

# Ecological role and bacterial grazing of *Halteria* spp.: small freshwater oligotrichs as dominant pelagic ciliate bacterivores

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**ABSTRACT:** We conducted extensive studies on bacterivory and bacterial production over several seasons in 2 reservoirs: the meso-eutrophic Římov Reservoir in the Czech Republic and the highly eutrophic Sau Reservoir in Spain. Based on abundance, seasonal dynamics, and cell-specific uptake rates of different ciliate taxa, as well as heterotrophic nanoflagellate bacterivory, we were able to quantify bacterivory by individual ciliate species, total ciliates, and aggregated protists in these systems. With increasing trophic status, a higher portion of bacterial production was consumed by protists, and there was a greater importance of ciliate grazing, accounting for 40 and 50% of the total protistan bacterivory in the epilimnion of the Římov and Sau reservoirs, respectively. Increases were attributable to the oligotrichs of the genus *Halteria* that often numerically dominate freshwater pelagic ciliate communities. In both reservoirs, the most important ciliate bacterivores in order of importance were: oligotrichs, primarily the bacterivorous *Halteria* spp., peritrichs, and scuticociliates. We also examined food vacuole content in natural populations of *Halteria* spp. to estimate the proportion of cells that had ingested algae. Our results and a review of previous reports on the abundance of *Halteria* spp. suggest that small halteriids are ecologically important bacterial consumers in meso- to eutrophic freshwater systems due to: (1) efficient uptake of prey over a large size spectrum (approximately 0.4 to 5 µm), (2) high clearance rates on picoplankton-sized particles along with (3) high potential growth rate, and (4) lower vulnerability to metazooplankton predation compared to other common pelagic ciliates. Correspondingly, we suggest a revised concept of planktonic ciliate bacterivory, where the principal role is attributed to small omnivorous filter-feeding oligotrichous ciliates.

**KEY WORDS:** *Halteria* cf. *grandinella* · Oligotrichous ciliates · Feeding rates · Feeding ecology · Ciliate bacterivory · Reservoirs · Lakes

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## INTRODUCTION

Abundance and biomass of planktonic ciliates are related to lake trophic status, as measured by chlorophyll *a* concentrations (e.g., Beaver & Crisman 1989, Müller 1989, Carrias et al. 1998). In a review paper, Beaver & Crisman (1989) concluded that taxonomic replacements occur with increasing eutrophication such that large-bodied forms (predominantly oligotrichs) are progressively replaced by smaller-bodied

ciliates (mainly scuticociliates). However, recent studies of temperate meso- and eutrophic lakes have shown that pelagic ciliate communities are often dominated by small (<30 µm) species, mainly oligotrichs and prostomatids (e.g., Müller 1989, Macek et al. 1996), while scuticociliates, haptorids, and peritrichs are usually less numerous.

Small heterotrophic nanoflagellates have been reported as the major consumers of bacterioplankton production in most aquatic systems (e.g., Fenchel 1982, Güde 1986, Sanders et al. 1989). However, there is increasing evidence that ciliates can also significantly

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contribute to total protistan bacterivory (e.g., Sherr & Sherr 1987, Šimek et al. 1995, 1998a). Studies of taxon-specific bacterivory have shown that among pelagic ciliates the most important consumers of bacterioplankton production in both marine and freshwaters are often small oligotrichs (Sherr & Sherr 1987, Sanders et al. 1989, Šimek et al. 1995, 1996, Stabell 1996, Hwang & Heath 1997a, Thouvenot et al. 1999), rather than bacterivorous species such as scuticociliates, which usually require bacterial concentrations higher than those found in most pelagic environments (e.g., Fenchel 1980). Such high bacterial abundances are found in hypertrophic systems which can support large populations of scuticociliates (mostly of the genera *Cyclidium* and *Uronema*, e.g., Nakano et al. 1998) or in specific environments, such as the chemocline, oxycline, etc. (Fenchel et al. 1990). Only occasionally are small scuticociliates, e.g., *Cyclidium* spp., found to be important bacterivores in the pelagial of meso- and eutrophic systems, probably due to micropatches such as organic aggregates that have high bacterial densities (Šimek et al. 1995, 1998b).

Among small oligotrichs, the genus *Halteria*, most probably the species *H. grandinella*, has been identified as an abundant bacterial consumer in several meso- and eutrophic lakes and ponds (Sanders et al. 1989, Šimek et al. 1995, 1998a, Stabell 1996, Nakano et al. 1998). This species has also been studied with respect to taxonomy (e.g., Tamar 1990, Foissner 1994), feeding ecology (Jürgens et al. 1996), and vulnerability to metazooplankton predation (e.g., Tamar 1979, Gilbert 1994, Wiackowski et al. 1994a). Recently it has been reported that the genus *Halteria* sensu lato comprises several rather similar species. *H. grandinella* Müller is likely the most important species, but *H. bifurcata* Tamar and *Pelagohalteria cirrifera* Kahl are quite similar (summary of taxonomic information in Foissner et al. 1999) and cannot always be routinely differentiated in quantitative examinations, as silver impregnations are necessary to examine the somatic ciliature. Thus, since the latter 2 species have been recently found in various European lakes (Foissner pers. comm.), and with respect to the fact that they probably cannot be differentiated in quantitative studies, we pooled these halteriids together and used the term '*Halteria*' throughout this paper, being aware that it might contain heterotrophic species of the 2 genera *Halteria* and *Pelagohalteria*.

Here we report on abundance, seasonal and spatial dynamics, and cell-specific uptake rates of *Halteria*, as well as the contributions of different ciliate taxa to total protistan bacterivory in 2 systems. By combining recent and some previously published field data (Šimek et al. 1995) on uptake rates and food vacuole content, with additional laboratory experiments for estimating

the rate of ingestion and digestion of typical food items (Jürgens & Šimek 2000, in this issue), we tried to elucidate the most important factors affecting abundance, growth rate, feeding ecology, and carbon requirements of this apparently common and important ciliate species.

## MATERIALS AND METHODS

**Sampling.** We conducted studies in 2 dam reservoirs, the meso-eutrophic Římov Reservoir and the eutrophic Sau Reservoir. In the Římov Reservoir (South Bohemia, Czech Republic, for more details see Šimek et al. 1995), the sampling site was located above the former river valley (a 30 m depth) close to the reservoir dam. Samples were collected from the epilimnion (a mixed sample from  $1 \pm 0.5$  m depth) and the metalimnion (a mixed sample from the thermocline  $\pm 0.5$  m) of the reservoir at 2 to 3 d intervals from August through September 1993 (see Šimek et al. 1995). Additional samples were collected from the surface layer (1 m depth) during a *Halteria* peak at the beginning of October 1994. In 1997, samples were collected from the surface layer (1 m depth) at 3 to 6 d intervals during the spring bloom period (late April–May) and clear water phase (June) and sampled at 1 to 3 wk intervals over the rest of the study period.

The eutrophic Sau Reservoir is an 18.5 km long, canyon-type reservoir located in the middle stretch of the River Ter (Catalonia, NE Spain, for a detailed description see Vidal & Om 1993). The reservoir was sampled during the period of summer stratification in June–July 1996; samples were collected from 0.5 and  $2 \times$  the Secchi depth from 2 stations located about 1.5 and 3 km from the reservoir dam. During 1997, water samples were collected in 2 intensive sampling campaigns consisting of 9 points (all  $\sim 1.8$  km apart; for details see Armengol et al. 1999) along the longitudinal axes of the reservoir: in April, when the temperature of the river inflow was the same as that of the epilimnetic reservoir water ( $\sim 16^\circ\text{C}$ ), and in July, with well-developed water stratification (for details see Comerma et al. in press). In both cases mixed water samples from the top 3 m were collected.

**Bacterial abundance, biomass, and production.** Subsamples were fixed with formaldehyde (2% final concentration), stained with DAPI (final concentration 0.2% wt/vol) and enumerated by epifluorescence microscopy (Olympus BH2 or BX60). Between 400 and 600 DAPI-stained bacterial cells were recorded at a magnification of  $1250\times$  using an analog monochrome LCD camera (Cohu) mounted to the Olympus BX60 microscope. The recorded bacterial cells were then processed with the semiautomatic image analysis

system LUCIA D (LUCIA 3.52, resolution  $750 \times 520$  pixels, 256 grey-levels, Laboratory Imaging, Prague, Czech Republic, <http://www.lim.cz>). Cell area and cell perimeter were chosen as the most reliable parameters of pixel measurements. Details of the image processing (grey transformation, edge finding) are described in Posch et al. (1997).

Bacterial production was measured by [ $^3\text{H}$ ]-thymidine incorporation using the method modified from Riemann & Søndergaard (1986); for details, see Šimek et al. (1995). For different sampling periods (see above), corresponding empirical conversion factors (ECF) of thymidine incorporation rate to bacterial cell production were determined by incubating replicate 750 ml subsamples of  $1.0 \mu\text{m}$  filtered water for 24 h at *in situ* temperature (see Šimek et al. 1995, 1999). In the present study, we applied the following ECF: 2.27 to 2.74, 3.0, and  $1.75 \times 10^{18}$  cells  $\text{mol}^{-1}$  of thymidine incorporated for the Řimov Reservoir in 1993, 1994, and 1997, respectively, and  $4.7 \times 10^{18}$  cells  $\text{mol}^{-1}$  for the Sau Reservoir in April 1997. A theoretical conversion factor of  $2 \times 10^{18}$  cells  $\text{mol}^{-1}$  was applied to the Sau Reservoir data in July 1997.

**Protistan grazing and abundance.** To measure protistan grazing on bacterioplankton, we used fluorescently labelled bacterioplankton (FLB) prepared according to Sherr & Sherr (1993), as slightly modified by Šimek & Straškrabová (1992). Bacterioplankton from the reservoirs was concentrated on  $0.2 \mu\text{m}$  pore-size filters after pre-filtration through  $2 \mu\text{m}$  pore-size filters (Poretics). Bacterial cells were detached from the filter surface by several sonication pulses and fluorescently labelled in  $\sim 30$  ml of a staining solution. This small modification minimized the loss of very small cells, resulting in a good fit of size distributions of bacterioplankton and FLB. Heterotrophic nanoflagellate (HNF) and ciliate FLB uptake rates were determined using 500 ml samples for short-term FLB direct uptake experiments with tracer amounts of FLB (5 to 17% of natural bacterial concentration). In cases where small oligotrichs were abundant, we used a separate treatment for the ciliates where FLB tracers amounted to  $< 5\%$  of bacterial abundance. Subsamples of 30 to 50 ml were taken at 0, 3, 6, 10, 20, and 30 min, or 0, 5, 10, 15, 20, 40, and 60 min after tracer addition and fixed by 0.5% of alkaline Lugol's solution, immediately followed by 2% borate-buffered formaldehyde (final concentration) and several drops of 3% sodium thio-sulphate to clear the Lugol's color. This preservation technique is recommended to prevent egestion of food particles by HNF (Sherr & Sherr 1993). Within 3 d after fixation, 5 to 15 ml (flagellates) or 20 to 30 ml (ciliates) subsamples were stained with DAPI, filtered through  $1 \mu\text{m}$  (HNF) or  $2 \mu\text{m}$  (ciliates) black polycarbonate filters (Poretics), and the protozoa inspected and counted on

the filters via epifluorescence microscopy (Šimek et al. 1995, 1997). Up to 200 HNF and 50 to 100 ciliates were inspected at randomly selected microscopic fields at each time point. Non-pigmented, HNF and plastidic flagellates were always differentiated. Ciliate uptake rates as FLB  $\text{cell}^{-1}$  were estimated at 3, 6, and 10 min, or alternatively at 5, 10, and 15 min exposure. HNF uptake rates were estimated at 10, 20, and 30 min, or alternatively at 20, 40, and 60 min; the longer times were used during cold water periods. Samples from time zero were also inspected to avoid potential bias of our data due to attachment of non-ingested tracers on protozoan surfaces. Uptake rates were calculated by linear regression of average number of tracers per protozoan cell versus time. To estimate total protistan grazing rate, average grazing rates of HNF and ciliates were multiplied by their total *in situ* abundances.

**Community structure of ciliates.** Ciliate community structure was evaluated by combining: (1) DAPI-stained samples in epifluorescence microscopy, (2) live sample observation, and (3) protargol staining (for details see Macek et al. 1996). For more details of the above approaches and criteria used for grouping ciliates into different taxonomic categories, see Šimek et al. (1995; and references therein). The taxonomy of oligotrichous ciliates is undergoing revision and we based our identifications on the publications of Foissner et al. (1991, 1999), Foissner (1994), and Foissner & Berger (1996) and detailed references therein.

**Field data—*Halteria* tracer ingestion and food vacuole content.** During the examination for FLB uptake, the ciliates with ingested tracers were tentatively identified, which in the case of *Halteria* was possible using cell size, shape and size of nuclei, and the arrangement of FLB in food vacuoles. Only heterotrophic halteriid species were considered, thus excluding for example the mixotrophic *Pelagohalteria viridis*. Each individual of unambiguously identified *Halteria* (the taxon identifications were confirmed in protargol-stained impregnations) was measured with an ocular micrometer in a fluorescence microscope, numbers of ingested FLB were counted, and the food vacuole content was also inspected for uptake of natural phytoplankton based on autofluorescence of chlorophyll. Ingested algae or cyanobacteria were measured with an ocular micrometer and recorded as either pico- ( $< 2 \mu\text{m}$ ) or nano-sized ( $> 2$  to  $< 20 \mu\text{m}$ ) phytoplankton prey. Thus each individual ciliate was characterized by its cell volume (calculated by approximation to prolate spheroid), uptake rate of bacteria under *in situ* temperature, and presence (enumerated and sized) or absence of phytoplankton prey in food vacuoles.

A total of 879 individuals of *Halteria* from grazing experiments were inspected in both reservoirs at different periods or seasons as specified below. From the

Římov Reservoir, 585 individuals of *Halteria* were examined with 235 cells from the epi- and metalimnion of the reservoir during August–September 1993, 125 epilimnetic specimens from October 1994, and 225 epilimnetic individuals from April through October 1997. From the Sau Reservoir, a total of 294 individuals from the epilimnetic populations of *Halteria* were inspected during 3 periods: 86 cells from July 1996, and 113 and 95 individuals from the longitudinal sampling campaigns in April and July 1997, respectively.

***Halteria* — calculated doubling time based on picoplanktivory.** Potential doubling times were calculated based on the estimated amount of bacterial carbon consumed, and in a 1993 subset of data from the Římov Reservoir, the amount of carbon consumed as autotrophic picoplankton (APP) as well. The amount of carbon ingested by individual ciliates was calculated from grazing rates multiplied by the amount of organic carbon per food particle (bacteria and/or APP; for details of APP see Šimek et al. 1996). Cell volumes of ciliates and those of their ingested picoplankton prey were transformed to carbon using the following conversion factors (in fg C  $\mu\text{m}^{-3}$ ): ciliates, 140, recommended for formaldehyde-fixed samples (Putt & Stoecker 1989); bacteria, 231 and 192 (calculated according to Norland [1993], corresponding to the mean cell volumes of bacteria in both study sites, i.e., 0.062 and 0.105  $\mu\text{m}^3$  in the Římov and Sau reservoirs, respectively); and picocyanobacteria, 200 (Weisse 1993). The mean cell volumes of bacteria used were based on 52 (Římov) and 22 (Sau) bacterial size determinations (always >400 bacterial cells measured per sample) conducted along with the measurement of uptake rates of *Halteria* on bacteria. To convert the carbon data into potential doubling times of the ciliates, we used 35% gross growth efficiency for bacterivorous ciliates (see Šimek et al. 1996, and references therein).

## RESULTS

In most cases, the mean uptake rates were between 6 and 20 FLB per *Halteria* cell during 5 to 10 min exposure to a tracer concentration that was typically <10% of bacterial concentration. The distributions of the uptake data were not significantly different from a normal distribution of prey item per ciliate. Fig. 1 shows 3 examples from dates when the highest number of the ciliate individuals was inspected in samples collected from the same locality. In each example, the data distribution was not significantly different from a normal distribution and, except for the data set from October 1994, it differed significantly from a Poisson distribution (Kolmogorov-Smirnov test,  $p > 0.5$ ). Thus, with regard to the typical data distribution, we used the

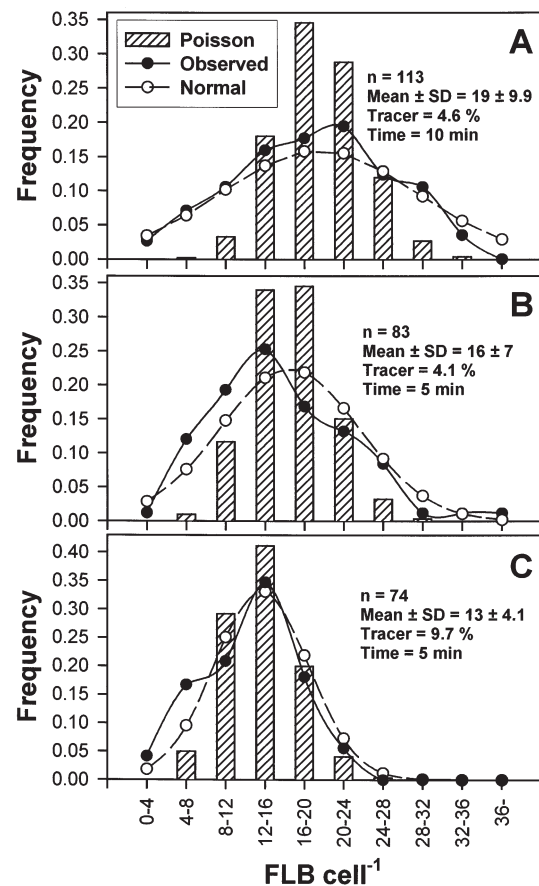


Fig. 1. Three examples of the frequency distribution of FLB uptake data of *Halteria* spp. representing samples with the highest abundance and number of ciliate individuals inspected. (A,B) The Sau Reservoir, 16 April 1997 and 10 July 1996, water temperature 16°C and 23.2°C, respectively; (C) The Římov Reservoir, 4 October 1994, water temperature 14°C. Each panel shows the corresponding parameters of mean uptake rate (fluorescently labelled bacteria [FLB] per cell  $\pm$  SD), number (n) of individuals inspected, tracer amount of FLB added, and time of incubation of the sample

mean uptake rate per ciliate for calculating total ciliate grazing rate.

To illustrate the importance of *Halteria*, and of total ciliates, as bacterial consumers in the different meso- and eutrophic systems, we present details of 2 data sets (Figs. 2 & 3) out of the entire database, which is summarized in Fig. 4. Fig. 2 shows the seasonal development of selected microbial parameters in the Římov Reservoir in 1997. Between April and October, 1 conspicuous peak and 2 less remarkable increases of ciliate abundance occurred, i.e., 102, 45, and 41 ciliates  $\text{ml}^{-1}$ , in the middle of May, July, and September, respectively. In general, they occurred with or just after peaks of bacterial and HNF abundances, which varied from 2.23 to  $6.32 \times 10^6$  bacteria  $\text{ml}^{-1}$  and 0.44 to  $2.92 \times 10^3$  HNF  $\text{ml}^{-1}$ , respectively (data not shown) over the study period.

Grazing rates of HNF ranged from 5 to 31 bacteria  $\text{HNF}^{-1} \text{h}^{-1}$  (mean  $\pm$  SD,  $14.4 \pm 6.4$  bacteria  $\text{HNF}^{-1} \text{h}^{-1}$ ), with the lowest values at the cold water period in April. Separately, we enumerated unambiguously identifiable individuals of the group *Halteria*. Their numbers ranged from  $<1$  cell  $\text{ml}^{-1}$  in early April to 55 cells  $\text{ml}^{-1}$  in the middle of May (Fig. 2A) and temporal changes paralleled shifts in total ciliate abundance.

Bacterial production (BP) showed 2 apparent maxima, in the middle of May and in early August (Fig. 2B), i.e., shortly after the spring phytoplankton peak, and coinciding with the summer phytoplankton peak, respectively (data not shown). Minima of BP were observed at the beginning of April (before stratification) and during the transient stage between the clear water phase (with the minimum chlorophyll *a* concentration of  $4 \mu\text{g l}^{-1}$  in early June) and the onset of the summer phytoplankton peak by the end of June. On average, 58% of BP was consumed by total protozoa, with slightly more important ciliate bacterivory (32%) compared to that of HNF (26% of the total BP grazed). On a seasonal basis, however, there were significant differences in absolute and relative values of the bacterial loss rate due to protistan bacterivory. During the late April-early May period and the clear water phase (first half of June), protistan bacterivory was generally low and removed only a small proportion of BP ( $<25\%$ ). However, protistan bacterivory almost balanced BP for most of May and the late summer-early fall period.

Grazing of *Halteria* alone accounted for, on average, 54% of total ciliate bacterivory; thus, changes in total protozoan grazing rate were tightly correlated with the abundance of *Halteria* ( $r^2 = 0.789$ ,  $n = 17$ ,  $p < 0.001$ ). Fig. 2C clearly documents, except for a few data points, the dominating role of *Halteria* and of other oligotrichs in ciliate bacterivory. This holds especially true for the June period when only 2 small oligotrichs, *Halteria* (Fig. 2C) and the closely related mixotrophic *Pelagohalteria viridis* (data not shown), ingested bacteria, with the latter species shortly dominating ciliate bacterivory. Oligotrichs dominated bacterivory in 14 out of 17 assays. In the remaining 3 samples, the most important group, designated as 'others' (see Fig. 2C), was largely peritrichs, dominated by the genera *Vorticella*, *Epistylis*, *Carchesium*, and by some unidentified species attached to zooplankton (data not shown). Uptake of bacteria by these forms accounted for most of the ciliate bacterivory in the samples from April and October. Bacterivory by scuticociliates, especially of *Cyclidium* spp., while detectable in about half of the plankton samples (Fig. 2C), was never quantitatively important ( $<15\%$ ).

Fig. 3 shows changes in selected microbial parameters in April 1997 along the longitudinal axis of the Sau Reservoir, which is supplied with organically loaded

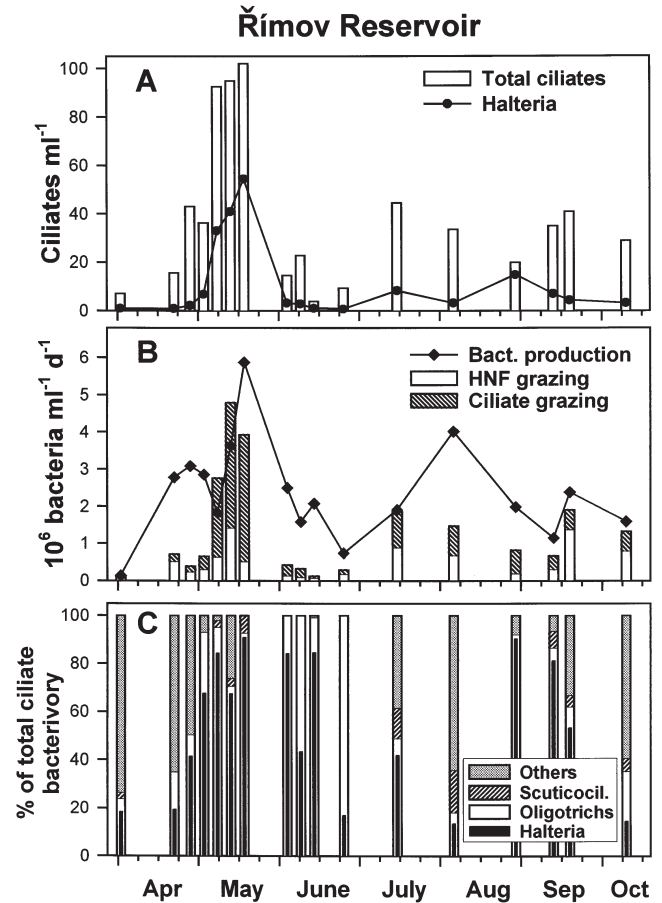


Fig. 2. The Římov Reservoir, April to October 1997. (A) Total ciliate abundance and abundance of *Halteria*, (B) bacterial production and total protistan bacterivory divided into heterotrophic flagellate (HNF) and ciliate grazing, and (C) the role of different ciliate taxa in total ciliate bacterivory. Note that the group 'oligotrichs' represents the aggregated bacterivory of all oligotrichous ciliates compared to the bacterivory of *Halteria* spp. only, and the group 'others' was dominated by grazing activity of peritrichous ciliates (for details see text)

river water with a high allochthonous bacterial biomass and production (see Fig. 3B). Bacterial densities declined from  $16 \times 10^6$  cells  $\text{ml}^{-1}$  at the river to  $<5 \times 10^6$  cells  $\text{ml}^{-1}$  downstream (Stn 1); HNF numbers ranged from  $\sim 2$  to  $5 \times 10^3$  HNF  $\text{ml}^{-1}$ , except for a conspicuous peak abundance ( $22 \times 10^3$  HNF  $\text{ml}^{-1}$ ) at Stn 7. HNF grazing rates ranged from 12 to 67 bacteria  $\text{HNF}^{-1} \text{h}^{-1}$  (mean  $\pm$  SD,  $24.1 \pm 17.1$  bacteria  $\text{HNF}^{-1} \text{h}^{-1}$ ), with the highest values at Stn 7 along with a peak of large chrysomonads (see Šimek et al. 1998a). Total ciliate and *Halteria* numbers showed a similar pattern with minima at the river inflow and close to the reservoir dam (Stn 1) and sharp maxima of 144 and 105 cells  $\text{ml}^{-1}$ , respectively, at Stn 4 (Fig. 3A).

There was a negligible grazing impact of protists on the extremely high production of the allochthonous

bacterial populations brought by the river to the reservoir ('river' and Stn 8, Fig. 3B). However, downstream, at Stn 7, there was a distinct HNF peak, corresponding to HNF bacterivory that was roughly double the rate of BP. However, from Stn 6 downstream to Stn 2, ciliates clearly dominated bacterivory. *Halteria* consumed the bulk of BP at Stns 6, 4, and 3 and slightly less at Stn 2, and contributed about equally with the ciliate group 'others' to total bacterivory at Stn 5 (Fig. 3B,C). Among other oligotrichs ingesting FLB, we observed mainly small strobiliids. The ciliate group 'others' was dominated by bacterivory of the peritrich genera of *Vorticella* and *Epistylis* (data not shown). Scuticociliates (i.e., the genera *Cyclidium* and *Uronema*) were more

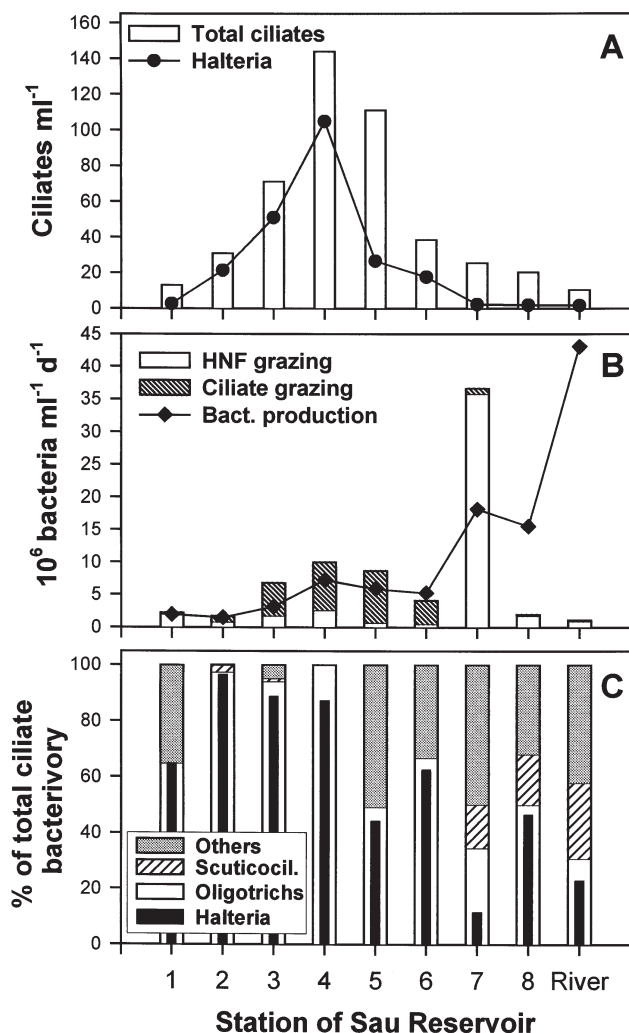


Fig. 3. An example of the longitudinal transects through the Sau reservoir, April 1997. (A) Total ciliate abundance and abundance of *Halteria*, (B) bacterial production and total protistan bacterivory divided into HNF and ciliate grazing, and (C) the role of different ciliate taxa in total ciliate bacterivory. For other explanations see Fig. 2

important in total ciliate bacterivory in the upper, inflow parts of the reservoir. However, due to their generally low abundance, their contribution to total bacterial loss rate caused by ciliates was small (always <24%; cf. Fig. 3A,C).

We summarized all our published and unpublished results from both reservoirs where bacterivory of total HNF and ciliates, as well as individual ciliate taxa, were analyzed to illustrate the overall importance of *Halteria* as a bacterial consumer (Fig. 4). This summary of protistan bacterivory in the epilimnetic waters was based on the average values, representing 52 analyses conducted in the Římov Reservoir: 32 in 1993 (Šimek et al. 1995), 3 in 1994, and 17 in 1997 (see Fig. 2). From the Sau Reservoir we analyzed 22 samples: 4 in 1996 and 18 in 1997 split into two 9-sample subsets from the 2 longitudinal sampling campaigns. On average, HNF and ciliates together consumed a total of 65 and 75%, and *Halteria* alone 13 and 22% of total BP in the epilimnion of the Římov and Sau reservoirs, respectively (Fig. 4). While in the meso-eutrophic Římov Reservoir HNF populations contributed on average 60% and cil-

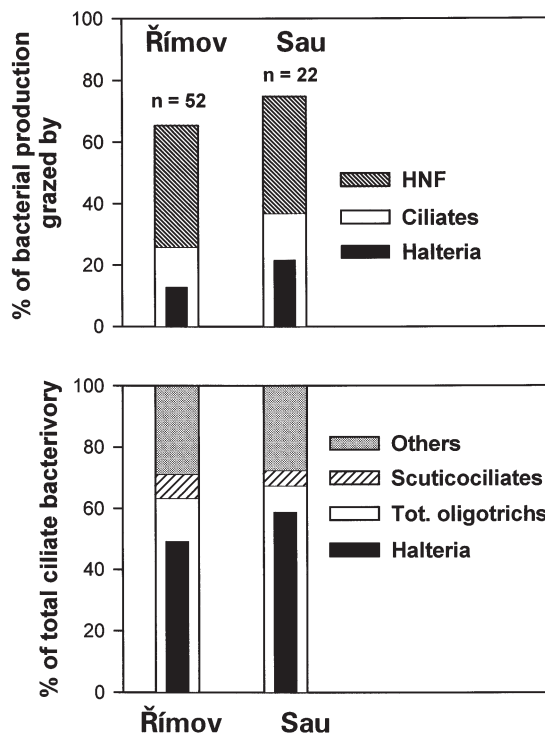


Fig. 4. (A) Overall averages (of n measurements) of the proportions of bacterial production grazed by all protozoans (the full size of the bars), grazed by HNF and ciliates separately, and grazed only by *Halteria* in the Římov (data from seasons 1993, 1994 and 1997) and Sau reservoirs (data from June 1996 to July 1997). (B) Overall averages of the role of different ciliate taxa in total ciliate bacterivory. For other explanations see Fig. 2

iates 40% of the total protistan grazing, in the Sau Reservoir, their contributions to total protistan bacterivory were approximately equal. Plastidic flagellates were not important bacterivores in either reservoir, as they consumed <1% of BP (data not shown).

The 4 major groups of ciliates we distinguished showed different, but for the respective group in both systems similar, contributions to the total ciliate bacterivory (Fig. 4). Oligotrichs clearly dominated with 63 and 68%, mainly due to bacterivory of *Halteria* accounting for 49 and 59% of the total ciliate bacterivory in the Římov and Sau reservoirs, respectively. The contributions of scuticociliates were within the range of 5 to 8%, but 'others', mainly peritrich ciliates (*Vorticella*, *Epistylis*, and *Carchesium*), significantly contributed (~30%) to ciliate bacterivory in both reservoirs.

The important role of *Halteria* in bacterivory was not only a result of the frequent numerical dominance of halteriids in our studies (e.g., Figs. 2A & 3A), but also of its very high bacterial consumption rates. Table 1 shows mean, median and ranges of values of the ciliate cell volumes, and grazing and clearance rates. Since the parameters of the populations of *Halteria* from both reservoirs differed remarkably (see Table 1), we treated the data set separately. Mean uptake rates and mean cell volumes ( $\pm$ SD) of *Halteria* were:  $1782 \pm 864$  and  $3220 \pm 1920$  bacteria cell<sup>-1</sup> h<sup>-1</sup>, and  $2497 \pm 1025$  and  $1950 \pm 860$   $\mu\text{m}^3$  in the Římov and Sau reservoirs, respectively (Table 1). We tested if there was a positive correlation between cell volume and grazing rate of the ciliate. There were significant, but rather weak, relationships between cell volume and grazing rate of *Halteria* ( $r^2 = 0.086$  and  $0.118$ ,  $n = 585$  and  $294$ ,  $p < 0.001$ , in the Římov and Sau reservoirs, respectively). Different water temperatures in the reservoirs could also influence grazing rates of ciliates. To correct the potential effect of this factor, we normalized the grazing data to the mean temperature at both study sites using  $Q_{10} = 2.5$ . However, there was no positive effect of this correction on the correlation between the cell volume of *Halteria* and its grazing rate ( $r^2 = 0.053$ ,  $n = 585$ ,  $p < 0.001$ ) in the Římov Reservoir. Only the correlation of the data from the Sau Reservoir became slightly closer ( $r^2 = 0.162$ ,  $n = 294$ ,  $p < 0.001$ ).

For a rough estimate of doubling times of *Halteria* based exclusively on carbon from bacteria, the mean cell volumes of ciliates (Table 1) and of ingested bacteria were transformed into carbon units (for details see 'Materials and methods'). Assuming a gross growth efficiency of 35% and using our data on the mean uptake rates (Table 1), the growth rate of *Halteria* would be  $0.49$  d<sup>-1</sup> in the Římov Reservoir and  $1.10$  d<sup>-1</sup> in the Sau Reservoir. During the 1993 study, we measured grazing rates on bacteria and picocyanobacteria in the Římov Reservoir (see Šimek et al. 1995). Estimating the

Table 1. *Halteria*. Major characteristics of cell volume and grazing rates on bacteria for populations from the Římov and Sau reservoirs. Growth rates ( $\mu$ ) were calculated only on the basis of organic carbon ingested in bacteria or a combination of bacteria and picocyanobacteria (pcyano) (for mean cell volumes and corresponding carbon content see 'Materials and methods') assuming a 35% gross growth efficiency. n: number of individuals inspected

Reservoir	Cell volume of <i>Halteria</i> ( $\mu\text{m}^3$ )			Grazing rates on bacteria (bacteria ciliate <sup>-1</sup> h <sup>-1</sup> )			Clearance rate (nl ind. <sup>-1</sup> h <sup>-1</sup> )			Grazing rates on pcyano (pcyano ciliate <sup>-1</sup> h <sup>-1</sup> )		$\mu$ (d <sup>-1</sup> )	Algivity <sup>a</sup> (% of total ciliates)
	Mean (SD)	Median	Range	Mean (SD)	Median	Range	Mean (SD)	Median	Range	Mean (SD)	(SD)		
<b>Římov</b> n = 585	2497 (1025)	2278	470–6880	1782 (864)	1703	100–4960	432 (222)	415	29–1426	–	–	0.49	9.5
n = 235 <sup>b</sup>	2860 (1380)	2770	470–6650	1580 (1120)	1310	100–4960	–	–	–	210 (69)	–	0.74	2
<b>Sau</b> n = 294	1950 (860)	1780	580–4820	3220 (1920)	3120	0–8820	572 (405)	457	0–2687	–	–	1.10	8

<sup>a</sup>Percentage of the ciliate individuals that ingested *in situ* algae > 2  $\mu\text{m}$

<sup>b</sup>This subset represents the data from the Římov Reservoir (August–September 1993), when uptake rates on both bacteria and picocyanobacteria were measured in parallel (for details see Šimek et al. 1995)

doubling time of the ciliates based on carbon ingested as both heterotrophic bacteria and picocyanobacteria yields a generation time of  $0.74 \text{ d}^{-1}$  (Table 1). Our inspection of food vacuole content of *Halteria* (Table 1) revealed that only a very small percentage of ciliate cells ingested phytoplankton other than picocyanobacteria, on average 9.5 (Římov) and 8% (Sau). Almost all ingested algal preys (0 to 4 cells ciliate<sup>-1</sup>) were within a size range of 2 to 4  $\mu\text{m}$ , and algal prey  $>5 \mu\text{m}$  were not found in food vacuoles of the ciliate.

## DISCUSSION

The high protist-induced bacterial mortality in both reservoirs can be associated with a rather moderate top-down control of protistan populations by metazooplankton. A common feature of both systems is that a pronounced grazing impact by cladocerans (mainly *Daphnia* spp.) is usually limited to a short clear water phase in the Římov and Sau reservoirs. In the Římov Reservoir, there was a sharp decrease in total ciliates, *Halteria*, and HNF (data not shown) abundance during the clear water phase, June 1997 (Fig. 2). This phenomenon corresponded with marked seasonal maxima of abundance and bacterivory of daphnids and has been previously reported for the reservoir (Šimek et al. 1990) and some lakes (Pace et al. 1990, Jürgens 1994). The clear water phase also yielded a seasonal minimum of the role of protists in consuming BP (Fig. 2). In general, 1997 (Fig. 2) was rather exceptional, as ciliate grazing accounted for, on average, more than 50% of total protistan bacterivory. In contrast, during 1987 (Šimek et al. 1990) and 1988 (Šimek & Straškrabová 1992) ciliate grazing exceeded HNF bacterivory only during a late summer-fall period. In general, the increased importance of ciliates in total protistan bacterivory (Fig. 2) was closely linked to seasonal changes in the abundance of *Halteria*.

In the Sau Reservoir (Fig. 3), there was a clear downstream trend in the abundances and succession of microbial communities, i.e., bacteria-HNF-ciliates, which was perhaps linked to their potential growth rates and changes in water flow regime. The river inflow showed a conspicuous peak in BP and negligible protistan bacterivory corresponding to very low protist abundances (Fig. 3). A few hundred meters downstream a marked HNF population peak occurred. From Stn 6 downstream to Stn 2, HNF, as the major bacterivores, were replaced by ciliates largely due to bacterivory of *Halteria* (cf. Fig. 3A,C).

Overall, our data indicated 2 important findings from the lower (Římov) towards the higher trophic status (Sau) in the reservoirs: (1) an increasing portion of BP consumed by protists, and (2) an increasing role of cil-

iate grazing accounting for 40 and 50% of the total protistan bacterivory in the Římov and Sau reservoirs, respectively (Fig. 3). Several possible sources of over- and underestimates of the production and grazing data (for details see Sherr et al. 1989) could have influenced these conclusions. Specific details of our modified protocols for the FLB uptake measurements have been discussed in Šimek & Straškrabová (1992) and Šimek et al. (1995, see also Fig. 1). McManus & Ocubo (1991) reported 3 major potential sources of error present in such surrogate experiments:

(1) Ingestion is concentration dependent; thus, addition of surrogates may itself increase grazing. To minimize such an error, we kept FLB additions as low as possible within a rather narrow range, i.e., mostly below 15% (9 to 17%) in the case of HNF and below 10% (3.7 to 10%) in the case of ciliates, with the majority of samples with oligotrichs receiving FLB additions  $<5\%$ . Hence, HNF uptake data, rather than the estimates for ciliates, could be more significantly overestimated. (2) A linear approximation of uptake is assumed in short time uptake experiments. Our data showed a near-linear increase of food particles per protozoan cell for both HNF and ciliates (see, e.g., Fig. 2 in Jürgens & Šimek 2000). (3) As shown for several species of flagellates (McManus & Ocubo 1991), the distribution of surrogates in grazers does not support the idea of random encounter and ingestion, even for a uniform population of grazers. Thus, data on HNF grazing seem to be prone to a larger statistical error than those for ciliates, since at different tracer exposure times there is a significant and varying proportion of HNF cells with no FLB ingested. It can also partly reflect the fact that HNF represent a mixed community of a largely unknown taxonomic composition, or a community where only a few dominant bacterivorous HNF could be tentatively identified (cf. Šimek et al. 1997). Among typical bacterivorous HNF, we always included 'non-responders' (i.e., those HNF with zero FLB cell<sup>-1</sup>) into the calculation of the mean uptake per cell. To minimize the error that can result from such a data distribution, we inspected up to 200 HNF individuals per time point.

On the other hand, a non-normal data distribution does not seem to be inherent in the uptake of the monospecific ciliate populations (e.g., Fig. 1). Due to a very low proportion of ciliates with zero FLB per cell, a generally higher number of FLB per ciliate (as opposed to HNF), and a close match between mean and median values of grazing rate per ciliate (see, e.g., Table 1), the distribution of the uptake data (as FLB per ciliate cell) is not statistically different from a normal distribution (Fig. 1). Our data on ciliate bacterivory could also have been overestimated due to FLB counted in ciliate food vacuoles that were primarily ingested by HNF and



then secondarily consumed by ciliates. However, considering typical densities and grazing rates of HNF (see 'Results'; Šimek et al. 1995, 1997), clearance rates of *Halteria* (Table 1; Šimek et al. 1996), and the short incubation times and low FLB tracer amounts used (see 'Material and methods'), this source of error seems to be negligible. For instance, for *Halteria* we calculated that indirect FLB uptake via HNF would always account for <5% of its estimated bacterivory. Thus, we conclude that our FLB approach produced reliable evidence on the role of ciliate bacterivory in the Římov and Sau reservoirs.

The most important parameter that could bias our estimates of BP is the factor used for converting thymidine incorporation rate to cell production of bacteria. Therefore, we applied our ECF whenever possible. Our values of ECF are close to the theoretical ones, matching the typical range of values reported for freshwater bacteria (Smits & Riemann 1988).

There was a difference between the Římov and Sau reservoir populations of *Halteria* in cell volumes, with larger cells found in the Římov Reservoir (Table 1). When a maximum shrinkage of individuals of *Halteria* fixed with Lugol's solution is assumed (30 to 35%, Wiackowski et al. 1994b), and we use their mean cell volumes reported in Table 1, this would yield a live volume of 3246 to 3371 and 2535 to 2633  $\mu\text{m}^3$  for the Římov and Sau reservoirs, respectively. The calculated mean live volume of *Halteria* in the Římov Reservoir is very close to that of well-fed individuals of the ciliates from batch cultures with algae (3754  $\pm$  890  $\mu\text{m}^3$ , Jürgens & Šimek 2000). The individuals from the Sau Reservoir were much smaller, but without a large difference in clearance rates compared to the populations from the Římov Reservoir (Table 1). Thus, with a similar clearance rate these *Halteria* populations in the Sau Reservoir could: (1) meet their carbon requirements much faster, (2) thus also realize shorter doubling times than in the Římov Reservoir, and (3) compete more efficiently for bacterial food sources, with a higher volume-specific clearance rate in the Sau Reservoir.

We also tried to determine if individual ciliate uptake was positively correlated with an individual cell volume of the ciliate. Assuming that the larger individuals should have higher grazing rates, the changes in the cell volume of *Halteria* would explain only between ~9% (Římov) and 12% (Sau) of the variability in our uptake data. Normalizing for potential temperature effects ( $Q_{10} = 2.5$ ) improved the correlation from the Sau Reservoir only slightly, explaining ~16% of the uptake data measurements. A similar weak relationship between cell volume and uptake rates on bacteria was also found for a natural lake population of *Cyclidium* sp. (Šimek et al. 1998b). There are probably other factors, besides temperature and cell volume, which

affect the feeding rate, such as physiological state, cell cycle (the largest, dividing ciliates had usually very low uptake rates), food availability and food quality (see also Legner 1975, Jürgens & Šimek 2000). There is also the possibility that the pooled group *Halteria* indeed did not comprise only the most frequently identified *H. grandinella*, but also the closely related species *H. bifurcata* and *Pelagohalteria cirrifera* (Foissner et al. 1999), or a species complex with different subspecies of slightly deviating morphology and ecological behavior.

Laboratory experiments showed that the typical food items, i.e., hetero- and autotrophic picoplankton and 3 to 4  $\mu\text{m}$  sized *Chlorella* sp. were efficiently ingested and then digested by *Halteria* sp. within ~2.5 to 4 h (Jürgens & Šimek 2000). Both the laboratory and field experiments indicate that *Halteria* feeds on different trophic levels (hetero- and autotrophic picoplankton and small HNF). This likely species complex has a large prey size spectrum compared to a strictly bacterivorous species, though some authors consider, e.g., *H. grandinella* as primarily bacterivorous (e.g., Taylor 1978). By virtue of its omnivory and very high clearance rates on bacteria, *Halteria* can compete with HNF by feeding on the same food sources, moreover the ciliates can also prey on HNF (Cleven 1996, Jürgens et al. 1996).

The high uptake rates of bacteria and picoalgae by *Halteria* in the reservoirs imply that these ciliates can meet most of their carbon requirements through picoplanktivory (Table 1). The existing evidence that *Halteria* can subsist on bacteria alone is contradictory: Skogstad et al. (1987) and Jürgens & Šimek (2000) were not successful in cultivating members of this species complex on bacteria alone, whereas Taylor (1978) reared *H. grandinella* in batch cultures exclusively on a purely bacterial culture of *Aerobacter aerogenes*. Our analyses of food vacuole content of *Halteria* from both reservoirs (Table 1) indicate a rather limited importance of algae in the diet of natural populations of the ciliates. Small algae (2 to 5  $\mu\text{m}$ ) were usually observed at low abundances and not more than 9% of pelagic *Halteria* individuals were found with ingested algae (2 to 4  $\mu\text{m}$  large cells). Thus, our data suggest that picoplankton was the major source of organic carbon for the ciliate in our systems.

For instance, multiplying the mean cell volumes of bacteria by the grazing rates of *Halteria* on bacteria in the Římov (0.062  $\mu\text{m}^3$ , 1782 cells ind.<sup>-1</sup> h<sup>-1</sup>) and Sau reservoirs (0.105  $\mu\text{m}^3$ , 3220 cells ind.<sup>-1</sup> h<sup>-1</sup>) yields a total of 111 and 338  $\mu\text{m}^3$  of bacterial volume biomass ingested hourly, respectively. In comparison, even in the rare case of a ciliate cell with 4 ingested algae with a maximum diameter of 4  $\mu\text{m}$ , this would yield only about 100  $\mu\text{m}^3$  of algal volume biomass ingested. Fur-

ther, experimental data showed (Dolan & Šimek 1997, Jürgens & Šimek 2000) that for the full digestion of algal cells, involving also the complete disappearance of their chlorophyll autofluorescence, oligotrichs need at least 2 to 3 h. Hence, the algae distinguished according to their autofluorescence within ciliate food vacuoles represent algivory over 2 to 3 h prior to fixing the ciliates. Thus, among the food items distinguishable within ciliate food vacuoles, bacteria were quantitatively the most important food source.

This is also indicated by our estimates of *Halteria* growth rates, assuming exclusive picoplanktivory, i.e., 0.75 and 1.1 d<sup>-1</sup> for the Římov and Sau reservoirs, respectively (Table 1). To compare the latter estimates with those independently derived from changes in the ciliate abundance with time, we summarized available published and unpublished data on the maximum net growth rate of the ciliate determined in predator-removal experiments with water samples pre-screened through meshes of different sizes (for details see Table 2). Our estimates, derived from 20 µm treatments incubated in the Římov Reservoir in dialysis bags during 1997 (see Šimek et al. 1999), matched quite well those listed in Table 1. It provided additional support to our finding that picoplanktivory significantly contributed to the diet of the ciliate. The highest growth rate estimates of *Halteria* (Table 2) were reported by Jürgens et al. (1999) from a hypertrophic Danish lake during a bloom of pico- and nanoalgae (including *Chlorella* spp.), suggesting that phytoplankton can be an important food resource for *Halteria* in some lakes. On the other hand, almost the same maximum net growth rate (1.73 d<sup>-1</sup>) was also found when *Halteria* sp., reported as *H. grandinella*, was reared on a pure bacterial culture (Taylor 1978). Legner (1975) reported a maximum growth rate as high as 3.1 d<sup>-1</sup> for *H. grandinella* growing in organically enriched sam-

ples from 2 reservoirs. Hence, the above references and Table 2 clearly document an apparent food flexibility of the small halteriids and their high growth potential under food-satiated conditions. Other potential food items, falling into the size range of particles ingested by the omnivorous halteriids (Jürgens & Šimek 2000) are HNF and small detritus particles. They represent potentially important carbon sources, but we cannot distinguish them within ciliate food vacuoles.

To document also the numerical importance of small halteriids, mostly reported as *Halteria grandinella* in different lakes and reservoirs, we collected the available published and unpublished data (Table 3). *Halteria* has been found worldwide across the trophic spectrum of lakes (see also Table 4.1 in Laybourn-Parry 1992). This suggests that *Halteria* might be an important bacterivore in a broad variety of temperate aquatic systems (Stabell 1996, Figs. 2 to 4), becoming more dominant in eutrophic lakes. It is reported in abundances ranging from <1 to 389 ind. ml<sup>-1</sup> along the trophic gradient from oligo- to hypertrophy. *Halteria* has uptake and clearance rates on bacteria (Table 1) about 2 orders of magnitude higher than the typical *in situ* uptake rates of freshwater HNF, ~10 to 25 bacteria ind.<sup>-1</sup> h<sup>-1</sup> (e.g., Sanders et al. 1989, Vaqué et al. 1994, Šimek et al. 1997). Since abundances of *Halteria* and small oligotrichs increase towards eutrophic and hypertrophic systems (cf. Figs. 2 & 3, Table 3; Nakano et al. 1998, Jürgens et al. 1999), it is not surprising that total ciliate bacterivory becomes as important as HNF bacterivory (Fig. 4). Regarding the role of ciliates as bacterivores, 2 important points should be stressed:

(1) While a general trend towards an increasing role of bacterivorous ciliates with increasing trophic status was suggested by Beaver & Crisman (1989), HNF have been ascribed the role as the most important bacteri-

Table 2. Literature and unpublished data on *in situ* measured maximum net growth rate of *Halteria* in predator-removal experiments. Numbers of ciliate individuals represent a range of values between the initiation and end of the experiment

Lake/reservoir	Country	Trophic status	No. ml <sup>-1</sup>	Max. net growth rate (d <sup>-1</sup> )	Source/experimental treatment
Lake Søbygård	Denmark	Hypertrophic shallow lake	<10–380	1.64–1.90	Jürgens et al. (1999)/ 10 and 50 µm screened samples
Rixdorfer Teich	Germany	Eutrophic pond	0.1–21	1.30–1.38	Langenheder & Jürgens (unpubl.)
Hasselburger Teich	Germany	Eutrophic pond	0.5–19	0.82–1.20	Langenheder & Jürgens (unpubl.)/ 200 µm screened samples
Heiligensee	Germany	Eutrophic	<1–10	1.25–1.40	Skibbe (1998) 60 µm screened samples
Římov Reservoir, 1993	Czech Republic	Meso-eutrophic	1–10	0.8	Macek et al. (1996)/ 100 µm screened samples
Římov Reservoir, 1997	Czech Republic	Meso-eutrophic	2–14	0.75–1.05	Šimek et al. (1999) <sup>a</sup> 20 µm screened samples

<sup>a</sup>Values that were not collected from the original papers

Table 3. Literature values of densities of *Halteria*, mostly reported as *H. grandinella*, in waters of different trophic status, including unpublished data from several studies

Lake/reservoir/pond	Country	Trophic status	No. ml <sup>-1</sup>	Source
Furuike Pond	Japan	Hypertrophic	25–389	Nakano et al. (1998) <sup>a</sup>
Lake Stigsholm	Denmark	Hypertrophic	15–104	Jürgens & Jeppesen (1998) <sup>a</sup>
Lake Søbygård	Denmark	Hypertrophic	3–99	Jürgens et al. (1999)
Pries Pot	UK	Hypertrophic	10–61	Finlay et al. (1988)
Pries Pot	UK	Hypertrophic	1–9	Berninger et al. (1993) <sup>a</sup>
Lake Heiligensee	Germany	Hypertrophic	<1–10	Skibbe (1998)
Poppelsdorfer Weihers Pond	Germany	Eutrophic	10–289	Wilbert (1969)
Two ponds	Canada, Ontario	Eutrophic	~100	Archbold (1983) <sup>a</sup>
Stagno di Favale Pond	Italy	Eutrophic	1–40	Madoni (1991)
Sau Reservoir, lacustrine part, 1997	Spain	Eutrophic	7–105	This study
Sau Reservoir, lacustrine part, 1998	Spain	Eutrophic	4–58	Comerma (unpubl. data)
Lake Oglethorpe	USA	Eutrophic	0–5	Sanders et al. (1989) <sup>a</sup>
Lake Erie, coastal sites	USA	Eutrophic	2–30	Hwang & Heath (1997b)
Řimov Reservoir, 1993	Czech Republic	Meso-eutrophic	1–10	Šimek et al. (1995)
Řimov Reservoir, 1997	Czech Republic	Meso-eutrophic	2–14	Šimek et al. (1999) <sup>a</sup>
Řimov Reservoir, 1997	Czech Republic	Meso-eutrophic	1–55	This study
Řimov Reservoir, 1999	Czech Republic	Meso-eutrophic	1–63	Jezbera & Šimek (unpubl. data)
Neusiedler See	Austria	Mesotrophic	0–7	Schönberger (1994)
Ruster Poschen Pond	Austria	Mesotrophic	1–27	Schönberger (1994)
Lake Erie, offshore sites	USA	Meso-oligotrophic	1–6	Hwang & Heath (1997b)
Traunsee	Austria	Oligotrophic	0–2.2	Sonntag (unpubl. data)
Loch Ness	UK	Oligotrophic	0.1–0.2	Laybourn-Parry et al. (1994)

<sup>a</sup>Values that were not collected from the original papers

vores (e.g., Fenchel 1982, Sanders et al. 1989, Berninger et al. 1991), independent of the trophic state of aquatic systems. The presumed importance of HNF is mainly due their ability to exploit and grow on low *in situ* bacterial abundances (see also Jürgens 1992). However, this argument does not apply to systems characterized by relatively high bacterial concentrations. Thus, while we still have little information about ciliate bacterivory in eutrophic and hypertrophic lakes, data from the Sau Reservoir (Figs. 3 & 4; Comerma et al. in press) and a hypertrophic pond in Japan (Nakano et al. 1998) indicate that ciliate bacterivory can exceed that of HNF.

(2) Restricted sets of ciliate types are important pelagic bacterivores. When reviewing data on ciliate bacterivory, there is a close concordance between our results (Fig. 4) and literature data, which enables a certain level of generalization. Based on a set of 100 taxonomic analyses of ciliate bacterivory in 21 systems, i.e., 17 Norwegian lakes of different trophic status (only once sampled, Stabell 1996), 4 samples from coastal and 4 samples from offshore sites of Lake Erie (Hwang & Heath 1997a), 1 seasonal study on Lake Oglethorpe (Sanders et al. 1989), and 2 seasonally studied reservoirs (52 and 22 samples from the Řimov and Sau reservoirs, respectively), we can conclude that only 3 groups are important pelagic ciliate bacterivores.

These groups with the typical representative genera, in order of their overall decreasing importance as bacterivores, are: (1) small oligotrichs (*Halteria*, *Pelagohalteria*, *Strobilidium*, *Strombidium*) (2) peritrichs (*Vorticella*, *Epistylis*, *Carchesium*), and (3) scuticociliates (*Cyclidium* and less frequently *Uronema* spp.).

Beaver & Crisman (1989) reviewed an extensive data set characterizing ciliate dynamics in subtropical Florida lakes and suggested that there was an increasing role of scuticociliate bacterivory with increasing trophic status. The situation might be different in temperate lakes. In none of 17 Norwegian lakes (Stabell 1996), nor in the reservoir data presented here (Figs. 2 to 4), did mean values of scuticociliate grazing exceed 17%; they were usually below 10% of total ciliate bacterivory. Two exceptions to this pattern, where bacterivory of *Cyclidium* spp. clearly dominated, were reported from rather extreme ecosystems, a hypertrophic Japanese lake (Nakano et al. 1998) and a naturally acidic, mesotrophic lake in Germany (Šimek et al. 1998b). Another deviation from the prevalence of bacterivory by oligotrichs has been documented when peritrichs, attached to colonies of cyanophytes (Stabell 1996), large diatoms (Carrias et al. 1996), or to carapaces of large crustacean zooplankton (Kankaala & Eloranta 1987), are abundant. The vulnerability of the attached peritrichs to metazoan predation is probably

strongly reduced, compared to small free-living ciliates. Thus, high abundance of metazooplankton can result in dominance of bacterivory by peritrichous ciliates.

It is somewhat unclear whether the jumping response of *Halteria* sp., reported as *H. grandinella* (e.g., Tamar 1979, Gilbert 1994), is an effective escape behavior in response to all metazoan predators. Results of recent laboratory (e.g., Gilbert 1994, Jack & Gilbert 1997) and field studies (Havens & Beaver 1997, Jürgens et al. 1999) imply that the jumping response of *Halteria* is probably an effective escape reaction against predation by rotifers but not so much against *Daphnia* spp. or *Cyclops* spp. (Gilbert 1994, Jack & Gilbert 1997, Jürgens et al. 1999). Zooplankton communities in both reservoirs were only briefly dominated by *Daphnia* spp. (Šimek et al. 1990), or possibly by *Cyclops* spp. Thus, the escape response and the high growth rate of *Halteria* (e.g., Legner 1975, Taylor 1978, Jürgens et al. 1999; Table 2) can explain why the ciliate communities dominated by *H. cf. grandinella* co-existed with abundant rotifer populations for most of the time in these systems (Šimek et al. 1995, Armentgol et al. 1999).

We suggest that there are 4 important reasons behind the exceptional position of *Halteria*, most frequently identified as *H. grandinella*, in planktonic food webs: (1) high uptake and clearance rates on picoplankton-sized particles, (2) omnivory with an efficient uptake of a large prey size spectrum (~0.4 to 5 µm) which covers autotrophic and heterotrophic pico- and nanoplankton and detritus (Jürgens & Šimek 2000), (3) very high growth rate and abundances *in situ* (Tables 2 & 3), and (4) lower vulnerability as prey for metazooplankton than other common ciliate species. Concerning the former 2 points, *Halteria* showed both the highest uptake and clearance rates on auto- or heterotrophic picoplankton among all *in situ* studied oligotrichs (Šimek et al. 1996, Stabell 1996; Table 1). Another ecologically important aspect is the very high volume-specific clearance rates of this species measured on bacterial prey, from 0.5 (Stabell 1996) to  $1.6 \times 10^5$  cell volumes  $\text{h}^{-1}$  (Šimek et al. 1995). They indicate the ability of *Halteria* to compete efficiently for the picoplankton food resources with some typical bacterivorous HNF (cf. Fenchel 1986).

We conclude that most of the pelagic ciliates that are efficient bacterial grazers are not bacterivorous in the strict sense, since autotrophic picoplankton and small algae also significantly contribute to their diet (Skogstad et al. 1987, Šimek et al. 1996, Jürgens & Šimek 2000; Table 1). Thus, we suggest revising the concept of pelagic ciliate bacterivory suggested by Fenchel (1980), since recent data have shown that not specialized bacterivorous ciliates, but small, omnivorous oligotrichs are the major ciliate bacterivores in meso- and

eutrophic waters (Šimek et al. 1995, 1996, Stabell 1996, Hwang & Heath 1997a, Thouvenot et al. 1999; Figs. 1 to 4). Thus, corresponding to the latter, the term 'bacterivorous ciliates' should be used rather for the ciliates that have bacteria not necessarily as an exclusive, but as a major food source. *Halteria* seems to be the most important taxon within that ecological group which frequently dominates in meso- and eutrophic plankton. Given its strong grazing impact on a wide prey spectrum within the pico- and nanoplankton including small HNF, *Halteria* might occupy a specific structuring role for the microbial food web in meso- to eutrophic systems.

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