Dominance of ciliate grazing on bacteria during spring in a shallow eutrophic lake

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ABSTRACT: The objective of this study was to investigate the relationships between bacterioplankton biomass and activity and protistan grazing during the spring in shallow Lake Võrtsjärv, Estonia. Bacterial and heterotrophic protistan (flagellate and ciliate) abundance was determined by fluorescence direct counts, protistan grazing on planktonic bacteria was measured from fluorescently labeled bacteria uptake rates, and the estimate of bacterial heterotrophic activity was obtained from leucine and thymidine incorporation rates. The abundance of heterotrophic nanoflagellates (HNF) was low, ranging from 8.4 to 27.1 cells ml^{-1}, while ciliate numbers dominated, ranging from 55 to 180 cells ml^{-1}. The population of ciliated protozoans was dominated by scuticociliates (*Uronema* sp., *Cyclidium* spp., and 1 unidentified scuticociliate) and oligotrichs (*Strobilidium* spp. (diameter > 50 µm), *Strobilidium* spp. (diameter < 50 µm), and *Strombidium* sp.). Ciliates were predominant grazers of bacteria, showing higher clearance rates (14 to 65 nl ciliate^{-1} h^{-1}) than HNF (1 to 11 nl HNF^{-1} h^{-1}); the total grazing rate of ciliates (on average 2398 bacteria h^{-1} ml^{-1}) was 28 times higher than total grazing of HNF (87 bacteria h^{-1} ml^{-1}). In general terms protozoan grazing balanced with bacterial production but was not sufficient to support ciliate growth: on the basis of conversion factors the calculated generation time of bacterivorous ciliates was long, on average 121 d (ranging from 43 to 198 d).

KEY WORDS: Bacterioplankton · Protist grazing · Ciliates · Shallow lake

INTRODUCTION

Previously, ciliates were only considered to be primarily bacterivores in isolated cases (Hall et al. 1993 and references therein). It is generally thought that ciliates are not effective grazers at concentrations of bacteria found in the field; rather, they are likely consumers of relatively large cyanobacteria and nanoplankters (Epstein & Shiaris 1992 and references therein). To date, several reports are available in which bacterivory by freshwater pelagic ciliates has been well documented *in situ* (Šimek et al. 1990, 1995, 1998b, Šimek & Straskrabova 1992, Stabell 1996).

Previous studies on bacterioplankton in Lake Võrtsjärv, Estonia, have shown that bacterial numbers are low during spring; despite considerable bacterioplankton productivity the abundance of bacteria did not increase. Sufficient organic substrates were produced by the spring bloom of diatoms (Kisand & Nõges 1998) and no nutrient deficiency could be expected (Kisand et al. unpubl.) during this season. The aim of the present study was to test the hypothesis that bacterioplankton is controlled by protistan grazing during the spring, and to compare the importance of ciliates and heterotrophic nanoflagellates in planktonic bacterivory. Also, we attempted to determine the relative importance of different ciliate taxa as bacterivores in Lake Võrtsjärv. In order to address to these questions, weekly samples were taken from the lake for the 6 wk period from March 31 to May 12, 1998; the grazing rate of protists was estimated along with the abundance of bacteria and protists, and the activity of bacteria (thymidine and leucine incorporation rates).

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MATERIAL AND METHODS

Samples were collected weekly from eutrophic (1.6 g N m^{-3} mean total nitrogen concentration and 54 mg P m^{-3} total phosphorus) and shallow (mean depth 2.8 m) Lake Võrtsjärv during spring 1998 (March 31 to May 12, 1998). The sampling station was situated in the deepest area of the lake (max. depth 6 m), near to Võrtsjärv Limnological Station. Samples were taken at 0.5 m intervals throughout the water column with a 2 l Ruttner sampler and mixed in a barrel to make a 20 l pooled sample, which was transported to the onshore laboratory. Several previous studies (Nõges et al. 1997, 1998a,b) have shown that pooled samples represent the whole water column of the lake fairly well.

The abundance of heterotrophic bacteria was determined by staining with DAPI (Porter & Feig 1980). Water (20 ml) was fixed with buffered formalin (1% final conc.) and 1 to 5 ml of subsample was filtered through 0.2 µm membrane filters (Poretics) immediately after sampling. Filters were frozen at –20°C until counting on a Leica DMBR fluorescence microscope at 1250× magnification using violet light (425/460 nm, GG475). The abundance of heterotrophic nanoflagellates (HNF) and small ciliates (∅ < 50 µm) was counted on the same filters which were used in short-term grazing experiments (see below). Auto- and mixotrophy of flagellates was checked on the basis of autofluorescence of chlorophyll under green light (546/565 nm, OG 590). A total of 250 (if >30 cells were encountered) to 400 (if <15 cells were encountered) fields of view were counted on each filter. The total biomass and taxonomic groups of ciliates (usually to the genus level) were determined from Lugol's fixed samples by inverted microscopy (Olympus IX50 or Nikon diaphot-TMD) at 200 to 600× magnification using the Utermöhl (1958) technique. Volumes of 50 ml were settled and the entire content of each Utermöhl chamber was surveyed. Ciliate identification was based on Patterson & Hedley (1992) and Foissner & Berger (1996) and taxonomy followed Corliss (1979). The dimensions of the first 20 measurable specimens encountered for each taxon were measured. Biovolumes of each taxon were estimated by assuming standard geometric shapes (Finlay 1977).

^{3}H-leucine and -thymidine incorporation was used to estimate bacterial heterotrophic activity. Saturation curves were always used to determine the rate of incorporation: ^{3}H-leucine (Amersham International, SA [specific activity] = 62.0 Ci mmol^{-1}) or ^{3}H-thymidine (Amersham International, SA = 26 Ci mmol^{-1}) was added to 5 ml samples (2 samples + 2 formalin-killed controls; 2% final conc.) at a concentration range of 0.5 to 54 nM. The vials were incubated at *in situ* temperature for 60 or 30 min for leucine or thymidine incorporation, respectively. The incubation was stopped by

adding 40% formalin (2% final conc.). Cold TCA-ethanol extraction was applied after filtering of samples on cellulose acetate (Millipore) 0.2 µm filters. The filters were dried and placed in a scintillation vial with 5 ml Quickscint (Zinssler Analytic Inc.) scintillation cocktail. Samples were measured by a Rackbeta 1211 liquid scintillation counter; the external standard ratio method was applied for quenching correction. Incorporation rate of leucine (TLI) was used to calculate biomass production of bacteria (BPB) and incorporation rate of thymidine (TTI) for cell production (BPC). Empirically determined conversion factors (ECF) from earlier studies (Kisand & Nõges 1998) were used in our calculations: ECF$_{TLI}$ was 4.25×10^9 µg C mol^{-1} leucine and ECF$_{TTI}$ was 3.8×10^8 cells mol^{-1} thymidine.

Preparation of fluorescently labelled bacteria (FLB) and grazing experiments. Bacterioplankton from the lake was concentrated on 0.2 µm pore-size filters after prefiltration through GF/C filters. Bacteria were grown in 0.2 µm filtered lake water batch cultures and harvested by centrifugation (Šimek et al. 1995, Dr K. Šimek pers. comm.). FLB (heat killed and DTAF stained) were obtained according to the protocol of Sherr & Sherr (1993). The size of FLB was comparable to cell size in natural populations of bacteria (although no real measuring was performed). In each FLB uptake experiment, bacterial density in the lake water was measured, and FLB were added to give a final concentration of 4 to 22% of the native bacterial counts. Samples were incubated for 45 to 360 min, but usually no longer than 60 min at the ambient temperature of the lake water; in calculations, only incubation times up to 75 min, which corresponded to the linear phase of uptake rate, were used. Subsamples for FLB counts in food vacuoles of protists were taken at 10 to 20 min intervals and the average uptake rate was caclulated on the basis of linear range of FLB uptake (usually the shortest and the longest incubations resulted in lower rates but at least 3 time points had similar rates in the middle). Samples were fixed with buffered formalin (1% final conc.). Preserved samples were stained for 1 to 2 min with DAPI at a final concentration of 2 µg ml^{-1} and 5 to 15 ml of water was gently filtered through 0.8 µm pore-size black isopore (Poretics Inc.) filters. Protists and the contents of their food vacuoles were examined with a Leica DMBR fluorescence microscope at 1250× magnification using blue light (470/505 nm, OG 515). The results of staining with both DTAF and DAPI were examined on the same microscopic field by switching filter sets without disturbing the position of the slide, and between 200 and 400 fields were examined. The dominant taxa of fluorescently stained ciliates were identified as much as possible based on knowledge of the composition of parallel Lugol's fixed samples.

Calculations. Biomass of different organisms was calcuated on the basis of published conversion factors: bacteria, 20 fg C cell^{-1}; heterotrophic flagellates, 220 fg C µm^{-3} (Børsheim & Bratbak 1987); ciliates 190 fg C µm^{-3} (Putt & Stoecker 1989). Grazing rates of protists were calculated directly from FLB uptake values considering total number of cells in incubation bottles (FLB + natural concentration). To estimate total protistan grazing rate, average uptake rates of HNF and ciliates were multiplied by their total *in situ* abundance. The doubling time of bacteria was calculated from TTI and TLI; the doubling time of protists assuming bacteria as the only food was estimated taking into account the biomass of protists, carbon content of bacteria, growth efficiency 40% (Fenchel 1987) and specific grazing rate of protists (bacterial cells ind.$^{-1}$ h^{-1}).
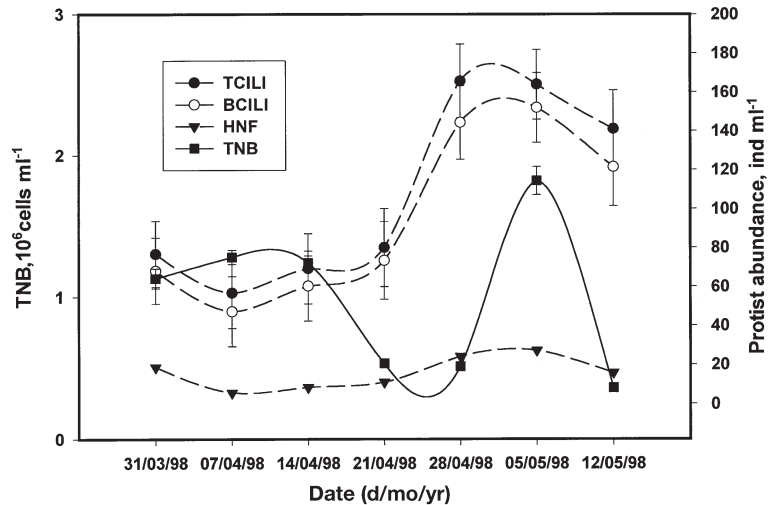

Fig. 1. Total number of bacteria (TNB), heterotrophic nanoflagellates (HNF) and ciliates (TCILI: total number of ciliates; BCILI: bacterivorous ciliates). Error bars represent ±SE

RESULTS

Physical-chemical parameters and phytoplankton

The investigated period (from March 31 to May 12, 1998) represented the period between last weeks of ice cover on the lake, ice break (in April 11) and warming up of water column. The period was characterized by relatively low temperatures and a well-mixed water column. Under the ice the water temperature was around 1.5°C and the water had warmed up to 12°C by May 12 (temperature increased almost linearly). Water transparency decreased to 1.3 m from the initial values of 1.8 to 2.0 m. The total phytoplankton biomass measured as chlorophyll *a* (chl *a*) concentration increased about 3 times (from 15 to 46 µg chl *a* l^{-1}) in a similar manner to the temperature. Total nitrogen (N$_{tot}$) and inorganic forms of nitrogen (N$_{in}$) decreased during the study period (N$_{tot}$: from 2.1 to 1.4 mg N l^{-1} and N$_{in}$: from 1.31 to 0.45 mg N l^{-1}), whilst total phosphorus (P$_{tot}$) almost doubled (35 µg P l^{-1} at the beginning and 66 µg P l^{-1} at the end). The phosphate concentration was quite stable at a level around 4 to 10 µg P l^{-1}.

Bacterioplankton

Bacterial numbers were relatively stable and low during the whole sampling period: 0.36 to 1.82 × 10^6 cells ml^{-1} (Fig. 1). The activity of heterotrophic bacteria (measured as TLI and TTI) were also at a low level; only at the end of investigated period did both parameters increase sig-

nificantly (Fig. 2). Biomass production of bacteria calculated on the basis of TLI and cell production calculated from TTI ranged from 0.045 to 0.80 µg C l^{-1} h^{-1} and 2.5 to 12.1 × 10^6 cells l^{-1} h^{-1}, respectively. In these calculations ECFs from earlier studies (Kisand & Nõges 1998, Kisand et al. unpubl.) were used: ECF$_{TLI}$ was 4.25 × 10^9 µg C mol^{-1} leucine and ECF$_{TTI}$ was 3.8 × 10^{18} cells mol^{-1} thymidine. Median generation time of bacteria was 7.8 (range from 1.2 to 30) and 8.9 (range from 0.4 to 15) d^{-1}, calculated trom TTI and TLI, respectively.
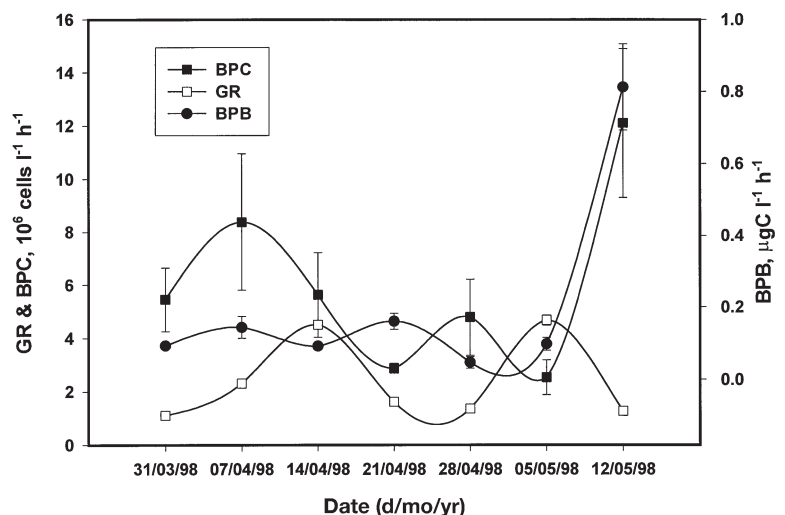

Fig. 2. Bacterial biomass (BPB, µg C l^{-1} h^{-1}), cell production (BPC, cells l^{-1} h^{-1}) estimated by TLI and TTI, respectively, and protistan grazing rate on bacteria (GR, bacterial cells l^{-1} h^{-1}) during investigated period. Error bars represent ±SE

Protozooplankton

In protozooplankton HNF abundance was low, ranging from 8.4 to 27.1 cells ml^{-1} (Fig. 1), while ciliate numbers dominated, ranging from 55 to 180 cells ml^{-1}. HNF cell volume ranged from 2.4 to 170 µm^{-3} (median 25). Abundance of these 2 main groups of protists gave an exceptionally low numerical HNF/ciliate ratio of 0.1 to 0.24 (average 0.15).

During the investigation period the population of ciliated protozoans was dominated by scuticociliates and oligotrichs (Fig. 3). The most common scuticociliates were *Uronema* sp. (8 to 25 ind. ml^{-1}), *Cyclidium* spp. (1 to 4 ind. ml^{-1}) and 1 unidentified scuticociliate (Scutico., 16 to 49 ind. ml^{-1}). Oligotrichs were dominated by *Strobilidium* spp. ($\varnothing > 50$ µm, 5 to 68 ind. ml^{-1}; $\varnothing < 50$ µm 13 to 24 ind. ml^{-1}), and *Strombidium* sp. (2 to 30 ind. ml^{-1}). Also, haptorids (*Mesodinium* sp., 0.1 to 12 ind. ml^{-1}) and prostomatids (*Urotricha* sp., 4 to 10 ind. ml^{-1}; *Coleps* spp., 0.7 to 2.3 ind. ml^{-1}) were always present. At the beginning of the investigation period the community was dominated by smaller species like *Uronema* sp., *Cyclidium* sp. and *Urotricha* sp. In the middle of April the abundance of large ($\varnothing > 50$ µm) *Strobilidium* and *Strombidium* species rose quickly, as well as the abundance of some large haptorids (*Dileptus* sp., ~0.1 ind. ml^{-1}; and *Monodinium* sp., ~0.12 ind. ml^{-1}). Altogether 12 identifiable taxa were recorded during the investigation period.

Protist grazing of FLB

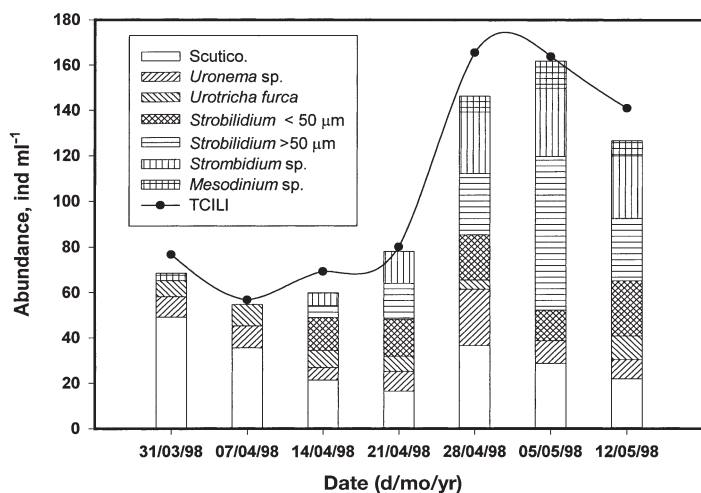The uptake rate of FLB by protists was usually linear during incubations of 15 to 75 min; these values were

Fig. 3. Abundance of identified taxa of ciliates ind. ml^{-1}. TCILI: total number of ciliates

used to calculate the average rate of FLB uptake. Ciliates were predominant grazers of bacteria, and showed higher clearance rates (median 23; range: 14 to 65 nl ciliate^{-1} h^{-1}) than HNF (median 6; range: 1 to 11 nl HNF^{-1} h^{-1}, Fig. 4A). The total grazing rate of ciliates was 28 times higher than the total grazing of HNF: ciliates grazed, on average, 2398 bacteria h^{-1} ml^{-1}, HNF only 87 bacteria h^{-1} ml^{-1} (Fig. 4A).

The main grazers of bacteria among quite small ciliate species (see also Table 1) were: *Uronema* sp., *Urotricha* sp., *Strobilidium* sp. ($\varnothing < 50$ µm) and Scutico., with average clearance rates of about 38 to 53 nl ciliate^{-1} h^{-1}. Species-specific grazing rate was the highest for *Cyclidium* sp. (123 bacterial cells ind.$^{-1}$ h^{-1}) but its abundance was low during the period investigated. Other taxa showed specific grazing rates in the range of 25 to 62 bacterial cells ind.$^{-1}$ h^{-1} (Table 1). The unidentified scuticociliate (Scutico.) was responsible for the highest proportion of the total grazing (on average 1205 cells ml^{-1} h^{-1}), small *Strobilidium* sp. ($\varnothing < 50$ µm) had a lower grazing rate (970 cells ml^{-1} h^{-1}), and *Uronema* sp. and *Urotricha* sp. grazed 390 and 160 cells ml^{-1} h^{-1}, respectively (Fig. 4b).

Protistan grazing and bacterial production

In general terms protozoan grazing balanced with the production of bacteria, being on average 61% (Fig. 2). In these calculations an ECF for calculating the cell production was used (ECF$_{TTI}$ was 3.8×10^{18} cells mol^{-1} thymidine). If the ECF$_{TTI}$ was actually lower (literature average is ~2×10^{18}), protists could consume about 100% of bacterial production. On the basis of published conversion factors and specific grazing rate the mean generation time of bacterivorous ciliates was rather long (121 d^{-1}). That calculation assumes that bacteria are the only food source for these ciliates. The median of HNF generation time was 6.7 d^{-1} (range from 2.8 to 98), assuming that bacteria are the only food source.

DISCUSSION

Ciliates versus HNF as grazers of bacteria in Lake Võrtsjärv

Among protozoans, HNF, and not ciliates, are known to be the most important grazers of bacteria. This knowledge is based on 2 basic factors: HNF abundance is 1 to 2 orders higher than that of ciliates (Šimek et al. 1997, Sommaruga & Conde 1997) and ciliates are considered to graze mostly on nano-sized organisms (Sherr et al. 1990). There is clear evidence that ciliates, especially smaller ones, are able to graze effectively on

pico-sized particles (including bacteria), and specific grazing rates of ciliates are higher than those of HNF (Epstein & Shiaris 1992, Iriberri et al. 1993). Earlier studies have suggested that ciliates cannot survive exclusively on bacteria in pelagic systems because they require high bacterial concentrations. Still, data from coastal waters indicate that 10^6 bacteria ml^{-1} might be sufficient to allow ciliates $\varnothing < 15$ µm to grow at a rate of 1 doubling per 48 h (Sherr et al. 1989). Small species (mostly $\varnothing < 30$ µm) often numerically dominate ciliate communities in most of the meso- to eutrophic lakes and they can exploit a variety of food resources ranging from picoplankton to nanophytoplankton (Beaver & Crisman 1989, Sherr et al. 1991). Recent laboratory experiments (Zubkov & Sleigh 1995) have shown that *Uronema* sp. reduced the bacterial concentration to a limiting level of less than 8×10^5 cells ml^{-1} during 2 h. In Lake Võrtsjärv, bacterivorous ciliates showed moderate clearance (average 30 nl $ciliate^{-1}$ h^{-1}); the clearance rate of HNF was about 6 nl HNF^{-1} h^{-1}. The main reason for these rather low clearance rates was probably environmental conditions, mainly low temperature.

The abundance of HNF was very low, indeed there is no literature reference of such a low numerical ratio of HNF/ciliates (~0.15). In the naturally acidic bog lake (Große Fuchskuhle) in northeastern Germany, the populations of protists were also characterized by a low numerical proportion of HNF to ciliates (~1.5 to 3.5; Šimek et al. 1998b). However, these 2 lakes are different, as Lake Võrtsjärv is slightly alkaline (pH 7.6 to 8.5) and is not considered to be a humic lake. It is noteworthy, however, that average organic carbon concentrations are quite high (total [TOC] ~ 10 mg C ml^{-1}, particulate [POC] ~ 5.6 mg C ml^{-1}, and dissolved humic [DHC] ~3.9 mg C l^{-1}). To date, 1 other example of a eutrophic environment (backwater system of the Alte Donau) in which HNF

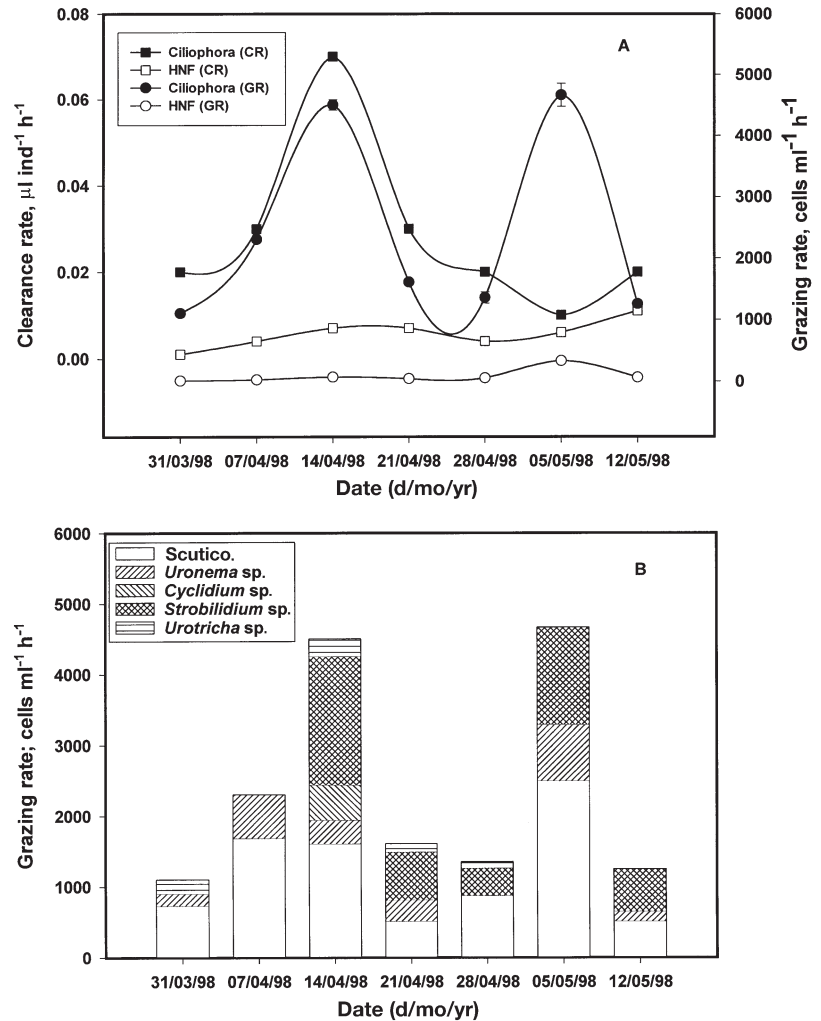Fig. 4. Clearance rate (CR, µl $protozoa^{-1}$ h^{-1}); total grazing rate (GR, bacterial cells h^{-1} ml^{-1} of protist). (A) CR and GR of total ciliates and HNF. Error bars represent ±SE. (B) GR of the main bacterivorous ciliates

are present at a very low abundance (2 to 400 HNF ml^{-1}) and graze at a low rate on bacteria, is known (Wieltschnig et al. 1999). These waterbodies conform to the rule established mostly from marine systems that

Table 1. Species-specific characteristics of main bacterivorous ciliates

Taxon	Biovolume µm^{-3}	SE	Clearance rate (ml ind.$^{-1}$ h^{-1})			Specific grazing rate (bacterial cells ind.$^{-1}$ h^{-1})		
			Average	Min.	Max.	Average	Min.	Max.
Scutico.	3812	28	0.044	0.014	0.062	44	15	87
Uronema sp.	4530	60	0.047	0.022	0.091	46	17	79
Cyclidium sp.	3195	42	0.099[a]	–	–	123[a]	–	–
Urotricha furcata	4469	37	0.038	0.034	0.045	25	17	33
Strobilidium $\varnothing < 50$ mm	3323	62	0.053	0.027	0.084	62	20	125

[a]*Cyclidium* sp. was encountered only in 1 sample

in most cases HNF dominate both in abundance and in the control of bacterial populations, but there can be exceptions, e.g., eutrophic lakes. According to unpublished data from 1997 in Lake Võrtsjärv, HNF abundance is low throughout the whole season. At the same time abundance of ciliates found in Lake Võrtsjärv is in the range found in other eutrophic waterbodies (Sanders et al. 1989, Šimek et al. 1995). Studies from 1995 to 1997 (Kisand et al. 1998, Zingel 1999) indicated high biomass of ciliates in this lake. The species composition of ciliates in Lake Võrtsjärv is highly variable. Oligotrichs, haptorids, scuticociliates and prostomatids dominate the community of ciliates. The most common oligotrichs are *Strobilidium* spp., *Strombidium* spp., and *Tintinnidium fluviatile*. On some occasions scuticociliates (*Uronema* sp., *Cyclidium* sp.), haptorids (*Mesodinium* sp., *Dileptus* sp., *Askenasia volvox*, *Monodinium* sp.), prostomatids (*Urotricha* sp., *Coleps* spp.) and peritrichs (*Vorticella* spp., *Epistylis procumbens*) are also quite abundant. The annual maximum abundance is usually found during late July or early August, when the community of ciliates is mostly dominated by small ($\varnothing$ < 30 μm) bacterivorous species. One might speculate that the ciliates could keep the numbers HNF low (Šimek et al. 1990, Weisse et al. 1990, Jürgens et al. 1996). For example, *Urotricha* spp. and omnivorous oligotrichs could efficiently control HNF dynamics. The ciliate community is extremely rich in this lake. In 1995 the mean abundance of ciliated protozoa was 39 cells ml^{-1} and mean biomass was 0.68 mg WW (wet weight) l^{-1}. In 1996 these numbers were 60 cells ml^{-1} and 2.91 mg WW ml^{-1}, respectively. Of the whole zooplankton biomass of Lake Võrtsjärv the planktonic ciliates formed up to 50% in 1995 and up to 64% in 1996 (Zingel, 1999). Thus, the high grazing pressure of ciliates on HNF could be the main reason why HNF population is kept at such a low level. There is no serious reason to believe that the counting methodology used (which is also routinely used in other waterbodies) missed most HNF or that extremely delicate species should dominate in this lake. The volumes of 5 to 10 ml should be sufficient for counting HNF and a filtration pressure below 80 mm Hg (in this case a pressure of 20 mm Hg was used) has been reported to avoid cell breakage (Gasol & Moran 1999 and references therein).

Although, to date, comparatively few reports are available in which bacterivory of freshwater pelagic ciliates has been well documented *in situ*, the importance or even prevalence in grazing on bacteria is stressed in several works from various types of lakes and reservoirs (Sanders et al. 1989, Christoffersen et al. 1990, Šimek & Straskrabova 1992, Šimek et al. 1995). In most cases ciliates appeared to become important grazers at the end of summer or even in autumn. How-

ever, with increasing trophy of the system, ciliates become more important as bacterivores (Šimek et al. 1998a). The minor effect of HNF on the bacterial population (on average 5% of cell production) was also observed in the eutrophic backwater system of the Alte Donau (Wieltschnig et al. 1999). Unfortunately, however, ciliate grazing was not measured in this case.

Due to high abundance and more efficient grazing rate (clearance rates of ciliates are almost always found to be higher than those of HNF), grazing of bacterivorous nanociliates on bacteria predominated. In a similar study of Lake Frederiksborg Slotssø, Denmark (Hansen & Christoffersen 1995), HNF grazing on bacteria was assumed to prevail, while ciliates were assumed to graze preferentially on primary producers and only marginally on bacteria. Bacterial abundance was much higher in this Danish lake, but the abundance and species composition of ciliates were similar to Lake Võrtsjärv. Hansen & Christoffersen (1995) assumed that HNF grazed preferentailly on bigger bacterial cells, while at the same time bacterial size distribution was skewed toward small cells. If this population of small and inactive cells could escape from predation by both HNF and ciliates, this could account for the huge standing stock of bacteria. At the same time, the productive part of the population, which is often found to have larger cells, could be quickly grazed by HNF and ciliates. In Lake Võrtsjärv, the standing stock of bacteria was much lower and the proportion of grazed bacteria was higher and more or less equal to the production of bacteria. Thus, the prevalence of small cells was not observed and ciliates played the most important role in bacterial grazing.

According to the literature, oligotrichs dominate (Šimek et al. 1998a) the total ciliate bacterivory (65 to 70%), and the other important bacterivorous ciliate groups are scuticociliates, accounting for 8 to 15% of the total ciliate bacterivory (Šimek et al. 1998a), and peritrichs (Carrias et al. 1996, Stabell 1996, Šimek et al. 1998a). In Lake Võrtsjärv, bacterivorous ciliates were mostly fine suspension-feeding ciliates such as scuticociliates and small oligotrichs. By virtue of their elaborate oral membranelles, scuticociliates seem especially well adapted to concentrate very small food particles from the environment (Fenchel 1986). The only bacterivorous ciliate whose feeding apparatus was not equipped for filter feeding was the prostomatid *Urotricha* sp. This species is considered to be a raptorial feeder. In addition, in Lake Võrtsjärv, *Urotricha* sp. showed the lowest total grazing rates. The other ciliates such as haptorids (*Dileptus* sp., *Monodinium* sp., *Mesodinium* sp.) large oligotrichs (*Tintinnidium fluviatile*, *Codonella cratera*, *Strombidium* sp.) and some prostomatids (*Coleps* spp.) did not show any ability to take up bacterioplankton.

In conclusion bacterivorous ciliates were extremely important grazers of bacteria during spring in the shallow and eutrophic Lake Võrtsjärv. They were more abundant than HNF and had a higher specific grazing rate on bacteria. Oligotrichs and small scuticociliates were responsible for >97% of total mortality of bacteria due to grazing. At the observed gazing rates, bacterivorous ciliates must also have a food source other than bacteria.

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