CHAPTER 3

"Planktonic food web structure along the Sau Reservoir (Spain) in summer 1997"

ABSTRACT

We studied the planktonic food web in eutrophic Sau Reservoir (Catalonia, NE Spain). Along the longitudinal axis from the River Ter downstream to the dam, we characterized a microbial succession of food web dominance of bacteria-HNF-ciliates. The River Ter transports a large load of organic material into the reservoir, with a bacterial density of ~$9 \cdot 10^6$ large cells per ml. While at the first lacustrine station of the Reservoir, HNF were the dominant bacterial consumers, at the others, an oligotrich ciliate, *Halteria grandinella,* was the main protozoan bacterivore. Most of the bacterial production in the reservoir epilimnion was consumed by grazing. The spatial succession of the reservoir microbial food webs was followed downstream by maximum densities of their potential predators among zooplankters – rotifers, and early developmental stages of copepods.

INTRODUCTION

The microbial food web was initially described in oligotrophic ecosystems as a source or a sink for carbon which potentially mediated energy flow to higher trophic levels (POMEROY, 1974). The pelagic microbial loop consists of bacteria, phagotrophic flagellates, ciliates, and other protists and is primarily fuelled by organic carbon released from phytoplankton exudates (AZAM et al., 1983). Bacteria make efficient use of the dissolved organic matter (e.g. excretions from pelagic organisms), before being consumed by heterotrophic protozoans. The heterotrophic protozoans (mostly flagellates) are consumed by metazoan zooplankton, thereby channelling the energy from the microbial loop into the "classic" food chain (LAMPERT and SOMMER, 1997). A high biomass of picoplankton, especially that of bacteria, can sequester a marked proportion of nutrients (N, P) and limit the overall efficiency and production of a system. The principal role of microbial consumers, namely of phagotrophic protozoa, is the liberation of the nutrients bound in the picoplankton biomass (CARON and GOLDMAN, 1990), thus mediating their availability to primary producers. In eutrophic systems the "new" production levels are high due to large allochthonous nutrient inputs (WEISSE and STOCKNER, 1993). Under such circumstances, the significance of microbial food webs is even so important in eutrophic and hypereutrophic lakes, as to frequently contribute >50% to the annual carbon production and nutrient cycling (WEISSE and STOCKNER, 1993).

Several studies exist on microbial food webs in lakes (e.g. BERMAN, 1990; RIEMANN and CHRISTOFFERSEN, 1993) and in the sea (e.g. AZAM et al., 1983). However, these communities are starting to be considered in reservoirs, which have substantial limnological differences from lakes (STRAŠKRABA, 1998). Reservoirs have horizontal gradients of environmental variables (temperature, oxygen, and nutrients), controlled by water circulation (KENNEDY and WALKER,

1990). In our belief, these specific features also result in the distinctive spatial distribution of the plankton community, determining its structure and processes. To date some specific aspects of the longitudinal succession of zoo- and phytoplankton communities have been reported (URABE, 1989; PINEL-ALLOUL, 1995). However, to our knowledge, only limited data are available on longitudinal changes in microbial food web in relation to other biological and chemical variables.

Based on our preliminary research in an eutrophic reservoir (ŠIMEK et al., 1998; ARMENGOL et al., 1999) we hypothesised that depending on the amount and the ratio of biologically-degradable organic carbon to biologically available nutrients in the river inflow, different longitudinal succession patterns will occur (ŠIMEK et al., 1998; ŠIMEK et al., 2000). Bacteria, protists, phytoplankton and zooplankton could take part in the processes of organic matter and nutrient transformations. Thus, downstream parts of reservoirs behave more as lake ecosystems (with less pronounced gradients in microbial food webs) while the upper, inflow parts are likely to show much more pronounced gradients in microbial food web dynamics. This could be particularly evident in canyon-shaped reservoirs. The Sau Reservoir represents a system with a rather extreme organic matter load in its inflow part (VIDAL and OM, 1993).

The goal of this study was to estimate the range of microbial activities along the trophic gradient in a eutrophic reservoir from the river to the dam. Special attention was given to comparing levels of bacterial production and mortality induced by protistan grazing. The role of ciliate bacterivory is known to increase along the trophic gradient from oligo- to eutrophy (BEAVER and CRISMAN, 1989; ŠIMEK et al., 1998). The dominant groups of bacterivores from among the ciliate taxa were determined at different sites in this highly heterogeneous reservoir. Since the specific features of the studied reservoir, i.e. the high input of allochthonous organic matter and microbial food webs functioning in the detritus-rich environment, might also affect zooplankton development (URABE, 1989; LAMPERT, 1997), we also considered changes in the zooplankton composition along the longitudinal axis of the reservoir.

SAMPLING AND METHODOLOGICAL REMARKS

In July, the reservoir is well stratified and the river is colder than surface layers of the reservoir (i.e. 0-5 m). This explains why the interflow circulation occurs below the mixing depth of the epilimnion. During the sampling interval (15th to 17th July 1997), water inflow was low (8.8-15.7 $m^3 sec^{-1}$, compared with a yearly average of 18 $m^3 sec^{-1}$; VIDAL and OM, 1993). Consequently, the plunge point was close to the river entrance (i.e. between stations 9 and 8).

The contribution of the river Ter water and dissolved salts to the epilimnion occurs at the plunge point (see Chapter 1). As calculated by ARMENGOL *et al.* (1999), around 14 % of dissolved salts transported by the river in July 1997 were injected into the epilimnion at station 8, thus, salinity could contribute to establishing the trophic gradient in the reservoir.

RESULTS

Development of physical and chemical parameters
## and chlorophyll *a*

The water in the river inflow was highly turbid, resulting in very low water transparency as indicated by the Secchi depth (Fig. 3.1a-b). This indicates that light was likely a limiting factor for phytoplankton development at stations 8 and 9 although they are clearly nutrient-unlimited (Fig. 3.1c). Along with a sharp decrease in particulate material (PM) and turbidity, the maximum values of chlorophyll *a* were observed at stations 7 and 6 (Fig. 3.1b). The stations downstream (5 to 1) showed a decline in chlorophyll *a* concentrations.

In the upper half of the reservoir, heterotrophic processes

predominated as shown by the level of oxygen saturation (Fig. 3.1a). The oxygen saturation percentage in the river was very low but increased downstream as autotrophic activity increased, as shown by increased chlorophyll *a* concentrations.

Figure 3.1
Development in the main physical and chemical para-meters at the nine stations from the Sau Reservoir dam to the river. The x axis comprises two scales: the numbers of the stations and the distance from the dam in kilometres. **a**) Percent of oxy-gen saturation and Secchi depth; **b)** particulated mate-rials (PM), Chlorophyll *a* concentration, and nephelo-metric turbidity; **c)** soluble reactive phosphorous (SRP) and ammonium concentra-tions.
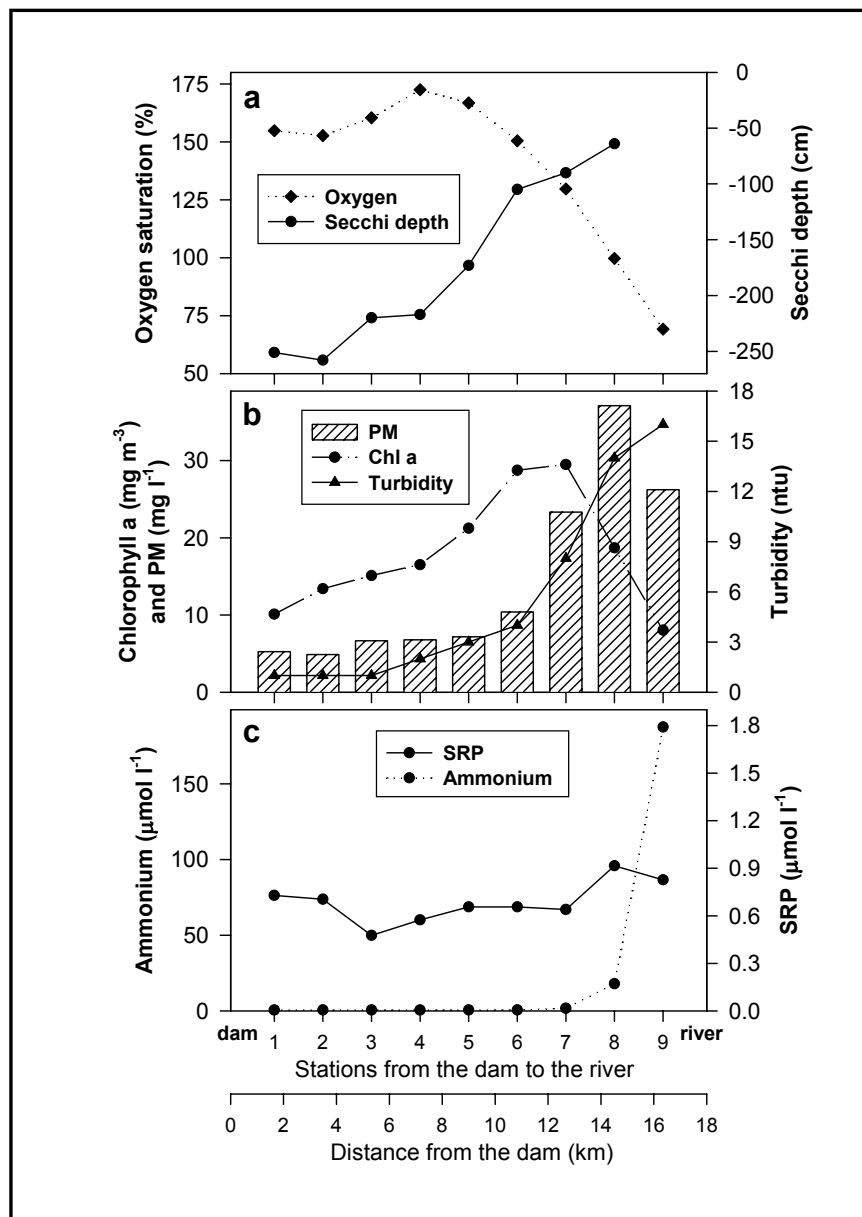
Longitudinal trophic succession

Bacterial density was highest at station 9 ($9 \cdot 10^6$ cells ml^{-1}) and much lower at the downstream stations (within a range of $3\text{-}5 \cdot 10^6$ cells ml^{-1}, Fig. 3.2a), with the minimum being recorded at station 1 (close to the
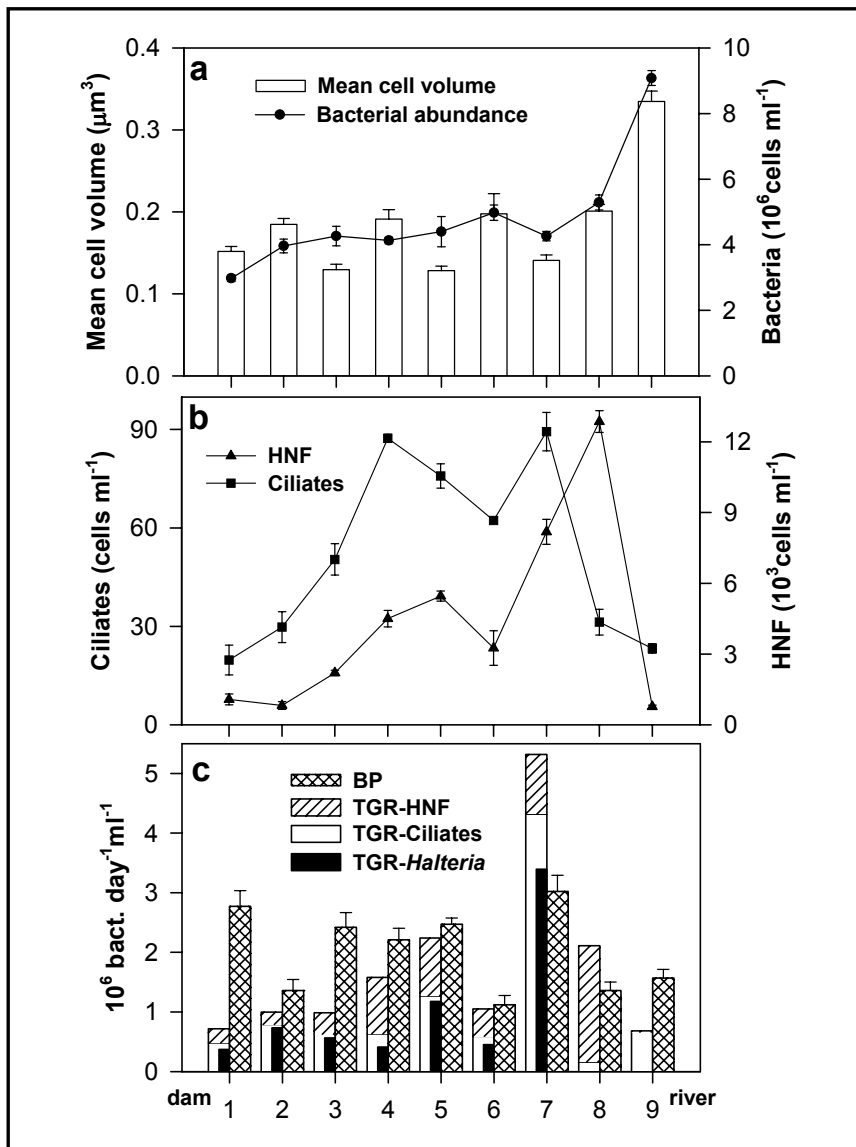

Figure 3.2
Longitudinal pattern along the Sau reservoir of: **a)** Mean bacterial abundance (±se, n=3) and mean cell volume (+1se, n=400); **b)** mean abun-dances (±se, n=3) of hetero-trophic nanoflagellates (HNF) and ciliates (CIL); **c)** mean bacterial production (BP, +1se, n=5) and total grazing rates of HNF (TGR-HNF), ciliates (TGR-CIL), and *Halteria grandinella* only (TGR-*Halteria*).

dam). Together with the marked changes in bacterial abundance, we also observed considerable differences in bacterial mean cell volumes and carbon content per bacterial cell in the river, which were twice as high as those of the rest of the reservoir (Fig. 3.2a).

Maximum abundances of bacteria, HNF, and ciliates showed a marked longitudinal succession along the course of the reservoir (Fig. 3.2a-b). HNF abundance peaked at station 8 ($12.4 \cdot 10^3$ cells ml^{-1}), ciliate abundances showed two conspicuous maxima, at station 7 (dominated by *Halteria grandinella*), and station 4 (86 cells ml^{-1}), dominated by *Coleps*. A successional pattern of bacteria-HNF- ciliates was also apparent though not so markedly, in the stagnant parts of the reservoir (stations 6-4).

The percentage abundances of the main groups of ciliates are shown in Fig. 3.3a. The most abundant groups were oligotrichs, mainly of the genus *Halteria*, scuticociliates (dominated by the genus *Cyclidium*) and prostomatids, basically from the genera *Coleps*. The genus *Vorticella*, *Acineria* and scuticociliates accounted for ~60% of total ciliates in the riverine stations (9 and 8), from which *Halteria* were largely absent. However, *H. grandinella* was clearly dominant at station 7 and from the station 4 downstream. The genus *Coleps* was only dominant in the intermediate stations 6, 5, and 4: 56%, 50%, and 33% respectively. The proportion of Prostomatids 2 increased at stations close to the reservoir dam.

In the riverine zone (stations 9 and 8), the genera *Vorticella* and *Acineria* as well as the Scuticociliates were the largest group of ciliate feeding on bacteria (Fig. 3.3b). In the rest of the reservoir the grazing rates of ciliates on bacteria were dominated by the oligotrichs, where *H. grandinella* was the most important bacterivore in the Sau Reservoir.

Bacterial production and protistan bacterivory

Maximum bacterial production occurred at station 7 ($3 \cdot 10^6$ bacteria

day^{-1} ml^{-1}; Fig. 3.2c). Although the bacterial production was also high at stations 1 and 5 to 3.
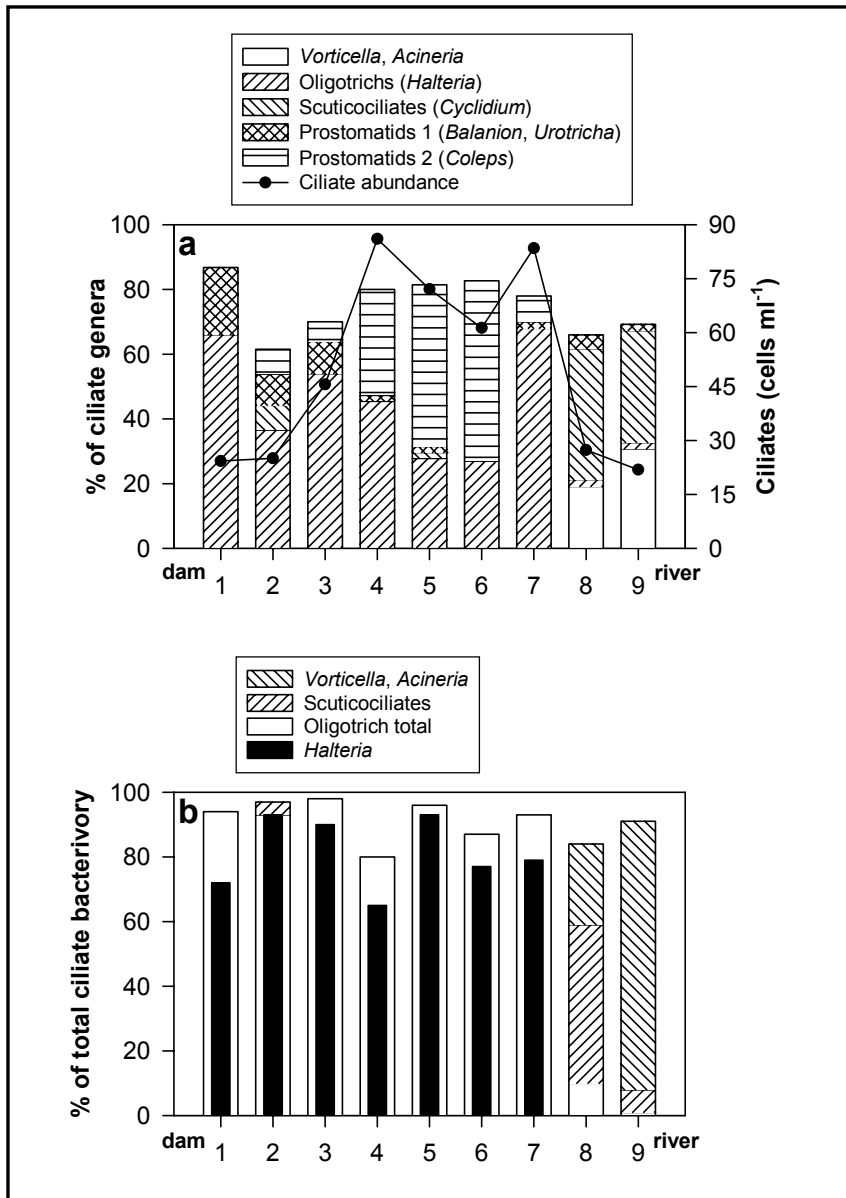

Figure 3.3
a) Composition of ciliate genera at each sampling station. **b)** The role of different ciliate groups as bacterivores.

Total protistan grazing was subdivided into HNF and ciliate bacterivory (Fig. 3.2c). The total grazing rate of ciliates (TGR-CIL) was higher than that of HNF (TGR-HNF) in all stations except those of 8 and 4, where the maximum density of bacterivorous HNF occurred. Ciliates

had the highest abundance and total grazing rate at station 7 ($4.32 \cdot 10^6$ bacteria day^{-1} ml^{-1}). Most of the TGR-CIL at stations 7 through to 1 was the result of the grazing activity of *H.grandinella* (TGR-*Halteria*, Fig. 3.2c).

On average, 76% of bacterial production was consumed by protists, with HNF and ciliate bacterivory accounting for 39% and 61% respectively of total protistan bacterivory. *H. grandinella* alone accounted for 75% of total ciliate grazing. Total protistan grazing was higher than bacterial production at stations 8 and 7, and roughly equal at stations 6 and 5. From station 4 downstream, bacterial production was higher than protist-induced bacterial mortality (Fig. 3.2c).

Zooplankton

Rotifera was the most abundant group of zooplankton in the reservoir (Fig. 3.4), achieving a maximum abundance between stations 7 and 5 ($9 \cdot 10^6$ ind. m^{-2} at the last one).

Figure 3.4
Abundances of the main groups of zooplankton at the sampling stations.
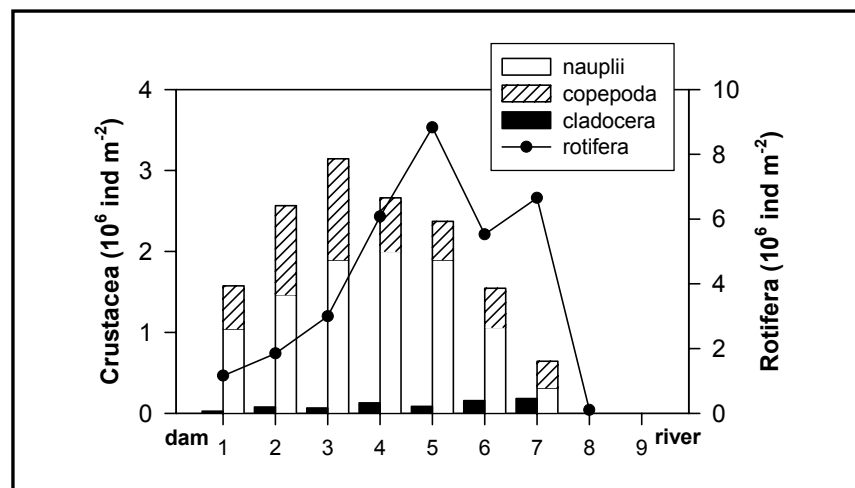
Cladocera were less abundant and they decreased from station 7 to the reservoir dam (station 1). Copepoda showed slightly shifted maxima

downstream, nauplii at station 4 and adults at station 3 ($1 \cdot 10^6$ ind. m^{-2}).

The percentage contribution of the most abundant groups of zooplankton at each station are described in Table 3.1. Some typical river species, as *Euclanis dilatata* and Bdelloidea, were dominant at the stations 8, near to the river. The most abundant genera of rotifera from station 1 to 7 were *Keratella*, *Polyarthra* and *Pompholyx*. Only two species of copepoda appeared in the reservoir, *Acanthocyclops vernalys* and *Cyclops abyssorum*, and they had high percentages from station 1 to 3.

% of ZOOPLANKTON COMPOSITION								
Sampling stations								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
ROTIFERA								
Bdelloidea	0	0	0	0	0	0	0	46
Brachionus angularis	0	0	0	1	1	3	13	3
Euchlanis dilatata	0	0	0	0	0	0	0	19
Hexarthra mira	6	6	0	3	1	1	3	1
Keratella cochlearis f. *tecta*	7	16	14	8	12	14	33	7
Keratella cochlearis	16	12	12	18	43	32	5	7
Polyarthra major	10	3	12	26	3	7	13	7
Pompholyx sulcata	2	3	9	11	19	13	17	2
CLADOCERA								
Daphnia galeata	1	1	0	0	0	0	0	0
Moina brachiata	0	1	1	1	1	1	0	0
Bosmina longirostris	0	0	0	1	0	1	1	1
Alona sp.	0	0	0	0	0	0	1	1
COPEPODA (*Acanthocyclops vernalis*+*Cyclops abyssorum*)								
adults+copepodites	19	24	20	7	4	6	4	0
nauplii	37	33	31	23	17	15	4	0
OTHERS	2	1	1	2	1	6	5	3

Table 3.1
Zooplankton composition at each sampling station. Percentage contribution calculated from densities of zooplankton (ind. m^{-2}).

DISCUSSION

The longitudinal pattern of physical and chemical parameters (Fig. 3.1) showed a clear gradient with notable changes in water quality towards from the river to the dam. Sau is supplied by a polluted river inflow that is rich in organic material; however, intensive self-purification processes result in significant changes in water quality (cf. Figs 3.1-3.4). These changes are most apparent in decreasing SRP concentrations, decreasing turbidity, number and biomass of bacteria, and vice versa in increasing water transparency downstream. The general factors operating in these processes can be compared to a sequential chemostat, such as waste-treatment lagoons that reduce the concentration of easily-degradable organic material from the inflow (ULHMANN, 1991).

One might argue that if we longitudinally sampled the reservoir stations within ~ 48 hours (i.e. within 3 consecutive days, 15-17 July), we might have taken the same packet of water more than once. However, we calculated that even for the river water masses it took 4-29 days to move between two consecutive lacustrine stations (station 7 downstream) of the reservoir. Moreover, the river water flowed through the reservoir metalimnion and had little effect on the epilimnetic layers that we sampled. Regarding the volume of the epilimnion and only a small portion of the river inflow mixed into the epilimnion (estimated round 14%), the move of the epilimnetic water masses was much slower than that of the metalimnetic river interflow. Thus, it seems safe to conclude that our downstream-consecutively taken samples did represent spatially different water masses.

Heterotrophic activity was high at the first two stations (reflected in low levels of oxygen saturation), while autotrophic activity increased from stations 7 and 6 (see Chl. *a* concentration, Fig. 3.1). Primary production in the middle zone of the reservoir was maintained at a high level

(GARCÍA, unpublished data) since the phytoplankton community receives a continuous supply of nutrients from the inflow water and from the sediment (COLE and HANNAN, 1990). In the case of Sau Reservoir, this difference between the inflow and the transition zone is magnified because light acts as a limiting factor on primary production at the first two stations because of the high levels of river water turbidity (Fig. 3.1b). The inflow part is highly turbit and receives the highest organic load and, thus, is functionally dominated by bacteria.

The results show a longitudinal trophic succession consisting of three sequential steps within the microbial food webs dominance of: bacteria, HNF, and ciliates (Fig. 3.2). Another example of such a typical longitudinal pattern (detected in April 1997) of the microbial parameters could be found in ŠIMEK *et al*. (1998) and in ŠIMEK *et al*. (2000).

About half the bacterial production of the river water (station 9) was consumed by ciliates, with scuticociliates and oligotrichs being the dominant bacterivores (cf. Fig. 3.3). At stations 8 and 7, however, protistan grazing rates were higher than bacterial production. Between these two stations the surface flow of the river water mass began to mix with the water masses of the reservoir. This implied that a part of large bacteria from the substrate-rich river were admixed into the reservoir epilimnetic bacterioplankton, i.e. into much more substrate-limited conditions. Moreover, the large bacterial cells at stations 7 and 8 (Fig. 3.2b) could be preferentially removed by the highly abundant HNF populations, known as size selective bacterivores (GONZALEZ *et al*., 1990; ŠIMEK and CHRZANOWSKI, 1992). Thus an interplay of the described substrate availability and size selective grazing likely resulted in a decreased proportion of river–carried large cells (having also lower surface/volume ratio) within bacterioplankton from station 8 downstream. Corres-pondingly, we observed a significant decrease in the mean cell volume of bacteria between stations 9 to 7. This partly contradicts our finding of a spatially limited increase in bacterial production at station 7 with no marked changes in bacterial abundance being recorded. However, this bacterial "regrowth" was probably mediated by the growth activity of other groups of bacteria, as indicated by a significant shift in bacterial community composition between stations 8 and 7 in a

preliminary study (ŠIMEK *et al*., 1998; ŠIMEK *et al*.,1999). The intensive protistan bacterivory might have increased substrate and nutrient availabilities locally (BLOEM *et al*., 1988; CARON and GOLDMAN, 1990), thus permitting the faster bacterial growth of the reservoir bacterioplankton found at station 7.

The station 6 point up from the upstream stations because there is a minimum protistan abundance, as well as bacterial production and grazing on bacteria but the bacterial abundance no change in comparison to the other stations. The large differences in microbial parameters between station 6 and the upstream stations could simply reflect the distinct character of the riverine versus lacustrine water masses (ARMENGOL *et al*., 1999) or could be a consequence from high grazing pressure on bacterial populations upstream.

Between stations 6 to 5 bacterial growth and loss rates were roughly equal, due to similar rates of HNF and ciliate bacterivory. From station 4 downstream, protistan numbers fell sharply and their grazing activity consumed only between 20-50% of bacterial production. This phenomenon was associated with a marked increase in the abundances of various groups of zooplankton. While ciliate dynamics do not seem to be influenced by rotifers (JÜRGENS *et al*., 1999), along with the first peak of rotifers and *Halteria*-dominated ciliate populations, we observed a dramatic drop in HNF abundance (cf. Figs 3.2b and 3.4). Both rotifers and *H. grandinella* are known to be efficient HNF consumers (DOLAN and GALLEGOS, 1991; ARNDT, 1993; JÜRGENS *et al*., 1996). From station 4 downstream, there was a clearly decreasing trend in ciliate and rotifer abundances in parallel with the maximum numbers of predatory copepods. This could be related to the fact that certain members of the latter group prey efficiently upon ciliates and rotifers (WICKHAM *et al*., 1993).

Cladocerans, which usually have a considerable impact on microbial food webs structures (e.g. PACE *et al*., 1990; JÜRGENS, 1994), were of minor importance in all parts of the reservoir. In our study, cladocerans did not appear in great numbers in contrast with copepods. In the absence of planktivorous fish as the case of Sau, copepods could limit the density of cladoceran populations (GLIWICZ and UMANA, 1994).

Protist-induced bacterial mortality was clearly the most important factor controlling bacterial production from the river inflow downstream to station 4. However, other loss factors in addition to protistan bacterivory which might have affected bacterial dynamics from station 4 downstream cannot be clearly deduced from our data.

The apparent differences in the balance between bacterial production and protozoan grazing are also potentially affected by the method used to estimate bacterial production. The largest inaccuracy in bacterial production estimates is usually associated with the factor used for converting thymidine incorporation into bacterial cell production (BELL, 1993; ŠIMEK et al., 1995). The differences between the bacterial production estimates derived from an empirical conversion factor (ECF) and from that of a theoretical conversion factor (TCF) can be considerable (BELL, 1993). In this study, we used TCF for all our estimates of bacterial production. On the other hand, the reservoir showed extreme longitudinal gradients for microbial parameters, together with significant shifts in bacterial community composition (ŠIMEK et al., 1998; ŠIMEK et al., 1999). Future studies need to establish ECF separately at least for the upper inflow part and for the downstream lacustrine parts of the reservoir.

In various freshwater lakes, it has been found that HNF are the main grazers of bacteria (BLOEM et al., 1989; SANDERS, 1990; WEISSE et al., 1990; CHRZANOWSKI and ŠIMEK, 1993). However, in other lakes ciliates have been temporarily identified as the main bacterivores (ŠIMEK et al., 1990 a and b; NAKANO, 1998). In our sampling of the Sau Reservoir, we found ciliates to be more significant bacterivores than HNF, except at stations 8 and 4, because of enhanced HNF numbers in these two sections of the reservoir. In line with data from marine systems (SHERR and SHERR, 1987), ciliates were found to be voracious consumers of bacteria in the Sau Reservoir, consuming 12-146% of bacterial production. Values of ciliate bacterivory were, on average, very high and highly variable along the longitudinal axis compared to bacterial production estimates. A similar range of ciliate bacterivory has also been documented in the meso-eutrophic Římov Reservoir (ŠIMEK and STRAŠKRABOVÁ, 1992; ŠIMEK et al., 1995; ŠIMEK et al., 1998) and in

a hypereutrophic pond (NAKANO, 1998). The main bacterivorous ciliates have been identified as small (<30 μm) oligotrichs (ŠIMEK *et al*., 1995; STABELL, 1996). Here, the oligotrich *Halteria grandinella* dominated the ciliate community and accounted for the highest total grazing rates on bacteria. The second maxima of ciliate abundance (station 4) was not reflected in high grazing rates (Figs. 3.2 and 3.3) because the ciliates were mostly composed of the genus *Coleps* which does not depend on bacterial food. *Coleps* is omnivorous, feeding on autotrophic organisms, protozoa, and sometimes even on small metazoans (FOISSNER and BERGER, 1996). This ciliate clearly followed the trophic gradient pattern because it occurred at those stations where phytoplankton and zooplankton were more abundant.

The spatial distribution of zooplankton composition also showed a marked trend from the inflow to the outflow. At the upstream stations, two typical groups appeared, inhabiting littoral and riverine conditions - *Euchlanis* and *Bdelloidea*. These groups are not adapted to life in the plankton but can survive in highly polluted areas (ARNDT, 1993). The rotifers that developed between stations 7 to 5 (Fig. 3.4), basically followed the spatial succession of the microbial food web show in Fig. 3.2. About 10-40% of rotifers' food is composed of heterotrophic organisms affiliated to the microbial food webs (ARNDT, 1993). Arndt (1993) also considers many bdelloids to be effective feeders on bacteria and these were abundant at the station with the second highest amount of bacteria. Arndt (1993) suggests that *Brachionus,* which was most abundant at stations 7 and 6, select for HNF having the highest numbers just at these stations. When HNF and protozoans are cropped by zooplankton, as our data suggest, they represent an important mechanism by which DOM, bacteria and ultrafine detritus enter plankton food chains (PORTER *et al*., 1979).

Copepods became more abundant than rotifers at the intermediate stations 5 to 2 (Fig. 3.4). The copepod distribution pattern along the reservoir axis reflected their development stages (naupli, copepodites and adults). Their abundances seemed to follow chlorophyll *a* maxima at stations 7 and 6, which might mean that phytoplankton is their main food source while rotifers primarily fed upon microorganisms.

In short, this study establishes how the different steps of the trophic chain, which were spatially segregated, contributed to water purification in the Sau Reservoir. The high allochthonous organic matter inputs formed the basis of a heterotrophic food web (bacteria-HNF-ciliates-rotifers) developed through the first half of the reservoir. Following the microbial food web, an autotrophic gradient (phytoplankton-copepods) started the autochthonous organic matter fluxes in the reservoir.

CHAPTER 4

"Seasonal changes in the epilimnetic microbial food web dynamics along a eutrophic reservoir"

ABSTRACT

In the eutrophic Sau Reservoir (Catalonia, NE Spain) microbial food web structure and activities varied on both spatial as well as on temporal scales. We have analysed 8 longitudinal transects (i. e. one for each sampling date), conducted between July 1996 and April 1999, covering a wide range of both seasonal and spatial water circulation patterns.

Enhanced abundances and activities of microbes were detected during the spring and summer periods. Applying a model of geometric distances, we analysed all samplings together from a longitudinal perspective (from the River Ter downstream to the dam). Along the longitudinal gradient, we characterized a downstream food-chain succession with spatial dominance of bacteria, heterotrophic nanoflagellates, ciliates, phytoplankton, and zooplankton. The river circulation pattern through the reservoir controlled this longitudinal gradient. The amplitude of microbial peaks was related to nutrient and organic carbon loads in the river inflow and the percentage of river water mixed to the epilimnion. Ciliates, not HNF, were the major consumers of the bacterial production and showed two conspicuous abundance maxima. From almost 1500 ciliates inspected, *Halteria grandinella* was the most abundant and the most significant bacterivore.

INTRODUCTION

Seasonal trends of protozooplankton have been described as a function of trophic status of lakes, lake thermal regimes and depth (BEAVER and CRISMAN, 1990; BENNETT *et al*., 1990; JAMES *et al*., 1995; LAYBOURN-PARRY, 1994; PACE, 1982). Several investigations of spatial distribution of ciliate populations have been conducted within the water column in lakes and reservoirs (BARK, 1985; GUHL *et al*., 1994; HADAS and BERMAN, 1998; JAMES *et al*., 1995; PACE, 1982). However, relatively little information is available on the factors controlling the distribution of ciliate taxa and HNF dynamics along the longitudinal axis in canyon-shaped reservoirs (ARMENGOL *et al*., 1999; ŠIMEK *et al*., 1999; ŠIMEK *et al*., 2000; COMERMA *et al*., 2001). These systems are well known for their longitudinal zonation (ARMENGOL *et al*., 1999; THORNTON *et al*., 1990), frequently covering a wide range of trophic states within the same water body. The larger the differences in biological and chemical parameters from river inflow to the lacustrine part of the reservoir, the more pronounced the longitudinal gradients of planktonic parameters.

The Sau Reservoir (NE Spain) represents a specific system characterized by: (I) high nutrient and organic inputs (ŠIMEK *et al*., 1998; COMERMA *et al*., 2001); (II) typical morphology (ARMENGOL *et al*., 1999; COMERMA *et al*., 2001; 18.5km long; 1.5km max. width) for a deep and narrow river valley reservoir; and (III) relatively high residence times (90 days, median from 1996 to 2000) allowing for efficient water self-purification processes. Thus, we expected to find a marked longitudinal pattern in limnological and biological parameters along the reservoir during any season of the year.

Aims were, (I) to compare the dynamics of microbial populations along the longitudinal axis of the reservoir (i. e. from the river to the dam area) and, at the same time, to analyse seasonal changes in these, (II) to determine major factors controlling microbial food web dynamics,n (III) to

compare the relative importance of heterotrophic nanoflagelates and ciliates in planktonic bacterivory, and specifically, to determine species-specific grazing rates of ciliates on bacteria. We analysed 8 samplings between July 1996 and April 1999 looking at data from two points of view, seasonally, and examining spatial heterogeneity using a geometric distances model.

METHODOLOGICAL REMARKS

Hydrological descriptors. Current inflow, volume of the reservoir and outflow were calculated from the averages of the sampling days and the day prior to sampling (Table 4.1). The Catalan Water Agency (ACA) provided the daily data. Previous inflow was estimated from the average of inflows 4 to 2 days before sampling began. The plunge point or the border between the riverine and the lacustrine zones of the reservoir was calculated as in ARMENGOL *et al*. (1999). After situating the plunge point, we calculated the differences between epilimnion and river water temperature. Percentages of river water mixed with the epilimnion were calculated from conductivity measurements, which is a conservative parameter (for details see Chapter 1). A combined multiparameter-approach using these hydrological descriptors, allows an approximate description of the major features of the river water circulation in the reservoir, above or below the thermocline.

Thymidine conversion factor. A two-way ANOVA was performed on the data considering space and circulation pattern (overflow, interflow and underflow, which are related to seasons, see details in ARMENGOL *et al*., 1999) as sources of variation on the empirical thymidine conversion factor (empirical TCF). No significant differences between empirical TCF in different circulation patterns ($F_{2,4}$ = 2.023, P<0.05) and zones of the reservoir ($F_{2,4}$ = 0.349, P<0.05) were found, neither any significant interaction between them ($F_{4,4}$ = 1.455, P<0.05). Therefore, the mean from all empirical TCF ($4.7 \cdot 10^{18}$ cells mol^{-1} thymidine incorporated, se = 0.98, n = 13) was used to estimate bacterial production.

Date	Current Inflow m³ s⁻¹	Previous Inflow m³ s⁻¹	Volume h m³	Outflow m³ s⁻¹	Plunge point km from the river	$T_{epil} - T_{river}$ °C	River water mixed % (Cond.)	River circulation in the water column through the reservoir
Jul-96	9.9	10.2	113	24.0	4.3	3.8	24	interflow
Apr-97	11.6	11.5	114	5.6	4.5	1.8	75	overflow
Jul-97	13.2	20.7	122	23.3	6.9	2.5	14	interflow
Oct-97	4.1	3.6	118	8.8	4.8	4.5	36	interflow
Dec-97	13.1	3.8	129	23.5	4.3	5.2	15	underflow
Feb-98	5.7	6.3	103	2.5	7.6	0.8	51	overflow
May-98	7.3	6.8	116	1.3	6.4	1.0	88	overflow
Apr-99	4.8	6.0	44	4.7	11.5	0.8	-	overflow

Table 4.1
Hydrological descriptors for each longitudinal transect (July 1996, April 1997, July 1997, October 1997, December 1997, February 1998, May 1998 and April 1999). Differences in temperature between the river inflow (T_{river}) and the epilimnion (T_{epil}) were calculated. Percentages of river water mixed with the epilimnion were calculated from conductivity (Cond.) measurements, details in Chapter 1.

Ciliate volume versus ingestion rate regressions. To establish the specific relationship between volume and ingestion rates for main groups of ciliates we used the model II regression method described in (SOKAL and ROHLF, 1995), because both variables are subject to error.

A geometric mean regression was calculated from individual ingestion rates (bacteria ingested cell⁻¹ h⁻¹) as dependent variable on individual volume (μm^3). We selected the most abundant genera of ciliates in the Sau Reservoir for this statistical analysis. The large abundance of *Halteria* through the year allowed us to compare its grazing activity in cold against warm months (Autumn-Winter, Oct-97, Dec-97 and Feb-98; and Spring-Summer, Jul-97 and May-98).

The slopes of regression lines were compared using a test which depends on the calculation of the t-value, as described in (FOWLER and COHEN, 1990). Two-tailed tests at p = 0.05 were accepted as significant.

Geometric distances. Geometric distances reflect where along the longitudinal axis of the reservoir peaks in studied variables occur. We used the following equation to obtain the geometric distances from the river for each plankton group (i.e. bacteria, HNF, ciliates, phytoplankton and zooplankton):

$$d_{G_{tv}} = \frac{\sum (v_i - v_{min.}) \cdot d_i}{\sum (v_i - v_{min.})}$$

Equation 4.1

where d_{Gtv} is the geometric distance for a longitudinal sampling t (Jul-96, Apr-97, Jul-97, Oct-97, Dec-97, Feb-98, May-98 or Apr-99) and a variable v (bacteria, HNF, ciliates and zooplankton abundances or Chlorophyll *a* concentrations), v_i is the value of this variable at station i, $v_{min.}$ is the minimum value adopted by this variable in this longitudinal transect, and d_i is the standardised distance from the river inflow to station i. Finally, mean d_{Gtv} value (±se), for all longitudinal transects were calculated for each variable.

Distances were standardised taking 0 as the position of the river inflow and 1 as the dam. This was because water level in the Sau Reservoir changed seasonally and correspondingly so did its total length.

RESULTS

Seasonal and spatial changes in protistan abundance, bacterial production and grazing

Protistan abundances and activities varied seasonally with high amplitudes. In the autumn-winter period of 1997 (Oct-97 and Dec-97, in Fig. 4 1) bacterial, HNF and ciliate abundances, bacterial production, and protozoan bacterivory were 0.5-1 orders of magnitude lower than in the winter-spring period of 1998 (Feb-98 and May-98, in Fig. 4. 2). Note the change in scales between Figures 4.1 and 4.2. High microbial abundances and activities were also found in Jul-96 (ARMENGOL *et al*., 1999), Apr-97 (ŠIMEK *et al*., 1999) and Jul-97 (COMERMA *et al*., 2001).

Total bacterial abundances in all longitudinal transects ranged between 2 and $16 \cdot 10^6$ cells ml^{-1}, and their mean cell volumes between 0.1 and 0.5 μm^3. Abundance and volume decreased from river to dam. Total HNF abundances generally ranged between 1 and $4 \cdot 10^3$ cells ml^{-1}, with exceptional high values (7-22 $\cdot 10^3$ cells ml^{-1}) at stations near to the river inflow, found in Jul-96, Apr-97, Jul-97 and May-98. Total ciliate abundances usually ranged between 50-200 cells ml^{-1} in lacustrine zone, although higher values were common in the intermediate stations (e.g.

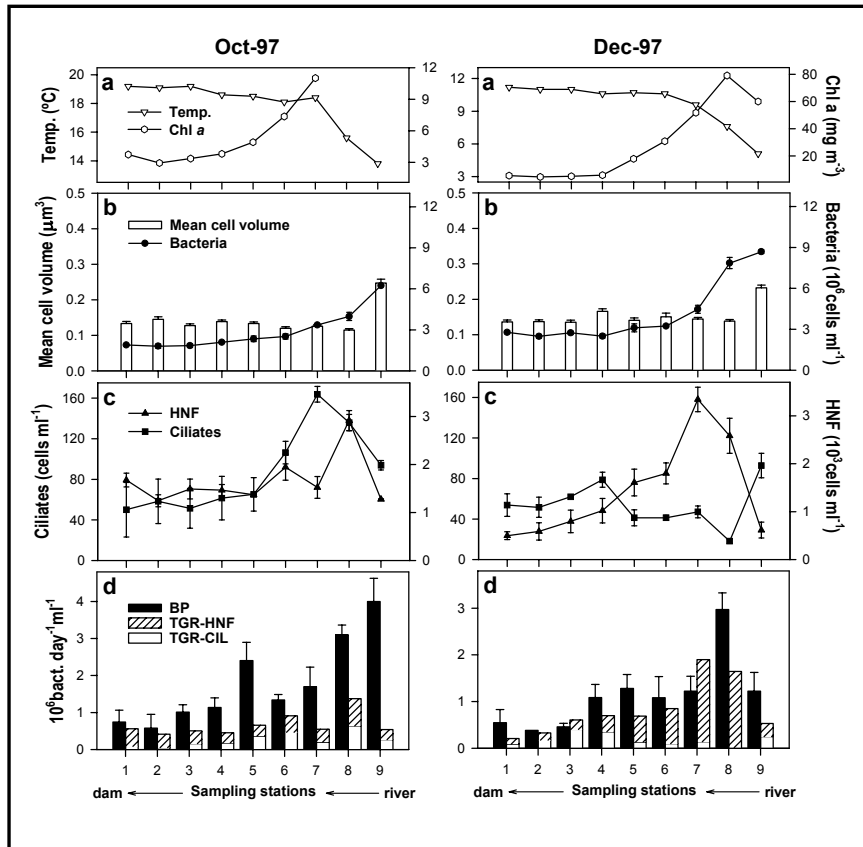almost 600 ciliates ml^{-1} at station 6 in Feb-98, Fig. 4.2).

Figure 4.1
Variables measured in longitudinal samplings from the river to the dam in October 1997 and December 1997.
**a)** Temperature (Temp.) and Chlorophyll *a* (Chl *a*) at the sampling stations; **b)** Mean bacterial abundance (±se, n=3) and mean cell volume (+se, n>400); **c)** mean abundances (±se, n=3) of heterotrophic nanoflagellates (HNF) and ciliates; **d)** mean bacterial production (BP, +se, n=5) and total grazing rates of HNF (TGR-HNF) and ciliates (TGR-CIL).

Bacterial production reached clear peaks at riverine stations, with high nutrient inputs (see e.g. COMERMA *et al.*, 2001). Correspondingly, at upstream stations we also found enhanced bacterivory of protists (see Figs. 4.1 and 4.2). Bacterial production measured at the eight samplings was recalculated using empirical TCF ($4.7 \cdot 10^{18}$ cells mol^{-1} thymidine incorporated). Bacterial activity was highly variable, ranging between 0.3 and $48.2 \cdot 10^{6}$ cells day^{-1} ml^{-1}. Highest values were found in Apr-97 and May-98 samplings.

Individual grazing rates of HNF and ciliates ranged between 1 and 68 bacteria HNF^{-1} h^{-1} and between 11 and 4763 bacteria $ciliate^{-1}$ h^{-1}, respectively, considering all measurements made. Marked fluctuations in HNF and ciliate total grazing rates were tightly related to the spatial

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distribution of these organisms (see Fig. 4.3).

Figure 4.2
As for Figure 4.1 but for February 1998 and May 1998 samplings.
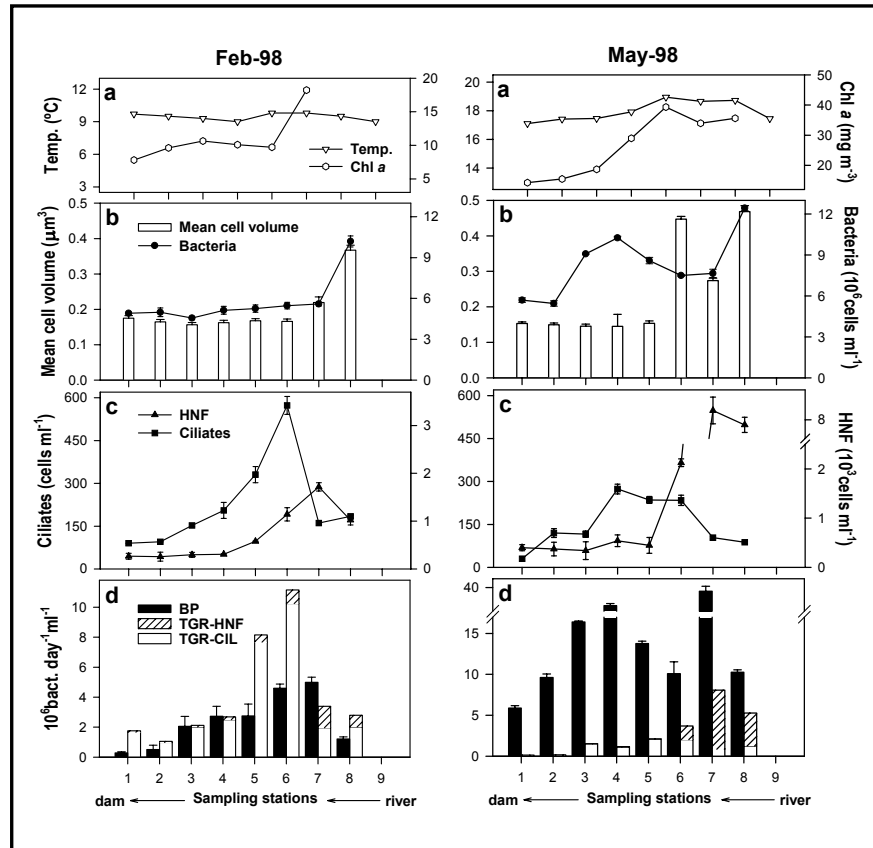
Maximum total grazing rates were found at stations near the river inflow (Figs 4.1 and 4.2), corresponding to the high HNF or ciliate abundances. Considering only the lacustrine stations, with no marked direct impact of the significant organic load brought in by the river inflow, ciliate grazing rates were higher than those of HNF, except for Oct-97.

Spatial food web succession versus hydrology

The microbial food web composition varied strongly at spatial as well as at temporal scales (Figs 4.1 and 4.2). In a previous study,

COMERMA *et al.* (2001) have described a spatial trophic succession (bacteria, HNF and ciliates) from river to dam in a summer sampling (Jul-97). However, essentially the same longitudinal pattern of the microbial parameters was also found in autumn, winter and spring, with only few deviations (cf. Figs 4.1 and 4.2). In Oct-97, the spatial trophic succession showed a clear pattern with maximum bacterial abundance at station 9, followed by a HNF maximum at station 8, and a ciliate maximum at station 7. In Dec-97 (Fig. 4.1), only HNF abundance followed the high bacterial density in the river. Ciliate abundance varied little along the reservoir and was lower than in all other samplings. The complete succession was observed in Feb-98 and May-98 (Fig. 4.2), although starting from station 8 due to low water levels in the reservoir. This implied that both stations 8 and 9 were typically riverine stations.

Figure 4.3 gives a summary of the microbial food web succession observed on a spatial scale, based on all longitudinal transects sampled in the Sau Reservoir from 1996 to 1999. To better describe the major steps in the longitudinal food web succession, we also implemented parameters characterising the succession of phytoplankton (as measured by Chlorophyll *a* concentration) and zooplankton. Mean abundance or concentration percentages from eight samplings showed a spatial succession from the river to the dam of bacteria, HNF, chlorophyll a, ciliates, and zooplankton. Calculated geometric distances from the river inflow (Fig. 4.3, below) for each plankton group showed the position of the maxima along the main axis of the reservoir. In all groups the maximum occurred relatively near to the river inflow (i. e. between 4 to 10 km from the river). However, distance from the river inflow also indicates the role of the development of a single food chain compartment in the reservoir.

Figure 4.3
Mean percentages at each
sampling station of bacterial,
HNF, ciliates and zooplankton
(Zoopl.) abundances, and
chlorophyll *a* (Chl *a*) concen-
trations from eight longitudinal
transects (Jul-96, Apr-97, Jul-
97, Oct-97, Dec-97, Feb-98,
May-98 and Apr-99). The sum
of the nine values through the
reservoir for each line is =
100%. Below, the mean
geometric distances (+se,
n=8) from the river inflow for
the same variables and
samplings.
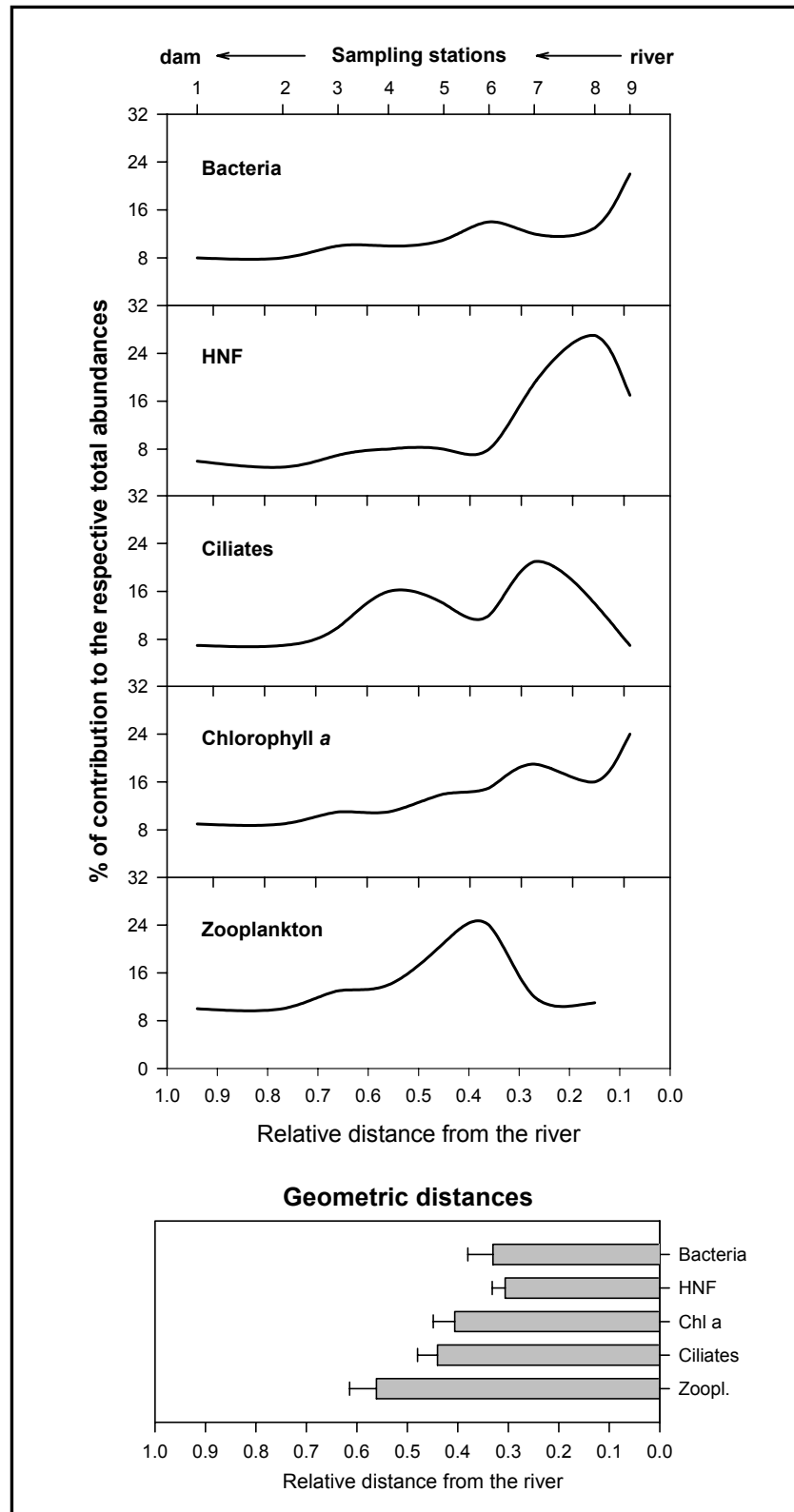
Hydrological conditions (Table 4.1) were determinant for nutrient loadings from the River Ter to the epilimnion of the reservoir, initiating marked longitudinal gradients through the reservoir. When the river temperature was notably lower than the epilimnion (e. g. Jul-96, Jul-97, Oct-97 and Dec-97), the river water mass plunged to the hypolimnion near to the river inflow by virtue to its higher density. The 30 % of river water were injected to the epilimnion. Finally, the proportion of river water that mixed with the epilimnion in cases when the river circulated below the epilimnion, depended on the river flow rate. We found on numerous occasions that a lower proportion of river water was injected to the epilimnion when the river water flow was high, except for Apr-97 (see Table 4.1). For the rest of samplings, with moderate to low river flow rates, the proportion of river water mixed with the epilimnion was very high (i. e. 50-90 %, the river flowed mostly in the epilimnion) because of similar temperatures of river and epilimnion, and it significantly contributed to the pronounced gradients and activities occurring in these samplings. Note that the maximum values of bacterial, HNF and ciliate abundances occurred in Apr-97 (ŠIMEK *et al.*, 1999) and May-98, with very high proportions of the river water mixing with the epilimnion.

Main genera of ciliates in the Sau Reservoir and their role

Seasonally, ciliate composition varied markedly (Fig. 4.4). Oligotrichs were present in the reservoir in all samplings. The genus *Halteria* was quite abundant, except in Dec-97. When *Halteria* sp. was present in the epilimnion, most ciliate bacterivory was attributed to its activity, owing to its very high bacterial consumption rates (see Table 4.2). Grazing of *Halteria* alone accounted for, on average, 39 % of total ciliate bacterivory.

Prostomatids were also highly abundant throughout the year, but were dominated by genera *Coleps* and *Urotricha*, which prefer to feed on phytoplankton. Thus, their role in aggregated ciliate bacterivory was negligible. Scuticociliates, mainly the genus *Cyclidium*, dominated the

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ciliate populations and were responsible for most bacterivory in Dec-97, when the water column was well mixed. Highest ciliate densities per unit water volume, however, occurred in Feb-98 (Fig. 4.2). The dominant ciliate was the Oligotrich *Rimostrombidium*. *Rimostrombidium* together with the Peritrich *Vorticella* were the main ciliate bacterivores in Feb-98 (Fig. 4.4).

Figure 4.4
a) Composition of ciliate groups at each sampling station in Jul-97, Oct-97, Dec-97, Feb-98 and May-98.
b) The role of these ciliate groups as bacterivores.
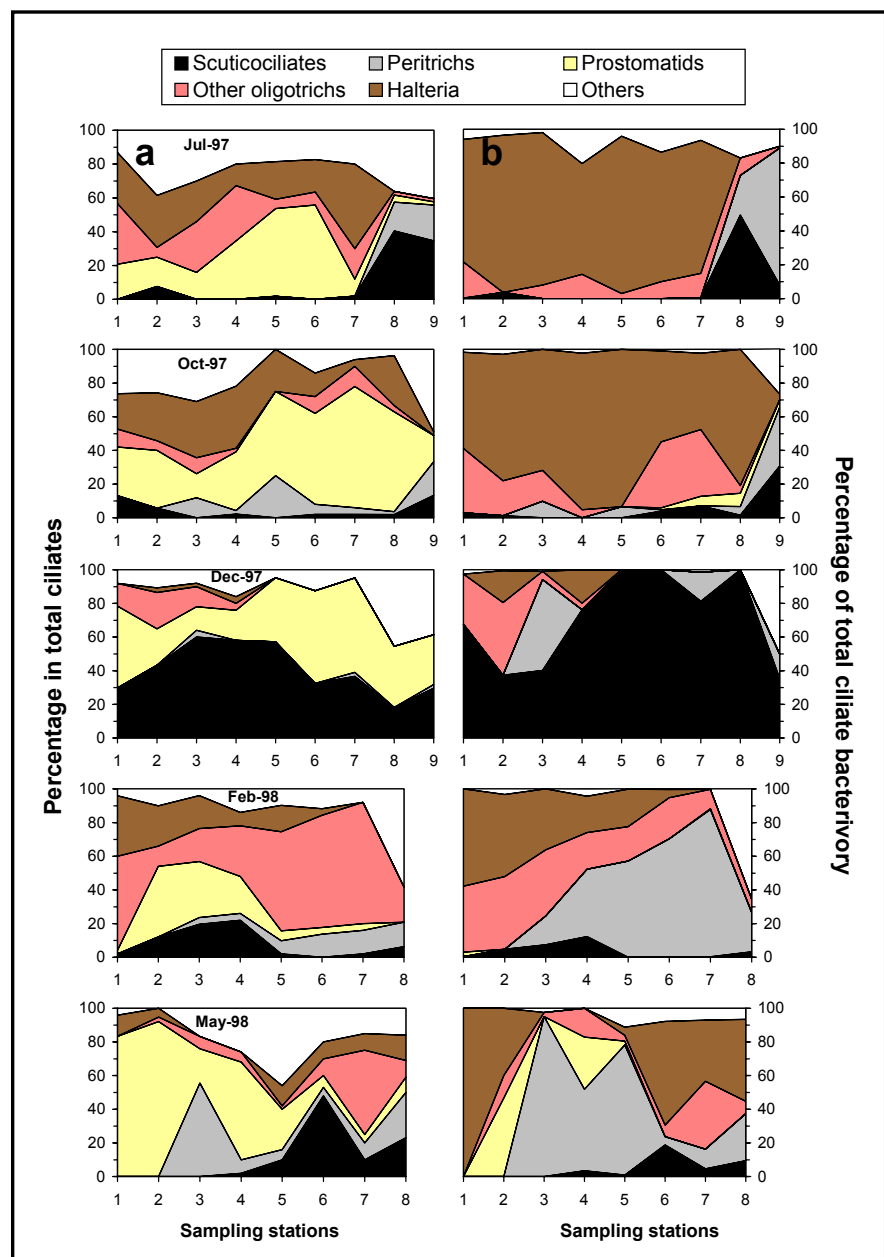
Epistylis was another Peritrich accounting for a large proportion of total ciliate bacterivory when present (stations 3 to 5 in May-98, cf. Fig. 4.4). We have observed in monthly zooplankton samples (collected in the monitoring of the Sau Reservoir from 1996-1999 period, using 53-μm mesh) an annual bloom of *Epystilis* after the clear water phase (around May).

Oligotrichs *Codonella* and *Tintinnidium* were conspicuous in the protozooplankton of the Sau Reservoir in Oct-98 and Dec-98, respectively, due to their large body volume, although abundance and bacterivory were not large in the ciliate community.

Group _Genera_	Grazing rate (bact. cell^{-1} h^{-1})			Clearance rate on bact. (nl cell^{-1} h^{-1})			Mean cell volume (μm^3)			Vol. specific clear. rate (10^4 h^{-1})
	Mean	SE	n	Mean	SE	n	Mean	SE	n	
Gymnostomatida										
Askenasia	46	22	17	8	4	17	27138	13807	17	0.03
Monodinium	98	98	3	16	16	3	2707	724	3	0.59
Hymenostomata										
Cyclidium	201	11	212	59	3	212	754	34	102	7.84
Oligotrichida										
Codonella	377	129	9	116	47	9	35420	6674	8	0.33
Halteria	1547	97	240	402	23	240	1765	64	227	22.75
Rimostrombidium	423	36	286	100	9	286	2765	105	166	3.63
Tintinnidium	0	-	5	0	-	5	51746	4497	3	-
Peritrichia										
Epistylis	972	95	37	108	11	37	16959	983	24	0.63
Vorticella	1891	355	92	314	51	92	29789	3693	67	1.06
Pleurostomatida										
Litonotus	170	50	22	18	5	22	2179	521	4	0.81
Prostomatida										
Balanion	52	48	21	12	10	21	2901	331	21	0.40
Coleps	28	7	173	14	1	173	9973	520	78	0.14
Urotricha	0	-	331	0	-	331	1011	85	126	-

Table 4.2
Mean individual grazing and clearance rates on bacteria (bact.), mean cell volume, and volume specific clearance rates (Vol. specific clear. rate) for the most abundant genera of ciliates in the Sau Reservoir from Jul-97, Oct-97, Dec-97, Feb-98 and May-98.

All together we have inspected grazing rates and cell volumes of 1448 individuals belonging to the main ciliate groups in the Sau Reservoir (Table 4.2). The highest grazing rates were observed in peritrichs, followed by oligotrichous ciliates and *Cyclidium*.

The genera *Halteria* and *Vorticella* differed markedly from other ciliate taxa in their higher clearance rates on bacteria. However, when

their volume specific clearance rates were calculated, *Halteria* was clearly the most voracious consumer of bacteria. *Cyclidium* occupied the second position in terms of its volume specific clearance rate due to its lower cell volume and its exclusive feeding on bacteria.

Table 4.3
Descriptors for geometric mean regression lines (volume Vs grazing rates) calculated for the 5 most abundant genera of ciliates in the Sau Reservoir. Comparisons are shown between every two regression lines. *Halteria* in spring and summer (Jul-97 and May-98; s-s) have been separately calculated from autumn and winter (Oct-97, Dec-97 and Feb-98; a-w).

GEOMETRIC MEAN REGRESSION

Genera	Slope	Y-intercept	SE of slope	95% confidence limits for slope	n
Vorticella	0.062	238.367	0.009	0.045-0.080	54
Rimostrombidium	0.456	-732.698	0.035	0.386-0.526	143
Cyclidium	0.464	-98.339	0.048	0.368-0.560	93
Halteria (a-w)	0.590	-570.190	0.050	0.491-0.690	114
Halteria (s-s)	2.656	-449.141	0.262	2.136-3.175	102

DIFFERENCE BETWEEN TWO REGRESSION LINES

Genera	*Vorticella*	*Rimostrom.*	*Cyclidium*	*Halteria (a-w)*
Halteria (s-s)	0.0001	0.0001	0.0001	0.0001
Halteria (a-w)	0.0001	0.05	n.s.	-
Cyclidium	0.0001	n.s.	-	-
Rimostrombidium	0.0001	-	-	-

These taxon-specific differences became more apparent when we calculated geometric mean regressions between volume and clearance rates (Table 3). All regression slopes were positive and significant ($p=0.05$), but they differed between taxa and in the case of *Halteria* between seasons. *Halteria* had the highest slope in spring-summer, and differed in a highly significant way ($p=0.0001$) from the rest of taxa and also from *Halteria* individuals in autumn-winter. *Cyclidium* and *Rimostrombidium* had similar slopes to those of *Halteria* in autumn-winter. In contrast, *Vorticella* had a very low slope, which differed in a highly significantly way from the rest of taxa.

DISCUSSION

The seasonality and spatial variation in abundance and activity of microbial epilimnetic populations of this reservoir was highly influenced by the river. The River Ter transports a large load of organic material into the Sau Reservoir (COMERMA *et al*., 2001) causing a remarkable longitudinal microbial succession throughout the year. It is well known that reservoir longitudinal gradients in physical, chemical, and biological factors result from the combined effects of hydrodynamics and basin morphology (KENNEDY and WALKER, 1990). Hydrological conditions in this very narrow-valley reservoir were the major forces controlling the nutrient inputs to the epilimnion (from percentages of river water mixed with the epilimnion) and, in consequence, also the rate of microbial community development. Hydrology is in turn influenced by the water thermal conditions which are related to weather or season. The general river circulation model in the Sau Reservoir is characterized by river underflow in winter, overflow-interflow in spring and interflow in summer-autumn (ARMENGOL *et al*., 1999). More direct effects on microbial development upstream in the reservoir can be deduced from hydrology than from season of the year. Note the high abundance of ciliates in the winter Feb-98 sampling, when underflow was expected and an overflow was caused by a flash flood.

The geometric distance model is a good tool for observing the spatial heterogeneity in abundances of groups from samplings with data of high variability. Results show a clear food chain succession (bacteria, HNF, ciliates, phytoplankton and zooplankton) from the river to the dam (Fig. 4.3), with the fast microbial development appearing fairly close to the riverine zone of the reservoir. Phytoplankton and zooplankton developed downstream at the transitional zone, peaks often associated with the plunge point (KIMMEL *et al*., 1990). All these biotic activities, together with the physical processes, mainly sedimentation and stratification, contributed to a decreasing trophic status downstream

towards the lacustrine zone, as one can deduce from values of the studied parameters (ŠIMEK *et al.*, 1998; ARMENGOL *et al.*, 1999; COMERMA *et al.*, 2001).

The abundance and composition of microbial planktonic populations (bacteria, HNF and ciliates, cf. Figs 4.1, 4.2 and 4.4) found in the Sau Reservoir were very similar to those reported from eutrophic lakes and reservoirs (BENNET *et al.*, 1990; RIEMANN and CHRISTOFFERSEN, 1993; ŠIMEK *et al.*, 1995). Ciliate abundance was related to lake trophic status, as measured by chlorophyll a concentrations (preponderantly 8-60 mg m^{-3}), just as BEAVER and CRISMAN (1989) described.

In particular, highest bacteria, HNF and ciliate abundances, and largest bacterial production and protozoan grazing rates, were measured in spring-summer near to the river inflow part of the reservoir. HNF and ciliate populations developed here, exploiting the river bacterioplankton food source, as one can deduce from the measured protistan grazing abundances and rates at stations close to the river inflow (cf. Figs 4.1 and 4.2). Corresponding with the peak of protist bacterivory, a significant compositional shift in bacterioplankton was found (ŠIMEK *et al.*, 1999; ŠIMEK *et al.*, 2001), with changes in the morphotypic and genotypic structures of their populations. Coupled with the decrease in mean cell volume (cf. Figs 4.1 and 4.2), use of fluorescently labelled RNA probes for the main groups of the class *Proteobacteria* showed a decrease downstream in the proportions of the subclass β-Proteobacteria and the group of Cytophaga/Flavobacterium. Selective grazing by protists could explain this significant shift in the size and community structures of bacteria, indicating in fact the existence of two different bacteriplankton populations – allochthonous and authocthonous ones.

If bacterial mortality was mainly due to protozoan grazing, then total protozoan bacterivory should, on average, balance the bacterial production as occured in the Sau Reservoir. On average, protozoa in the Sau Reservoir consumed 95 % of bacterial production. HNF and ciliates consumed 40 and 47 %, respectively of total bacterial production in the riverine part of the Sau Reservoir, where HNF peaked in abundance. Downstream, especially at intermediate stations, ciliates increased in abundance and became the prime protist consumers of bacteria,

consuming 64-74 % of total bacterial production, while the ranges in HNF consumption decreased to 24-37 %. These percentages, however, are the average of results from eight longitudinal transects. We measured grazing rates in warm months (see Jul-97 in COMERMA *et al.*, 2001; and May-98 in Fig. 4.2) which could not explain high bacterial productions found (2-5 times higher) and in some cases where protozoan grazing rates exceeded largely the bacterial production (e.g. Feb-98 in Fig. 4.2). What is important to remark here are: (1) the high portion of bacterial production consumed by protists, and (2) the role of the ciliate community as main bacterivores in this eutrophic reservoir.

An additional comment on differences between bacterial production and bacterial mortality by protistan grazing pressure is to note the problematic nature of an empirical thymidine conversion factor (ECF) to obtain precise bacterial production rates. Although in our initial studies along the Sau Reservoir (COMERMA *et al.*, 2001) differences in ECF were expected, measurements through the 1997-1999 period have established a unique value ($4.7 \cdot 10^{18}$ cells mol^{-1}) for the reservoir. We want to emphasize that ECF for the Sau Reservoir is at least twice the theoretical conversion factor (i. e. $2 \cdot 10^{18}$ cells mol^{-1}; BELL, 1993) and other ECFs measured in several freshwaters (BELL, 1990; BLOEM *et al*., 1989).

The main bacterial consumers among the HNF of the Sau Reservoir were chrysomonads, bodonids and choanoflagellates (ŠIMEK *et al*., 1999). The Peritrichs *Vorticella* and *Epistylis*, Oligotrichs <30μm (*Halteria* and *Rimostrombidium*) and the Scuticociliate *Cyclidium* were the main grazers of bacteria in the pelagic ciliate community. Other pelagic ciliates able to ingest bacteria were of negligible importance, either due to low abundance or low clearance rates (cf. Fig. 4.4 and Table 4.2). This results agrees well with the composition of bacterivorous ciliates reported for 17 Norwegian lakes (STABELL, 1996), the eutrophic Lake Oglethorpe (SANDERS *et al*., 1989), and the eutrophic Řimov Reservoir (ŠIMEK *et al*., 1998), corroborating the general value of these findings. Our data set show not only total grazing rates of HNF and ciliates in a eutrophic reservoir, but can provide information on the ranges of species-specific

grazing rates and volume specific clearance rates of distinct ciliate taxa groups, which could elucidate their distinct role in the plankton.

A detailed analysis of the community of bacterivorous ciliates documented an exceptional role for oligotrichous ciliates, especially *Halteria*, which was clearly the most voracious ciliate consumer of bacteria (cf. Table 4.2 and 4.3). This small filter-feeding ciliate is an omnivorous species, which is able to efficiently exploit the planktonic prey size spectrum from 0.5 to 5 μm, covering heterotrophic and autotrophic pico- and nanoplankton in its diet (JÜRGUENS and ŠIMEK, 2000). *Halteria* has uptake and clearance rates on bacteria more than 2 orders of magnitude higher than the typical *in situ* uptake rates of freshwater HNF (ŠIMEK *et al*., 2000), which means that it is a serious competitor to the flagellates. This genus has been identified as an abundant bacterial consumer in several meso- and eutrophic lakes and ponds (SANDERS *et al*., 1989; STABELL, 1996; NAKANO *et al*., 1998; ŠIMEK *et al*., 1998). All this particularities have conducted to affirm that *Halteria* might occupy a specific structuring role for the microbial food web in meso- to eutrophic systems (ŠIMEK *et al*., 2000).