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Growth rates of dominant planktonic ciliates in two freshwater bodies of different trophic degree

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Abstract. The *in situ* growth rates of dominant ciliate species were studied during and shortly after phytoplankton peaks in two water bodies: the eutrophic Římov Reservoir (South Bohemia, Czech Republic) and the oligo-mesotrophic Piburger See (Tyrol, Austria). Growth rate estimates based on changes in ciliate abundances in incubated pre-screened samples (E_N) were compared with those derived from the ciliate cell volume and ambient temperatures (E_T). The values of E_N were always rather lower than those of E_T. During the studies, the food supply limited the ciliate growth depending on the ciliate feeding mode. An ecological grouping into filter feeding versus raptorial feeding ('hunting') species, on the one hand, and attached/crawling (browsing) versus free swimming species, on the other hand, clearly affected experimental estimation. Both fine filter feeders (namely attached) and browsers exhibited a calculated E_N closer to the theoretical (maximum) E_T than did hunters and coarse filter feeders. It was apparent, for example, comparing E_N and E_T (day^{-1}) of the following species: filter feeders *Halteria grandinella* (E_N = 0.42; E_T >1.4), *Strobilidium hexakinetum* (0.34; >1.9), *Pelagohalteria viridis* (0.27; >0.9), *Vorticella aquadulcis* complex (0.75; >1.0); raptorial *Balanion planctonicum* (0.65; >1.5), *Urotricha furcata* (in Římov Reservoir 0.65; >2.1; in Piburger See 0.20; >1.5), *Rhabdoaskenasia minima* (0.22; >1.0), *Askenasia acrostomia* (0.12; >0.6); opportunistic *Cyrtolophosis mucicola* (0.42; >1.6) and *Cinetochilum margaritaceum* (0.86; >1.4). Predation by rotifers apparently affected measurements in several samples containing ~400 rotifers l^{-1}; however, it seemed to be of little importance in the water column.

Introduction

The temporal and spatial changes in the distribution of ciliates within lotic plankton communities have been well documented, and the importance of the microbial food webs in this environment demonstrated, during recent years (reviewed by Beaver and Crisman, 1989; Müller, 1989; Sanders *et al.*, 1989; Pace *et al.*, 1990; Šimek *et al.*, 1990; Hansen and Christoffersen, 1995). Ciliate pelagic assemblages are mostly numerically dominated by minute species in meso- and eutrophic systems (Sheldon *et al.*, 1986; Rassoulzadegan *et al.*, 1988; Sherr *et al.*, 1988, 1991a,b; Šimek *et al.*, 1990, 1995, 1996; Müller, 1991; Müller and Weisse, 1994). These ciliates may be voracious bacterivores (Sherr *et al.*, 1986, 1989; Šimek *et al.*, 1995, 1996) or they may utilize directly primary production, particularly of picocyanobacteria and picoalgae (Müller, 1989, 1991; Sherr *et al.*, 1991a,b; Müller and Weisse, 1994; Šimek *et al.*, 1995). On the other hand, large mixotrophic taxa which frequently dominate ciliate biomass in oligotrophic environments are not efficient picoplankton consumers and feed particularly upon nanoplankton (Rassoulzadegan *et al.*, 1988; Sherr *et al.*, 1988; Beaver and Crisman, 1989).

Studies documenting the carbon flow within plankton communities (e.g. Pace *et al.*, 1990; Weisse, 1990, 1991) have shown that protozoan development may be both top-down controlled (e.g. by zooplankton, the composition of which is

strongly linked to fish stock composition) and bottom-up controlled (e.g. via exhaustion of limiting nutrients for primary production). In marine habitats, seasonal protozoan cycles are apparently controlled by top-down processes, mainly by crustacean zooplankton predation (Smetacek, 1981; Sheldon *et al.*, 1986; Gifford, 1991). Rotifers can also play an important role in removing protozoa, particularly in freshwater ecosystems (Gifford, 1991; Arndt *et al.*, 1992). In a seasonally stratified freshwater environment, a spring protozoan peak following a phytoplankton peak suggests 'bottom-up control', but eventually zooplankton predation upon protozoa increasingly dominates, thus limiting their development (Pace *et al.*, 1990; Šimek *et al.*, 1990; Weisse, 1991; Jürgens, 1994). However, zooplankton feeding upon protozoa observed in small-scale experiments is not always verified *in situ* or in enclosures (e.g. Gilron and Lynn, 1989; Šimek *et al.*, 1995).

A general relationship between growth rate, ciliate species volume and temperature proposed for planktonic ciliates by Montagnes *et al.* (1988) is widely used to estimate growth rates and production of ciliates. However, such calculated growth rates of small species showed contradictory results when compared with those directly measured in *in situ* conditions (Müller, 1989, 1991; Taylor and Johannsson, 1991; Leakey *et al.*, 1994; Hansen and Christoffersen, 1995). Müller and Geller (1993) included a robust data set for freshwater pelagic ciliates and accordingly reconsidered this relationship to be more applicable. Nevertheless, the estimated and measured values are frequently inconsistent (Leakey *et al.*, 1994). The feeding mode of ciliates seems to be of high importance in ciliate growth strategy (Taylor and Johannsson, 1990). However, Müller and Geller (1993) did not find significant differences between measured and theoretically estimated growth rates (derived from cell volume and temperature) of algivorous and bacterivorous ciliates. Generally, directly obtained data on the feeding mode of many pelagic ciliates are still scarce in the literature (cf. Foissner *et al.*, 1991, 1992, 1994, 1995; Šimek *et al.*, 1995).

The aim of this study was to compare the apparent change in biomass of ciliate species following phytoplankton peaks in two different water bodies with their growth rates measured under *in situ* conditions in pre-screened water and those estimated using theoretical equations.

Method

Study sites and sampling

Water samples were collected at ~8:00–9:00 h, three times a week, from (i) the eutrophic Římov Reservoir (RIM), South Bohemia, during 16 August–23 September 1993 and (ii) the oligo- to mesotrophic alpine lake, Piburger See, Tyrol, Austria (PIB) during 4 May–1 June 1994. For more details on the water bodies, see Šimek *et al.* (1995) and Sommaruga and Psenner (1993), respectively. For the following experiments, the samples were screened through a plankton net of 100 μm (RIM) and 50 μm (PIB) mesh size both to remove and quantify zooplankton.

Prior to sampling, oxygen and temperature profiles were obtained using an oxymeter type OXY 196 (WTW, FRG). Samples were taken with a 2 l Friedinger sampler (RIM) or a 5 l Schindler–Patalas sampler (PIB) from two layers: the

epilimnion (a mixed sample from 0.5, 1.0 and 1.5 m) and the metalimnion (a mixed sample from the thermocline and 0.5 m above and below this layer) characterized by a strong decrease of temperature (PIB) or temperature and oxygen (RIM).

Ciliate identification and species-specific abundance

Ciliate identification was performed (i) immediately after sampling by inspecting a live sample in a labyrinth chamber under a microscope and (ii) on samples fixed (RIM) or post-fixed (PIB) with Bouin's fixative (5% final concentration). For post-fixed samples, water was first fixed with acid Lugol solution (1% final concentration), samples were allowed to sediment for 1 week and then Bouin's fixative was added to 10× concentrated samples. Ten to 40 ml of RIM sample, or 2–4 ml of PIB sedimented sample, were filtered onto a nitrocellulose membrane filter (1.2 μm pore size; Millipore, USA), mounted in agar, fixed with formalin (2%) and stained in protargol (Roques, France) at 40–60°C according to Skibbe's (1994) modification of the quantitative protargol staining method (QPS) of Montagnes and Lynn (1987). Membranes were dehydrated in an ethanol series (70%, 96%, 96%, phenol–xylene and xylene) and mounted in Canada balsam. The total area of the membrane was inspected for the enumeration of ciliates (pre-screened samples) and rotifers (both pre-screened and unscreened samples) using an Olympus BH2 (Japan) microscope equipped with Nomarski interference contrast at ×1250 and ×250 magnification, respectively.

The taxonomic system of Small and Lynn (1985) including the comments of Foissner (1994) was used. Species identification was based on Foissner *et al.* (1991, 1992, 1994, 1995) and references therein, namely Krainer (1981) and Krainer and Foissner (1990). Species-specific abundance derived from QPS data was corrected to total abundance derived from counts in DAPI-stained samples (see below), mostly higher by 10–20%, assuming proportional distribution of taxa.

Individual ciliate and total community biomass

Pre-screened samples were fixed by adding alkaline Lugol's solution (0.5% final concentration), immediately followed by borate-buffered formalin (2% final concentration) and cleared by several drops of 3% sodium thiosulphate (Sherr and Sherr, 1993). Twenty to 40 ml aliquots were concentrated onto 2 μm pore size black Poretics filters, DAPI stained (Porter and Feig, 1980) and observed by epi-fluorescence microscope (Olympus or Zeiss Axioplan, FRG). Since DAPI staining does not visualize typical taxonomic features of the ciliates, we needed to add some criteria for determination, such as the size and position of nuclei, and the way in which prey were arranged in the food vacuoles, i.e. species-specific feeding modes were evaluated (Šimek *et al.*, 1995). This was possible based on the comparison of fluorescence images of ciliates with the ciliates in protargol preparations. Usually between 5 and 15% of ciliates could not be identified.

Ciliates were enumerated and the length and width of at least 30 cells were measured. Cell volumes were calculated by approximation to prolate sphaeroids. Live cell volumes for growth rate estimates were calculated by multiplying fixed volumes by a factor of 1.4, suggested for Lugol iodine-preserved ciliate cells (Müller

and Geller, 1993), as formalin will not produce additional shrinkage (Wiąckowski *et al.*, 1994). Ciliate cell organic carbon was estimated using a conversion factor of 140 fg μm^{-3} (Putt and Stoecker, 1989).

Owing to the low inspected number of individuals per ciliate species in some samples, we pooled the individual volume data of the same taxa from the whole study period. The biomass of the total ciliate assemblage was calculated by multiplying total abundance by the average ciliate cell volume. QPS data multiplied by the species-specific cell volume derived over the whole period were used to estimate the contribution of individual species to total ciliate biomass.

Ciliate specific growth rates

Duplicate 500 ml water samples pre-screened through a plankton net of 100 μm (RIM) and 50 μm (PIB) mesh size were incubated in the dark at *in situ* temperature for 1–2 days (RIM) or in transparent glass bottles *in situ* for 2–3 days (PIB). Since the difference of the individual cell biomass was not measurable, population specific growth rate was approximated by the specific division rate; growth rates of each species were calculated assuming exponential growth according to the equation: $\mu = (\ln N_t - \ln N_0)/t$ where μ is the intrinsic rate of increase (day^{-1}), N_0 and N_t are QPS cell abundances at the beginning and end of the experiment (cells ml^{-1}) and t is the duration of the experiment (days). In the following text, the symbol E_N designates for estimates derived from measured abundances.

The maximum specific growth rate was estimated using the following equations: (i) $\ln \mu_{max} = 0.1438\ T - 0.3285 \ln (V \times 10^{-3}) - 1.3815$ (Montagnes *et al.*, 1988) and (ii) $\ln \mu_{max} = 1.52 \ln T - 0.27 \ln V - 1.44$ (Müller and Geller, 1993), where μ_{max} is the maximum intrinsic growth rate (day^{-1}), V is the ciliate (live) volume (μm^3) and T is the ambient temperature (°C). The symbol E_T designates these theoretical estimates of growth rates.

Phytoplankton growth rates

Growth rates of PIB phytoplankton were calculated from changes in chlorophyll *a* concentrations in the same samples incubated at *in situ* conditions as for ciliate growth rate estimates. In addition, phosphorus was added (30 $\mu g\ l^{-1}$) to one set of samples (ciliates were not enumerated in those samples). Fresh samples were filtered onto a glass fibre filter (GF/C, Whatman), dried and desiccated on silica gel in a freezer (–18°C). Pigments were extracted with acetone and chlorophyll *a* concentrations were measured fluorometrically (Phinney and Yentsch, 1985). Potential limitation by phosphorus concentration was estimated according to Løvstad (1984).

Results

Římov Reservoir

During the summer ciliate peak, the water column was thermally stratified. In the epilimnion (1 m depth), temperatures slowly decreased from 22 to 15°C, in the metalimnion (located between 3.5 and 5 m depth during the first days of the study,

and between 5 and 7 m towards the end) from 20 to 14°C. For more details, see Šimek *et al.* (1995).

Phytoplankton biomass was dominated by diatoms and chlorophytes, namely by *Fragilaria crotonensis* and *Staurastrum pingue*, in the epilimnion also by *Ceratium hirundinella* (Dinophyceae), but only during the first days of the study. Picocyanobacteria (mostly species resembling *Synechococcus* and partly *Microcystis incerta*) fell sharply from ~3 to 4 × 10^5 at the beginning of the study to <2 × 10^3 cells ml^{-1} by the end of the study. Bacterial numbers were stable, ranging from 2.1 to 4.4 × 10^6 cells ml^{-1} (Šimek *et al.*, 1995).

Although rotifers, dominated by *Keratella cochlearis*, contributed only little to net zooplankton (mean abundance 38 individuals l^{-1}; range 2–129), total counts (from QPS preparations) were much higher (mean abundance 300 individuals l^{-1}; range 33–1000). Since *K.cochlearis* and *Brachionus* sp. might pass through a 100 μm plankton net, the epilimnetic pre-screened samples contained rotifers. Their abundance peaked before 1 September (mean 200; range 100–400 individuals l^{-1}, i.e. up 200 rotifers per cultivation bottle). Rotifers were not observed in the metalimnetic pre-screened samples.

Among large zooplankton >100 μm, crustaceans of the genera *Cyclops* (39 individuals l^{-1}; range 10–74), *Daphnia* (12; 3–29), and *Ceriodaphnia* and *Diaphanosoma* (summed together 12; 2–41) were dominant. Abundances were generally low and similar in both layers without any clear trend, except for rotifers, which were significantly more abundant in the epilimnion, but only at the end of the study period. For more details, see Šimek *et al.* (1995).

The identified ciliates and their mean cell volumes are presented in Table I. Since the general development of the ciliate species composition during the study period has been discussed elsewhere (Šimek *et al.*, 1995), only the seasonal trends in total ciliate biomass in the epilimnion (screened samples) are shown in detail in Figure 1 (changes in the metalimnetic layer were similar to the epilimnetic ones).

Among algivorous raptorial species (Foissner *et al.*, 1994), the genus *Urotricha* (>90% *Urotricha furcata*) dominated numerically. Although this ciliate formed up to ~20% of total ciliate abundance, its biomass did not exceed 9%. During the first 2 weeks, the proportion of the dominant picoplankton filter feeder, *Halteria grandinella* (Fenchel, 1986; Foissner *et al.*, 1991), exceeded 50% of both abundance and biomass. Later, this species was partly replaced by another oligotrich, *Strobilidium hexakinetum*, which accounted for nearly 20% of total ciliate abundance, but for only 10% of biomass. Ciliates known to live in organic debris, i.e. *Cyrtolophosis mucicola* and *Cinetochilum margaritaceum* (Foissner *et al.*, 1991, 1994), contributed ~50 and 20% to total abundance and biomass, respectively, by the end of the study period. The above five species represented on average 65% of total ciliate biomass.

The remaining ciliate biomass consisted of a varying assemblage of rare but large ciliate species, such as *Litonotus* sp., *Lacrymaria* sp. and *Strobilidium humile*. Specimens of the genera *Tintinnidium*, *Codonella* and *Epistylis* were not included in calculations because they were observed only in centrifuged samples, but never on QPS membranes.

Table I. Ciliates of the Římov Reservoir: average cell volumes (μm³) and ranges of growth rates derived indirectly from live cell volume, minimum and maximum temperature (E_T), and directly from measured changes in abundance (E_N)

Taxa	Cell volume (μm³)		Growth rate (day⁻¹)		
	Fixed[a] (mean ± SD)	Live[b] (mean)	E_T[c] (min; max)	E_T[d] (min; max)	E_N[e] (mean ± SD)
Oligotrichida					
Tintinnidium sp.	25000	35000	0.71; 0.90	0.89; 1.56	nd[f]
Strobilidium hexakinetum	1230 ± 690	1720	1.90; 5.12	2.00; 3.53	0.34 ± 0.21
Strobilidium sp. (~35 μm)	10050 ± 4850	14100	0.95; 2.56	1.14; 2.00	nd
Attached unidentified	1530 ± 1130	2140	1.77; 4.76	1.89; 3.33	nd
Halteria grandinella	2860 ± 1380	4000	1.44; 3.88	1.60; 2.81	0.42 ± 0.25
Prostomatida					
Urotricha spp. (*U.furcata* >90%, *U.ristoi*)	930 ± 690	1300	2.08; 5.61	2.16; 3.80	0.65 ± 0.41
Unidentified ciliate[g]	1160 ± 630	1620	1.94; 5.22	2.04; 3.59	nd
Coleps sp.	2850 ± 890	3990	1.44; 3.88	1.60; 2.81	nd
Small *Urotricha* sp.	450 ± 210	630	2.64; 7.12	2.63; 4.63	nd
Haptorida					
Lacrymaria sp.	15500 ± 1760	21700	0.83; 2.22	1.01; 1.78	nd
Pleurostomatida					
Litonotus sp.	6500 ± 3950	9100	1.10; 2.96	1.28; 2.25	nd
Sessilida					
Vorticella aquadulcis	8940 ± 4940	12500	0.99; 2.67	1.17; 2.06	0.75 ± 0.42
Scuticociliatida					
Cyclidium sp.	1070 ± 510	1500	1.98; 5.35	2.08; 3.66	0.80 ± 0.67
Cinetochilum margaritaceum	3290 ± 1400	4610	1.37; 3.70	1.54; 2.70	0.86 ± 0.64
Cyrtolophosida					
Cyrtolophosis mucicola	2050 ± 1590	2870	1.60; 4.33	1.74; 3.07	0.42 ± 0.39

[a]Measured in Lugol–formalin-fixed samples.
[b]Estimated multiplying the fixed volume by a factor of 1.4 (Müller and Geller, 1993).
[c]Formula used: $\ln E_T = 0.1438\ T - 0.3285 \ln (V \times 10^{-3}) - 1.3815$ (Montagnes *et al.*, 1988).
[d]Formula used: $\ln E_T = 1.52 \ln T - 0.27 \ln V - 1.44$ (Müller and Geller, 1993).
[e]Formula used: $E = (\ln N_t - \ln N_0)/t$.
[f]nd = non-defined, i.e. too low data set.
[g]Resembles *Balanion* sp.

The estimates of growth rates (both E_N and E_T) of the most abundant species measured in the laboratory at *in situ* temperature are shown in Table I, changes in species abundance during incubation are shown in Figure 2. Among oligotrichs, the growth rates of *S.hexakinetum* and *H.grandinella* were estimated. Mean E_N of 0.34 and 0.42 day⁻¹, respectively, were calculated from positive values only, i.e. from those samples where an increase in ciliate abundance at the end of the incubation period was found. We observed differences between the epilimnion and metalimnion, which were also connected with rotifer occurrence. *Strobilidium hexakinetum* grew regularly in the metalimnion ($E_N \leq 0.56$ day⁻¹) and even faster in the epilimnion (≤0.69 day⁻¹), but during September the population was decreasing (also confirmed by negative E_N on 1 September). *Halteria grandinella* showed positive E_N up to 0.45 day⁻¹ (mean 0.28) and up to 0.80 day⁻¹ (mean 0.68) in the epilimnion and metalimnion, respectively. However, several negative values of E_N were

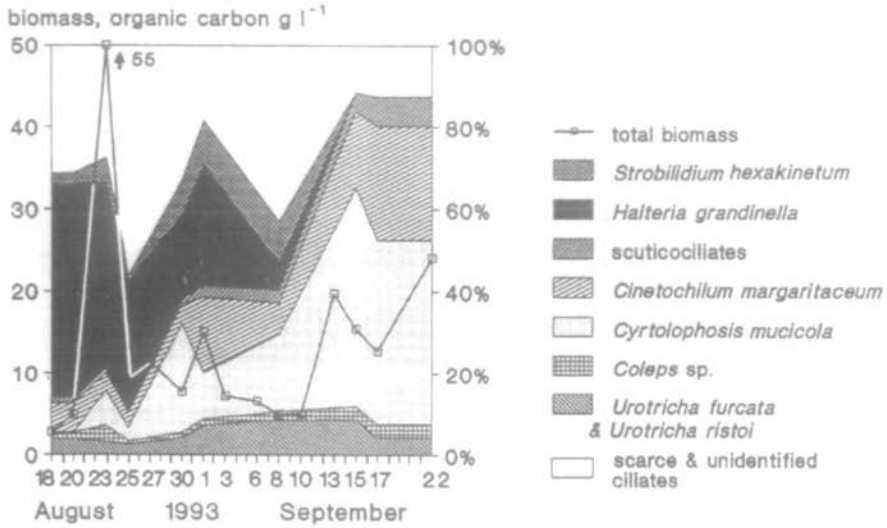

Fig. 1. Seasonal changes in the epilimnetic total ciliate biomass (g organic carbon l^{-1}) and relative contribution of ciliate taxa (%) to this in Římov Reservoir during the summer phytoplankton peak.

calculated both in the metalimnion (23 August) and in the epilimnion (30 August–1 September). Theoretical estimates (E_T) for both ciliates were ~2 day^{-1}.

Among prostomatids, *U.furcata* showed similar E_N in most of the epilimnetic and metalimnetic experiments (0.65 day^{-1}), but E_T was >2 day^{-1}. E_N of vorticellids, *Vorticella aquadulcis* complex, varied around 0.75 day^{-1}. Also, scuticociliates represented by *Cyclidium* sp. and *Cinetochilum margaritaceum* (Figure 2) showed quite high E_N, around 0.8 day^{-1}, except for 1 September. For these species, E_T (>1.5 day^{-1}) was less different from calculated E_N. However, the first measurements showed negligible changes in abundance in the metalimnion. *Cyrtolophosis mucicola* (mean E_N 0.42 day^{-1}) reached maximum $E_N > 1.0$ day^{-1} during the second week of the study. When abundances increased to a higher level, E_N fell below 0.25 day^{-1}, whereas E_T was >1.6 day^{-1}. Other species were not present in sufficient numbers to estimate E_N.

Piburger See

Sampling at the lake started when the thermal stratification of the water column had stablized (first week of May). During the study period, temperatures increased from 13.0 to 16.5°C and from 9.5 to 13.9°C in the epilimnion and metalimnion, respectively. Except for the first and last sampling, the thermocline temperature was relatively stable at ~12°C, but the position of the thermocline shifted from 4.0 to 5.0 m depth. While the metalimnetic waters were frequently oxygen oversaturated (12.4–14.3 mg l^{-1}), dissolved oxygen concentrations in the surface layer were found to be lower (8.9–11.1 mg l^{-1}).

Phytoplankton biomass was always higher in the metalimnion (as chlorophyll *a* concentration; minimum 1.71 and 2.09, maximum 2.83 and 4.12, mean 2.36 and 2.83 μg l^{-1} in the epilimnion and metalimnion, respectively; Figure 3). The epilimnetic

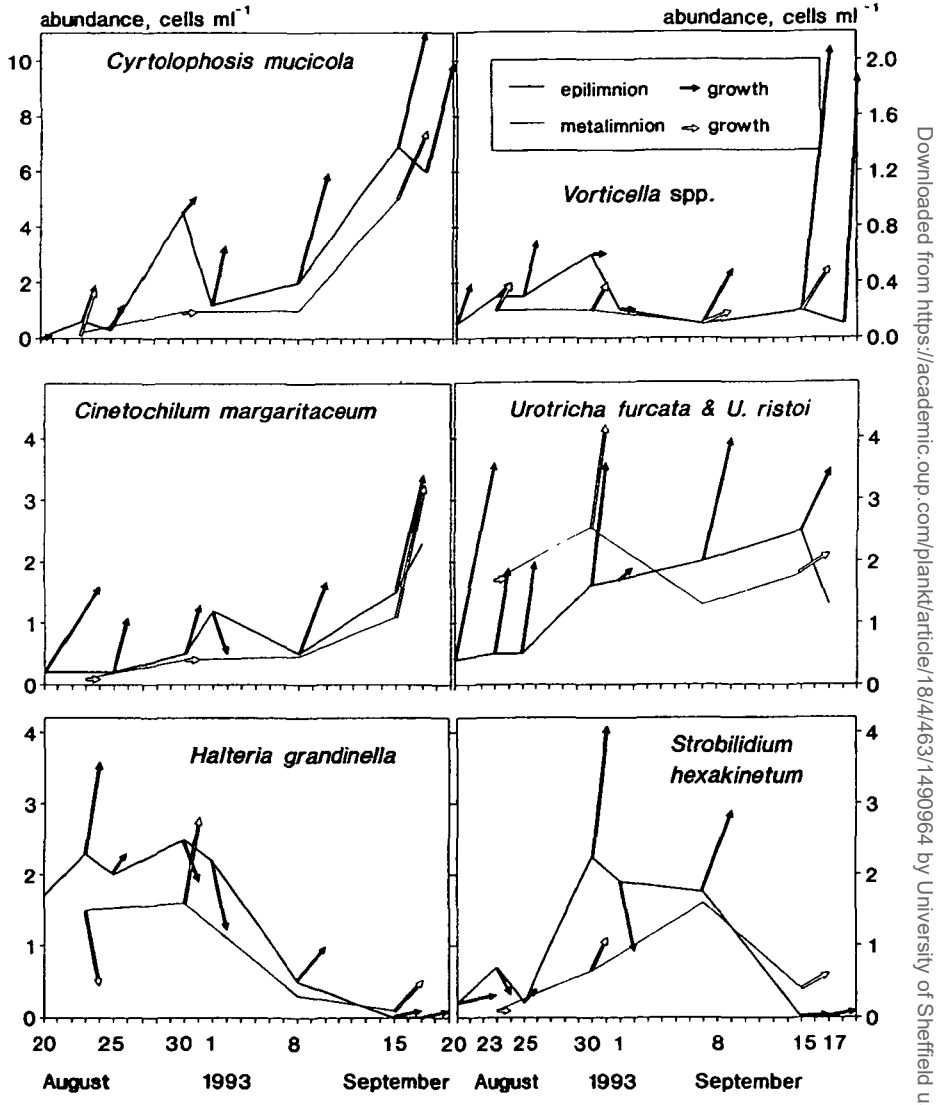

Fig. 2. Changes in abundance (from QPS preparations) of ciliates (cells ml⁻¹) in Římov Reservoir samples incubated in the laboratory at *in situ* temperatures.

phytoplankton consist mainly of dinoflagellates, chrysophytes and chlorophytes, namely of the genera *Gymnodinium*, *Peridinium*, *Dichrysis* and *Stichogloea*. In the metalimnion, dinoflagellates, diatoms (*Fragilaria crotonensis*) and chlorophytes accounted for the main proportion of the phytoplankton biomass during the first samplings, later on diatoms decreased to almost zero abundances. In the epilimnion, a peak of *Microcystis incerta* was observed between 16 and 23 May, and single cells of species resembling *Synechococcus* increased during the study period from

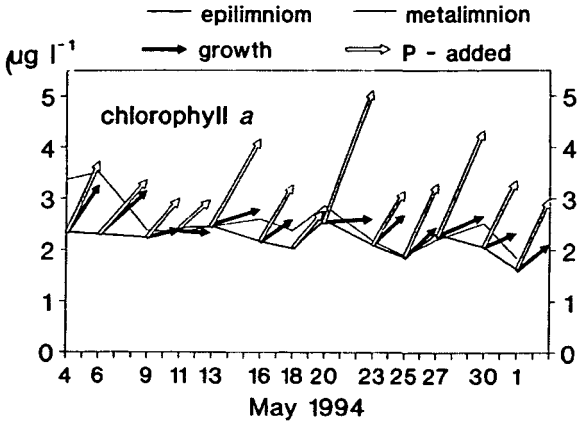

Fig. 3. Changes in chlorophyll *a* concentration (μg l^{-1}) in Piburger See epilimnetic samples incubated in *in situ* conditions in the presence and absence of additional phosphorus (30 μg l^{-1}).

2.3 to 11.5 × 10^4 cells ml^{-1}. Bacterial numbers were stable, ranging from 1.7 to 3.5 × 10^6 cells ml^{-1}.

In the bottles incubated in the epilimnion, phytoplankton achieved an average growth rate of 0.07 day^{-1}; however, after adding phosphorus this value increased to 0.2 day^{-1} (based on chlorophyll *a* measurement).

Conochilus unicornis, *Keratella cochlearis* and *Polyarthra dolichoptera* in the epilimnion, and *C.unicornis* and *Kellikottia longispina* numerically dominated rotifer assemblage (from 12 at the first sampling to >600 individuals l^{-1} at the end of study). *Asplanchna priodonta* and *C.unicornis* were the most important contributors to rotifer biomass in both layers. As no rotifers passed through the 50 μm plankton net, the samples were incubated without any metazoans. Among large zooplankton, the most common crustaceans were *Daphnia longispina*, *Bosmina longirostris*, *Cyclops vicinus* and *Acanthodiaptomus denticornis*. Crustacean abundance was very variable, with maxima in the metalimnion (summed together, range 25–50 and 25–120 individuals l^{-1} in the epilimnion and metalimnion, respectively). For more details, see Pernthaler *et al.* (1996).

Ciliate abundance in the lake peaked at the end of the first week of the study period (Figures 4 and 5). Ciliate species composition was quite different from that found in Římov Reservoir with a significant proportion of mixotrophic ciliates, particularly by the end of the study (data from screened samples pooled in Figures 4 and 5; Table II).

Among algivorous ciliates, the genus *Urotricha*, and later on *Balanion* (syn. *Pseudobalanion*) *planctonicum* (Foissner *et al.*, 1994) dominated. Although the proportion of the latter ciliate frequently exceeded 30% (maximum 53%) of total ciliate abundance, its proportion never accounted for >10% of the total biomass due to its very small cell volume (Table II). Likewise, the common species *Urotricha furcata* and *Urotricha ristoi*, which together contributed up to 10% of abundance, typically shared only <2% of total biomass. The contribution of the larger *Urotricha pelagica* to biomass was significant during the first weeks (maximum

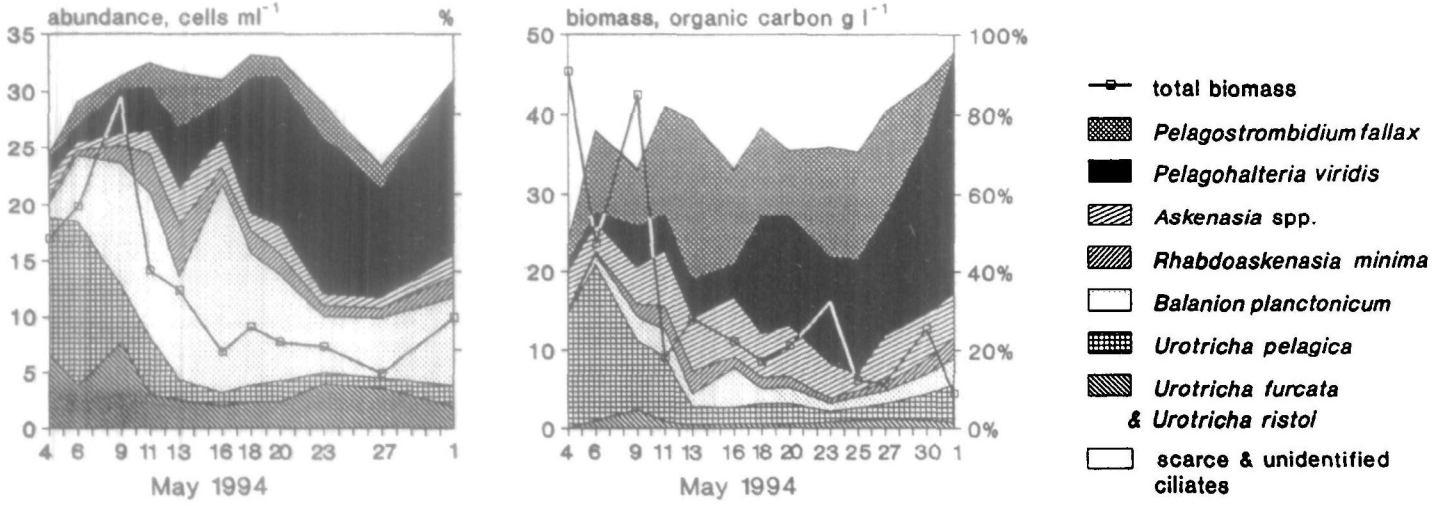

Fig. 4. Seasonal changes in the epilimnetic total ciliate abundance (cells ml^{-1}) and relative contribution of ciliate taxa (%) to this (**left panel**) and seasonal changes in the epilimnetic total ciliate biomass (g organic carbon l^{-1}) and relative contribution of ciliate taxa (%) to this (**right panel**) in Piburger See during the decay of the spring phytoplankton peak.

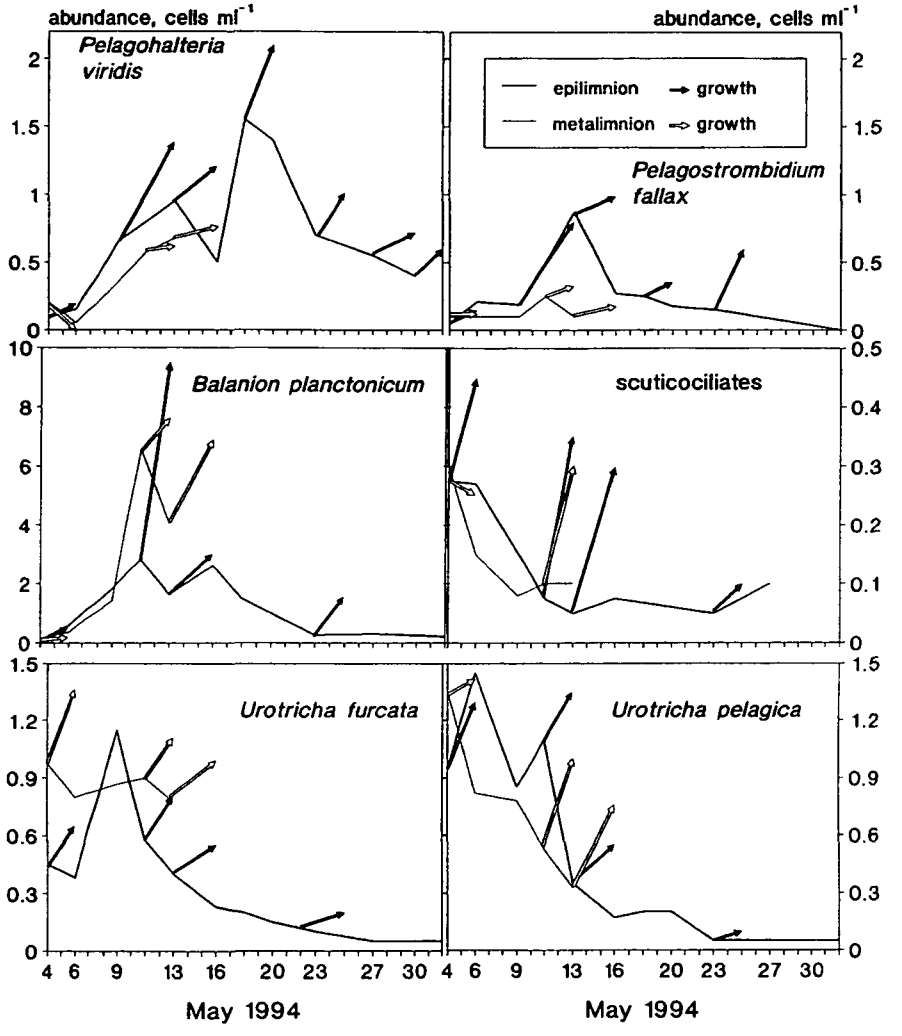

Fig. 5. Changes in abundance (from QPS preparations) of ciliates (cells ml $^{-1}$) in Piburger See samples incubated in *in situ* conditions.

40%, mean 12% of the total biomass). Algivorous ciliates, namely *B.planctonicum*, were frequently observed in higher concentration in the metalimnion. Besides raptorial algivorous species, the coarse filter feeder, *Pelagostrombidium fallax*, was common and contributed on average 21% to the total biomass (maximum 40%). Species feeding upon organic debris were less abundant, except for *Lagynophrya* sp. which was frequently encountered in the metalimnion, particularly during the first week.

Typical filtering bacterivores were represented by scuticociliates (among them, *Cyclidium* sp. identified), but they were present in low abundances. Other effective filter feeders were more important, in particular the mixotrophic species,

Table II. Ciliates from Piburger See: average cell volumes (μm^3) and ranges of growth rates derived indirectly from live cell volume, minimum and maximum temperatures, and directly from measured changes in abundance. For more details, see the legend to Table I

Taxa	Cell volume ± SD (μm^3)		Growth rate (day^{-1})		
	Fixed[a] (mean ± SD)	Live[b] (mean)	E_T[c] (min; max)	E_T[d] (min; max)	E_N[e] (mean ± SD)
Oligotrichida					
Strobilidium sp.	27900 ± 17400	39000	0.53; 0.74	0.71; 0.91	nd[f]
Pelagohalteria viridis	5260 ± 2940	7360	0.91; 1.28	1.12; 1.43	0.27 ± 0.01
Pelagostrombidium fallax	2460 ± 11000	34400	0.55; 0.77	0.74; 0.95	0.34 ± 0.21
Strichotrichida					
Stichotricha secunda	75000 ± 56500	105000	0.38; 0.54	0.55; 0.70	0.19 ± 0.06
Prostomatida					
Urotricha furcata	1170 ± 1110	1630	1.49; 2.11	1.68; 2.15	0.20 ± 0.10
Urotricha ristoi	500 ± 210	700	1.97; 2.78	2.11; 2.71	0.59 ± 0.11
Urotricha pelagica	6770 ± 2620	9480	0.84; 1.18	1.04; 1.34	0.19 ± 0.11
Balanion planctonicum	1110 ± 500	1560	1.51; 2.14	1.70; 2.18	0.65 ± 0.32
Coleps spetai	3060 ± 1830	4280	1.09; 1.53	1.29; 1.66	nd
Haptorida					
Monodinium sp.	17000	23800	0.62; 0.87	0.81; 1.04	nd
Askenasia acrostomia	22800 ± 5760	31900	0.56; 0.79	0.75; 0.97	0.12 ± 0.12
Askenasia chloreligella	7750 ± 1740	10800	0.80; 1.13	1.01; 1.29	nd
Rhabdoaskenasia minima	3800 ± 1150	5300	1.01; 1.43	1.28; 1.71	0.22 ± 0.15
Lagynophrya sp.	23300 ± 11600	33000	0.55; 0.78	0.75; 0.96	0.85 ± 0.10
Scuticociliatida	2850 ± 1130	3980	1.11; 1.57	1.32; 1.69	0.49 ± 0.24

[a–f]As Table I.

Pelagohalteria viridis (Foissner *et al.*, 1991). In the second half of the study, this species typically accounted for 30% of both total abundance and total biomass, and 60% on the last sampling date. Also, the very large *Stichotricha secunda*, bearing zoochlorellae (Foissner *et al.*, 1991) and feeding also partly upon picoplankton, was observed regularly but in very low abundance.

Growth rates measured *in situ* (E_N) are shown in Table II, and Figure 5 shows changes in the abundance of individual species during incubation. The metalimnetic growth rates were measured only during the first week.

The numerically dominant ciliate *B.planctonicum* grew at a mean E_N of 0.65 day^{-1} with a maximum of 0.91 day^{-1} (23 May) and $E_T > 1.5$ day^{-1}. Although the metalimnetic abundance was higher, E_N was lower in this layer (maximum 0.18 day^{-1}). Among the representatives of the genus *Urotricha*, *U.furcata* showed E_N of 0.20 day^{-1} (measured maximum E_N 0.35 day^{-1}; $E_T > 1.5$ day^{-1}), the much smaller *U.ristoi* of 0.59 day^{-1} (0.69 day^{-1}; >2 day^{-1}) and the large *U.pelagica* of 0.19 day^{-1} (0.35 day^{-1}; >0.8 day^{-1}). Values of E_N of these ciliates varied significantly only in the metalimnion. Scuticociliates grew at rates of ~0.5 day^{-1} (maximum E_N of 0.77 day^{-1}; $E_T > 1.1$ day^{-1}).

Among mixotrophic ciliates, E_N was measured for the picoplankton filter feeder, *Pelagohalteria viridis* and a larger coarse filter feeder, *Pelagostrombidium fallax* (E_N of 0.27 and 0.34 day^{-1}, respectively). In comparison with E_N, E_T values were significantly higher (>0.9 day^{-1}) for the smaller *Pelagohalteria viridis*, but more

similar for *Pelagosrombidium fallax* (>0.55 day^{-1}). On the other hand, growth was not regularly observed in bottles incubated in the metalimnion, where in particular *Pelagostrombidium fallax* frequently failed to grow. Extremely large *Stichotricha secunda* grew at a reasonable rate (mean E_N 0.19 day^{-1}, $E_T > 0.4$ day^{-1}), but it was present in a very low abundance.

The flagellate hunters (Weisse, 1990; Krainer, 1991) *Rhabdoaskenasia minima* and *Askenasia acrostomia* achieved mean E_N of 0.22 and 0.12 day^{-1}, respectively, but E_N varied significantly. The mixotrophic *Askenasia chloreligella* showed no apparent growth. Owing to the low concentration of both haptorids and *S.secunda*, growth rate measurements of these species are of limited precision.

Discussion

The development of the ciliate assemblages in both sites was in accordance with previously published results regarding the respective water bodies (Šimek *et al.*, 1990; Macek, 1994; Sommaruga and Psenner, 1993) and did not differ from generally accepted seasonal patterns of freshwater planktonic ciliates [reviewed by Beaver and Crisman (1989) and supported by numerous recent data, e.g. Müller, 1989; Sanders *et al.*, 1989; Madoni, 1990; Sherr *et al.*, 1991a; Taylor and Johannsson, 1991; Carrias *et al.*, 1994]. One may argue that two different seasons in two different water bodies are not suitable for methodical comparison. However, the aim of the study was to compare estimates of growth rates of various ciliate species obtained on the basis of two different approaches under various environmental conditions.

According to the literature data (Sommaruga and Psenner, 1993; Macek, 1994; Macek *et al.*, 1994; cf. Sherr *et al.*, 1991a; Sime-Ngando and Hartmann, 1991; Carrias *et al.*, 1994), maximum ciliate abundances may be associated with the thermocline and/or with phytoplankton maxima. On the other hand, analyses of the mixed epilimnetic samples showed the most reproducible data (Macek, 1994). Only a few species were found to be concentrated below the thermocline (in RIM, tintinnids, *Strobilidium humile*, *Lacrymaria* sp.; in PIB, *B.planctonicum*). Furthermore, the surface layer and the thermocline appeared to be two distinct habitats regarding ciliate development, which is also indicated by the remarkable differences in measured E_N (see below).

The information about the growth pattern of phytoplankton is required as a background to explain possible food limitation. In the RIM sampling site, phytoplankton are frequently limited by phosphorus concentration and do not show any growth (Vyhnálek, 1989; Vyhnálek *et al.*, 1991; Komárková, 1994). The superficial phytoplankton bloom mostly builds up near the inflow of the reservoir, and from there, it is transported to the dam (Vyhnálek, 1989). The predominance of *Staurastrum pingue* among the phytoplankton in 1993 was quite surprising, since this algal species peak replaced the common cyanobacterial bloom (Komárková, 1994). This alga is non-ingestible even by large zooplankton, thus decreasing the possible food resources of ciliates. Also, picocyanobacteria were observed in conspicuous abundance only during the first weeks of the study period (Šimek *et al.*, 1995).

In PIB, picocyanobacteria were slowly increasing throughout the study period (Pernthaler *et al.*, 1996). The phytoplankton growth was phosphorus limited, but the measured growth rates were comparable with those of ciliates (Figure 3). Estimates of growth rates calculated from changes in chlorophyll *a* concentration could only be of limited informative value without a taxonomic analysis of phytoplankton. However, the growth of bacterivorous ciliates may be indirectly related to this parameter, as the growth of bacteria in a water body is also significantly correlated with chlorophyll *a* (Straškrabová *et al.*, 1994). Then the observed values of E_N may be strongly affected by varying food limitation during both studies.

In the literature, the differences between maximum specific growth rates of ciliates (non-limited) and intrinsic ones have scarcely been discussed, except for Müller and Geller (1993) and Leakey *et al.* (1994). According to Montagnes *et al.* (1988), intrinsic ciliate growth rates in the field are mostly in accordance with the predicted model (growth rate as a function of ciliate volume and environmental temperature), but recently published data do not always support this (Gilron and Lynn, 1989; Taylor and Johannsson, 1990; Müller and Geller, 1993; Leakey *et al.*, 1994; Hansen and Christoffersen, 1995). The theoretical (maximum) estimate (E_T) published by Montagnes *et al.* (1988) has been reconsidered by Müller and Geller (1993). Measured growth rates (E_N) were frequently below 50% of estimated rates, which also holds true for our data (Tables I and II). Such low growth rates may be related in particular to food limitation (e.g. Leakey *et al.*, 1994) which apparently did not occur in other studies (e.g. Montagnes *et al.*, 1988; Taylor and Johannsson, 1991).

In the present study, mean estimates derived from maximum and minimum measured temperatures are listed in Tables I and II. The formula of Müller and Geller (1993) seems to give more realistic estimates. Unfortunately, the relationships could not be analysed in each sample during the study period due to the fact that individual species appeared in sufficient abundance only within a temperature range of ~3°C.

In addition, the relationship might be modified by ciliate feeding mode; however, data to attempt such an analysis have been scarcely published for pelagic ciliates (except for, for example, Taylor and Johannsson, 1990; Foissner *et al.*, 1991, 1992, 1994, 1995; Müller and Geller, 1993). So we are forced to rely mostly on our own data (see also Macek *et al.*, 1994; Šimek *et al.*, 1995, 1996).

Among the efficient picoplanktivorous ciliates—*H.grandinella*, *S.hexakinetum*, *P.viridis* and *V.aquadulcis* complex (Šimek *et al.*, 1995, 1996; compare with Fenchel, 1986)—the measured values of E_N were low in comparison with E_T, although frequently higher than corresponding natural changes in species abundance. *Vorticella aquadulcis*, which apparently profits from growth on bottle surfaces, achieved a mean E_N near to E_T. In comparison with oligotrichs and peritrichs, the collection of suspended particles by spirotrichs (*Stichotricha secunda*) or by some scuticociliates may be less effective, although a high cell volume-specific clearance rate was confirmed for *Cyclidium* sp. (e.g. Šimek *et al.*, 1995, 1996). These ciliates frequently slide on surfaces [e.g. Fenchel (1986) and references therein] and thus also profit from the 'bottle effect'. This is probably a reason why some E_N values

were closer to E_T in the present study. The same was observed for species typically living in organic debris (detritus) such as *Cinetochilum margaritaceum* and *Cyrtolophosis mucicola*, found in high abundance during the conspicuous *Staurastrum* peak in RIM.

Surprisingly, all the above-mentioned filter feeders ingested both bacteria and picocyanobacteria (Šimek *et al.*, 1995, 1996), although at very different rates. Raptorial algivorous ciliates *Urotricha* spp. (namely *U.furcata*) and *B.planctonicum* (Foissner *et al.*, 1994) showed very low uptake rates on fluorescently labelled (heat-killed) picoplankton (Šimek *et al.*, 1995, 1996). Owing to the decreasing concentration of unicellular phytoplankton concentration, they probably faced increased food limitation. We observed a wide spectrum of ingested prey within food vacuoles among raptorial haptorids that may feed on both autotrophic and heterotrophic flagellates (Weisse, 1990)—*Rhabdoaskenasia minima*, *Askenasia acrostomia*, *Askenasia chloreligella*. *Coleps* spp. may, in addition, be detritophagous and carnivorous (K.Šimek and J.Pernthaler, unpublished data). E_N values of all raptorial ciliates were low and varied substantially during the study. We conclude that the development of both HNF, as food of the latter ciliates, and algae as the food resource for urotrichas and *B.planctonicum*, was affected by experimental conditions. The feeding mode of *Lagynophrya* sp. remains partly unclear, but we consider this species to be detritophagous due to the observed higher growth rate in the apparent presence of detritus visualized by the QPS preparation.

Mixotrophic species, mainly *Pelagohalteria viridis*, but also *Pelagostrombidium fallax*, *Stichotricha secunda*, *A.chloreligella* and *Coleps spetai*, were abundant in the more oligotrophic PIB (cf. Beaver and Crisman, 1989). *Pelagohalteria viridis* may dominate freshwaters (may be misidentified as 'zoochlorellae-bearing *H.grandinella*' or *Halteria chloreligella*; compare, for example, Taylor and Johannsson (1991) and Foissner *et al.* (1991), (K.H.Krainer, unpublished). The low estimated E_N in the metalimnion may be a consequence of light limitation, as no or very low growth was observed there (Figure 5). To our knowledge, comparative data dealing with the energetic budgets of mixotrophy have not been published, but only the photosynthetic rates of mixotrophic ciliates have been evaluated (e.g. Perriss *et al.*, 1994). As recently estimated by Šimek *et al.* (1996), the autotrophy of *Pelagohalteria viridis* in PIB could account for ~45% of its carbon requirements.

The role of metazoan predation can be shown on RIM data. The measured E_N of *H.grandinella* and *Strobilidium hexakinetum* were apparently affected by the presence of rotifers in 100 μm pre-screened (epilimnetic) water observed after incubation. Although rotifers did not decrease the abundance of larger ciliates in mesocosms (Gilron and Lynn, 1989), a decrease in abundance has been observed in experiments performed in bottles (Arndt *et al.*, 1992). The growth rate minimum of *H.grandinella* observed between 25 August and 1 September may be related to higher rotifer abundance (up to 400 individuals l^{-1}), while the growth of *S.hexakinetum* was only affected on 1 September concomitantly with the rotifer peaking abundance. Also, the *in situ* abundances of these species were decreasing, perhaps both due to increasing rotifer abundance and decreasing picoplankton food resources (Šimek *et al.*, 1995). In Piburger See, however, E_N values were not affected by rotifers, quantitatively removed by 50 μm screening.

In the light of the above, we can discuss the realized growth rates of the investigated ciliates (Tables I and II, and Figures 2 and 5). Very high differences were found between the predicted and measured growth rates of minute herbivorous ciliates such as *U.furcata*, *U.ristoi* and *B.planctonicum*. In oligotrophic Piburger See, E_N was very low but in accordance with possible food limitation (in Římov Reservoir, $E_N = 0.65$; $E_T > 2.1$; in Piburger See, 0.20; >1.5). Only the maximum E_N values were similar to published ones (Müller, 1991; Müller and Geller, 1993), so apparently food limitation was observed in both laboratory experiments (RIM) and in experimental bottles incubated *in situ* (PIB). For example, *B.planctonicum* grew faster in the light-unlimited epilimnetic samples than in metalimnetic samples, while *in situ* abundances were mostly higher in the metalimnion than epilimnion. This can be explained by considering this species as an r-strategist (Müller and Weisse, 1994), being able to eliminate prey very quickly. Incubation of samples in diffusion chambers (Stoecker *et al.*, 1983) may diminish the growth limitation of phytoplankton by carbon dioxide; however, phytoplankton also grew relatively well in PIB samples despite being limited by phosphorus (Figure 3). The inhibition of ciliates by increasing pH was not observed. It seems likely that some species migrate between the respective layers (Sime-Ngando and Hartmann, 1991) to reach optimum growth rate. Thus, the incubation of samples at the fixed layer might partly bias our data.

Less significant differences were found comparing E_N and E_T of some bacterivorous and detritophagous ciliates such as attached *V.aquadulcis* and crawling scuticociliates (namely *Cyclidium* spp., *Cinetochilum margaritaceum*). Detritophagous *Lagynophrya* sp. grew even faster than was predicted using minimum values in the equation of Müller and Geller (1993), while the growth of *Cyrtolophosis mucicola* apparently depended on the presence of detritus.

Conclusions

(1) The measured values of E_N were closer to the estimates based on water temperatures and cell volumes (E_T) using the equation of Müller and Geller (1993) than to those based on a formula of Montagnes *et al.* (1988).
(2) During the studies, food supply limited ciliate growth differently, depending on the ciliate feeding mode. The ecological grouping into filter feeding versus raptorial feeding ('hunting') species, on the one hand, and attached/crawling (browsing) versus free-swimming species, on the other hand, clearly affects experimental estimation. Both fine filter feeders (namely attached) and browsers exhibited calculated E_N closer to theoretical (maximum) E_T than did hunters and coarse filter feeders.
(3) Predation by rotifers apparently affected measurements (samples containing ~400 individuals l^{-1}); however, it seemed to be of little importance in the water column.

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