes in eastern Norway. On average, bacteria equivalent to 19% (range: 0.8 to 62%) of the bacterial production were consumed by ciliates. The most important bacterivorous ciliates were small (<30 µm) oligotrichs; *Halteria grandinella* and *Strobilidium* spp. These ciliate taxa were found to have average clearance rates of 183 and 103 nl cell^{-1} h^{-1} respectively, corresponding to specific clearance rates of 0.5 and 0.9 × 10^5 cell volumes h^{-1}. In addition, *Vorticella* sp., a peritrich ciliate that was attached to colonies of the cyanophyte *Anabaena flos-aquae*, was found to be important in several lakes. On average, these 3 ciliate taxa alone accounted for >80% of total ciliate bacterivory. Species-specific clearance rates did not vary much between lakes, indicating that the ciliates were always food limited. These results confirm other recent studies, showing that pelagic ciliates can be significant grazers on bacterioplankton.

KEY WORDS: Ciliates · Bacterivory · Lakes

INTRODUCTION

Ciliates are now recognized as an important component in pelagic food webs (Porter et al. 1985), but investigations into the population dynamics or ecology of ciliates are few compared to other groups of plankton. In addition, pelagic ciliates are by no means a functionally uniform group. They range in volume over 3 orders of magnitude, they can eat bacteria (Sherr & Sherr 1987, Sanders et al. 1989, Šimek et al. 1995), heterotrophic flagellates (Weisse 1991), and a wide range of phytoplankton (Skogstad et al. 1987, Šimek et al. 1995). Also, many common pelagic ciliates are mixotrophic (Dolan 1992, Jones 1994). Ciliates are in turn mainly consumed by crustaceans (Hamilton & Taylor 1987, Jack & Gilbert 1993, 1994). A better understanding of the ecological role of different ciliate taxa would thus contribute significantly to our understanding of the functioning of microbial food webs.

One of the links in the pelagic food web that deserves attention is the one between bacteria and ciliates. Numerically, a pelagic ciliate community is very often dominated by small (<30 µm) species (Beaver & Crisman 1982, Pace 1982, Gates 1984) and over the last decade it has been shown that some of these are efficient grazers of bacterioplankton (Sherr & Sherr 1987, Sanders et al. 1989, Šimek & Straškrabová 1992, Šimek et al. 1995). However, it now seems clear that most of the pelagic ciliates that are efficient grazers of bacteria are not bacterivorous in the strict sense, as autotrophic picoplankton also contributes significantly to their diet (Šimek et al. 1996). Thus, the term 'bacterivorous ciliates' is here used for ciliates which have bacteria not necessarily as an exclusive, but as a major, food source.

Results from several studies indicate that the incipient limiting food concentration (ILC) for bacterivorous ciliates is much higher than the bacterial density found in most natural lakes (Taylor 1978a, Rivier et al. 1985, Sanders 1988). In theory, the clearance rate should be constant below the ILC. For a pelagic bacterivorous ciliate, large variations in clearance rate from one lake to another should therefore not be expected.

With a few notable exceptions (Sanders et al. 1989, Šimek et al. 1995), no systematic studies on ciliate bacterivory in lakes have been conducted. As a result, information on grazing and clearance rates, distribution of important bacterivorous species, or total ciliate grazing pressure on bacteria is very limited. At the

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moment, it is therefore difficult to estimate the magnitude of ciliate bacterivory without careful and laborious investigations.

Both Sanders et al. (1989) and Šimek et al. (1995) followed protozoan bacterivory in 1 lake over a period of time. In the present study a different approach was taken. Instead of taking many samples from 1 lake, 1 sample was taken from the epilimnion of 17 lakes in eastern Norway in late July/early August 1994. The objectives of the study were to provide a general overview of the magnitude of ciliate bacterivory in a summer situation in temperate lakes, to identify which ciliates are most important as grazers of bacterioplankton, and to evaluate clearance rate variability within distinct ciliate taxa.

MATERIALS AND METHODS

Study lakes. All the lakes in this study are located in the same climatic region within a radius of 35 km of the center of Oslo (Oslo: 59° 59' N, 10° 45' E) at an altitude of 1 to 180 m. The lakes were selected so as to cover the maximum possible range of environmental parameters, but only lakes deep enough to have a marked thermal summer stratification were considered. Detailed morphological data were only available for some of the lakes, but maximum depth ranged between 6 and 64 m and lake surface area from 0.003 to 2.4 km^2.

Sampling. In each of the 17 lakes a pooled sample was made from 3 to 4 discrete samples taken at different depths within the epilimnion. All subsamples for incubations or counting were taken from the pooled samples. The samples were taken from the deepest part of the lake if this was known. Otherwise, they were taken in the central part of the basin (small lakes), or where the depth was at least 10 m (larger lakes). The epilimnion depth was determined from temperature measurements, using a YSI 33 SCT-combined temperature/salinity probe.

All incubations were performed either immediately *in situ*, or within 2 h of sampling in the laboratory at ±1°C of *in situ* temperature.

Bacterial production. Bacterial production was measured using the [^{3}H]thymidine (69 Ci $mmol^{-1}$, Sigma) incorporation method, following the protocol of Robarts & Zohary (1993). From each pooled epilimnion sample, five 10 ml subsamples were placed in 20 ml polyethylene scintillation vials. Three of these were live replicates, two NaOH-killed (0.5 ml 5 M NaOH) time-zero controls. Labeled thymidine was added to each vial to give a final concentration of 20 nM. The vials were incubated submerged for 30 min. Thymidine incorporation in the live replicates was stopped by addition of 0.5 ml 5 M NaOH. When performed *in situ*, the vials were stored on crushed ice until further processing. Labeled DNA was precipitated by adding 1.25 ml of ice-cold TCA to each vial. The precipitate was collected onto 0.22 µm pore-size cellulose nitrate membrane filters that had been presoaked in 10 mM cold thymidine solution for at least 2 h. To remove labeled proteins and lipids, the filters were washed with ice-cold 5% TCA, phenol-chloroform (50% w/v) and finally with 80% ethanol. After removing the non-filtering area with a circular cutter, the filters were completely dissolved in 5 ml of Filter-Count (Packard Instruments). Tritium incorporation into DNA was determined with the use of a Packard Tri-Carb liquid scintillation counter.

Bacterial cell production was calculated using a conversion factor of 2.0×10^{18} cells produced mol^{-1} thymidine incorporated.

Bacterial counts. Subsamples of 20 ml were preserved with formalin (2% final conc.). One ml was stained with 4',6-diamidino-2-phenylindole (DAPI) and gently filtered onto black 0.2 µm pore-size Nuclepore filters (Porter & Feig 1980). At least 300 bacteria were counted at 1000× magnification from each sample using epifluorescence microscopy.

Preparation of fluorescently labeled bacteria (FLB). Water from an oligotrophic lake (Sognsvann) was filtered through a 2 µm pore-size Nuclepore filter, and subsequently through a 0.4 µm Nuclepore filter. One drop of this filtrate was added to 75 ml of algal growth medium, to which 0.1 g l^{-1} of yeast extract and 0.025 g l^{-1} of peptone had been added. This produced a culture of rod-shaped bacteria. The culture was left at room temperature, and harvested in early stationary growth phase. Preparation of FLB followed the protocol of Sherr et al. (1987), except that the culture was not centrifuged prior to the addition of 5-(4,6 dichlorotriazin-2-yl)-aminofluorescein (DTAF). The FLB were frozen in small aliquots, thawed and shaken vigorously before use. Inspection showed no aggregation of FLB. The size of the FLB was estimated by measuring 50 cells with an eyepiece graticule at 1000× magnification.

Ciliate grazing and abundance. For the grazing experiments, 500 ml samples were dispensed into 1 l flasks. After 10 min (for recovery), FLB were added to a final concentration of 0.8 to 1.0×10^5 ml^{-1}. A subsample of 10 ml was taken out for exact determination of FLB concentration. The same procedure was followed as for bacterial counts, except that no DAPI was added and 3 ml was filtered instead of 1 ml. Subsamples of 200 ml were taken at time 0 and 10 min after tracer addition, and fixed by adding 0.4 ml of Lugol's solution, immediately followed by 1.2 ml 3% sodium thiosulfate and 4 ml formalin (B. F. Sherr et al. 1989). The ciliate density usually found in lakes will often make it necessary to concentrate relatively large volumes of

water to get good estimates of species-specific clearance rates. Filtration techniques were therefore considered inadequate. After fixation the samples were left for at least 24 h. To concentrate the material (when necessary), 0 to 120 ml was carefully siphoned off the the top of the flasks. The residue was resuspended and transferred to a 50 ml settling chamber. After a sedimentation time of at least 12 h, the samples were examined using a Nikon inverted microscope with epifluorescence. The bottom of the settling chamber was scanned at a magnification of 200× with transmitted light on. When a ciliate was found, the magnification was switched to 600× and transmitted light was blocked. Ciliate taxa where none of the first 10 cells examined had uptake of FLB were not examined further. In those taxa where uptake was found among the first 10 cells, at least 50 cells were examined.

For quantification of ciliates, a sample of 1 l was fixed with Lugol's solution (1% final conc.). The samples were concentrated and settled as above, but now the exact volume of the water siphoned off, and of the residue, was determined. At least 50, and in most cases 100 to 150, ciliates of each bacterivorous ciliate taxa were counted.

Chlorophyll *a*. Between 200 and 1000 ml of water was filtered through Whatman GF/C filters. Chlorophyll *a* (chl *a*) was extracted in a mixture of dimethylsulfoxide and acetone, and measured spectrophotometrically according to Stauffer et al. (1979).

Water colour. Water colour was estimated by comparing filtered lake water to a standard Pt scale with the use of a Hellige comparator.

RESULTS

The epilimnion depth was always found to be between 3 and 4 m, and the epilimnetic temperatures varied from 20.1 to 23.8°C. Values of chl *a* ranged from 3.4 to 39.5 µg l^{-1}, Secchi depths from 1.1 to 6.1 m, and pH from 6.0 to 9.8. Bacterial abundances ranged from 0.8 to 6.4 × 10^6 bacteria ml^{-1}, while daily production estimates ranged from 0.08 to 1.9 × 10^6 bacteria ml^{-1} d^{-1} (Table 1).

The average size of the FLB used in grazing experiments was found to be 1.2 × 0.6 µm. The abundance of ciliates which ingested FLB ranged from 2 to 25 cells ml^{-1}, and they grazed between 0.005 and 0.24 × 10^6 bacteria d^{-1}, equivalent to 0.8 to 62% (average 19%) of the bacterial production (Table 1).

The contribution from different ciliate taxa on total ciliate bacterivory in each lake is shown in Fig. 1. Small oligotrichs were clearly the most important bacterivorous ciliates in this material. *Halteria grandinella* (18 to 26 µm) was present in 13 of the 17 lakes, and was found to have clearance rates between 142 and 273 nl $cell^{-1}$ h^{-1} (mean: 183; standard deviation, SD: 38). The other important oligotrichs were 12 to 18 µm, belonging to the genus *Strobilidium*. They appear similar to *S. humile*, but Protargol staining for species determination was not performed, and they will therefore be referred to as *Strobilidium* spp. (see Foissner et al. 1991). Clearance rates for *Strobilidium* spp. were found in the range 76 to 199 nl $cell^{-1}$ h^{-1} (mean: 105, SD: 35). As can be seen in Fig. 2, the variability in clearance rate between lakes for the 2 taxa *Halteria*

Table 1. Some lake characteristics: Temp: epilimnetic temperature; Sd: Secchi depth; Cond: conductivity (25°C); Colr: water colour; Bact: epilimnetic bacterial density; BP: bacterial production; CG: ciliate community grazing rate

Lake	Temp (°C)	Sd (m)	pH	Cond (µS cm^{-1})	Colr (mg Pt l^{-1})	Chl *a* (µg l^{-1})	Bact (10^4 cells ml^{-1})	BP (10^4 cells ml^{-1} d^{-1})	CG (10^4 bact ml^{-1} d^{-1})	CG/BP
Bogstadvann	20.1	2.6	7.3	45	40	12.2	145	19	4.6	0.24
Bondivann	21.0	1.7	7.7	189	35	35.7	529	190	11.6	0.06
Gjellumvann	21.6	3.0	8.3	155	25	16.1	638	113	14.8	0.13
Gjersjøen	21.7	4.2	7.8	173	25	6.7	288	28	4.7	0.17
Kolbotnvann	23.8	1.1	9.8	203	35	39.5	556	85	0.7	0.01
Pollen	22.0	2.4	8.3	343	35	7.0	225	29	7.1	0.24
Semsvann	21.1	2.5	8.9	94	25	8.7	133	17	7.1	0.42
Skraperudvann	21.4	4.1	7.4	54	10	7.1	185	13	6.3	0.49
Snipetjern	20.5	–	6.0	62	80	3.5	312	27	1.1	0.04
Sognsvann	21.1	6.1	7.0	33	15	3.4	76	8	0.9	0.12
Steinsrudvann	21.6	3.2	7.5	149	45	9.4	322	67	2.1	0.03
Svinsjøen	21.6	4.4	8.3	239	15	4.0	458	58	9.9	0.17
Sværsvann	20.5	2.2	6.7	66	50	16.5	349	72	24.0	0.33
Tussetjern	21.4	–	7.6	126	45	7.5	288	18	2.1	0.12
Ulsrudvann	22.4	1.8	7.1	55	40	17.0	319	12	0.5	0.04
Verkensvann	22.0	4.9	8.1	192	20	4.4	269	59	2.3	0.04
Årungen	23.5	2.5	9.2	203	30	19.0	545	20	12.3	0.62

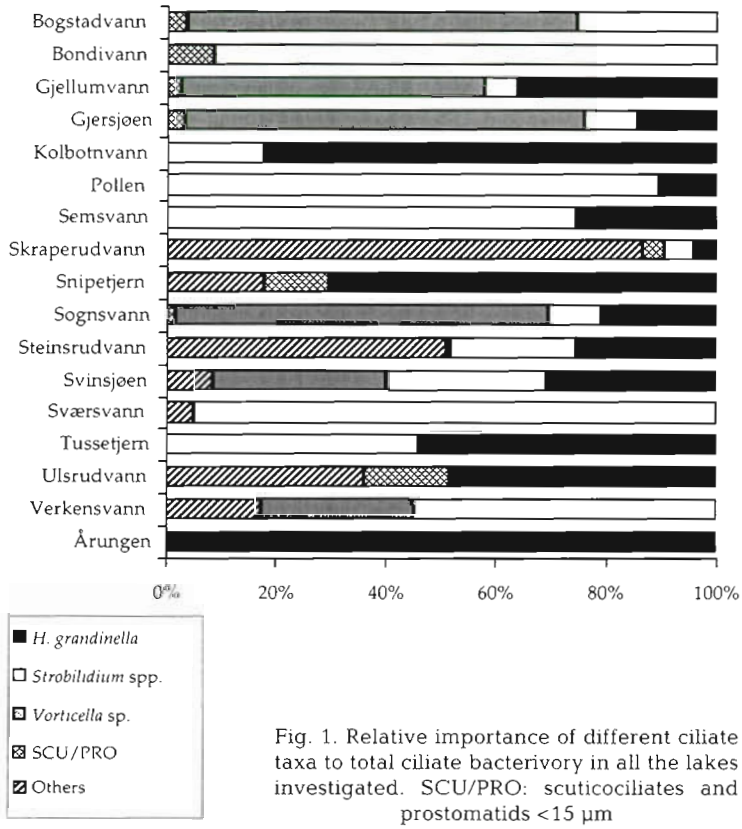

Fig. 1. Relative importance of different ciliate taxa to total ciliate bacterivory in all the lakes investigated. SCU/PRO: scuticociliates and prostomatids <15 µm

grandinella and *Strobilidium* spp. was relatively small, indicating that they were always food limited. Grazing rates are dependent on the bacterial abundance, and a larger variability must therefore be expected. For *H. grandinella* grazing rates of 140 to 1008 (mean: 598) bacteria ciliate^{-1} h^{-1} were found, while *Strobilidium* spp. ingested 65 to 911 (mean: 348) bacteria ciliate^{-1} h^{-1} (Fig. 3). In the samples where these ciliates were present, 5 to 10 cells of each were measured. The average volumes were 3840 µm^3 for *H. grandinella* and 1180 µm^3 for *Strobilidium* spp. By using these values and the average clearance rates, this gives specific clearance rates of 0.5×10^5 and 0.9×10^5 cell volumes h^{-1} respectively.

The contribution from larger oligotrichs (>30 µm) to total bacterivory was small. They made up a significant portion of total ciliate grazing in one lake only (Steinsrudvann), and except in one case, clearance rates were found to be very low (5 to 32 nl cell^{-1} h^{-1}). The only exception was in Steinsrudvann, where a clearance rate of 182 nl cell^{-1} h^{-1} was found for *Strobilidium* sp. (35 to 40 µm).

Scuticociliates never dominated among the bacterivorous ciliates in the lakes investigated in this study. Ciliates belonging to the genus *Cyclidium* were hardly found at all, but some smaller species (10 to 15 µm), which may have included both scuticociliates and prostomatids (hereafter called SCU/PRO) were somewhat more abundant. However, these all had low clearance rates (1 to 42 nl cell^{-1} h^{-1}). The maximum contribution to total ciliate bacterivory from SCU/PRO in one single lake was 17%. When taking an average of all the lakes, they only contributed 3% of the total.

Peritrich ciliates contributed significantly (28 to 85%) to total ciliate grazing on bacteria in 7 of the 17 lakes. A large, unidentified species dominated in Skraperudvann. In the 6 other lakes the peritrichs were represented by a vorticellid ciliate attached to

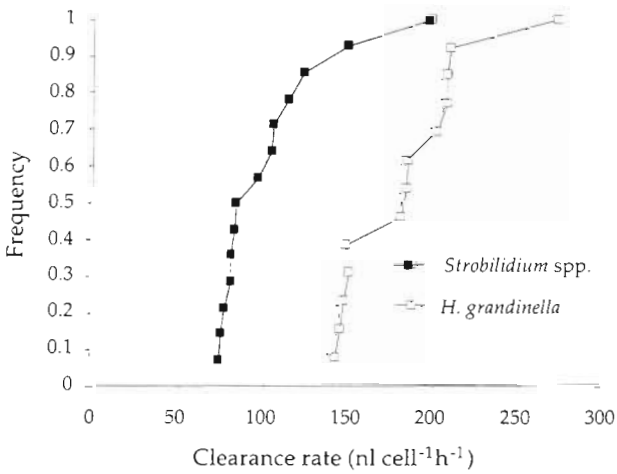

Fig. 2. Cumulative frequency plot of clearance rates for the 2 most important bacterivorous ciliates, *Strobilidium* spp. and *Halteria grandinella*

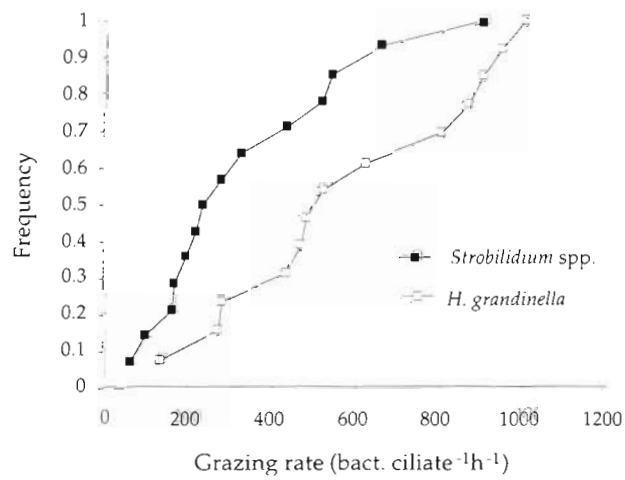

Fig. 3. Cumulative frequency plot of grazing rates for the 2 most important bacterivorous ciliates, *Strobilidium* spp. and *Halteria grandinella*

colonies of the cyanophyte *Anabaena flos-aquae*. On average 15 ciliates were attached to each colony, and they had an individual clearance rate of 250 to 797 nl cell^{-1} h^{-1} (mean: 490, SD: 186), giving grazing rates of 377 to 3445 bact. ciliate^{-1} h^{-1}.

Clumping of FLB in food vacuoles was never a problem for the small oligotrichs, which usually ingested 1 to 6 FLB during the incubation. Each *Vorticella* ingested 10 to 20 FLB, and in a few cases clumping caused some difficulties. With the concentration of FLB used here, the incubation time should therefore not exceed 10 min.

DISCUSSION

There are several problems connected to both the estimates of bacterial production and ciliate bacterivory (see B. F. Sherr et al. 1989). Ciliates grazing picoplankton (0.2 to 2 µm) seem to retain larger cells within this size category with a higher efficiency than smaller cells (Fenchel 1986, González et al. 1990, Epstein & Shiaris 1992, Šimek et al. 1995, 1996). Although this effect was not found to be dramatic for ciliates (González et al. 1990), this still means that when using FLB for estimating bacterivory, the clearance rates and grazing rates obtained will probably vary depending on the size distribution of the FLB. The average size of the FLB used in this study was 1.2×0.6 µm, which is larger than the average size of natural bacteria in most lakes. This means that the grazing rates may have been systematically overestimated. However, it is possible that it is mainly the larger-sized bacteria that are responsible for the bacterial production (González et al. 1990, Sherr et al. 1992), implying that ciliates might be cropping a larger proportion of the bacterial production than the bacterial standing stock. When comparing bacterivory and bacterial production, the most appropriate grazing rates might therefore be obtained by using FLB that are comparable to the larger size classes of the natural bacterioplankton.

If ciliates are able to discriminate against heat-killed FLB in favour of live bacteria, there is also a possibility for systematic underestimations of grazing rates. Sherr et al. (1987) found that a small scuticociliate had the same growth rate when fed on FLB as when fed on unstained bacteria of the same clonal strain, and the oligotrich ciliate *Strobilidium conicum* showed no significant difference in uptake of FLB and live bacteria (B. F. Sherr et al. 1989). However, González et al. (1990) found different clearance rates using FLB of the same size, but made from 2 different bacterial strains, indicating that factors other than size might be of importance for rates of ingestion. Ciliate clearance rates obtained by using FLB are in most cases probably close to, or slightly lower than, actual clearance of similar-sized natural bacteria.

The use of filtration techniques can also cause underestimations. Small oligotrichous ciliates are very fragile, and even gentle filtration can cause disruption of cells. Thus, if quantified on the filter, their abundance can be seriously underestimated. Also, often a rather small volume of water (≤30 ml) is filtered. Numerically inferior, but still potentially important bacterivorous ciliates (e.g. *Vorticella* or *Epistylis*) can then easily be missed out if only a small part of the filter is examined.

In this material, bacterial abundances ranged from 0.8 to 6.4 $\times 10^6$ ml^{-1} and production estimates from 0.003 to 0.08 $\times 10^6$ cells ml^{-1} h^{-1}, corresponding to doubling times of 53 to 462 h. Both are within the range of values that have been found in freshwater and marine systems, but the production rates are in the lower end (Sanders et al. 1989, Ducklow & Carlson 1992). The low production estimates could be due to the use of an incorrect conversion factor. Both in the sea and in lakes, empirically derived conversion factors seem to cluster around a value of 2×10^{18} cells produced mol^{-1} thymidine incorporated (Bell 1990, Ducklow & Carlson 1992). This factor was therefore used in this study. However, significant variations in conversion factors have been reported (Bell 1990, Ducklow & Carlson 1992), and production estimates obtained by using a fixed factor must be interpreted with caution. Moreover, empirical conversion factors are most often based on thymidine uptake into the cold TCA fraction, not the DNA fraction. This is not likely to cause serious systematic underestimations as the DNA fraction in most cases is >80% of the TCA fraction (Bell 1990). In an oligotrophic lake an empirical conversion factor of 1.8×10^{18} was obtained using the same protocol for DNA purification as in this study (Stabell unpubl.).

If bacterial mortality is mainly due to protozoan grazing, then total protozoan bacterivory should, on average, balance the bacterial production. The percentage of bacterial production removed by ciliates should thus give an impression of the relative importance of ciliates as bacterial grazers. However, because of all the methodical uncertainties involved, a comparison of bacterivory and bacterial production is problematic. Still, with many observations it is likely that such comparisons produce a reasonably good picture of the possible magnitude of ciliate bacterivory.

In this study, the ciliates were found to graze bacteria equivalent to 0.8 to 63% (mean: 19%) of the bacterial production. In 2 very thorough works on community bacterivory, Sanders et al. (1989) found that ciliates accounted for up to 30% of total bacterivory, with an average of 11% throughout the year, while

Šimek et al. (1995) found that ciliate grazing ranged from 8 to 42%, with an average of 18% of total protozoan bacterivory in the epilimnion and 21% in the metalimnion. On average both authors found total bacterivory to be somewhat lower, but close to the bacterial production, leaving the grazing impact from ciliates on bacteria close to what was found in this study. Vaqué et al. (1992) found that ciliates contributed significantly to total bacterivory, but due to much lower total bacterivory than bacterial production, they only grazed bacteria equivalent to ~0 to 10% of the bacterial production. In other studies, values of ciliate bacterivory have been found to be negligible (Bloem et al. 1989, Pace et al. 1990), very significant (Sherr et al. 1987, B. F. Sherr et al. 1989, Christoffersen et al. 1990, Sherr et al. 1991), and highly variable (Šimek & Straškrabová 1992) compared to bacterial production estimates.

When averaging the entire material in this study, *Strobilidium* spp. accounted for 34%, *Halteria grandinella* 31%, peritrichs (mainly *Vorticella*) 19%, and SCU/PRO for 3% of total ciliate bacterivory. Thus, the 3 most important ciliate taxa accounted for >80% of total ciliate bacterivory. The low contribution from oligotrichs >30 µm is in accordance with other studies which show that these ciliates mainly ingest food particles >2 µm (Jonsson 1986, Bernard & Rassoulzadegan 1990, Kivi & Setälä 1995).

Based on results from this and other studies, it appears that the only pelagic ciliates that are of importance as grazers of bacteria in lakes are *Cyclidium* spp., oligotrichs <30 µm (*Halteria, Pelagohalteria, Strobilidium*) and a few peritrichs (*Vorticella, Epistylis*) (Sanders et al. 1989, Christoffersen et al. 1990, Sherr et al. 1991, Šimek & Straškrabová 1992, Šimek et al. 1995). Other pelagic ciliates able to ingest bacteria are usually of no importance either due to low abundance or low clearance rates. However, these few important bacterivorous ciliates are very efficient filter feeders (Šimek et al. 1996). Here *H. grandinella* and *Strobilidium* spp. were found to have volume-specific clearance rates of 0.5 and 0.9 $\times 10^5$ h^{-1} respectively, which is somewhat lower than, but in the same order of magnitude as, has been found for small oligotrichous ciliates by others (E. B. Sherr et al. 1989, Šimek et al. 1995), and comparable to values usually found for bacterivorous flagellates (Fenchel 1982, Tobiesen 1990). This means that these ciliates are serious competitors to the flagellates. Despite this, ciliates are only occasionally of importance as grazers of bacteria, while bacterial mortality due to grazing from heterotrophic flagellates always seems to be significant. This can probably be explained by the low number of bacterivorous ciliates. In a situation with few functionally similar species, temporarily favourable/unfavourable conditions for a single bacterivorous ciliate can lead to rapid changes in ciliate community bacterivory.

Both *Halteria grandinella* and *Strobilidium* spp. are very common. They can be found at any time of the year, and in oligotrophic as well as in eutrophic lakes (Pace 1982, Beaver & Crisman 1989, Foissner et al. 1991, Müller et al. 1991). Small oligotrichous ciliates eat bacteria and autotrophic picoplankton, while ingestion of larger food particles appears to be rare (Šimek et al. 1996).

The most common peritrichs found in lake plankton seem to be *Vorticella* spp. and *Epistylis* spp. Several species within these genera are voracious grazers of bacteria (Foissner et al. 1992, Šimek et al. 1995). Information on seasonal abundance or trophic preferences for these ciliates are very scarce, but they usually peak in summer or autumn (Müller et al. 1991), and are probably more common in eutrophic than in oligotrophic lakes (Bark 1981, Pace & Orcutt 1981, Beaver & Crisman 1989, Sanders et al. 1989, Christoffersen et al. 1990, Müller et al. 1991, Šimek et al. 1995). However, in this study *Vorticella* sp. attached to *Anabaena flos-aquae* was found in many of the clearly least productive lakes. This is not surprising, as this cyanophyte is common in oligotrophic lakes (Rosén 1981).

It has been questioned whether ciliates that are able to ingest bacteria can subsist on bacteria alone. E. B. Sherr et al. (1989) calculated that this would be possible for a small (<15 µm) oligotrichous ciliate even at a bacterial concentration of 1×10^6 bacteria ml^{-1}. Nevertheless, probably all 'bacterivorous' ciliates ingest autotrophic picoplankton in addition to bacteria (Šimek et al. 1996). Based on ciliate ingestion of bacteria and autotrophic picoplankton, Šimek et al. (1996) found a good match between calculated and observed ciliate growth, showing that for some efficient fine-filter feeding ciliates (i.e. *Cyclidium, Vorticella*, small oligotrichs), ingestion of nanoplankton is not essential for survival. In the present study bacterivorous ciliates were found even in Lake Sognsvann, where the bacterial concentration was as low as 7.6×10^5 ml^{-1}. The fact that 'bacterivorous' ciliates also ingest autotrophic picoplankton makes it impossible to assume that ciliate bacterivory can only be important above a certain bacterial concentration. In general the abundance of bacterivorous ciliates increases with increased trophic status (Beaver & Crisman 1982), but so does the bacterial production (Cole et al. 1988). The relative importance of ciliates as grazers of bacteria can therefore be just as high in oligotrophic as in eutrophic lakes.

If a pelagic ciliate ingests nothing but free-living bacteria, clearance rate estimates should not differ much from one lake to another, as the incipient limiting food concentration for bacterivorous ciliates appears to be 10^7 to 10^8 bacteria ml^{-1} (Taylor 1978a,

Rivier et al. 1985, Sanders 1988), which is much higher than what is found in most lakes. The observed variations in clearance rates for *Halteria grandinella* and *Strobilidium* spp. must be considered to be small, taking into account that for both taxa there must have been some variability in average cell size. These results indicate that bacteria are indeed an important food source. If nanoplankton had been the main food source, it is likely that the ciliates would have been food saturated in some of the more productive lakes. Clearance rate estimates from those lakes would be low, and the overall clearance rate variability would be larger than observed here. Despite the very likely ingestion of autotrophic picoplankton in addition to bacteria, these results also show that the ciliates are still always food limited. In agreement with this, Šimek et al. (1996) found growth rates for picoplanktivorous ciliates that were much lower than their expected maximum growth rate (Taylor 1978b, Müller & Geller 1993).

Despite uncertainties due to the methods involved, the results here and in other studies (e.g. Sanders et al. 1989, Šimek et al. 1995) show that ciliates in general are not the major grazers on bacteria, but they are sometimes important, and should not be ignored in investigations of pelagic food webs. The combination of few important taxa and the possibility of only small variations in clearance rates within each taxon can make it possible to assess their importance without too much work. With more information on the influence of temperature on the clearance rates of the important bacterivorous ciliates, fairly good estimates on ciliate bacterivory can probably be obtained by only quantifying a few key species.

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