

Seasonal dynamics of cyst formation of strombidiid ciliates in alpine Lake Mondsee, Austria

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ABSTRACT: The seasonal dynamics of strombidiid ciliates in alpine Lake Mondsee, Austria, were studied from September 1999 to November 2000 and in April/May 2001. Simultaneously, their resting cysts were collected in sediment traps. Concentrations of active strombidiids at 0 to 20 m depth ranged from 50 cells l⁻¹ (February) to 2100 cells l⁻¹ (May). The genera *Pelagostrombidium* and *Limnostrombidium* coexisted during all seasons, with *Pelagostrombidium* being the dominating taxon, contributing 70 and 83% to total strombidiids in September 1999 and May 2001, respectively. Throughout the study period, only 1 cyst type was observed, which in size and shape matched a previous description of *Pelagostrombidium* cysts. Maxima of cyst production (up to 2 × 10⁵ cells m⁻² d⁻¹) occurred in October/November, while virtually no cysts were detected in winter, spring and early summer. The absence of a spring maximum of cyst formation contrasts with earlier observations from pre-alpine Lake Constance. We explain this finding by a different timing of strombidiid development, relative to the phytoplankton spring bloom in both lakes.

KEY WORDS: *Pelagostrombidium* · *Limnostrombidium* · Cyst · Lake Mondsee · Lake Constance

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INTRODUCTION

Planktonic strombidiid ciliates are common in surface waters of oceans and lakes (Fenchel 1987), and several species can form resting cysts (Reid 1987, Kim & Taniguchi 1995, Müller 1996, Müller & Wünsch 1999). Up to now, our knowledge on the function of these resting stages and on the factors triggering encystment is very limited. Relevant studies have mainly been performed with marine ciliates (for a review see Müller 2000). In freshwater, there has only been 1 field study on strombidiid cysts: Müller & Wünsch (1999) described a pronounced seasonality of cyst formation in pre-alpine Lake Constance, Germany.

The site of the present study was the deep alpine Lake Mondsee, Austria. This lake is similar to Lake Constance in several aspects, such as range of ambient temperatures, stratification and community composition of planktonic ciliates (Salbrechter & Arndt 1994).

Both lakes underwent a period of accelerated eutrophication during the 1960s and 1970s, followed by a strongly reduced phosphorus nutrient load and subsequent re-oligotrophication over the past 20 yr (Häse et al. 1998, Schwarz & Jagsch 1998). Concerning annual mean and maximum chlorophyll *a* (chl *a*) concentrations, and mean total phosphorus content (Häse et al. 1998, IGKB 2000), Lake Constance is currently in a mesotrophic state, according to the OECD classification system (OECD 1982); Lake Mondsee is at present oligo-mesotrophic (Schwarz & Jagsch 1998). The crustacean zooplankton community and its response to eutrophication and re-oligotrophication differ in these lakes. Lake Mondsee is dominated by copepods in autumn, winter and spring (Dokulil et al. 1990). A pronounced clear-water phase, which is caused by grazing daphnids and characteristic of Lake Constance (Lampert 1978) has never been observed in Lake Mondsee (Dokulil & Skolaut 1986, Dokulil et al. 1990, Salbrechter & Arndt 1994).

This field study in Lake Mondsee was performed from September 1999 to November 2000; additional data were collected in April/May 2001. We recorded

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concentrations of strombidiids at 0 to 20 m depth together with total numbers of planktonic ciliates, chl *a* concentration and water temperature. The downward settling flux of strombidiid cysts was quantified by the use of sediment traps.

A different seasonal pattern of cyst formation emerged compared to the pattern reported from Lake Constance. We discuss this result, considering general differences in the plankton seasonal succession of both lakes.

MATERIALS AND METHODS

Study site and periods. Lake Mondsee is an alpine oligo-mesotrophic lake situated in central Austria (47° 50' N, 13° 23' E) at 480 m above sea level. It has an area of 13.8 km², a mean depth of 37 m and a maximum depth of 68 m (Schwarz & Jagsch 1998). Our sampling station was located in the central part of the lake (depth 45 m) where water currents due to inflowing rivers and lateral input were presumably low. Study periods were September 9, 1999 to November 21, 2000 and April 10 to June 5, 2001.

Temperature and chl *a*. Continuous profiles of water temperature (0 to 40 m) were recorded at the sampling site at each sampling occasion by means of a thermistor probe (Yellow Springs). Water samples for chl *a* measurements were obtained by an integrating Schröder water bottle (Züllig) over the upper 20 m of the water column. The volume of the water bottle was 800 ml; it collected 40 ml m⁻¹ during a vertical haul. Results, therefore, represent mean chl *a* values from 0 to 20 m. Chl *a* was measured after hot ethanol extraction according to Nusch (1980).

Cell concentrations. Water samples were taken weekly during the growing season with an integrating Schröder water bottle over the depth interval 0 to 20 m. Since strombidiid ciliates are known to live rather close to the lake surface (Müller et al. 1991), we did not take samples from below 20 m. In winter, sampling intervals were 2 wk, except for one 3 wk interval in January when the lake was frozen. Samples were fixed with acid Lugol's solution and used for counting ciliates with the Utermöhl technique (cf. Müller 1989). All planktonic ciliates were counted in 50 ml subsamples; 100 ml subsamples were scanned for strombidiids. In April/May 2001, only the strombidiids were recorded. Phytoplankton cell concentrations were determined by Claudia Skolaut (Institute for Limnology, Mondsee) in parallel to the present investigation with standard methods (Dokulil & Skolaut 1986).

Taxonomy. We use the term 'oligotrich ciliates' in the sense of the Oligotrichida Bütschli, 1887, as characterized by Foissner et al. (1999). Regarding strombidiid ciliates, we followed the nomenclature of Krainer (1991, 1995), who placed freshwater strombidiids into the newly established genera *Limnostrombidium* and *Pelagostrombidium*. In counts of Lugol-fixed samples, these 2 genera cannot be separated quantitatively, whereas they are easily recognized in protargol-stained material. Therefore, 500 ml water samples from 0 to 20 m depth were taken on 3 occasions (September 9 and 15, 1999, and May 22, 2001) and fixed with HgCl₂ (final concentration: 0.6 g l⁻¹). The samples were concentrated by sedimentation and centrifugation to a volume <0.5 ml; protargol-stained slides were prepared from this material following the protocol of Foissner (1991). The slides were scanned for strombidiids at 400-fold magnification to determine the ratio of *Limnostrombidium*:*Pelagostrombidium*. We did not attempt to identify strombidiid species (see 'Discussion').

Cyst identification and sizing. *Pelagostrombidium* cysts were identified with light microscopy, following the description of Müller (1996). Cyst dimensions were measured at 200-fold magnification with a calibrated eyepiece micrometer. Data sets from Lake Constance (Müller & Wünsch 1999) and Lake Mondsee were compared by the Mann-Whitney rank sum test, using the statistical software SigmaStat (Jandel Scientific).

Flux rates of cysts. Cyst production was measured with sediment traps as described by Müller & Wünsch (1999). We used the same traps as in this earlier study, with a design recommended by

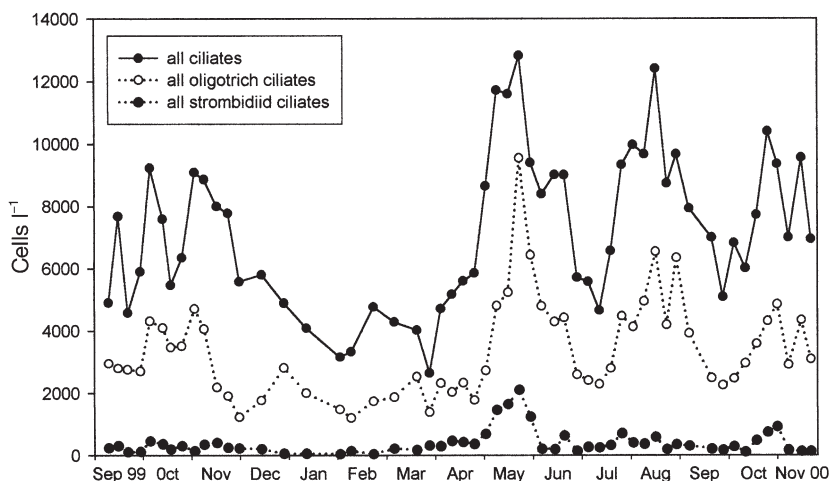


Fig. 1. Ciliate cell concentrations in Lake Mondsee at 0 to 20 m depth from September 9, 1999 to November 21, 2000

Bloesch & Burns (1980), i.e. cylindrical tubes made of transparent plexi-glas with a height of 100 cm and an inner diameter of 10 cm. Four replicates of these traps were exposed at 45 m depth, standing upright on the lake bottom. Müller & Wünsch (1999) measured a sinking velocity of *Pelagostrombidium* cysts at 8°C of approximately 14.4 m d⁻¹. According to Stokes' law, this value will increase considerably with increasing water temperature. Cysts produced between 0 and 20 m depths, therefore, could have reached the 45 m depth within 2 to 3 d. The effect of turbulence on settling particles <500 µm is low, as explained in detail by Bloesch & Burns (1980).

With consecutive exposures, we covered the entire study periods. Routinely, the traps were exchanged weekly. Biweekly exchanges were made from December 1999 to mid-March 2000, except for a period of ice cover in winter: between January 11 and February 1, the traps remained exposed on the lake bottom for 3 wk. After trap retrieval, the collected material was sieved through 200 µm mesh. The fraction of <200 µm of 1 trap was fixed with acid Lugol's solution for counting and sizing of the cysts. The rest of the material was stored at 4°C in the dark for live observation (Müller 2002). The Lugol-fixed subsamples were concentrated by sedimentation and centrifugation, and resuspended in a defined water volume, generally 40 or 80 ml, depending on the amount of sediment collected during

each exposure. One ml aliquots of this material were filled into Sedgewick-Rafter-chambers and scanned for cysts at 100-fold magnification. Two to 8 entire chambers were examined, the contents of which was 2.5 to 10% of the contents of 1 trap. Flux rates (cysts m⁻² d⁻¹) were calculated from these counts, the total area of the trap (78.5 cm²) and the exposure time. The protocol described above resulted in a detection limit of approximately 400 cysts m⁻² d⁻¹.

RESULTS

Ciliate abundance and community composition

Over the study period 1999/2000, mean concentrations at 0 to 20 m depth of all planktonic ciliates varied from 2600 to 12 800 cells l⁻¹ (Fig. 1). Oligotrich ciliates, namely strobilidiids, halteriids, strombidiids and tintinnids, were a major component of the community. Taken together, these taxa accounted for 47% of total ciliate numbers on average. Furthermore, ciliates of the genera *Balanion*, *Urotricha*, *Coleps*, *Askenasia* and *Histiobalantium* contributed significantly to ciliate concentrations. Ciliate maxima occurred on May 23 and August 16, whereas only moderate numbers were present in April, when chl *a* concentrations peaked (Fig. 2).

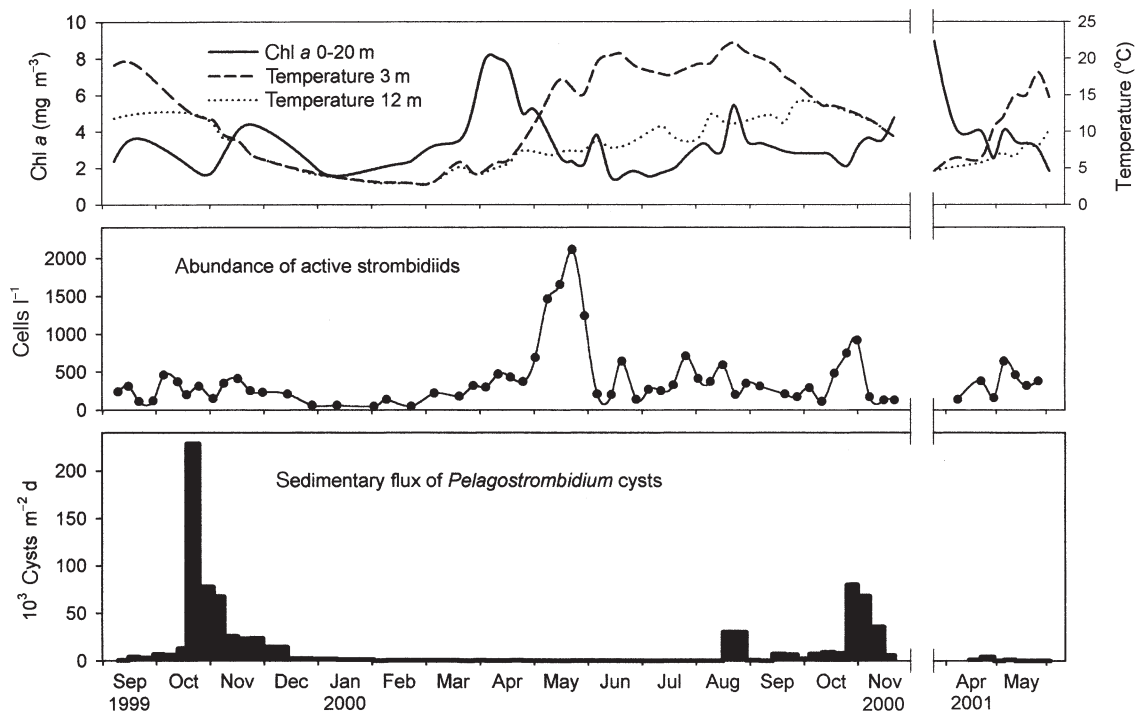
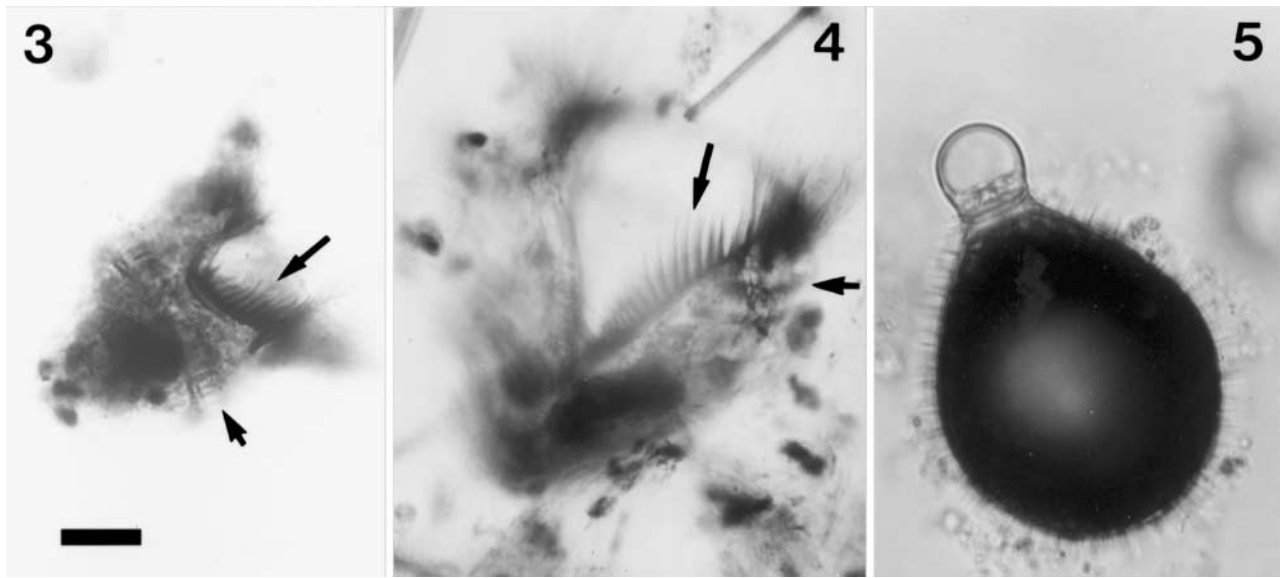


Fig. 2. Dynamics of strombidiid ciliates in Lake Mondsee, September 1999 to November 2000 and April/May 2001. Top: chlorophyll *a* concentrations at 0 to 20 m depth and water temperature in 3 and 12 m depth. Middle: concentrations of active strombidiids at 0 to 20 m depth. Bottom: flux rates of strombidiid cysts



Figs. 3 & 4. Protargol-stained specimens of *Limnostrombidium* (Fig. 3) and *Pelagostrombidium* (Fig. 4) from surface waters of Lake Mondsee. Long arrows point to row of inner membranelles of adoral zone. Short arrows point to extrusome girdle, which is complete in *Limnostrombidium*, but interrupted by row of inner membranelles in *Pelagostrombidium*. Scale bar = 10 μm . Fig. 5. Flask-shaped resting cyst of *Pelagostrombidium* from Lake Mondsee sediment sample. Lugol-fixation. Note the spines on the cyst surface and the clear plug. Scale as in Fig. 3

Composition of strombidiids

Two genera are presently known among freshwater strombidiid ciliates, namely *Limnostrombidium* and *Pelagostrombidium* (Foissner et al. 1999). We identified both taxa with the protargol technique in samples obtained from surface waters of Lake Mondsee during spring and autumn (Figs. 3 & 4). These non-quantitative preparations also served to determine relative frequencies and size ranges. In the combined samples from September 9 to 15, 1999, and in the sample from May 22, 2001 *Pelagostrombidium* was identified as the dominating genus (Table 1). Individuals of both genera covered the same size range, with their largest diameters ranging from 30 to 60 μm . Since distinguishing characters other than size and shape were not visible in Lugol-fixed specimens, we were not able to quantitatively separate

Table 1. Ratio of *Pelagostrombidium*:*Limnostrombidium* in Lake Mondsee (depth 0 to 20 m) in autumn 1999 and spring 2001. Genus identification by protargol staining. Damaged specimens which could not be determined to genus are not included

	Number of identified strombidiids	<i>Pelago-strombidium</i> (%)	<i>Limno-strombidium</i> (%)
Sep 9 + 15, 1999	93	70	30
May 22, 2001	112	83	17

both genera in the routine counts and, therefore, did not record strombidiid composition over the entire seasonal cycle. However, since a few specimens in each sample could be recognized unequivocally by their characteristic shape, we noticed that both genera coexisted throughout the study period.

Dynamics of active strombidiids

Strombidiid ciliates accounted for ca. 12% of the oligotrichs and for ca. 6% of total ciliate numbers. Their concentrations at 0 to 20 m depth varied from 50 to 2100 cells l^{-1} (Fig. 2). The strombidiid peak in May 2000 appeared unrelated to the phytoplankton spring bloom in April, when chl a concentrations reached 8 $\mu\text{g l}^{-1}$ (Fig. 2), and combined cell numbers of small cryptophytes (*Rhodomonas* spp. and *Cryptomonas pusilla*) exceeded 10³ cells ml^{-1} . Large numbers of strombidiids developed only 5 wk later, when water temperatures at 3 m depth increased from 11 to 17°C within 2 wk. The abundance of small cryptophytes ranged from 400 to 600 cells ml^{-1} during the ciliate peak. A comparable strombidiid peak was not observed in April/May 2001. Strombidiid concentrations ranged from 100 to 900 cells l^{-1} from June through November and from 50 to 200 cells l^{-1} from December through mid-March. Notably, low numbers of active strombidiids were present throughout the winter months.

Table 2. Dimensions of *Pelagostrombidium* cysts in sediment samples from Lake Mondsee (this study) and Lake Constance (Müller & Wünsch 1999, unpubl. data)

Location Period	n	Length (μm)		Width (μm)	
		Mean \pm SD	Range	Mean \pm SD	Range
Lake Mondsee					
Sep 9 to Oct 25, 1999	114	56 \pm 4	45–62	36 \pm 2	30–40
Oct 18 to 25, 1999	40	57 \pm 3	49–62	36 \pm 2	32–40
Lake Constance					
Apr 28 to May 5, 1997	30	67 \pm 3	61–75	41 \pm 1	39–43
Sep 22 to 29, 1997	30	59 \pm 2	55–61	36 \pm 1	33–39

Cyst formation

We observed only 1 type of strombidiid cyst, which by its flask shape, clear plug and spines was identified as the resting stage of *Pelagostrombidium* (Fig. 5). Cyst dimensions are presented in Table 2 together with earlier data from the Lake Constance population (Müller & Wünsch 1999). The Mann-Whitney rank sum test revealed significant differences in both length and width between spring cysts from Lake Constance and autumn cysts from both lakes ($p < 0.001$). Cysts collected during the autumn maxima in Lake Constance and Lake Mondsee differed slightly in length ($p = 0.006$) but not in width ($p = 0.967$). Thus, the overall size difference between autumn cysts from both lakes was small compared to the seasonal size difference within the Lake Constance population.

High cyst production occurred in October/November of 1999 and 2000, with a maximum rate of 2×10^5 cysts $\text{m}^{-2} \text{d}^{-1}$ (18 to 25 October 1999). One smaller peak was recorded in August 2000. Virtually no cysts were found from February to July 2000, whereas in April/May of 2001 encystment occurred at a very low rate, never exceeding 4000 cyst $\text{m}^{-2} \text{d}^{-1}$.

DISCUSSION

We present the second field study on encystment of strombidiid ciliates in freshwater, and the first one which covers an entire annual period. Our records during summer and autumn agree with observations of Müller & Wünsch (1999) from pre-alpine Lake Constance, whereas data collected during the spring period are in contrast to this earlier study. In the following, we will discuss the seasonal dynamics of strombidiids, comparing results from both field studies.

The species problem

In each of the genera under investigation, namely *Limnostrombidium* and *Pelagostrombidium* (both formerly *Strombidium*), 2 very similar species have been described. Kahl (1932) and Foissner (1994) treated *L. pelagicum* as a form of *L. viride*, whereas Krainer (1991) and Foissner et al. (1999) defined it as a separate species. Distinguishing features according to Foissner et al. (1999) are listed in Table 3.

While most of these features are overlapping, the characters <presence/absence of sequestered plastids> and <numbers of basal body pairs in the ventral ciliary row> seem to be decisive. However, with the methods used in our study, we were not able to recognize these details. Considering cell size, which rarely exceeded 60 μm , we believe that the majority of *Limnostrombidium* individuals in Lake Mondsee belong to the species

Table 3. Criteria separating the species *Limnostrombidium viride* and *L. pelagicum* according to Foissner et al. (1999)

	<i>L. viride</i>	<i>L. pelagicum</i>
Length (μm)	40–90	30–60
Width (μm)	30–55	25–45
Micronuclei	1–2	1–3
Color	Greenish to yellow-green	Colorless or greenish-gray or reddish brown
Sequestered plastids	Yes	No
Colourful granules	No	Often
Basal body pairs in ventral ciliary row	13–18	7–10
Inner buccal membranelles	6–16	8–12

Table 4. Criteria separating the species *Pelagostrombidium fallax* and *P. mirabile* according to Foissner et al. (1999). In parentheses: according to Krainer (1991) and Foissner (1994)

	<i>P. fallax</i>	<i>P. mirabile</i>
Size (μm)	40–90 \times 40–80 (60 \times 50)	30–70 \times 25–50 (45 \times 30)
Color	Orange (reddish brown)	Yellowish-green (greenish gray to orange yellow)
Extension of row of buccal membranelle	Ending below mid-body (at least half cell length)	Ending below mid-body (third of cell length)
Number of buccal membranelles	19–22 (19–22)	12–17 (12–15)
Polysaccharid plates	Polygonal (polygonal)	Polygonal (square)

(or form) *L. pelagicum*. In contrast, Müller & Wünsch (1999) encountered a large-sized population in Lake Constance (up to 100 µm in length), which they identified as *L. viride*.

Criteria separating *Pelagostrombidium mirabile* from *P. fallax* have been changed recently (Table 4). Müller & Wünsch (1999) observed 'a long row of buccal membranelles (>16) extending at least half cell length internally' and 'polygonal polysaccharide plates' in the Lake Constance population. Based on these characters, the ciliates were identified as *P. fallax* according to Krainer (1991) and Foissner (1994). However, using the more recent definitions by Foissner et al. (1999), the same criteria could also lead to *P. mirabile* (Table 4). These authors argue that the Lake Constance population has been misidentified. It should be considered, however, that in the list of Foissner et al. (1999) only 2 decisive characters remain, namely <numbers of buccal membranelles> and <color>. Since little is known about the variability of these characters, it cannot be excluded that *P. fallax* and *P. mirabile* might be synonyms, as already considered by Kahl (1932).

The *Pelagostrombidium* population in Lake Mondsee, in our judgement, was identical to that observed in Lake Constance. For the reasons explained above, we did not attempt identification to the species level.

Cyst identification

Our identification of *Pelagostrombidium* cysts was corroborated by laboratory experiments; by live observation, Müller (2002, this issue) identified excysting ciliates from a sediment sample collected during the present field study as *Pelagostrombidium*. In the present investigation, we did not find the large *Limnostrombidium viride* cysts (mean length 96 ± 5 µm) which have been described in Lake Constance. This is not surprising, since active strombidiids of a similar size did not occur in Lake Mondsee. *Limnostrombidium* cysts in this lake, if there are any, should be within the same size range as those of *Pelagostrombidium*. Other differences than size, separating the 2 cyst types in Lake Constance, were surface structure (hardly visible with light microscopy) and features of the plug. *Pelagostrombidium* cysts had a clear plug, whereas the plug of *Limnostrombidium* cysts was composed of several bubbles enclosed within a larger sphere (cf. Figs. 4 & 5 in Müller & Wünsch 1999). Since all cysts recorded in Lake Mondsee had the typical *Pelagostrombidium* plug (Fig. 5), we conclude that throughout our study the *Limnostrombidium* population did not form cysts.

Strombidiid dynamics in summer/autumn

From July through November numbers of active strombidiids in Lake Mondsee were within the same range as reported from Lake Constance. The timing and magnitude of cyst formation in both lakes were also comparable: significant cyst fluxes were observed from September through November, with a maximum rate of 2×10^5 cysts $m^{-2} d^{-1}$ (Lake Constance: September 22 to 29, 1997; Lake Mondsee: October 18 to 25, 1999). Notably, an additional peak occurred in August 2000 in Lake Mondsee during a period of high water temperatures (>20°C at 3 m depth). This observation challenges the hypothesis of Müller & Wünsch (1999), who suggested that high water temperatures may impede encystment of *Pelagostrombidium*.

Müller & Wünsch (1999) crudely estimated the quantitative importance of cyst production relative to total production of the active *Pelagostrombidium* population in Lake Constance. Assuming generation times in the range of 24 to 120 h, their model calculation yielded ratios of cyst production:total population production of 1 to 6%, when averaged over 3 mo in autumn, and of 16 to 80% during the peak of encystment in September 1997. The same model calculation, applied to the autumn period in Lake Mondsee, should yield similar results, since concentrations of active strombidiids and cysts fluxes were within the same order of magnitude. A more precise estimate of the quantitative importance of cyst formation could be achieved only by measuring *in situ* production rates in parallel to records of cyst fluxes.

Strombidiid dynamics in winter

Low numbers of active strombidiids were always present throughout the winter months, i.e. survival of the population during the cold season did not rely entirely on the resting stages. Very few cysts were found in the traps during this period. While these could have been produced in winter, it appears more likely that they were leftovers from the cyst production in autumn, which had not yet sedimented.

Strombidiid dynamics in spring

Müller & Wünsch (1999) reported a highly significant correlation of strombidiid abundance with chl *a* in Lake Constance from April through mid-June 1997, when chl *a* concentrations varied from 1 to 9 µg l^{-1} . In contrast, the strombidiids in Lake Mondsee did not respond to the chl *a* maximum (up to 8 µg l^{-1}) in April

2000 (Fig. 2). Phytoplankton counts revealed that diatoms and small cryptomonads contributed ca. 69 and 25, respectively, to algal cell concentrations during this bloom, and that small cryptomonads, a preferred food of strombidiid ciliates (Müller & Geller 1993, Müller 1996), reached concentrations of up to 10^6 cells l^{-1} . Similar cryptomonad concentrations are typical for the phytoplankton spring bloom in Lake Constance (Weisse et al. 1990). Notably, the entire ciliate community in Lake Mondsee (mainly algivorous taxa), responded only weakly to the chl *a* peak in April 2000 (Fig. 1). During the present study, we did not collect any data which could explain the differing response of strombidiid ciliates (and of planktonic ciliates in general) to cryptomonad spring peaks of similar magnitude in both lakes. Differences in the community composition of the crustacean zooplankton (see 'Introduction') could have played a role. Since the crustaceans in Lake Mondsee are known to be dominated by copepods (Dokulil et al. 1990, Nauwerck 1991), which may act as efficient predators of ciliates (Wickham 1995), copepod grazing could have caused the delay in the development of the ciliate spring community in Lake Mondsee.

Strombidiid encystment during spring is, most probably, linked to food availability. In Lake Constance, the strombidiid maximum and the onset of cyst formation were recorded at the culmination of the phytoplankton spring bloom. Cyst production increased further when food concentrations declined. Müller (1996) observed the same pattern in batch cultures of *Pelagostrombidium* from Lake Constance with cryptomonads as food; cyst formation started at high food levels, but was enhanced during phases of decreasing prey concentrations. In Lake Mondsee, in contrast, strombidiids developed with a delay of 5 wk and peaked when chl *a* values had decreased to $<3 \mu g l^{-1}$. Although strombidiids in Lake Mondsee did not form cysts in spring 2000, and only a negligible number in spring 2001, descendants of the same *Pelagostrombidium* population, grown in well-fed laboratory cultures, produced large numbers of cysts at the same time, as reported by Müller (2002).

CONCLUSIONS

A pronounced seasonality of cyst production is commonly observed in field studies on dormancy of marine and freshwater loricate and aloricate oligotrich ciliates (for a review see Müller 2000). Cysts formed in late summer or autumn are interpreted as 'overwintering stages' (e.g. Reid & John 1978, Paranjape 1980), whereas encystment in spring is assumed to serve as a defense mechanism against predation (e.g. Reid 1987).

The data on freshwater strombidiids collected in Lake Mondsee (this study) and in Lake Constance (Müller & Wünsch 1999) fit into this scheme. They suggest that the environmental 'spring signal' causing encystment of freshwater strombidiids is a period of high food availability. Since phytoplankton blooms are exploited not only by planktonic ciliates, but also by rotifers and crustaceans, and since metazoa have longer generation times than protozoa, it may be an efficient survival strategy of the ciliates to encyst and sink to the lake bottom prior to mass development of their metazoan predators. While in Lake Constance both genera, *Limnostrombidium* and *Pelagostrombidium*, showed a strong response to this 'spring signal', the strombidiids in Lake Mondsee apparently missed it due to a delay in their development.

The nature of the environmental 'autumn signal' triggering encystment of *Pelagostrombidium* at the end of the growing season remains unknown. Comparing the results from both field studies, we conclude that this signal was of similar strength in both lakes. Only *Pelagostrombidium* responded to this 'autumn signal'. Müller (2002) presents experimental evidence that the majority of cysts formed in late autumn will excyst a few months later in early spring. The term 'overwintering stage' for the autumn cysts therefore seems to be adequate.

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