

# Impact of metazooplankton on the composition and population dynamics of planktonic ciliates in a shallow, hypertrophic lake

Klaus Jürgens<sup>1,\*</sup>, Oliver Skibbe<sup>2</sup>, Erik Jeppesen<sup>3</sup>

<sup>1</sup>Max Planck Institute of Limnology, PO Box 165, D-24302 Plön, Germany

<sup>2</sup>Institute of Zoology, Free University of Berlin, D-14195 Berlin, Germany

<sup>3</sup>National Environmental Research Institute, PO Box 314, DK-8600 Silkeborg, Denmark

**ABSTRACT:** We conducted an enclosure study in Lake Søbygård, a shallow hypertrophic Danish lake, to examine the impact of metazooplankton on the structure of the microbial food web. Here we present results on ciliate abundance, species composition and trophic interactions during 2 consecutive stages of zooplankton succession. Over a 3 wk period, metazooplankton shifted from dominance of rotifers to cyclopoid copepods and thereafter to cladocerans. On 2 different dates with contrasting zooplankton assemblages we performed enclosure experiments where we compared the population dynamics of ciliates in size-fractionated (<50 µm) treatments with enclosures containing *in situ* densities of metazooplankton. The ciliate community in the lake and in the enclosures was mainly represented (>80% of total abundance) by 3 small-sized taxa: *Urotricha* spp., *Halteria grandinella* and *Rimostrombidium brachykinetum*, which showed different dynamics in response to metazooplankton. In the first experiment, with dominance of rotifers, zooplankton had only a modest predatory impact on the ciliates, and interactions within the ciliate community were probably more important. Larger, raptorial ciliates (e.g. *Monodinium* sp., *Lagynophrya* sp.) seemed to have been the main predators of the small ciliates. Different species-specific responses of ciliates within the same size range were observed. In contrast, the second experiment, with dominance of crustacean zooplankton (cladocerans, copepods), demonstrated a clear top-down control of the whole ciliate community by metazooplankton. Predation is probably the dominating regulating mechanism for ciliate abundance, biomass and species composition in Lake Søbygård. In contrast, food limitation is thought to be of minor importance because of generally high concentrations of edible phytoplankton. This view was also supported in our experiments by very high net growth rates of the dominating ciliate species after predator removal (in the range 1.0 to 2.4 d<sup>-1</sup>). The study revealed 2 characteristics of hypertrophic lakes: first, zooplankton composition and the resulting predation pattern is the decisive factor for the protozoan community structure, and second, the ciliate community is dominated by high densities of a few small-sized species.

**KEY WORDS:** Ciliates · Zooplankton · Microbial food web · Hypertrophic lake · Predation · Rotifers · Copepods · Cladocerans

## INTRODUCTION

The classical grazer food chain and the microbial food web are linked by several direct and indirect interactions. Metazooplankton grazing is important for the recycling of nutrients and the production of dissolved organic substrates for bacteria (Lampert 1978) but it is also a controlling factor for the protozoan com-

munity structure (Sanders & Wickham 1993). The coupling between zooplankton and protists can have cascading effects on planktonic bacteria (Jürgens et al. 1994) and thus be an important structuring factor for the entire microbial food web. Due to their potential as grazers of small phytoplankton and bacteria and their role as food for various metazoans, ciliates are especially important links in pelagic food webs. Their grazing impact on pico- and nanoplankton has been demonstrated in marine studies (Sherr & Sherr 1987) and more recently also in freshwater lakes (Šimek et

\*E-mail: juergens@mpil-ploen.mpg.de

al. 1995, Stabell 1996). The number of studies which have examined ciliate communities in the freshwater plankton has considerably increased in the last decade. However, our knowledge of the species composition, distribution and regulating factors of planktonic ciliates is still fragmentary.

The first comprehensive analysis of freshwater planktonic ciliate community structure was done by Beaver & Crisman (1982). They described the shift in species composition in subtropical Florida lakes with increasing eutrophication, and assigned the orders Scuticociliatida, Oligotrichida, and Haptorida as the numerically most important ciliates. More recent studies in temperate European (Müller 1989, Müller et al. 1991, Laybourn-Parry & Rogerson 1993) and North American lakes (Taylor & Heynen 1987, Carrick et al. 1992) deviate from the observations of Beaver & Crisman (1982). Small species from the orders Prostomatida and Oligotrichida were generally found to be the most abundant ciliate groups in temperate mesoeutrophic lakes.

Even less knowledge exists concerning the regulating mechanisms of planktonic ciliates, which show considerable seasonal dynamics with respect to species composition and abundance (e.g. Müller et al. 1991). Zooplankton predation, mainly by copepods, on ciliates is well documented in marine systems (see Stoecker & Capuzzo 1990). The zooplankton-protzoan link in freshwater planktonic food webs has been examined recently and metazooplankton predation is an important controlling factor for the major protozoan groups (Carrick et al. 1991, Sanders & Wickham 1993). Most metazooplankton groups can probably exert grazing pressure on ciliates; this has been demonstrated in laboratory experiments with cyclopoid copepods (Wickham 1995), calanoid copepods (Burns & Gilbert 1993), cladocerans (Jack & Gilbert 1993), and rotifers (Arndt 1993, Gilbert & Jack 1993). Due to their different feeding modes, different species-specific effects of metazooplankton on natural ciliate communities could also be identified (Wiackowski et al. 1994, Wickham 1995). The degree to which ciliates are affected by predation or mechanical interference depends on their size and the existence of defence mechanisms (Jack & Gilbert 1997).

Eutrophic shallow lakes are especially suitable for studying trophic interactions due to a relatively simple food web structure, high process rates and mostly prevailing top-down control on plankton organisms (Jeppesen et al. 1997). These lakes are characterized by the dominance of few species which replace each other during the seasonal cycle and cause great oscillations in the whole pelagic ecosystem (Jeppesen et al. 1990). Field experiments using intact natural communities can help to identify the various direct and indi-

rect effects of higher trophic levels on microbial populations and communities.

The goal of the present study was to examine the impact of different metazoan zooplankton communities on the major components of the microbial food web (ciliates, flagellates, bacteria). We used field enclosures in which zooplankton abundance and composition was manipulated by size-fractionation during 2 consecutive stages in the plankton succession of the shallow, hypertrophic Lake Søbygård. In this paper we report on the population dynamics of ciliates, at the community and the species level, in response to the changing metazooplankton composition. In a following paper (Jürgens & Jeppesen unpubl.) we analyse the cascading effects of the food web structure on autotrophic and heterotrophic pico- and nanoplankton.

## METHODS

**Lake Søbygård.** Lake Søbygård is a shallow, hypertrophic lake situated in central Jutland, Denmark (56° 15' 20" N, 9° 48' 35" E). It is 0.38 km<sup>2</sup> in area, with a mean depth of 1.0 m and maximum of 1.9 m. The hydraulic retention time is on average 15 to 20 d. Lake water is well mixed and thus without summer stratification. Submerged vegetation is sparse or absent. The average concentration of chlorophyll *a* during summer is between 130 and 730 µg l<sup>-1</sup> (Jeppesen et al. 1990). This lake was intensively studied over the last 14 yr and sediment-water interactions are described by Søndergaard et al. (1990), studies of the biological community are reported by Jeppesen et al. (1990, 1996, 1997, 1998), and Hansen & Jeppesen (1992).

**Enclosure experiments.** During 2 consecutive periods in July/August 1994 mesocosm experiments were performed in Lake Søbygård. Six 500 l polyethylene enclosures (0.9 m in diameter, 0.7 m in depth), closed at the bottom and fixed to a wooden frame, were located close to the shore in the lake. Size-fractionated filtrations were applied in order to manipulate the zooplankton. All enclosures were first gently filled with water collected at a mid-lake station and filtered through a 50 µm mesh in order to remove mesozooplankton. In 3 of the enclosures (further referred to as '+ZP') zooplankton was reintroduced at approximately natural densities. Three of the enclosures were left without additional zooplankton (referred to as '<50'). In addition to these enclosures, three 10 l glass bottles were filled with lake water filtered through a 10 µm mesh, in order to remove micro- and mesozooplankton. These were incubated near the other enclosures in the lake (referred to as '<10'). The manipulated enclosures and bottles were sampled for 5 to 6 d in the lake; the first experiment was conducted

from 6 to 11 July, the second experiment from 19 to 24 July 1994.

**Sampling, chemical and biological analysis.** Sampling of the enclosures for the microbial components (picoplankton, protozoans) was done once or twice daily during the experiments. Sampling for the chemical analysis and the determination of zooplankton abundance and species composition was done at the beginning and end of the experiments. Chemical analysis was performed according to standard methods (see Søndergaard et al. 1990); chlorophyll *a* was determined spectrophotometrically after extraction with ethanol according to Holm-Hansen & Riemann (1978). For zooplankton, 2 l samples were filtered through a 40 µm net, then fixed in Lugol. Ciliates and rotifers were counted and sized from Lugol's fixed samples using settling chambers and an inverted microscope. Selected samples for identification of ciliates to genus- or species-level were post-fixed with Bouin's fixative and impregnated with Protargol according to the quantitative technique of Montagnes & Lynn (1987), modified by Skibbe (1994). Dominant ciliate species could be related from Protargol-stained preparations to Lugol's fixed samples which were used for the quantification. Parallel to the sampling of the enclosures, water samples were taken from a mid-lake station (1.5 m depth) with a core sampler covering the upper 1 m of the water column.

**Data analysis.** We analysed all data of an experiment by using measurements of the same variable (ciliate taxa or group of organisms such as small and large ciliates, rotifers) within the same enclosure at different

times (repeated-measures ANOVA). We compared the development of organisms between the treatment with zooplankton to those where zooplankton was removed (<50, <10). Data were log-transformed before ANOVA to stabilize variances. ANOVAs were performed using the software package STATISTICA 5.1. Due to multiple simultaneous tests of the different organisms, a sequential Bonferroni test procedure (Rice 1989) was performed. The initial critical probability value was set at  $p < 0.05/n$ , where  $n$  = number of tests per experiment (11 or 12, respectively). Net growth rates of the dominant ciliate taxa were calculated for intervals where population abundance increased for more than 2 sampling dates and by taking the slope of the regression of cell number (natural logarithm) versus time.

## RESULTS

The enclosure experiments were performed during a period of warm and stable weather conditions with water temperatures of 20 to 25°C. The design of our size-fractionations (first filtering all enclosures through a 50 µm mesh, then refilling zooplankton in the +ZP treatments) proved to be adequate for this situation as it did not strongly alter the chemical conditions or the phytoplankton community compared to the lake (Table 1). Significant changes occurred within the phytoplankton assemblage during the study period, with a strong increase in all dominant algae during the time of the first experiment and a shift in species composition from the first to the second experiment. The

Table 1. Physico-chemical conditions (TP: total phosphorus; TN: total nitrogen), chlorophyll *a* and particulate organic carbon (POC) in the enclosures and in the lake during the 2 experiments. Values for the enclosures are mean values of the 3 replicate treatments (mean CV = 9.4%); values for the lake are mean values of duplicate measurements. nd: not determined

	PO <sub>4</sub> -P	TP	NH <sub>4</sub> -N (mg l <sup>-1</sup> )	NO <sub>3</sub> -N	TN	POC	Chl <i>a</i> (µg l <sup>-1</sup> )	Temp. (°C)
Expt 1 (July 7)								19.5–22.8
<50, +ZP	0.87	1.02	0.30	0.48	1.95	3.44	31.3	
<50	0.87	1.10	0.24	0.50	1.80	4.09	34.9	
<10	0.82	0.97	0.21	0.51	1.75	4.35	28.5	
Lake	0.98	1.14	0.58	0.43	2.30	3.21	26.0	
Expt 1 (July 11)								
<50, +ZP	0.25	0.73	0.01	0.00	1.57	9.81	38.3	
<50	0.26	0.68	0.00	0.00	1.52	9.21	41.3	
<10	0.13	0.96	0.02	0.00	1.84	13.54	55.7	
Lake	0.63	0.96	0.01	0.00	2.10	9.78	219.0	
Expt 2 (July 19)								21.2–25.2
<50, +ZP	0.61	1.02	0.01	0.00	2.70	10.61	139.0	
<50	0.61	0.95	0.00	0.00	1.80	11.05	134.2	
<10	0.62	0.93	0.00	0.00	1.70	9.88	120.8	
Lake	nd	nd	nd	nd	nd	nd	196.5	

dominating algae during the first experiment were *Actinastrum* sp., *Monoraphidium* sp., *Scenedesmus* spp., *Pediastrum* sp. and several species of cryptomonads. Prokaryotic and eucaryotic picoalgae increased during the course of the first experiment (*Synechococcus* spp. and *Chlorella* spp., both  $>10^5$  cells  $\text{ml}^{-1}$ ). During the second experiment the phytoplankton assemblage was dominated by a bloom of *Scenedesmus* spp. (mainly *S. quadricauda* and *S. acuminata*, coenobia and single cells). The increase in phytoplankton, which was much more pronounced in the lake than in the enclosures, was probably the reason for the depletion in ammonium and nitrate below the detection limit whereas P concentrations remained at a high level (Table 1).

### Zooplankton dynamics

During our experiments, 2 consecutive stages in the zooplankton succession occurred in Lake Søbygård. The beginning of the first experiment was characterized by the dominance of rotifers, with a large contribution of *Brachionus* species (mainly *B. calyciflorus*), *Keratella quadrata* and *Asplanchna* spp. (Table 2). The situation was already in a transient state and rotifer populations in the lake were declining strongly. *Keratella* spp. had disappeared totally by the end of the experiment, and *Brachionus* spp. decreased to less than 5% of its former values. Only *Asplanchna* spp. remained at high levels and became the dominant rotifer species at the end of that week (Table 2). One reason for the rotifer collapse under relatively stable food conditions was exposure to predation by *Asplanchna* spp. and *Cyclops vicinus*. In addition, *Brachionus* spp. was heavily infected by microsporidians (probably *Plistophora asperospora*, H. Holst, University of Hamburg, pers. comm.) which are known to cause mortality of planktonic rotifers (Ruttner-Kolisko 1977). The only zooplankton which increased during the course of the first experiment were cyclopoid copepods (mainly *C. vicinus*).

One week later, at the start of the second experiment, zooplankton composition was dominated by cyclopoid copepods (adult and copepodite stages of *Cyclops vicinus*) and daphnids. *Daphnia* spp. increased further towards the end of the experiment (Table 2) and were then, in terms of biomass, the dominating zooplankton group. Rotifers remained in low numbers during the second experiment. In summary, contrasting zooplankton compositions prevailed during the 2 experiments: the first experiment can be characterized as microzooplankton-dominated with high numbers of rotifers, whereas the second experiment was a mesozooplankton-dominated community

with high numbers of *C. vicinus* and *Daphnia* spp. However, during both experiments zooplankton shifted in species composition, in the lake as well as in the enclosures: first from rotifers to *C. vicinus* dominance, and second, from *C. vicinus* to *Daphnia* spp. dominance.

The manipulation of the metazooplankton community by our size-fractionation design proved to be successful and in both experiments we obtained manipulated treatments virtually without any metazooplankton ( $<10 \mu\text{m}$ ) or without crustacean zooplankton and brachionids ( $<50 \mu\text{m}$ ). Also, the treatment designed to result in a comparable composition of zooplankton to the lake (+ZP) worked well, with a modest reduction (Expt 1) or increase (Expt 2) in zooplankton abundance compared to the lake. However, due to the strong dynamics inherent in the lake zooplankton community, the situation also changed in the enclosures (Fig. 1). In the first experiment small rotifers (mainly *Filinia* sp.) increased in the zooplankton-free enclosures ( $<50$ ). In the +ZP enclosures, a collapse of

Table 2. Zooplankton composition and abundance (ind.  $\text{l}^{-1}$ ) in Lake Søbygård at the start and end of the 2 enclosure experiments

Zooplankton	Expt 1		Expt 2	
	7 July	11 July	19 July	24 July
<i>Cyclops vicinus</i>	5.7	12.9	28.6	1.8
<i>Eucyclops serrulatus</i>	1.1	0.3	0	1.8
Cyclopoid copepodites	29.7	55.2	290.5	86.0
Cyclopoid nauplii	63.5	121.6	461.9	164.9
<b>Total copepods</b>	<b>99.7</b>	<b>190.0</b>	<b>781.0</b>	<b>254.4</b>
<i>Daphnia</i> spp.	0.5	4.6	109.5	203.5
<i>Ceriodaphnia</i> spp.	0	0.2	0	0
<i>Bosmina longirostris</i>	0	0	2.4	5.3
<i>Alona</i> spp.	3.8	0	0	5.3
<i>Chydorus</i> spp.	1.7	4.1	9.5	1.8
<i>Pleuroxus uncinatus</i>	2.7	0	0	7.0
<b>Total cladocerans</b>	<b>8.8</b>	<b>8.7</b>	<b>121.4</b>	<b>222.8</b>
<i>Brachionus calyciflorus</i>	5843.2	124.6	0.0	0.0
<i>B. budapest</i>	462.9	0.0	0.0	0.0
<i>B. rubens</i>	587.3	0.0	0.0	8.8
<i>B. angularis</i>	98.7	32.5	0.0	54.6
<i>B. urceolaris</i>	0.0	0.0	0.0	5.3
<i>Keratella quadrata</i>	2421.7	0.0	0.0	0.0
<i>K. cochlearis</i>	19.7	0.0	0.0	0.0
<i>Filinia longiseta</i>	47.6	27.0	26.2	54.6
<i>F. cornuta brachiata</i>	209.8	27.8	0.0	0.0
<i>Synchaeta</i> spp.	7.9	27.8	0.0	0.0
<i>Polyarthra</i> spp.	531.6	484.4	169.2	1.8
<i>Euchlanis</i> spp.	7.9	0.0	0.0	0.0
<i>Trichocerca pusilla</i>	9.8	0.0	0.0	0.0
<i>Asplanchna priodonta</i>	119.0	120.6	0.0	0.0
<i>A. girodi</i>	666.7	482.5	52.4	1.8
<b>Total rotifers</b>	<b>11034.0</b>	<b>1327.3</b>	<b>247.7</b>	<b>126.7</b>

the *Brachionus* population and an increase of copepods occurred, which is similar to the situation in the lake. This resulted in a somehow reversed situation in which the <50 enclosures achieved a higher density of rotifers at the end of the experiments than the +ZP enclosures. In the second experiment, where large crustacean zooplankton dominated, a clearer difference between <50 and +ZP enclosures occurred. The +ZP treatments showed a shift from copepods to cladocerans (virtually *Cyclops vicinus* to *Daphnia* spp.) which corresponded to the shift in the lake but in higher abundance. The <50 enclosures developed only moderate densities of rotifers whereas mesozooplankton remained virtually absent (Fig. 1).

#### Ciliate species composition

Total ciliate abundance in the lake was within the range of 100 to 600 cells ml<sup>-1</sup> during the first experimental period and 30 to 100 cells ml<sup>-1</sup> during the second experiment. The ciliate community was dominated by typical planktonic species (see Foissner 1994). Altogether 22 taxa were identified from Protargol-stained samples (Table 3). The dominating species occurred in both experiments and all treatments but in different proportions. In the lake and in the experimental enclosures, ciliates were dominated by small prostomatids (*Urotricha* spp.) and small oligotrichs (*Halteria* spp., *Strobilidium* spp.).

We tried to determine the dominant species by assessing relevant taxonomic features from Protargol impregnations (Fig. 2). There were several small *Urotricha* species that were very common during the entire study period. The majority were probably *U. furcata* (Fig. 2A) and *U. farcta*. However, they could not quantitatively be distinguished because the only reliable criterion seems to be the second caudal cilium in *U. furcata* (Foissner et al. 1994), which was not always clearly visible. Therefore we lumped these 2 species (and possibly other small species of this genus) together as *Urotricha* spp. The other small prostomatid of temperate lakes, *Balanion planctonicum* (Müller 1991), was not found in our samples. The oligotrich *Halteria* sp., which occurred in considerable numbers

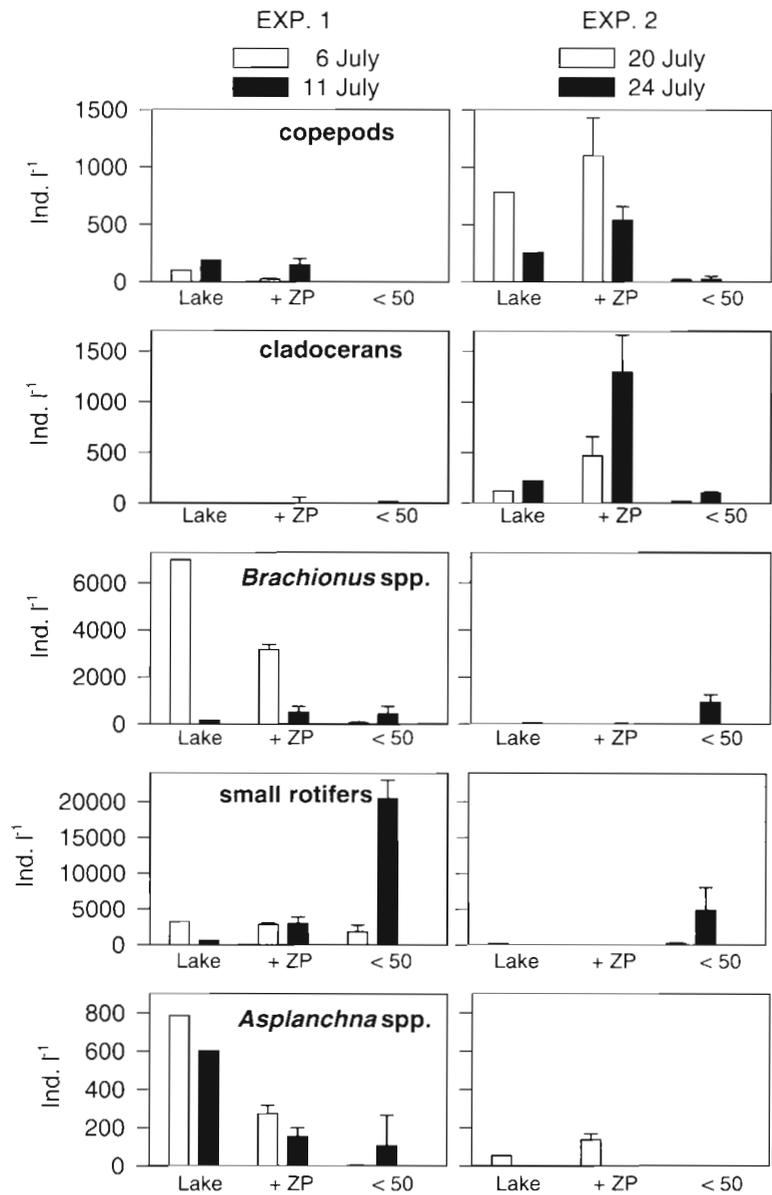


Fig. 1. Initial and final abundances of metazoan zooplankton in the mesocosms and in Lake Søbygård

in the experiments, closely resembles the descriptions of *H. grandinella* (Foissner et al. 1991), a widely distributed and common species in freshwater plankton (Foissner 1994, Šimek et al. 1995). The other abundant oligotrich was a small *Strobilidium* sp., characterized by 6 somatic kinetids and a body length of 15 to 20  $\mu\text{m}$ . This species, whose morphology was consistent among individuals (Fig. 2C), occurred in high numbers especially during the first experiment. It seems to be the same species (K. Šimek pers. comm.) which has been described and quantified in Rimov Reservoir by Šimek et al. (1995) under the name *Strobilidium hexakine-*

tum. However, no proper original description of *S. hexakinetum* exists and the same species was later described by Krainer (1995) under the name *Rimostrombidium brachykinetum* (Foissner pers. comm.). We refer to the name proposed by Krainer (1995) because we think that this species can clearly be identified from Protargol impregnations. However, we are aware that there is some controversy in the literature concerning the nomenclature of strobiliid ciliates and whether one should use the genera name *Rimostrombidium* or *Strobilidium* (Petz & Foissner 1992, Foissner 1994, Montagnes & Lynn 1991).

During the first experiment the 3 taxa *Urotricha* spp., *Halteria grandinella* and *Rimostrombidium brachykinetum* always comprised >90% and during the second

experiment >80% of total ciliate abundance. During the second experiment scuticociliates (*Cyclidium* spp., *Cinetochilum margaritaceum*) and *Cyrtolophosis mucicola* also developed in higher numbers (up to 20 ml<sup>-1</sup>) in the <50 enclosures.

Within the larger sized ciliate taxa, only haptorids increased in abundance and reached higher cell numbers in the experimental treatments when metazooplankton were reduced. The most abundant of these predatory ciliates, reaching numbers of up to 20–30 ml<sup>-1</sup> in the zooplankton-free enclosures, were *Monodinium* sp. and *Lagynophrya acuminata* (Fig. 2A,D). The latter resembled the species described by Wilbert (1986) and Foissner et al. (1995). *Monodinium* sp. were present with 1 or 2 ciliary bands; the latter are cells in division and might be confused with a small *Didinium*. However, within a larger *Didinium* population there are always some dividing cells with 4 ciliary bands (Skibbe unpubl. obs.) but this was not the case in our samples. Other predatory ciliates which frequently occurred were *Askenasia* sp., *Urotricha pelagica* and *Paradileptus elephantinus*.

Table 3. List of ciliate taxa determined from Protargol impregnations. Size range (max. dimensions) as determined from Lugol-fixed samples

Ciliate taxon	Size (µm)
Prostomatida	
<i>Urotricha</i> sp. 1 ( <i>furcata/farcta</i> )	12–18
<i>Urotricha</i> sp. 2 (c.f. <i>pelagica</i> )	35–60
Oligotrichida	
<i>Rimostrombidium brachykinetum</i>	15–19
<i>Strobilidium lacustris</i>	50–55
<i>Strombidium viride</i>	35–50
<i>Halteria grandinella</i>	17–25
Haptorida	
<i>Askenasia</i> sp.	25–32
<i>Monodinium</i> spp.	35–55
<i>Lagynophrya</i> sp.	32–50
<i>Paradileptus elephantinus</i>	100–160
<i>Actinobolina</i> sp.	55–70
<i>Enchelys</i> sp.	45–55
Scuticociliatida	
<i>Cyclidium</i> sp.	15–25
<i>Cinetochilum margaritaceum</i>	20–30
<i>Pleuronema</i> sp.	50–60
Peritrichida	
<i>Vorticella</i> spp.	20–25
<i>Vorticella meyeri</i>	25–30
Colpodea	
<i>Cyrtolophosis mucicola</i>	20–27
Pleurostomatida	
<i>Litonotus</i> sp.	60–80
<i>Amphileptus</i> sp.	80–120
Cyrtophorida	
<i>Chilodonella</i> sp.	30–35
Hypotrichia	
<i>Oxytricha</i> sp.	40–60

### Zooplankton-ciliate interactions

The development of the 3 dominant ciliate taxa in the lake and in the enclosures is shown for the 2 experimental periods in Figs. 3 & 4. For the first experiment (Fig. 3) large (predatory) ciliates and rotifers are also shown, for the second experiment (Fig. 4) large ciliates and other small ciliates (mainly scuticociliates and *Cyrtolophosis mucicola*) were included. Great differences occurred in the population development for the different ciliate species between experiments and treatments. The population dynamics in the enclosures with zooplankton (+ZP) closely resembled in both experiments the development in the lake, thus indicating that our treatment did not strongly alter the natural conditions. In contrast, the <50 and <10 enclosures exhibited deviating population developments for some of the respective ciliate species; we interpreted this mainly as a result of altered zooplankton composition. Results of statistical tests for comparison of the enclosures <50 and <10 with +ZP are shown in Table 4.

The repeated-measure ANOVAs revealed whether there are significant changes during time and between the treatments with and without zooplankton. This and the illustration of the general population developments (Figs. 3 & 4) demonstrate that the removal of metazooplankton >50 µm had different effects in the 2 experiments: in the first experiment there was a reduction and in the second one an increase in the population development of small ciliates relative to the controls (+ZP). In the first experiment the <50 µm-filtration

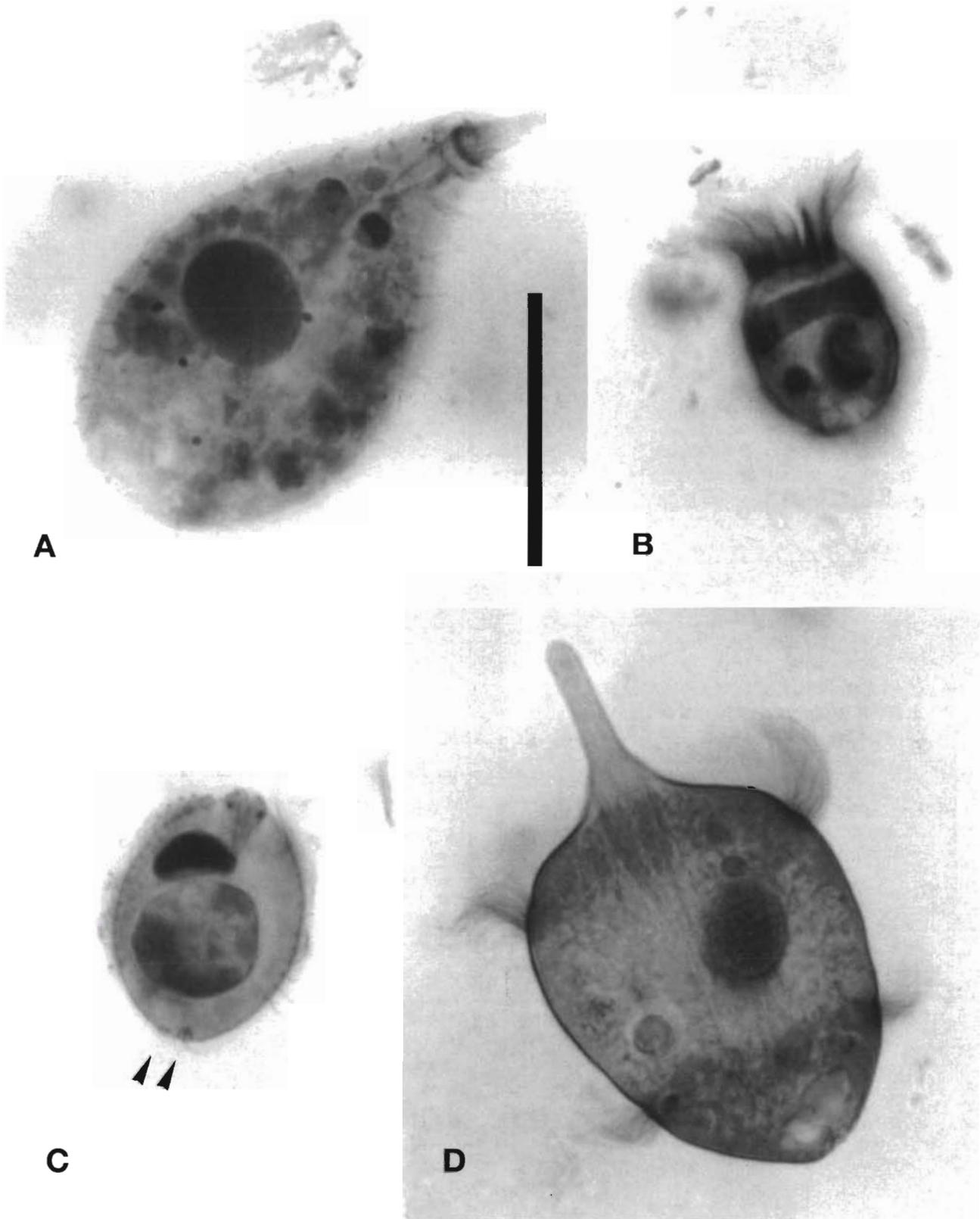


Fig. 2. Microphotographs of Protargol impregnations of some dominating ciliate species during the experiments. (A) *Lagynophrya acuminata*; (B) *Rimostrombidium brachykinetum*; (C) *Urotricha furcata*, arrows point to the 2 basal bodies of the caudal cilia; (D) *Monodinium* sp. Scale bar = 20  $\mu\text{m}$

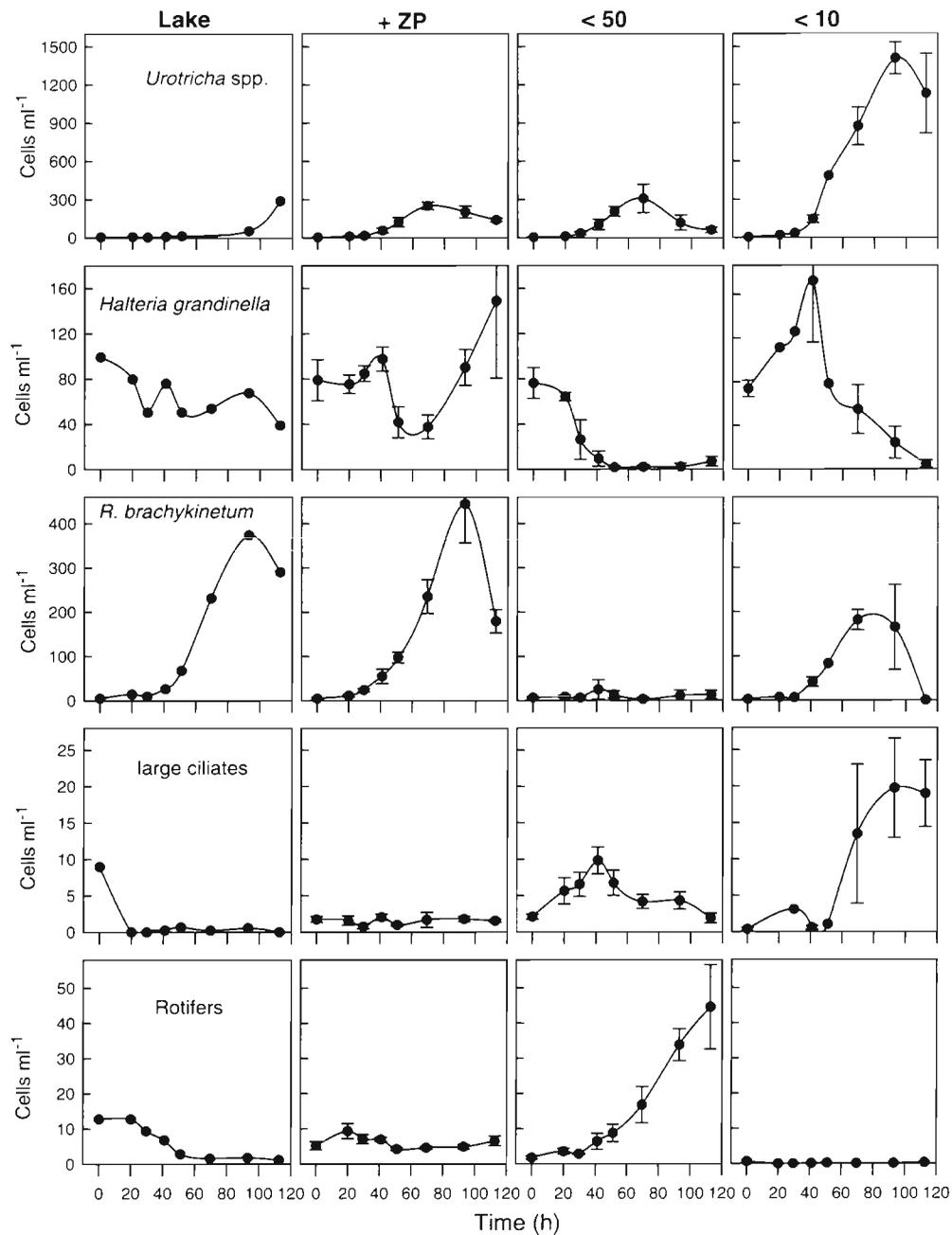


Fig. 3. Expt 1: population dynamics of the 3 dominating small ciliate species, total large ciliates and rotifers in the mesocosms (mean and standard deviation of the 3 replicate enclosures) and in the lake

removed cyclopoid copepods and strongly reduced the larger rotifers (*Brachionus* spp., *Asplanchna* spp.) (Fig. 1). For the 3 dominant ciliates, this resulted in either no (*Urotricha*) or negative (*Halteria*, *Rimostrombidium*) effects with strong declines compared to the zooplankton treatment. Possible predators on the small ciliates were rotifers and large, predatory ciliates which developed in the <50  $\mu\text{m}$  fraction. The main

species of ciliates in this group were the Haptorids *Lagynophrya* sp. and *Monodinium* sp., and the main rotifers were *Filinia* sp. and *Polyarthra* sp. The <10  $\mu\text{m}$ -filtration resulted first in an increase of all ciliate species, but towards the end of the experiment small species decreased again, parallel to the maximum of large, predatory ciliates. Although in maximum dimensions far larger than the net mesh size, some of these preda-

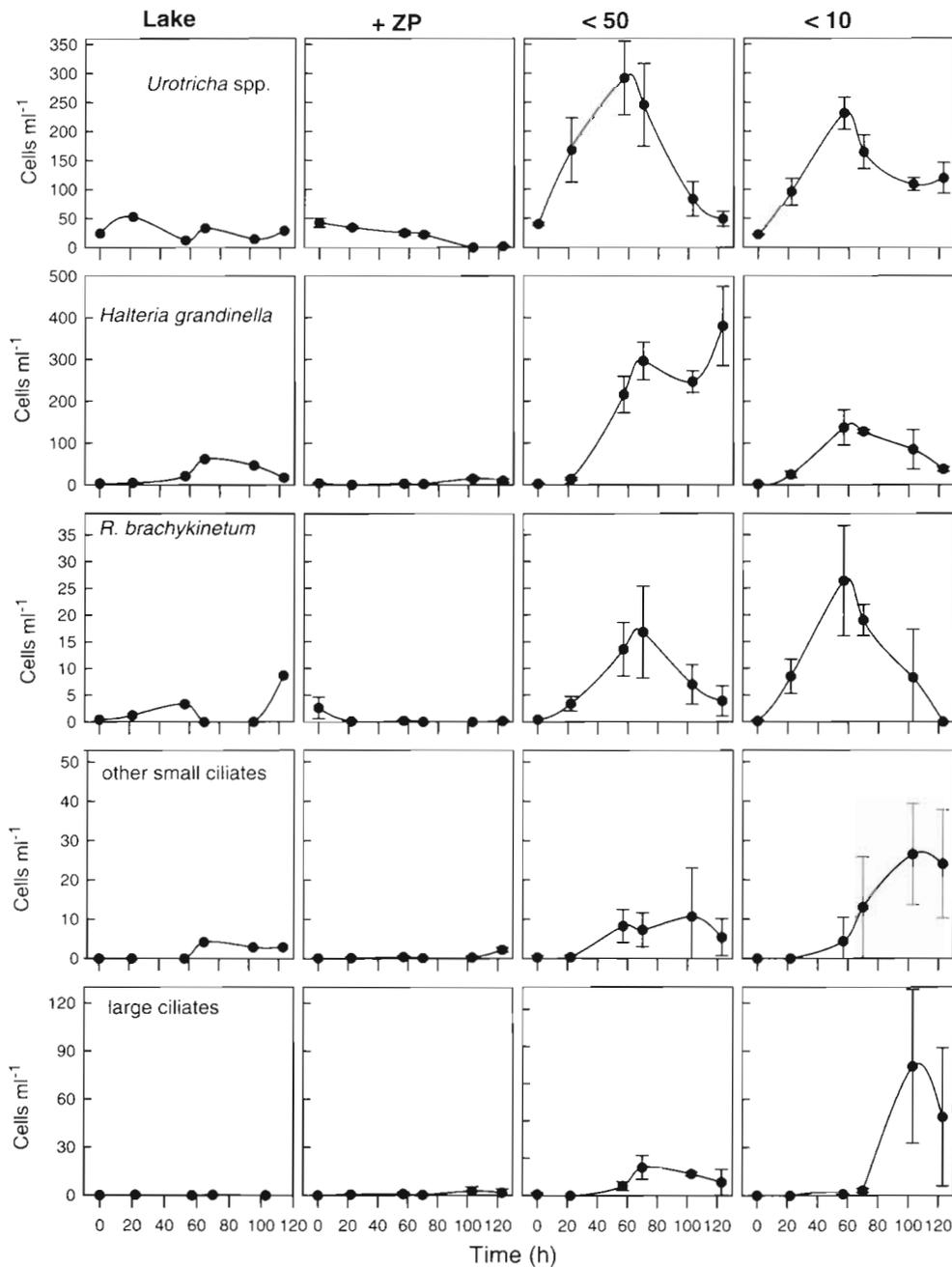


Fig. 4. Expt 2: population dynamics of the 3 dominating small ciliate species, large, predatory ciliates and other small ciliates (mainly *Cyclidium* spp., *Cinetochilum margaritaceum* and *Cyrtolophosis mucicola*) in the mesocosms (mean and standard deviation of the 3 replicate enclosures) and in the lake

tory ciliates can also pass through a 10 µm mesh and then rapidly increase in abundance.

The <50 µm fractionation in the second experiment, where crustacean zooplankton dominated, eliminated most of the metazooplankton and only rotifers (*Brachionus* spp. and *Polyarthra* spp.) appeared in moderate densities in these treatments (Fig. 1). The removal of mesozooplankton had a clear positive effect on all

ciliate taxa which showed a strong and immediate response after zooplankton removal. In addition to the 3 major ciliate taxa, Scuticociliates (mainly *Cyclidium* spp., *Cinetochilum margaritaceum*) and *Cyrtolophosis mucicola* also developed in higher abundance. Large, predatory ciliates (mainly *Lagynophrya* sp.) developed more towards the end of the experiment, again paralleled by a decrease in small ciliates.

From the population increases in the treatments without or with reduced metazoan predators (<10, <50) we calculated the net growth rates of the dominant ciliate taxa (Table 5). The values are within the range 1 to 2.35 d<sup>-1</sup> (doubling times 7 to 17 h). These high growth rates could be found for the 3 dominating small ciliate taxa and also for the larger raptorial species *Monodinium* sp. and *Lagynophrya* sp.

## DISCUSSION

Typical for hypertrophic lakes are the dominance of a few species which occur in high abundance, and large oscillations in the biological structure due to reduced homeostatic mechanisms within the plankton community when compared to oligo- and mesotrophic lakes (Jeppesen et al. 1990, Sommaruga & Robarts 1997). In Lake Søbygård strong fluctuations occur in the plankton community structure over short time scales, which can often be related to changes in fish predation pressure and cascading effects at lower trophic levels (Jeppesen et al. 1990, 1996). Increased fish predation results, for example, in a shift from *Daphnia* to *Bosmina* and copepods, and at even higher fish predation to dominance of rotifers and cyclopoid copepods (Jeppesen et al. 1990, 1998). Productivity in Lake Søbygård is extremely high and densities of phyto- and zooplankton are among the highest reported in the literature. Chlorophyll *a* levels regularly reached maxima of >500 µg l<sup>-1</sup> and summer means of zooplankton biomass (consisting mainly of rotifers, cyclopoids, *Bosmina longirostris* and *Daphnia hyalina*) are within the range 0.5 to 1.2 mg C l<sup>-1</sup> (Jeppesen et al. 1998). Although the lake now has reduced nutrient loading, it is still hypertrophic, and it is no surprise that ciliate concentrations proved to be among the highest reported in the literature.

The field situation examined during our enclosure experiments represented a typical summer situation for Lake Søbygård. A comparable zooplankton succession, with a shift from rotifers (mainly brachionids) to copepods and cladocerans, has been reported from previous years (Jeppesen et al. 1990). Lake Søbygård is one of the few examples where rotifers achieve sufficiently high numbers to produce a phytoplankton collapse and a clear-water phase (Jeppesen et al. 1990).

Table 4. Summary of the effects of zooplankton manipulation on the abundance of ciliates and rotifers. Results of ANOVA with repeated measure, in comparison to zooplankton treatments (+ZP). Data from all dates during the experiments were used. Reported levels of significance (p values) correspond to the univariate between-subject effect. ↑ and ↓ denote whether the fractionation significantly increased or decreased the mean population density, respectively. Significance was judged according to the sequential Bonferroni procedure, with an initial critical probability value of  $p < 0.0045$  (11 non-independent tests, Expt 1) or  $p < 0.0042$  (12 non-independent tests, Expt 2), respectively. nt: not tested due to low abundance

Variable	Expt 1		Expt 2	
	<50 µm	<10 µm	<50 µm	<10 µm
<i>Urotricha</i> spp.		↑	↑	↑
Zooplankton	0.8818	0.0006	0.0002	0.0002
Time	0.0000	0.0000	0.0000	0.0000
Zooplankton × Time	0.3045	0.0069	0.0000	0.0000
<i>Halteria grandinella</i>			↑	↑
Zooplankton	0.0260	0.0283	0.0000	0.0000
Time	0.0000	0.0000	0.0000	0.0000
Zooplankton × Time	0.0001	0.0000	0.0000	0.0000
<i>Rimostrombidium brachykinetum</i>	↓		↑	↑
Zooplankton	0.0065	0.047	0.0001	0.0025
Time	0.0290	0.0000	0.2058	0.0020
Zooplankton × Time	0.0001	0.0000	0.0002	0.0001
Other small ciliates			↑	↑
Zooplankton	nt	nt	0.0021	0.0077
Time	nt	nt	0.0001	0.0000
Zooplankton × Time	nt	nt	0.0394	0.0021
Total small ciliates	↓	↑	↑	↑
Zooplankton	0.0030	0.0006	0.0000	0.0000
Time	0.0000	0.0000	0.0000	0.0000
Zooplankton × Time	0.0000	0.0060	0.0000	0.0000
Large ciliates	↑		↑	↑
Zooplankton	0.0013	0.4705	0.0224	0.0009
Time	0.0008	0.0000	0.0161	0.0000
Zooplankton × Time	0.0000	0.0000	0.2608	0.0290
Rotifers				
Zooplankton	0.0385	nt	nt	nt
Time	0.0000	nt	nt	nt
Zooplankton × Time	0.0000	nt	nt	nt

Our experimental study covered the following successional sequences: (1) final stage of a rotifer-induced phytoplankton depression with the dominance of picoplanktonic algae; (2) collapse of the rotifer population probably due to predation and parasitism, strong population growth of *Cyclops vicinus*; (3) phytoplankton bloom (mainly *Scenedesmus*) and population maxima of cyclopoid copepods; (4) population increase of *Daphnia* spp.

The last stage, which was not entirely covered by our experiments, would probably have resulted in the next phytoplankton depression and clear-water phase due to a large *Daphnia* population (Jeppesen et al. 1990).

Table 5. Maximum abundances of the dominant ciliate species in Lake Søbygård and in the 2 enclosure experiments (mean  $\pm$  SD of 3 replicate enclosures). Maximum net growth rates are calculated from the population increase in the enclosures (mean  $\pm$  SD of 3 replicates)

Ciliate taxon	Lake	Max. abundance (ml <sup>-1</sup> )		Max. net growth rate (d <sup>-1</sup> )	
		Enclosure Expt 1	Enclosure Expt 2	Expt 1	Expt 2
<i>Urotricha</i> spp. ( <i>furcata/farcta</i> )	288	1406 $\pm$ 125	292 $\pm$ 63	2.24 $\pm$ 0.11	1.00 $\pm$ 0.16
<i>Rimostrombidium brachykinetum</i>	374	445 $\pm$ 88	17 $\pm$ 9	1.52 $\pm$ 0.32	1.51 $\pm$ 0.33
<i>Halteria grandinella</i>	99	170 $\pm$ 71	380 $\pm$ 95	1.64 $\pm$ 0.39	1.90 $\pm$ 0.16
<i>Monodinium</i> sp.	1	15 $\pm$ 7	0	2.10 $\pm$ 0.60	0
<i>Lagynophrya</i> sp.	3	27 $\pm$ 9	74 $\pm$ 49	1.64 $\pm$ 0.39	2.35 $\pm$ 0.71

### Ciliate community structure

The ciliate assemblage of Lake Søbygård was dominated by typical planktonic species (Foissner 1994), and, despite the mixing of the shallow water column, benthic species (e.g. hypotrichous ciliates) only occurred sporadically in the samples. The high ciliate densities found during our investigation period were well within the range normally observed in this lake, the summer means of previous years were 100 to 300 ciliates ml<sup>-1</sup> (Jeppesen et al. 1998), and fit to the generally high abundance of all plankton organisms in this productive system.

Although Lake Søbygård is an extreme habitat with respect to the mixing regime, high nutrient input, primary productivity and concentrations of organisms, it seems that the general composition of the ciliate community during our study period is comparable to other deeper and less eutrophic lakes.

Planktonic ciliate communities of several temperate lakes in central Europe have been recently examined: mesotrophic Lake Constance in southern Germany (Müller 1989), eutrophic Rimov Reservoir in southern Bohemia (Šimek et al. 1995, Macek et al. 1996) and oligo-mesotrophic Piburger See in Austria (Sommaruga & Psenner 1993, Macek et al. 1996). Some characteristic features are that ciliates <20 to 30  $\mu$ m numerically dominate and that the major taxa throughout most of the season are small prostomatids (*Urotricha* spp., *Balanion planctonicum*) and small oligotrichs (*Halteria* spp., *Strobilidium* spp.) whereas bacterivorous Scuticociliates are only temporarily more important.

The dominating taxa in our study, *Urotricha*, *Rimostrombidium* (or *Strobilidium*) and *Halteria*, were also among the most important ciliate species in the other lake studies. For example, in the Rimov Reservoir (Šimek et al. 1995, Macek et al. 1996) the dominant species were also *Halteria grandinella*, *Rimostrombidium brachykinetum* (referred to here as *Strobilidium hexakinetum*) and *Urotricha* spp.. Further, *Cine-*

*tochilum margaritaceum* and *Cyrtolophosis mucicola* occurred in significant numbers in both our study and in the Rimov Reservoir.

The filter-feeding small oligotrichous species, such as *Halteria* and *Strobilidium*, have a substantial grazing impact on heterotrophic and autotrophic picoplankton (Šimek et al. 1995, Stabell 1996) whereas small prostomatids, as raptorial feeders, can exert significant grazing pressure on nanophytoplankton such as cryptomonads (Müller 1991, Sommaruga & Psenner 1993) and the grazing activity of these ciliate groups can have a considerable impact on overall fluxes within the pelagic food web (Weisse et al. 1990, Šimek et al. 1995).

### Zooplankton predation impact

Our enclosure experiments suggest a strong impact of the metazooplankton on the abundance and community structure of the ciliate assemblage. The shift in zooplankton composition between the 2 experiments, from dominance of rotifers to dominance of cyclopoid copepods, was probably the decisive factor for the nearly 10-fold reduction in ciliate numbers from the first to the second experimental period. There are several reasons why changes in food supply (bottom-up control) were not responsible for the ciliate community decline. First, total phytoplankton increased from the first to the second period and, although the majority was composed of *Scenedesmus* colonies, other algae within the edible size range, e.g. cryptomonads, picoalgae and single cells of *Scenedesmus*, were present in fairly high numbers. Second, ciliates responded immediately to the zooplankton changes in the enclosure experiments, and finally the calculated net growth rates of the dominant species (Table 5) are among the highest values measured for these or related species in field or laboratory experiments (Müller & Geller 1993, Macek et al. 1996), thus suggesting saturating food conditions. Favourable growth

conditions for microzooplankton probably prevail during most of the season in Lake Søbygård, as well as in other Danish hypertrophic, shallow lakes, because they are generally dominated by small, edible green algae (e.g. *Scenedesmus* spp., *Chlorella* sp.) (Jensen et al. 1994) and not by cyanobacteria (of probably lower food quality) as found in many deeper, hypertrophic lakes (Sommaruga & Robarts 1997).

Predation rates on different ciliate taxa have been assessed for several metazooplankton groups under defined experimental conditions (e.g. Arndt 1993, Gilbert & Jack 1993, Wiackowski et al. 1994, Wickham 1995). These studies help us interpret the ciliate population dynamics in our experiments. The dominating ciliate species in Lake Søbygård during our experimental period were small-sized forms (15 to 25  $\mu\text{m}$ ) which have been shown to be most susceptible to metazooplankton grazers (Jack & Gilbert 1993, Gilbert & Jack 1993). Strong differences in the predation efficiency of different zooplankton groups may, however, occur (Wiackowski et al. 1994). This was also evident in our experiments where zooplankton predation pressure on ciliates differed substantially between Expts 1 and 2.

#### Expt 1: low predation impact by rotifers

Although the zooplankton population shift during the first experiment made the interpretation of the trophic interactions more difficult, some clear trends can be deduced from the very different developments in the +ZP and <50 enclosures. Contrary to what might be expected, the total number of small ciliates declined after the removal of zooplankton >50  $\mu\text{m}$  but the 3 dominant small ciliate taxa were affected differently: *Rimostrombidium brachykinetum*, which had achieved high growth rates in the lake and in the zooplankton enclosures, was entirely suppressed, *Halteria* declined to lower numbers and *Urotricha* spp. remained nearly unchanged compared to +ZP. Thus, overall top-down control of small ciliates appeared to increase after the removal of metazooplankton. Potential predators in the <50 enclosures were small rotifers (e.g. *Filinia*) and large, predatory ciliates (e.g. *Lagynophrya*, *Monodinium*) which both increased in abundance during the course of the experiment (Fig. 2).

Rotifers are potential predators on ciliates (reviewed by Arndt 1993) and it has been reported that microfiltrating species such as *Brachionus*, *Keratella* and *Filinia* have an impact on small ciliates whereas grasping species such as *Asplanchna* and *Polyarthra* will have a higher impact on large ciliate species (Arndt 1993). Gilbert & Jack (1993) showed that the rotifers *Asplanchna girodi*, *Brachionus calyciflorus* and *Syn-*

*chaeta pectinata* are effective predators of ciliates in the 45 to 60  $\mu\text{m}$  size range, ingesting up to 50 ciliates rotifer<sup>-1</sup> d<sup>-1</sup>. The large rotifer community (>10000 ind. l<sup>-1</sup>) at the start of the first experiment certainly exerted a substantial grazing pressure on the ciliates. It was probably the reason for only moderate ciliate densities at the beginning of Expt 1 and an increase in ciliates after the collapse of the rotifer community in the lake. However, by assuming ingestion rates to be within the range of 20 to 50 ciliates rotifer<sup>-1</sup> d<sup>-1</sup> and a ciliate abundance of 300 ml<sup>-1</sup>, the overall grazing rate of 0.7 to 1.7 d<sup>-1</sup> is still lower than the growth rates of the dominant ciliate species (Table 5).

It is evident that not all of the small ciliates were affected to the same extent by rotifers, despite only slight differences in body size. *Halteria* remained at relatively high levels before and after the collapse of the rotifer populations, suggesting only low impact by the rotifers. The jumping response of *Halteria* is an effective escape mechanism against rotifers (Gilbert 1994). Large ciliates were probably more efficient predators on *Halteria* as judged from the inverse development of the 2 groups. *Rimostrombidium brachykinetum* seems to be more vulnerable to predation, both by large rotifers and by predatory ciliates, as indicated by the inverse population development of this species and of rotifers in the lake and the +ZP enclosures. The smallest of the 3 dominating taxa, *Urotricha* spp., was obviously least effected by predation as the population developments in the +ZP and <50 treatments did not significantly differ (Fig. 3).

Evidence of the importance of predatory ciliates also comes from the <10  $\mu\text{m}$  fractionations (Fig. 3). Rotifers were not present in these treatments and all small ciliate taxa grew virtually without predation and achieved high population abundances. Later in the experiment large, predatory ciliates (*Lagynophrya*, *Monodinium*) appeared and probably caused the decline of the small ciliate species. Again a pronounced effect on *Halteria* was observed, emphasizing the important role of this predation force within the ciliate community.

In summary, rotifer dominated mesozooplankton seemed to have exerted only a weak top-down control on small ciliates but had an indirect positive influence by controlling predators in the microzooplankton size range. It confirms the general observations that ciliates and rotifers often co-occur in higher numbers in eutrophic lakes (Sommaruga 1995, Jürgens unpubl. obs.). A survey on zooplankton from 18 Danish lakes revealed that rotifers were the only zooplankton group which is strongly positively related to abundance and biomass of ciliates (Jeppesen unpubl. data). No or only modest effects of rotifers on planktonic ciliates in field

experiments were also reported by Jack & Gilbert (1997) and Havens & Beaver (1997). Complex interactions within the micro- and nanozooplankton and protozoan predation of other protozoans are typical for situations when large populations of mesozooplankton are absent. Rotifers and ciliates have considerable overlap in their food niches and in addition to direct predation and interference effects, exploitative competition might occur. The fact that rotifers can serve as alternate food sources for cyclopoid copepods (Adrian 1991, Jack & Gilbert 1997) is another indirect positive effect on ciliates, especially favouring the larger species.

### Expt 2: top-down control by cyclopoid copepods and *Daphnia*

The second experiment proved to be much clearer with regard to the impact of mesozooplankton on the ciliate community. Initial ciliate densities were about 1 order of magnitude lower than during the first experiment. Only the smallest of the dominant ciliate species, *Urotricha* spp., was still at moderate densities (25 cells ml<sup>-1</sup>). The immediate response and high net growth rates of all ciliate taxa after removal of zooplankton >50 µm suggest an efficient top-down control on the ciliate community (Fig. 4). The dominating mesozooplankton during this experiment, initially *Cyclops vicinus* and later *Daphnia* spp, can both cause significant mortality of planktonic ciliates (Jack & Gilbert 1993, Wickham 1995).

We suggest, however, that initially the copepods maintained ciliates at low numbers, as the high abundance of phytoplankton (mainly *Scenedesmus* spp.) indicated that grazing by daphnids was still not pronounced. The selective feeding behaviour of copepods can explain why ciliate numbers declined to low levels while phytoplankton remained rather unaffected. Cyclopoid and calanoid copepods detect their prey mainly by mechanoreception (DeMott & Watson 1991) which can be used to locate ciliates within dense phytoplankton. Further, some cyclopoid species actively select for motile prey species (Price 1988, DeMott & Watson 1991). *Cyclops vicinus*, the dominating copepod species in Lake Søbygård, has not been examined with regard to feeding on ciliates. Its feeding behaviour is, however, rather similar to the omnivorous *C. kolensis* (Adrian 1991), which has been shown to be an efficient predator of planktonic ciliates (Wickham 1995). Although larger ciliates are generally more effected by *Cyclops* predation (Wickham 1995, Dobberfuhl et al. 1997), smaller species such as *Halteria* are also consumed at rates of up to 20–30 ciliates copepod<sup>-1</sup> h<sup>-1</sup> (Wickham 1995).

The predation impact of *Daphnia*, which increased during the second experiment, affects a wide prey size range and most groups of planktonic protozoans (Jürgens 1994). The ability to suppress ciliate populations is well documented (Pace & Funke 1991, Jack & Gilbert 1993, Marchessault & Mazumder 1997, Pace et al. 1998). The shift from cyclopoids to daphnids even enhances grazing pressure on ciliates and includes the smallest species.

### General implications for metazoan-protozoan coupling in lake plankton

It is evident now that metazooplankton predation is a decisive factor for controlling population sizes and species composition of planktonic protozoans (Sanders & Wickham 1993). Protozooplankton is generally dominated by small forms (<30 µm in diameter) that are highly vulnerable to zooplankton predation. Zooplankton clearance rates of nanoflagellates resemble those of edible nano-phytoplankton (Carrick et al. 1991, Jürgens et al. 1996). For ciliates, predation vulnerability is taxon-specific for both the predators and prey (Wiackowski et al. 1994). Ciliate behavioural adaptations to lower grazing mortality (e.g. escape response) influence the outcome of the predator-prey interactions. This study and comparable ones performed in other systems reveal the importance of predation by different zooplankton groups (Wiackowski et al. 1994, Marchessault & Mazumder 1997) but results are to some extent still contradictory (e.g. Havens & Beaver 1997).

The controlling modes and the interactions between microbial and classical food webs can change within short periods of time. Whereas in the second experiment the whole ciliate community was equally effected by zooplankton predation, the first experiment revealed strong differences in the response of the different ciliate species within the same size range.

The planktonic ciliate assemblage reflects the metazooplankton community and its specific predation pressure. This is particularly pronounced in shallow, productive lakes where nutrient constraints are less important and food supply is sufficient to achieve high growth rate and population sizes. In those systems, alterations at the top of the food web propagate to lower trophic levels and affect phyto- and bacterioplankton (Jürgens et al. 1994, Dobberfuhl et al. 1997). The study on ciliate dynamics in Lake Søbygård reveals characteristics which support the overall picture of plankton organisms in shallow hypertrophic systems: top-down control is a dominating structuring force for the biological community and few species oscillate in exceptionally high numbers (Jeppesen et al. 1997).

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