

The annual cycle of protozooplankton in the alpine, mesotrophic Lake Mondsee (Austria)

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Abstract

The seasonal and vertical distribution of planktonic protozoans of the mesotrophic, alpine Lake Mondsee was investigated over a period of 12 months in the epi-, meta- and hypolimnion. Ciliates, heterotrophic nanoflagellates (< 15 µm; HNF) and large heterotrophic flagellates (LHF) — analysed in living and Lugol fixed samples — formed the major part of protozooplankton biomass and composed 44%, 24% and 30%, respectively, of the annual mean biomass. Sarcodines (naked amoebae and heliozoans) were occasionally significant (2% of annual mean biomass). The protozoan biomass of the epilimnion was about three times higher than that of the hypolimnion. Maximum values of protozooplankton biomass (mainly algivorous species) were recorded at the end of the phytoplankton spring bloom, when grazing by both groups, ciliates and heterotrophic flagellates, may have significantly contributed to phytoplankton mortality.

Oligotrichs, haptorids, prostomatids and peritrichs formed a significant part of ciliate biomass. HNF were dominated by chryomonads, and in diminishing importance by *Kathablepharis* sp., choanoflagellates and bodonids. LHF were composed not only of colourless dinoflagellates (mainly *Gymnodinium helveticum*) but also of colourless chryomonads. This important protozoan group is often overlooked in routine protozooplankton investigations. About 40% of total zooplankton biomass was composed of protozoans.

The simultaneous analysis of all major protozoan groups in Lake Mondsee indicated that general estimates of the role of zooplankton in the pelagic matter flux should consider the heterogeneity of protozooplankton.

Key words: Protozoa, Flagellates, Ciliates, Sarcodines, Metazoa, Vertical distribution, Biomass.

Résumé

Le cycle annuel du protozooplancton dans le lac alpin mésotrophe de Mondsee (Autriche)

La répartition saisonnière et verticale des protozoaires planctoniques du lac alpin mésotrophe de Mondsee a été étudiée sur une période de 12 mois dans l'épi-, le méta- et l'hypolimnion. Les ciliés, les nanoflagellés hétérotrophes (<15 µm) et les grands flagellés hétérotrophes — analysés dans des échantillons frais et fixés au Lugol — formaient la plus grande partie de la biomasse du protozooplancton et constituaient 44%, 24% et 30%, respectivement, de la biomasse annuelle moyenne. Les Sarcodines (amibes nues et héliozoaires) étaient significatifs occasionnellement (2% de la biomasse annuelle moyenne). La biomasse des protozoaires de l'épilimnion était environ trois fois plus

élevée que celle de l'hypolimnion. Les valeurs maximales de la biomasse du protozooplancton (principalement des espèces consommatrices d'algues) étaient enregistrées à la fin de la poussée printanière de phytoplancton, quand le broutage par les deux groupes, ciliés et flagellés hétérotrophes, peut avoir contribué de façon significative à la mortalité du phytoplancton.

Les oligotriches, les haptorides, les prorodontides et les pérित्रiches formaient une part significative de la biomasse des ciliés. Les flagellés hétérotrophes étaient dominés par les chrysomonades, avec une importance moindre de *Kathablepharis* sp., des choanoflagellés et des bodonides. Les grands flagellés hétérotrophes étaient composés non seulement de dinoflagellés incolores (surtout *Gymnodinium helveticum*) mais aussi de chrysomonades sans pigment. Ce groupe important de protozoaires est souvent négligé dans les investigations de routine sur le protozooplancton. Environ la moitié de la biomasse totale de zooplancton était constituée de protozoaires.

L'analyse simultanée de tous les groupes majeurs de protozoaires dans le lac de Mondsee a indiqué que les estimations générales du rôle du zooplancton dans le flux de matière pélagique devraient prendre en considération l'hétérogénéité du protozooplancton.

Introduction

At a first glance a seasonal cycle of a planktonic component in a lake may not seem to be of much interest, since seasonal cycles of plankton organisms and trophic interactions have well been studied in the last decades (for review see Sommer, 1989). However, classical studies have been concentrated mainly on phytoplankton and metazooplankton, some have incorporated bacterioplankton, but the knowledge regarding protozooplankton is very limited. Already in 1972, Sorokin and Paveljeva (1972) showed that heterotrophic flagellates and ciliates can contribute very significantly to flux of matter in a lake. During the last decade, planktologists, forced by marine studies (*cf.* Azam *et al.*, 1983), paid more attention to protozoans in routine plankton investigations. Major work on the seasonal cycle of protozooplankton in lakes has been carried out on ciliates (*e.g.* Nauwerck, 1963; Schlott-Idl, 1984a,b; Müller, 1989; Laybourn-Parry *et al.*, 1990a,b; Müller *et al.*, 1991b; Pace, 1982; Bennett *et al.*, 1990). Much less information is available on the seasonal cycle of heterotrophic flagellates (*e.g.* Rohde *et al.*, 1958; Bennett *et al.*, 1990; Jürgens and Güde, 1991; Weisse, 1991; Arndt and Mathes, 1991). And only a few data exist on the quantitative contribution of planktonic sarcodines (*e.g.* Kyle and Noblet, 1986; Laybourn-Parry *et al.*, 1990b; Arndt, 1993a). Simultaneous investigations on the seasonal changes in the whole zooplankton community comprising metazoans and all groups of protozoans seem to be available only for a few lakes (*e.g.* Geller *et al.*, 1991; Carrick *et al.*, 1991; Arndt and Nixdorf, 1991; Arndt *et al.*, 1993). Data from these lakes support the idea that protozoans form a very significant part of zooplankton biomass especially during spring and may significantly contribute to the pelagic matter flux.

The main aim of the present study was to add a relatively complete data set (including all major groups of proto- and metazooplankton), in the course of a seasonal cycle for a mesotrophic lake. Considering all groups of protozooplankton we were not able at the same time to determine, with some exceptions, the protozoans to the level of species. However, we will give an estimate regarding the relative contribution of each protozoan group to the biomass of zooplankton. We paid special

attention to large heterotrophic flagellates since recent findings from different types of lakes indicated that this group may have been underestimated in studies of protozooplankton (*e.g.* Arndt and Mathes, 1991; Carrick *et al.*, 1991; Mathes and Arndt, 1994, this issue), and we tried also to split HNF (heterotrophic nanoflagellates) into the major taxonomic groups.

The authors wish to thank Helga Müller and Arnold Nauwerck for constructive criticism on an earlier version of this manuscript.

Material and methods

Lake Mondsee is situated in central Austria (Fig. 1), it has a surface area of about 14.2 km², a mean depth of 36 m and a maximum depth of 68 m. The water retention time is about 1.7 years. The temperature profile and Secchi depth during the present investigation are illustrated in Figure 2. The water column was well oxygenated down to the bottom for the whole sampling period. The seasonal changes of phytoplankton, metazooplankton and bacterioplankton have been studied for several years (*e.g.* Findenegg, 1969; Dokulil and Skolaut, 1986; Nauwerck, 1988, 1991, 1993; Dokulil *et al.*, 1990; Krössbacher, 1991; Psenner and Sommaruga, 1992). Lake Mondsee has underwent significant eutrophication in the 60's, but the lake has now recovered to the mesotrophic status (*cf.* Jagsch and Dokulil, 1989; Dokulil, 1987; Nauwerck, 1991).

For 5 different stations (see Fig. 1) samples were integrated for each of the three depth strata, 3 m, 12 m and 30 m, respectively. These depths were chosen to give representative samples of the epilimnion, metalimnion (during summer stratification) and hypolimnion. Samples were generally taken at biweekly intervals. In some cases, nanoflagellates were investigated at monthly intervals. Annual mean values are based on 26 samplings for ciliates and 14 samplings for sarcodines and flagellates, respectively. Ciliates, dinoflagellates and small metazoans were counted in sedimented 50 ml Lugol-fixed samples by the Utermöhl method. Metazoans were counted in net samples (20 µm mesh size) of 2 l to 10 l lake water depending on the concentration of metazooplankton. Abundance and biomass of heterotrophic flagellates, amoebae and heliozoans were estimated by a live-counting technique under a light microscope (phase contrast). Unconcentrated samples were analysed in chambers of different size (5-10 µl; 50 µl; 2 ml; several parallel counts of each type of chamber) immediately (at least within 1-2 hours) after sampling. Generally, nanoflagellates were counted in the smallest chamber, microflagellates and nanociliates in the medium sized chamber, and ciliates in the largest chamber (for more details of the method *cf.* Arndt and Mathes, 1991). Naked sarcodines were investigated in all types of chambers. Protozoans were counted in size groups to the nearest 2 µm (interval: 2-20 µm), 5 µm (20-50 µm) or 10 µm (> 50 µm), respectively. Biovolumes of all protozoans were calculated from measurements of cell dimensions and approximations to simple geometrical forms. In addition living protozoans were investigated in 100-500 ml samples gently concentrated on a 10 µm sieve. Ciliate biovolumes were estimated from Lugol-fixed samples. Biovolumes of the other protozoans were estimated in living samples. Müller

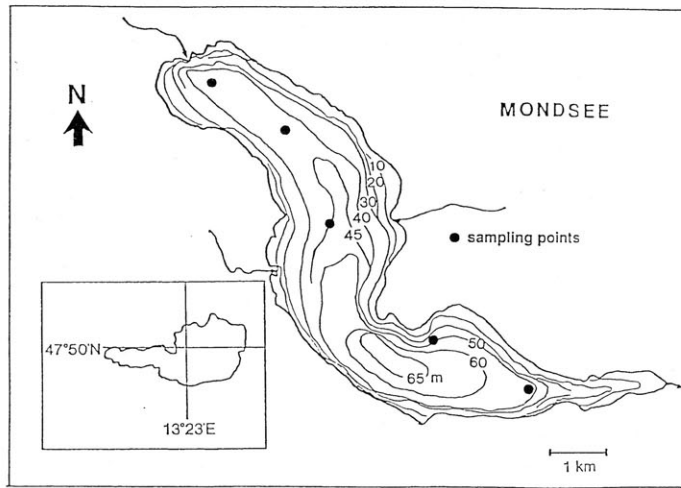


Fig. 1. Map of Lake Mondsee. Sampling stations are indicated by closed circles.

and Geller (1993) reported a shrinkage of small prostomatids and oligotrichs due to Lugol-fixation of about 70%. Since both groups of ciliates dominated the biomass of Lake Mondsee, a similar value was assumed during our investigation. For comparisons between different zooplankton groups, ciliate biovolumes were multiplied by a factor of 1.43. If possible, protozoans were determined to the species level; in many cases the determination was possible only to the level of genus or family, and in several cases — especially for many heterotrophic flagellates and sarcodines — only to major taxonomic groups following in general the taxonomic systems of Corliss (1979) and Patterson and Larsen (1991).

Metazoans were determined to the level of species except for some delicate rotifers and developmental stages of cyclopoids. Species of crustaceans were counted in size classes, for most other species at least 40 individuals of each species were measured by a micrometer. Biovolumes were calculated using length/weight regressions obtained for several crustacean species of Lake Mondsee by Mwebaza-Ndawula (1991), for the remaining species length/weight regressions summarized by McCauley (1984) were used assuming a dry weight/wet weight ratio of 0.15. Rotifer biovolumes were calculated using measurements of all three dimensions according to Ruttner-Kolisko (1977).

Results

Composition of protozooplankton

The annual mean and maximum abundance values of major groups of protozooplankton are given in Table I. Peak abundances, especially of flagellates, may have been missed due to long intervals between samplings, however, the values in Table I may provide a comparative overview of the different protozoan groups. We differentiated heterotrophic nanoflagellates (< 15 μm , HNF) and large heterotrophic

TABLE I.— Annual mean abundance, maximum abundance and annual mean biomass of different taxonomic groups of protozooplankton in three depths (3 m, 12 m and 30 m; integrated samples from 5 stations) of Lake Mondsee, Austria.

taxa	annual mean abundance [cells/l]			max. abundance [cells/l]	annual mean biomass [ngfw/l]		
	3 m	12 m	30 m		3 m	12 m	30 m
CILIATES							
prostomatids	3190	2280	1170	14000	3730	3330	2090
haptorids	330	310	120	1220	6730	7100	2730
peritrichs	110	150	40	960	1770	3090	730
oligotrichs	3090	1580	700	13120	21720	10270	47730
naked oligotrichs	2850	1320	610	7600	20590	8380	47060
tintinnids	240	260	80	5520	1140	1900	670
other ciliates	230	240	150	1400	7990	7460	4410
LHF $\geq 15 \mu\text{m}$							
dinoflagellates	5770	1470	350	56620	33300	21900	6800
chrysomonads	5400	6240	3000	29000	10700	12400	8900
HNF $< 15 \mu\text{m}$							
choanoflagellates	52400	13200	6100	233000	5310	1430	430
bodonids	19100	2000	—	340000	2870	300	—
bicoecids	6800	7300	—	80000	1300	1400	—
<i>Kathablepharis</i>	38700	23200	12800	100000	8900	5330	2950
other heterokont HNF (chrysomonads etc.)	265000	170100	53300	675000	17160	17200	4630
SARCODINES							
naked amoebae	800	2	—	8300	420	1	—
testate amoebae	1	—	—	16	25	—	—
heliozoa	198	80	92	1960	1980	620	610

flagellates ($\geq 15 \mu\text{m}$, abbreviated here as LHF). These LHF were much less abundant than HNF, however their contribution to protozoan biomass was remarkable. In addition to colourless dinoflagellates, large colourless and delicate chrysomonads were of considerable importance.

The seasonal changes of the biomass of protozooplankton were characterized by a spring peak of LHF and ciliates (Fig. 3). Maximum concentrations of metazoans occurred in early summer and summer (see also Nauwerck, 1993). During this time protozoan biomass decreased and then increased again in autumn. The biomass of protozooplankton was highest in the epilimnion (3 m depth), decreased to the 12 m samples (situated in the metalimnion during summer stratification, see Fig. 2) and were lowest in the hypolimnion (30 m). The composition of protozooplankton changed in the course of the year: ciliates were of relatively low importance in early spring, but were the most important component in summer. The opposite was the case for LHF. The average contribution of the different groups was similar at 3 m and 12 m depth

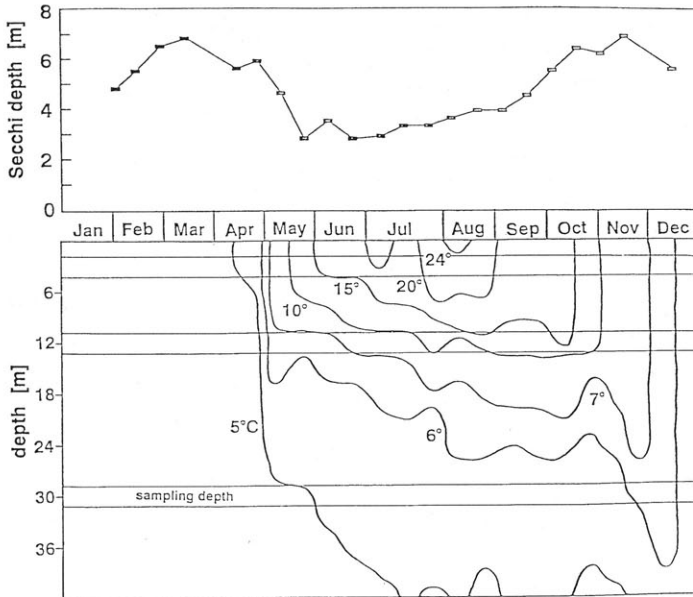


Fig. 2. Secchi-disk depth and depth distribution of isotherms in Lake Mondsee, 1992. The sampling depths are indicated by horizontal lines.

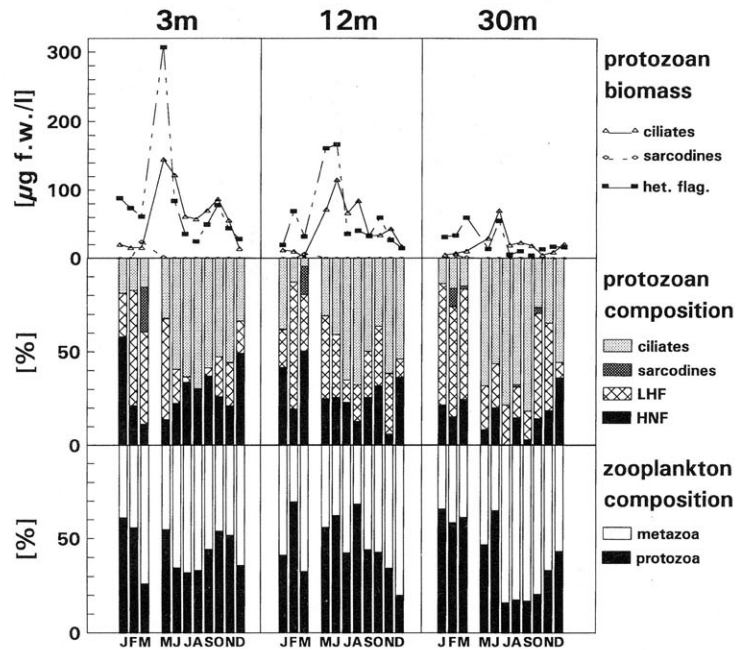


Fig. 3. Seasonal changes of monthly mean values of protozoan biomass (upper panel), the percentage composition of protozoan biomass (mid panel), and the percentage composition of zooplankton biomass (lower panel) in Lake Mondsee, 1992.

regarding the biomass of HNF (29 and 27% of protozoan biomass on annual average, resp.), LHF (25 and 30%), sarcodines (mainly heliozoans, 2.3 and 1.5%) and ciliates (43 and 42%), respectively. In the hypolimnion samples, the contribution by HNF (16%) was lower, however, that of LHF (36%) was higher than in the epilimnion. Average contributions to protozoan biomass of the hypolimnion by ciliates and sarcodines were 47% and 1.5%, respectively. The relative contribution of protozooplankton to total zooplankton biomass (including rotifers, cladocerans and copepods) was about 45% in 3 m and 12 m samples, and 38% in the hypolimnion. Though large cladocerans (*Leptodora*, *Bythotrephes*) may have been underestimated during metazooplankton sampling (too small subsamples), the protozoans seem to form very significant part (about 40%) of zooplankton biomass.

Ciliates

The ciliate abundance of Lake Mondsee was prevailed by prostomatids and oligotrichs. Regarding their biomass, however, only oligotrichs were of high significance (Fig. 4). Prostomatids (*Urotricha* spp., *Pseudobalanion planctonicum*, *Coleps* spp.) were always present in the samples. Most abundant in spring were small *Urotricha* and *Pseudobalanion planctonicum*. *Coleps* was common during all seasons, peak concentrations were found in the metalimnion during summer. The most important genus of haptorids was *Askenasia*, less important were *Mesodinium* spp., *Lacrymaria*, *Didinium nasutum* and *Monodinium balbiani*. During the warm season the biomass of haptorids may have been large enough to exert a significant grazing pressure on protists. Peritrichs were represented mainly by free-swimming large *Vorticella* species (which were present during all seasons), and by *Epistylis rotans* and species of *Epistylis*, *Vorticella* and other peritrichs attached to centric diatoms, daphnids and copepods. Oligotrichs were the most important group of ciliates. Species of the genera *Strobilidium* (e.g. *S. lacustris*), *Strombidium* as well as related genera, tintinnids (*Tintinnidium fluviatile*, *T. pusillum*, *Codonella cratera*, *Tintinnopsis cylindrata*) and halteriids (probably both species *Pelagohalteria viride*, *Halteria grandinella*) dominated the biomass of oligotrichs. The group "other ciliates" is very diverse. It includes e.g. *Stokesia vernalis*, *Staurophrya elegans*, *Euplotes*, *Paradileptus*, oxytrichids and other mostly undetermined ciliates. These "other" ciliates were especially of importance in the hypolimnion after summer stratification and require further taxonomic and ecological investigation. A large percentage of ciliates contained symbiotic chloroplasts, especially members of the genera *Strombidium* and *Askenasia* and halteriids. Up to 50 to 80 percent of naked oligotrichs contained chloroplasts irrespective of the season.

Heterotrophic nanoflagellates (HNF)

We differentiated 5 groups of heterotrophic nanoflagellates: kinetoplastids (e.g. *Bodo*), choanoflagellates (e.g. *Monosiga*, *Diploeca*), bicoecids (e.g. *Bicosoeca ovata*),

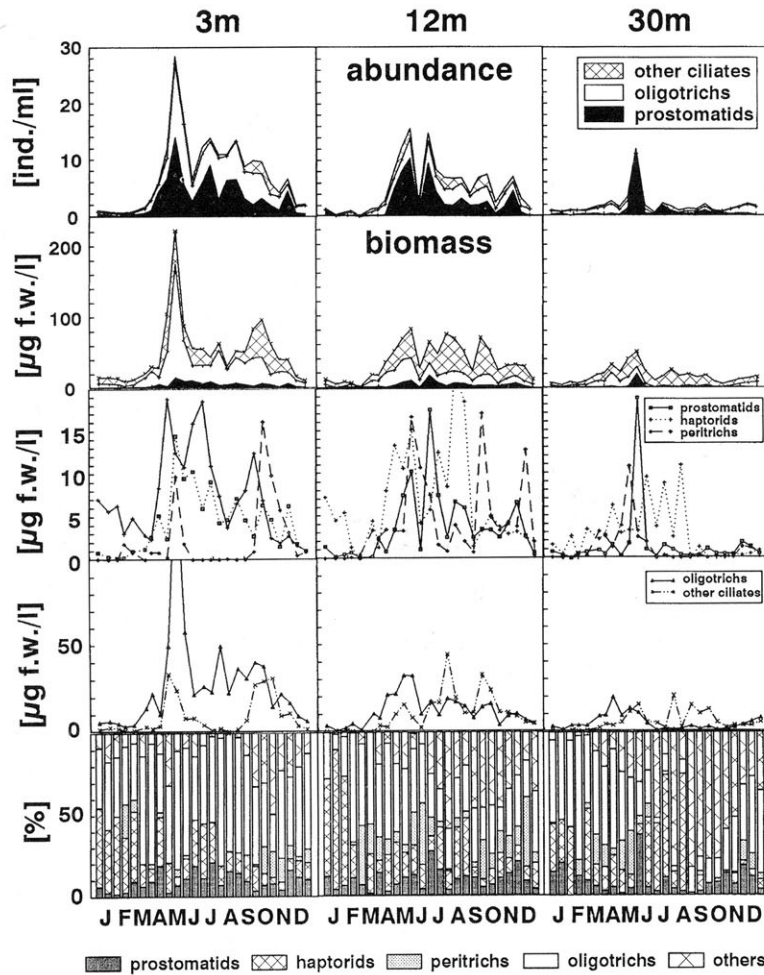


Fig. 4. Seasonal changes of ciliates in Lake Mondsee, 1992, in three different depths (3 m, 12 m, 30 m). 1. panel (from above): abundance of ciliates; 2. panel: biomass of ciliates; 3. panel: biomass of prostomatids, haptorids and peritrichs; 4. panel: biomass of oligotrichs and the remaining ciliates (other ciliates); 5. panel: percentage composition of ciliate biomass regarding different taxonomic groups.

other heterokont HNF (mainly chrysomonads, *e.g.* *Spumella*, and some undetermined HNF) and *Kathablepharis* (a genus of uncertain taxonomic position, *cf.* Patterson and Zölffel, 1991). Highest biovolumes of HNF were registered in the epilimnion. The annual mean contributions of the different groups to HNF biomass were: 28%, 22% and 28% by *Kathablepharis* in the 3 m, 12 m and 30 m samples, respectively, 49%, 65% and 66% by heterokont HNF, 4%, 6% and < 0.5% by bicoecids, 14%, 6% and 6% by choanoflagellates, and 5%, 1% and < 0.5% by bodonids. Bodonids and bicoecids were very rare in the hypolimnion, the relative contribution of the other groups did not change significantly (Fig. 5), though their absolute biomass decreased to about one

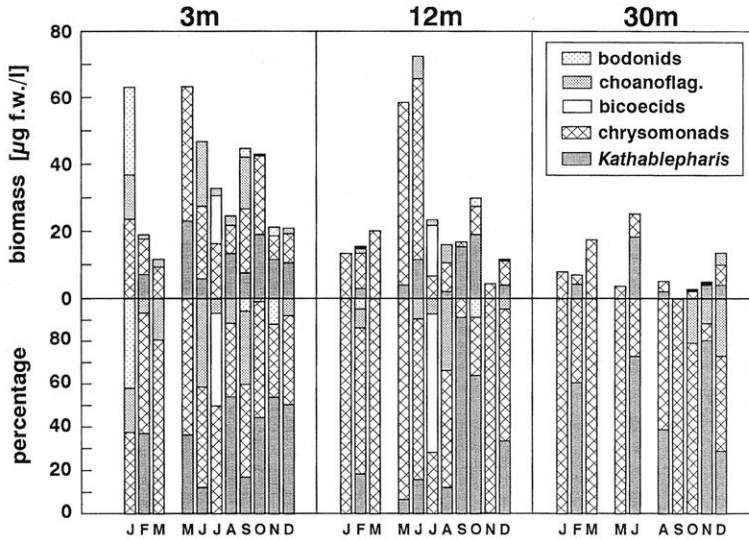


Fig. 5. Seasonal changes of heterotrophic nanoflagellates in Lake Mondsee (1992, three different depths) regarding biomass (upper panel) and percentage composition (lower panel) of major taxonomic groups.

quarter of that of the epilimnion. The most important group were chrysoomonads. The analysis of the composition of HNF gave clear evidence that a significant part of HNF was attached to substrates in the plankton community. The first three groups were generally attached (choanoflagellates, bicoecids) or in close contact to the substrate (bodonids). Sometimes up to one half of HNF were attached to the particles. Many chrysoomonads, in addition, were observed to be in contact with particles (live-observations). Another important result seems to be that at least one quarter on average, but sometimes much more, of the HNF biomass was due to *Kathablepharis*. This genus does certainly not only consume bacteria, but feeds also on nanoplankton (e.g. Skuja, 1948).

Mixotrophs like *Dinobryon* are common and sometimes abundant, but since their contribution to phagotrophy can vary significantly (Caron *et al.*, 1993), they were not considered among HNF.

Large heterotrophic flagellates (LHF)

This group includes all heterotrophic flagellates $\geq 15 \mu\text{m}$ in size. This size limit was used for pragmatic reasons, since organisms up to this size (HNF) are generally abundant and may be determined by epifluorescence microscopy on filters. During our investigations we found only chrysoomonads (mainly *Spumella*-like forms and *Paraphysomonas*) and colourless dinoflagellates (mainly *Gymnodinium* and esp. *G. helveticum*). Euglenids occurred, but were very rare among LHF. The seasonal cycle is

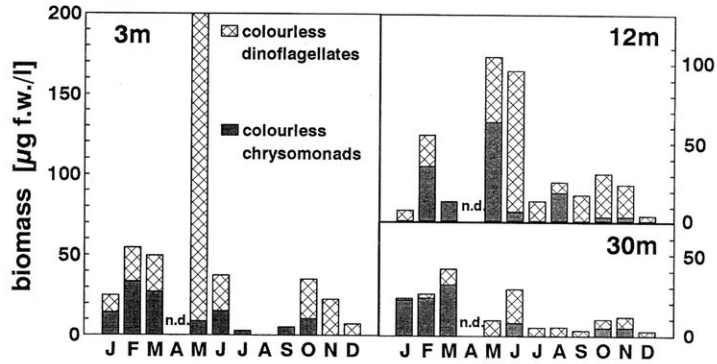


Fig. 6. Seasonal changes in the biomass of large heterotrophic flagellates in Lake Mondsee, 1992, at three different depths.

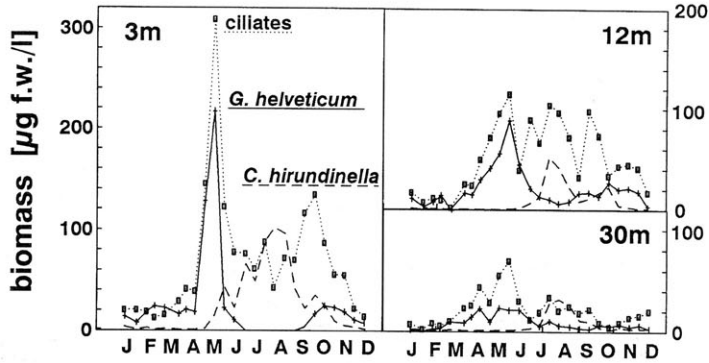


Fig. 7. Comparison of seasonal changes in the biomass of ciliates, the colourless dinoflagellate *Gymnodinium helveticum*, and the mixotrophic dinoflagellate *Ceratium hirundinella* in Lake Mondsee, 1992, at three different depths.

characterized by a spring peak of chrysomonads and dinoflagellates (Figs. 6 and 7). This spring peak in April/May was most pronounced in the epilimnion (just at the onset of stratification) and was mainly due to a mass development of *Gymnodinium helveticum*. Large chrysomonads increased their relative contribution to LHF biomass from 24% as an annual average for the epilimnion to 36% at 12 m and to 57% in the hypolimnion, respectively. The low importance in the epilimnion is mainly due to high abundances of *Gymnodinium*, which did not occur in deeper layers. When water temperatures rose above 15°C, *G. helveticum* disappeared from the epilimnion, but was present in the deeper layers for the whole year. The mixotroph *Ceratium hirundinella* was not included in LHF counts, though it may act up to a certain extent as a phagotroph (cf. Sandon, 1932; Arndt, unpubl.). However the relative importance of phagotrophy in this species is not yet known. There was an alternation of *G. helveticum* by *Ceratium hirundinella* during summer (Fig. 7).

Sarcodines

Sarcodines were generally of minor importance. All groups were most abundant in the epilimnion. The only testacean which occurred in considerable abundance was *Diffugia hydrostatica*. *Arcella* species were rare. The estimates of naked amoebae (e.g. *Vahlkampfia*, *Vanella*) are minimum estimates, since they may have been overlooked when attached to particles. Though abundances up to 8 per ml (integrated sample) occurred, their biomass was not important. Most naked amoebae were very small (3-10 μm) as it is known from a few investigations in estuarine or eutrophic limnetic waters (cf. Rogerson and Laybourn-Parry, 1992a; Arndt, 1993a). We found an enrichment of amoebae on planktonic particles in Lake Mondsee by a factor of about 600 (Arndt, 1993a). Heliozoans were most important among sarcodines, small size classes (10-20 μm) prevailed as well. Centrohelid forms (e.g. *Acanthocystis* species) dominated, but *Actinophrys sol* was also common. During March, heliozoans formed up to 20% of protozoan biomass.

Discussion

Ciliates

The seasonal cycle of ciliates in the surface water of Lake Mondsee characterized by a spring maximum, high concentrations during summer and low concentrations during winter seems to be a typical pattern for many lakes of the temperate region ranging from mesotrophic to highly eutrophic status (cf. Nauwerck, 1963; Laybourn-Parry *et al.*, 1990b; Arndt and Nixdorf, 1991; Müller *et al.*, 1991b). The spring peak of ciliates corresponded to the peak of cryptomonads (see also Dokulil, 1988). The peak of ciliates was formed by oligotrichs and small prostomatids, which are known to be effective users of cryptomonads (Müller, 1991; Müller and Geller, 1993). A typical clear-water phase as a result of intensive grazing activity by metazooplankton is generally missing in Lake Mondsee. A drastic decline of ciliates due to the grazing impact by daphnids or low food concentrations in early summer as known for other lakes (e.g. Müller *et al.*, 1991a; Arndt and Nixdorf, 1991) did not occur. The composition of ciliate abundance and biomass is similar to that of Lake Constance. The ciliate abundance in the epilimnion of Lake Mondsee during 1992 was in the same range of values from investigations during 1990 of the same lake by Macek (unpubl., cited in Krössbacher, 1991).

By sampling of only different strata rather than a whole water column we may have overlooked aggregations of protozoans at certain depths. However, the combined samples at one depth at very different stations (no oxygen stratification occurred) of the lake with slight differences in vertical profiles may offer an estimate regarding vertical differences. Assuming that the 3 m and 12 m samples were representative for the epilimnion and the 30 m sample for the hypolimnion, respectively, the biomass of

ciliates in the hypolimnion was only about one third of that of the epilimnion. About 55-60% of the ciliate biomass per square meter is concentrated in the epilimnion. This value is comparable to that of deep, large Lake Constance (Müller *et al.*, 1991a). Lakes with an oxygen stratification seem to have quite different vertical distributions of ciliates characterized by maxima of relatively large bacterivores at the oxycline (*e.g.* Schlott-Idl, 1984a; Laybourn-Parry *et al.*, 1990a).

Heterotrophic nanoflagellates

The total abundances of HNF may have been underestimated during our study, since picoflagellates were not adequately counted by the live-counting technique. Investigations by epifluorescence microscopy (Arndt, unpubl.) showed that these picoflagellates were sometimes abundant, but did not contribute significantly to HNF biomass. This is in accordance with results by Weisse (1991) from Lake Constance. This may explain, why abundances of HNF during our investigations were only about half of that estimated in Lake Mondsee by Psenner and Sommaruga (1992) and Šimek (unpubl., cited in Krössbacher, 1991) by epifluorescence microscopy. However, during live-counting we found only flagellated bacteria in the size range of about 2 µm, and maybe not all picoflagellates counted by epifluorescence microscopy are really heterotrophic flagellates. Large flagellated bacteria, swarming cells and small rhizopods may be taken for HNF by the epifluorescence technique as well. Therefore, counts by epifluorescence microscopy are often interpreted as heterotrophic nanoplankton (HNAN) rather than HNF (*e.g.* Caron, 1991). Nevertheless, small nanoflagellates may have been underestimated in our quantitative study. The first maximum of HNF biomass in January may be explained by especially high run-offs due to heavy rains which caused also a high turbidity of the water due to anorganic particles. The high concentration of bodonids, which were normally of minor importance in the plankton community, may indicate the inflow of wastewater. Maximum biomasses of HNF at the end of the phytoplankton spring bloom in May/June and in late summer are in agreement with long-term studies of Lake Constance (Weisse, 1991; Jürgens and Güde, 1991) and in the highly eutrophic Lake Müggelsee, Berlin (Arndt and Nixdorf, 1991).

The only available quantitative data on seasonal changes in the composition of HNF biomass in lakes seem to be those from the well-studied deep, mesotrophic Lake Constance (Springmann, 1993) and from the polymictic, shallow and highly eutrophic Lake Müggelsee, Berlin (Arndt, 1993b, 1994). Our results regarding the composition of Lake Mondsee agree well with data from both, though very different lakes: Chryomonads were most important in all lakes, *Kathablepharis* and colourless cryptomonads were the second most important group, followed by choanoflagellates and kinetoplastids (even percentage compositions of HNF groups were very similar in all investigations, though different methods were used). In estuarine Danish waters choanoflagellates were most abundant, followed by chryomonads, cryptomonads and bodonids (Andersen and Sorensen, 1986). The light that is brought into the black box

“HNF” allows some conclusions regarding the function of HNF in the planktonic community. The majority of flagellates, especially bicoecids, choanoflagellates and bodonids, but also a considerable part of other chrysomonads seem to be attached to substrates. During investigations of macroaggregates in Lake Mondsee in October, an enrichment factor of HNF compared to the surrounding water was found to be more than 500 (Arndt, 1993a). Enrichment of heterotrophic nanoplankton was also found on aggregates of American lakes (Caron, 1991) and Scottish estuaries (Rogerson and Laybourn-Parry, 1992b). Thus it seems very probable that HNF contribute significantly to bacterivory in the vicinity of or within macroaggregates. According to recent studies by Grossart and Simon (1993) these macroaggregates or lake snow may form a significant part of planktonic particulate material. The significant contribution of the nanophagous genus *Kathablepharis* to the HNF biomass indicates that HNF are not only important consumers of bacteria, but may contribute even to loss rates of small nanoplankton (food vacuoles often contained algae, Arndt, unpubl.). Some chrysomonads were also observed with pigments in food vacuoles. Thus HNF should be considered both as potential bacterivores and algivores. Though it has long been known that HNF are able to feed on algae (*e.g.* Skuja, 1948), it has only recently been proven quantitatively for estuarine HNF (Sherr *et al.*, 1991). In addition to HNF mixotrophic flagellates like *Dinobryon* may contribute to bacterivory in Lake Mondsee at certain times (Psenner and Sommaruga, 1992).

Large heterotrophic flagellates

Colourless dinoflagellates are traditionally counted by algologists. Only a few studies considered their quantitative importance as phagotrophs (*e.g.* Nauwerck, 1963; Arndt and Mathes, 1991; Carrick *et al.*, 1991), quantitative counts of large colourless chrysomonads are much more sparse (*e.g.* Suttle *et al.*, 1986) mainly due to the fact that most large chrysomonads are disrupted and unidentifiable after fixation. Therefore, we used the live-counting technique. Recent investigations of rivers and lakes ranging from oligotrophic to polytrophic status indicated that these LHF are a common and significant part of protozooplankton contributing on average about one third to total protozoan biomass (Arndt and Mathes, 1991; Mathes and Arndt, 1994, this issue). Our investigations from the alpine Lake Mondsee confirmed these observations. Most important among LHF was *Gymnodinium helveticum*. The seasonal cycle of this species characterized by maximum abundances in spring in the epilimnion and disappearance from the epilimnion during the summer while remaining at low abundances in the cold hypolimnion (or disappearing completely in unstratified lakes) seems to be a typical phenomenon for temperate lakes (*e.g.* Nauwerck, 1963; Arndt and Mathes, 1991; Wille and Hoffmann, 1991). Its phagotrophic behaviour is well-known. Many different kinds of food items were reported, especially algae (*e.g.* Nauwerck, 1963; Bertilsson and Gelin, 1975; Irish, 1979). Our feeding experiments indicated a considerable contribution of algae to the food of *G. helveticum* (Arndt and Salbrechter, in prep.). It is evident from Figure 7 that the biomass of *G. helveticum* is

in the same range as that of ciliates. Metabolic rates of both groups may be comparable (e.g. Carrick *et al.*, 1992). Thus *Gymnodinium* should be considered as an important consumer of the phytoplankton spring bloom.

Sarcodines

The sporadic occurrence of sarcodines in sometimes very high concentrations agreed well with observations from other lakes (see Arndt, 1993a). During the investigations of Lake Mondsee heliozoans contributed up to 20% of protozoan biomass in early spring. We observed their feeding on cryptomonads and on ciliates in living samples. The maximum abundances of heliozoans corresponded to a decline of ciliates in March (see Fig. 3), maybe that this was partly due to heliozoan predation. The quantitative estimates of sarcodines have to be considered as minimal estimates, since concentrations were often too low to be adequately estimated by the applied methodology. In addition, naked amoebae may have been overlooked when attached to particles.

Conclusions

The present study was carried out in order to get some more information regarding the seasonal changes in the quantitative and qualitative composition of the protozooplankton. There are only a few comparative studies of metazoan and protozoan biomass available from literature, which considered at the same time not only ciliates, but also heterotrophic flagellates (e.g. Geller *et al.*, 1991; Weisse and Müller, 1990; Carrick *et al.*, 1991; Arndt and Nixdorf, 1991; Arndt *et al.*, 1993). It seems to be very important to consider large heterotrophic flagellates among protozoan biomass, otherwise about half of potential herbivores among protozoans and about one third of protozoan biomass may be ignored. The traditional view that phytoplankton is under relatively low grazing pressure during spring (e.g. Sommer *et al.*, 1986) originated from data sets which included — when protozoans were considered — only ciliates as a part of zooplankton. A comparative study of lakes of different trophic levels revealed that ciliates may compose on average only about half of protozoan biomass (Mathes and Arndt, 1994, this issue). At the end of the spring phytoplankton maximum just at the onset of stratification (during investigation of Lake Mondsee in May), protozooplankton biomass (dominated by oligotrichs, prostomatids and dinoflagellates) reached its maximum (about 500 mm³/m³ of predominantly algivores). Assuming that 10% of this biomass is carbon and that the small protozoans need to consume about two times their body carbon per day, a carbon requirement of predominantly algivores of about 100 mg C/m³ per day would result. This could be a significant part of primary production according to the long-term analysis of primary productivity in Lake Mondsee (Dokulil, 1991). For the shallow

highly eutrophic Lake Müggelsee estimations reveal that LHF together with algivorous ciliates were able to consume a very significant part of primary production during spring (Arndt *et al.*, 1993). The relative contribution of protozoans to the zooplankton biomass was in the range of data from north German lakes (*cf.* Mathes and Arndt, 1994, this issue), but were high compared to data from Lake Constance (*cf.* Geller *et al.*, 1991). Even when it is considered that large heterotrophic flagellates are not included in the data set of Lake Constance, the relative contribution of protozoans was much lower than in Lake Mondsee. One possible explanation may be that the absolute abundance of metazoans was higher in Lake Constance. In contrast to Lake Mondsee, a clear-water phase in late spring generally occurs in Lake Constance indicating the stronger impact of metazoans in the latter lake.

The data on seasonal changes in the biomass of protozooplankton in Lake Mondsee give evidence for the significant contribution of very different groups of protozoans, which all require different methods of analysis. Ciliates (including nano-sized forms), heterotrophic nanoflagellates (including bacterivores and algivores), large heterotrophic flagellates (including delicate chrysomonads and dinoflagellates) and sometimes even sarcodines were found to be of significance (mixotrophic algae were not considered here). General estimates of the role of zooplankton in the pelagic matter flux should consider this heterogeneity of protozooplankton.

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