Biomass and composition of protozooplankton in relation to lake trophy in north German lakes

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Abstract

Comparative studies regarding the biomass and composition of protozooplankton were performed in nineteen different lakes in the Mecklenburg Lake District (Northern Germany) ranging from meso-eutrophic to hypereutrophic (polytrophic) state during spring and during summer. The contribution of protozoans to total zooplankton biomass (including metazoans) increased from 20% in meso-eutrophic lakes to about 50-60% in hypereutrophic lakes during spring. During summer, contributions by protozoans to zooplankton biomass were similar but were not as closely related to trophy. Ciliates (mainly oligotrichs), heterotrophic nanoflagellates (mainly chrysomonads), and large (≥ 15 μm) heterotrophic flagellates (mainly chrysomonads and dinoflagellates) formed the major part of protozooplankton biomass. The contribution of large heterotrophic flagellates ranged between 29-59% and 8-40% of protozooplankton biomass during spring and summer, respectively. Ignorance of large flagellates in many contemporary limnetic plankton studies could lead to a significant underestimation of the role of protozoans in planktonic food webs. Sarcodines (amoebae and heliozoans) were only occasionally of significance. When abundant, however, at least heliozoans should have been able to act as important predators within the plankton community.

Predominantly algivorous flagellates (mainly large forms) and ciliates dominated the protozooplankton in spring, whereas a more diverse protozoan community occurred during summer. There was no clear trend regarding the influence of lake trophy on the composition of protozooplankton within the investigated range of trophy.

The biomass of all protozoan groups was significantly correlated with phytoplankton biomass (and chlorophyll *a*). Predominantly algivorous large flagellates and ciliates showed the strongest response. The slope of the regression between the biomass of bacterivorous heterotrophic nanoflagellates and phytoplankton biomass was significantly lower than the corresponding slopes of ciliates and large flagellates, respectively. The significant increase of the contribution of protozoans to zooplankton biomass with increasing lake trophy indicated the high importance of the microbial food web for the ecosystem functioning of hypereutrophic lakes.

Key words: Flagellates, Ciliates, Sarcodines, Protozoa, Trophy, Biomass, Phytoplankton, Metazoans

Résumé

**Biomasse et composition du protozooplancton en relation avec l'état trophique
dans des lacs du nord de l'Allemagne**

Des études comparatives concernant la biomasse et la composition du protozooplancton ont été réalisées, pendant le printemps et l'été, dans dix-neuf lacs différents du District des lacs du Mecklembourg (Allemagne du Nord) s'étageant du méso-eutrophisme à l'hypereutrophisme. La contribution des protozoaires à la biomasse totale du zooplancton (métazoaires inclus) augmentait de 20% dans les lacs méso-eutrophes jusqu'à 50-60% dans les lacs hypereutrophes durant le printemps. Au cours de l'été les contributions des protozoaires à la biomasse du zooplancton étaient comparables mais n'étaient pas liées d'aussi près au régime trophique. Les ciliés (oligotriches surtout), les nanoflagellés hétérotrophes (principalement des chrysomonades) et les grands (≥ 15 µm) flagellés hétérotrophes (surtout des chrysomonades et des dinoflagellés) formaient la plus grande part de la biomasse du protozooplancton. La contribution des grands flagellés hétérotrophes oscillait de 29 à 59% et de 8 à 40% de la biomasse du protozooplancton durant le printemps et l'été, respectivement. La méconnaissance des grands flagellés dans de nombreuses études actuelles sur le plancton des lacs pourrait aboutir à une sous-estimation significative du rôle des protozoaires dans les réseaux nutritionnels planctoniques. Les sarcodines (amibes et héliozoaires) n'étaient significatifs que de façon occasionnelle. En cas d'abondance, cependant, les héliozoaires au moins devraient être capables d'être des prédateurs importants dans la communauté planctonique.

Les flagellés consommateurs d'algues (surtout de grandes formes) et les ciliés dominaient principalement le protozooplancton au printemps, tandis que pendant l'été la communauté des protozoaires était plus diversifiée. Aucune tendance claire n'était perceptible concernant l'influence du régime trophique des lacs sur la composition du protozooplancton dans le cadre des régimes trophiques étudiés.

La biomasse de tous les groupes de protozoaires était corrélée de façon significative avec la biomasse phytoplanctonique (et la chlorophylle *a*). Ce sont surtout les grands flagellés consommateurs d'algues et les ciliés qui montraient la plus forte réponse. La pente de la régression entre la biomasse des nanoflagellés hétérotrophes bactérivores et la biomasse du phytoplancton était inférieure de façon significative aux pentes correspondantes des ciliés et des grands flagellés, respectivement. L'augmentation significative de la contribution des protozoaires à la biomasse du zooplancton avec l'accroissement du niveau trophique du lac indiquait la grande importance du réseau alimentaire microbien pour le fonctionnement de l'écosystème des lacs hypereutrophes.

Introduction

Protozoans are now recognized as important constituents of plankton communities not only in marine (*e.g.* Azam *et al.*, 1983; Porter *et al.*, 1985) but also in limnetic waters (*e.g.* Pace, 1982; Gates, 1984; Geller *et al.*, 1991; Arndt and Nixdorf, 1991). Ciliate biomass is known to increase with increasing trophy of lakes (Pace, 1986; Beaver and Crisman, 1989) and recently the same was shown to be true for heterotrophic nanoflagellates (Berninger *et al.*, 1991; Gasol and Vaqué, 1993). The size frequency distribution of heterotrophic nanoflagellates shows a predominance of forms in the size range of 2-8 µm (*e.g.* Weisse, 1991). Forms with a size larger than 15 µm are much less abundant and not adequately counted, but they can contribute significantly to flagellate biomass (Arndt and Mathes, 1991; Arndt *et al.*, 1993, 1994). We differentiated in this study heterotrophic nanoflagellates (< 15 µm, HNF) and large heterotrophic flagellates (15-50 µm, abbreviated here as LHF). LHF have only seldom been incorporated into quantitative studies of protozooplankton (*e.g.* Nauwerck, 1963; Lewis, 1985; Carrick *et al.*, 1991). Recent investigations have shown that the biomass

of LHF, too, may increase with the trophy of lakes (Arndt and Mathes, 1991). Data on planktonic sarcodines (amoebae and heliozoans), which may sporadically occur in significant abundances, are even more sparse (*cf.* Arndt, 1993b). Up to now the groups of protozooplankton have generally only separately been considered regarding their response to trophy and regarding their contribution to total zooplankton biomass, respectively.

The idea of this study was to investigate the total and relative contribution of all these protozoan groups in plankton sample from very different lakes of varying trophic state and to analyse the relative contribution of protozooplankton biomass to total zooplankton biomass (including metazoans) with regard to the trophy of lakes. We included in the present investigation especially eutrophic and hypereutrophic lakes, since there are only a few studies on the microbial food web of highly eutrophic lakes (*e.g.* Beaver and Crisman, 1982; Riemann and Sondergaard, 1986). We will concentrate on the comparison of the two different seasons, spring and summer. Only data from the epilimnion are considered here to analyse the response of protozooplankton biomass to phytoplankton biomass as an indicator of lake trophy.

Methods

Nineteen lakes of the Mecklenburg Lake District (Northern Germany, see Fig. 1 and Table I) were investigated regarding their protozooplankton abundance and biomass during the period 1989-1991. The largest lake was Schaalsee (23.4 km^2), and the smallest was Schönlager See (0.16 km^2). Most of the investigated lakes in the North-German Lowland are naturally eutrophic, and many lakes have a higher trophic level today due to anthropogenic eutrophication (*cf.* Segebarth *et al.*, 1992). To consider differences between eutrophic lakes the trophic index was calculated according to the East-German Standard for Lake Classification (German Democratic Republic, 1982, TGL 27885/01, *Utilization and protection of waters: stagnant inland waters — classification*). This index is based on measurements of ranges of oxygen content, nutrients, epilimnetic chlorophyll *a* and biomass of phytoplankton and metazooplankton, and transparency, respectively. According to this classification the trophic status of the investigated lakes ranged from mesotrophic, to slightly and highly eutrophic, to polytrophic level. The characteristics of lakes within the different levels of trophy are given in Table I and Figure 2. The total phosphorus content ranged from about 90 µgP l^{-1} for mesotrophic lakes to about 600 µgP l^{-1} for polytrophic lakes (this would correspond to eutrophic and highly hypereutrophic levels according to Wetzel, 1983). For one lake, Krakower See, different basins were investigated and considered as different "lakes" as they significantly differed regarding their trophy.
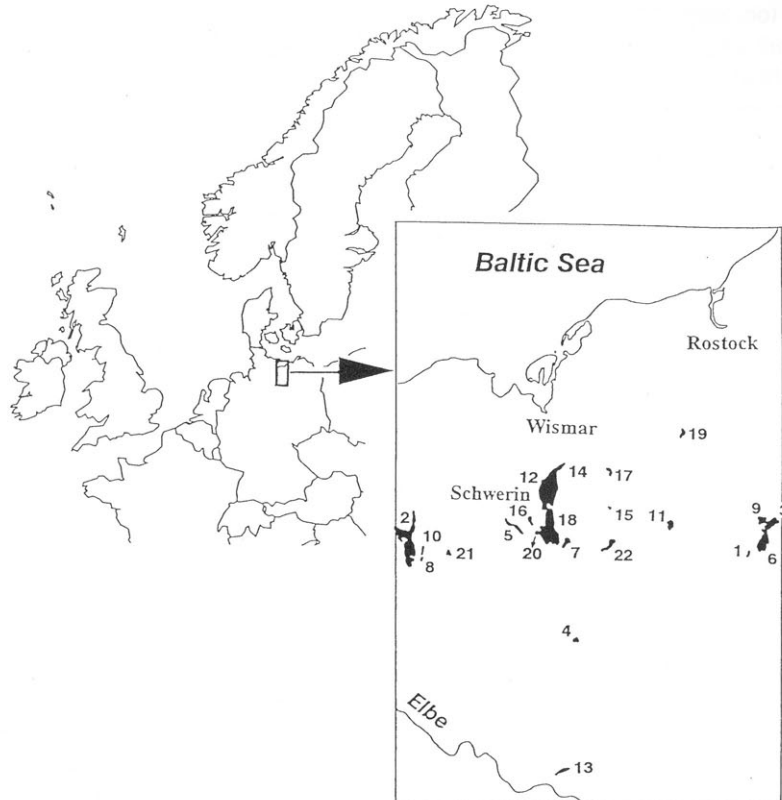
Fig. 1. Lakes in the Mecklenburg Lake District (Northern Germany) from which plankton samples were collected during 1989-1991. The numbers refer to the lakes listed in Table I.

The investigation of lakes was part of a routine monitoring programme of the water management authorities in Schwerin. For the purpose of this study samples taken during the spring period (phytoplankton spring bloom; generally March/April) and during the summer period (at well established stratification; generally July/August) were considered. The timing of sampling was based on routine seasonal records of chlorophyll *a* contents in the lakes. Samples were taken from the epilimnion above the deepest point of the different lakes only once per season. All samples were combined samples from 3-5 different samples of the epilimnion to reduce the influence of patchiness. A Secchi disk (25 cm diameter) was used to measure water transparency. Samples were taken during each investigation for the analysis of water chemistry (nutrients: soluable reactive phosphate, total P, nitrate, ammonium, pH, and oxygen according to standard methods: Legler *et al.*, 1988; Breitig and Tümpling, 1982). Chlorophyll *a* was extracted in ethanol. Phytoplankton was fixed with acid Lugol's iodine solution for microscopic analysis (species and biovolume) of sedimented

TABLE I. – Morphometric characterization of the investigated water bodies listed according to their trophy (numbers refer to Fig.1).

Lake (Nr.)	Surface area (km²)	Mean depth (m)	Maximum depth (m)	Catchment area (km²)	Trophic status
					mesotrophic
Paschensee (1)	0.52	7.9	18.0	4.3	1.9
Schaalsee (2)	23.4	14.1	72.0	180	2.3
Krakower Untersee (3)	4.1	8.0	12.5	154	2.4
Neustädter See (4)	1.44	5.0	29.5	1.0	2.4
Neumühler See (5)	1.72	5.2	17.5	18.4	2.4
					slightly eutrophic
Krakower Obersee (6)	8.2	10.0	29.0	107	2.6
Pinnower See (7)	2.69	7.0	16.0	6.3	2.6
Boissower See (8)	0.29	5.0	8.0	44.7	2.6
Krakower Stadtsee (9)	2.55	10.0	22.5	34.6	2.6
Neuenkirchener See (10)	0.56	6.0	10.0	42.2	2.7
Klein Pritzer See (11)	2.4	7.9	23.0	67	2.8
					highly eutrophic
Rudower See (13)	1.67	3.4	6.0	26	3.1
Schönlager See (15)	0.16	3.0	5.5	5.4	3.2
Medeweger See (16)	0.99	9.8	27.6	112	3.2
Tempziner See (17)	1.64	7.0	15.1	130	3.3
					polytrophic
Bützower See (19)	1.0	1.2	5.6	16	3.6
Schweriner See (Schloßbucht) (20)	0.2	4.0	8.0	-	3.7
Woezer See (21)	0.6	1.0	1.5	66.4	3.8
Barniner See (22)	2.52	2.2	8.0	199	4.0

material. Five or ten liters of lake water were concentrated on a net (mesh size 44 μm) and fixed with formaldehyde (final concentration 4%) for the analysis of metazooplankton (species and biovolume). Living samples for the analysis of protozooplankton were stored at in situ temperature, care was taken to prevent shaking of samples. Unconcentrated samples were analysed at least 1-2 hours after sampling.

Metazooplankton was counted and body dimensions of at least 20 individuals of each species for each sampling were measured with a micrometer. Fresh weight was calculated according to length weight regressions published by McCauley (1984), Ruttner-Kolisko (1977) and Balushkina and Winberg (1979). When only dry weight estimates were available, a dry weight/wet weight ratio of 0.17 was assumed. Phytoplankton species were counted in size groups and biovolumes were calculated from measurements of dimensions and approximations to simple geometrical forms. Abundance and biomass of protozoans (heterotrophic flagellates, amoebae, heliozoans, ciliates) were estimated by a live-counting technique using a light microscope with a temperature controlled microscope table. Unconcentrated samples were analysed in chambers of different size (5-10 μl; 50 μl; 2 ml; several parallel counts of each type of chamber). Generally, nanoflagellates were counted in the smallest chamber,
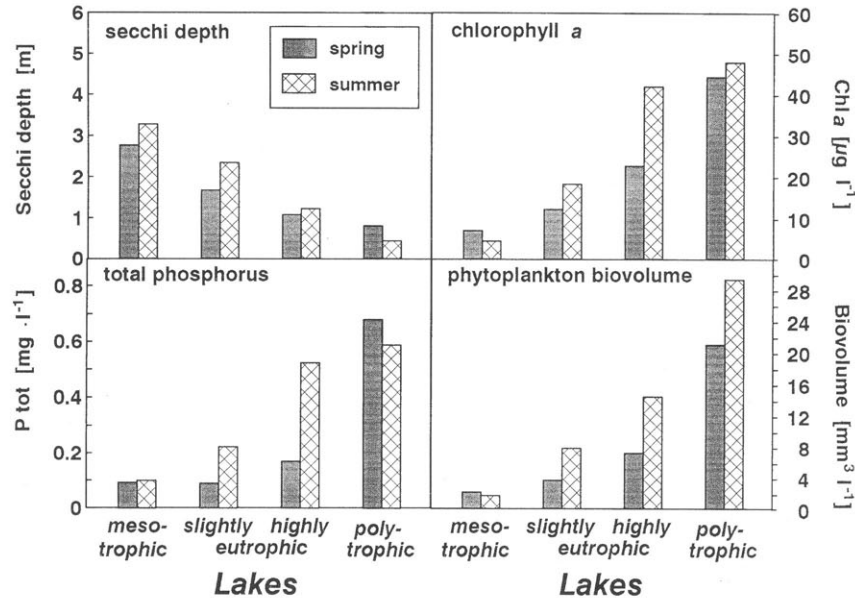
Fig. 2. Data for water transparency (Secchi depth), chlorophyll a, total phosphorus and phytoplankton biovolume in spring and summer are summarized for the groups of lakes defined in Table I.

microflagellates and nanociliates in the medium sized chamber, and ciliates in the largest chamber. Naked sarcodines were counted in all types of chambers. In addition, rare (< 100 ind./l) large protozoans were enumerated in sedimented samples fixed with Lugol's solution. Differentiation regarding autotrophy and heterotrophy of flagellates was done according to taxonomy. Comparative studies were done using parallel counts of fixed (2% cold glutaraldehyde) HNF by epifluorescence microscopy (*cf.* Caron, 1983) and the live individuals. Countings of flagellates which were ≥ 3 μm in size were in the same range as countings by means of epifluorescence microscopy, however picoflagellates were underestimated by live-counting (Arndt, unpubl.). In the meso-eutrophic Lake Constance and hypereutrophic Lake Müggelsee (Berlin) picoflagellates may be abundant but contributed only less than 10% to HNF biomass (Weisse, 1991; Arndt, 1994). Thus underestimations of the abundance of flagellates smaller than 3 μm may have not significantly affected the estimates of HNF biomass. Biovolumes of all protozoans were calculated from measurements of dimensions of living animals and approximations to simple geometrical forms. Protozoans were grouped in size intervals to the nearest 2 μm (interval: 2-12 μm), 5 μm (15-50 μm) or 10 μm (> 50 μm), respectively. If possible protozoans were determined to the level of species; in many cases the determination was possible only to the level of genus or family, and in several cases — especially for many heterotrophic flagellates — only to major taxonomic groups.
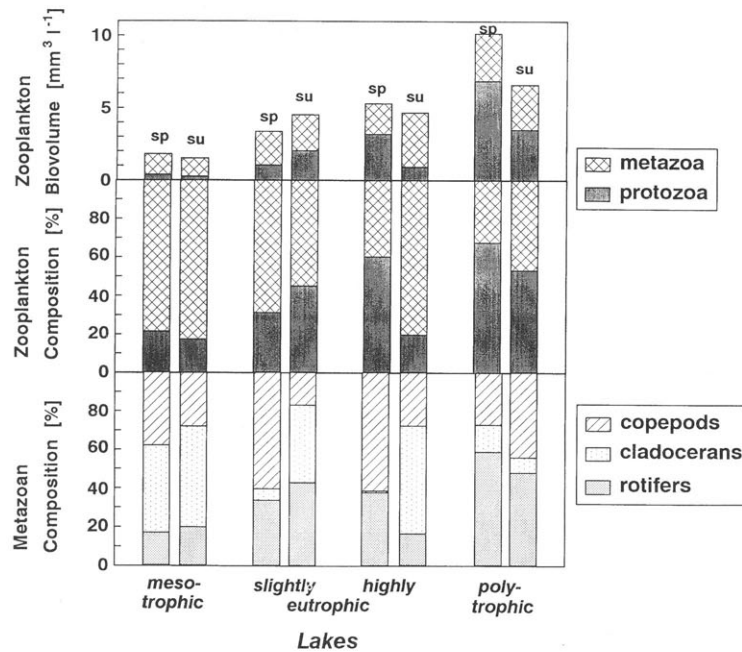
Fig. 3. Total zooplankton biovolume, percentage contribution of protozoans and metazoans to zooplankton, and metazooplankton composition with regard to the trophy of the Mecklenburgian lakes. Data were summarized for the groups of lakes defined in Table I and for spring (sp) and summer (su) samples.

Results

Relative contribution of protozoans to zooplankton biomass

Total zooplankton biomass of Mecklenburgian lakes increased significantly with an increase in trophy (p< 0.001), this was due to a significant increase of protozoan biomass, whereas metazoans did not increase significantly (see also below). Protozoans contributed about 20% to zooplankton biomass in mesotrophic lakes and about 50-60% in polytrophic lakes, respectively (Fig. 3). The increase in the relative contribution of protozoans to total zooplankton biomass was more clear for the spring values than for the summer values. Metazooplankton composition was relatively variable, there was a tendency for an increase in the contribution of rotifers to metazoan biomass with an increase in trophy. Figure 3 may indicate a close relationship between the percentage contribution of rotifers to metazooplankton biomass with the percentage contribution of protozoans to zooplankton biomass. However, the biomass and composition of metazooplankton varied strongly between
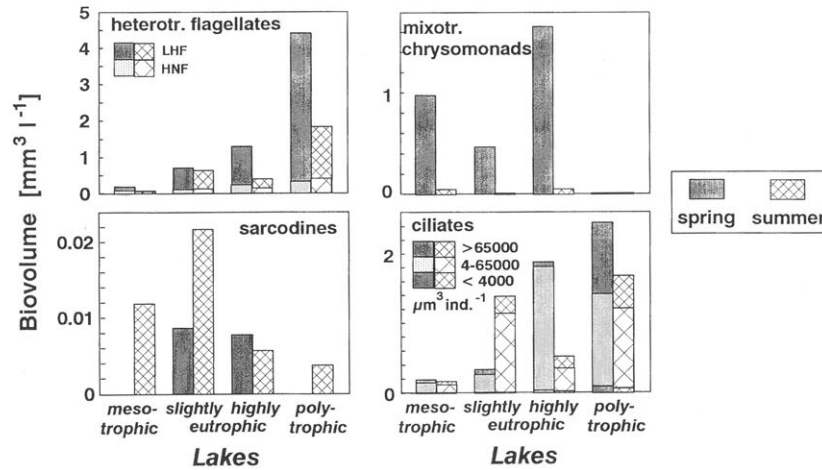
Fig. 4. Changes in the biovolume of different protozoan groups with regard to changes in the trophy of lakes. Data were summarized for the groups of lakes defined in Table I and for spring and summer samples. The columns for total flagellates are separated by horizontal lines; the lower and the upper parts represent HNF and LHF, resp. The columns of total ciliates comprise small ciliates (lower part, < 4000 μm^3/ind.), medium (middle part, 4000-65000 μm^3/ind.) and large ciliates (upper part; > 65000 μm^3/ind.).

the different lakes and revealed no significant trend regarding the relationship between metazoan composition and the protozoan biomass.

Changes in the biomass of the different protozoan groups

The differences in the mean biomass of heterorophic flagellates, sarcodines and ciliates in lakes of different levels of trophy during spring and summer are shown in Figure 4. The biomass of flagellates and ciliates increased towards the highest levels of trophy, sarcodine biomass showed no clear trend regarding the trophy of lakes. LHF were the most important heterotrophic flagellates in most of the lakes irrespective of their trophy. Their biomass was generally higher during spring than during summer. For comparison the biomass of mixotrophic HNF (chrysomonads: mainly genus *Dinobryon*) are shown in Fig. 4 (upper right panel). Since very little is known regarding the quantitative importance of phagotrophy among limnetic pigmented species of dinoflagellates, they have not been included here. Mixotrophic chrysomonads were not important during summer, but they were of remarkable importance regarding their biomass in mesotrophic lakes during spring when their biomass was about three times higher than that of heterotrophic flagellates. In eutrophic lakes their contribution was similar to heterotrophic flagellate biomass, but it was negligible in polytrophic lakes. The ciliate biomass was separated into three

Fig. 5. Changes in the biovolume of different groups of heterotrophic flagellates and ciliates with regard to changes in the trophy of lakes. Data were summarized for the groups of lakes defined in Table I and for spring and summer samples.
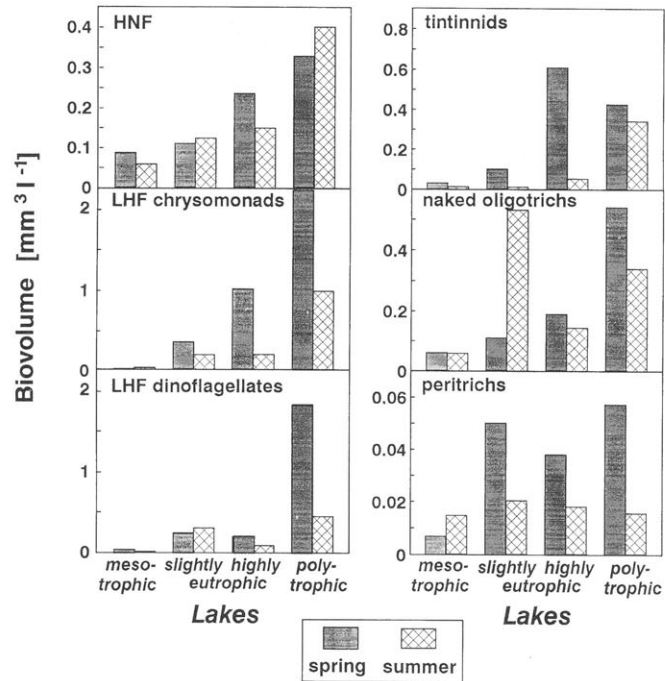
different size classes (Fig. 4, lower right panel). Small ciliates (< 4000 μm^3/ind., generally smaller than 20 μm) formed a very significant portion of ciliate abundance, but they did not contribute significantly to ciliate biovolume. The contribution of large ciliates (> 65000 μm^3/ind., generally larger than 50 μm) to the total ciliate biovolume varied with respect to the different lakes and to seasons. The increasing biomass of large ciliates from eutrophy to polytrophy corresponded to relatively stable biomasses of metazooplankton and to a decrease of the relative contribution of crustaceans in polytrophic lakes (*cf.* Fig. 3).

The biomass of HNF was prevailed by colourless chrysomonads. LHF were mainly composed of colourless chrysomonads and dinoflagellates (Fig. 5, left panels), only occasionally other groups were found. The most important colourless dinoflagellates were *Gymnodinium helveticum*, small *Gymnodinium*-like dinoflagellates, and *Diplopsalis acuta* in the lakes of the Mecklenburg Lake District. Among the delicate chrysomonads, *Spumella*-like and *Paraphysomonas* species were apparently dominant.

Naked amoebae were recorded in samples of most lakes. However, important abundances were only occasionally registered. Maximum abundances found were 6 ind. ml^{-1} (Lakes Neumühler See and Tempziner See). Testaceans (only the genus *Difflugia* was abundant) occurred only sporadically in plankton samples of Mecklenburgian lakes during this study (maximum abundance 0.2 ind. ml^{-1}; Neustädter See). Heliozoans were the most important group of planktonic sarcodines registered.
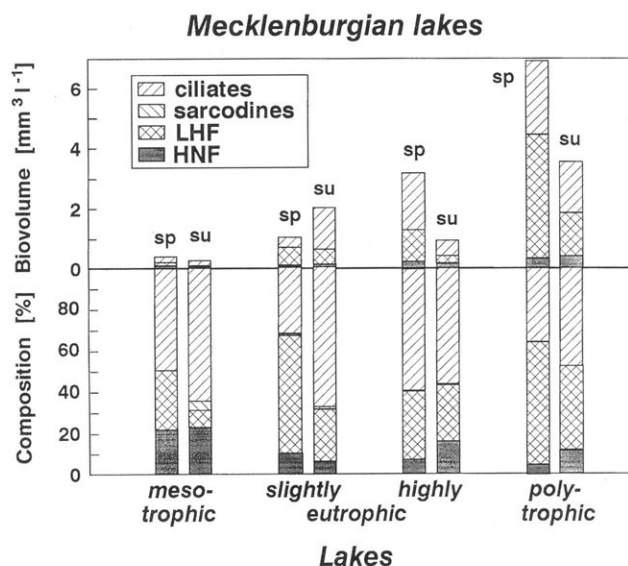
Fig. 6. Total biovolume and percentage contribution of protozooplankton with regard to Mecklenburgian lakes trophy. Data were summarized for the groups of lakes defined in Table I and for spring (sp) and summer (su) samples.

Maximum abundances were recorded as high as 77 ind. ml^{-1} (Neumühler See, Schaalsee). The irregular pattern of sarcodine distribution with regard to the trophy of lakes (Fig. 4, lower left panel) may reflect the sporadical occurrence rather than a trend for high biovolumes in slightly eutrophic lakes.

Prostomatid ciliates formed the major part of ciliate biovolume in the smallest size class in spring, while small scuticociliates occurred in high abundances in addition to prostomatids during summer. The biomass of the major representatives of medium sized ciliates (4000-65000 μm^{-3} ind.$^{-1}$) tintinnids (mainly *Tintinnidium* spp. and *Codonella cratera*), naked oligotrichs (mainly strombidiids, strobilidiids and halteriids), and peritrichs (mainly epizoic and epiphytic species of *Vorticella* and *Epistylis*) is shown in Figure 5. Spring maxima were found for tintinnids and naked oligotrichs in most of the lakes. There was no clear response of the occurrence of peritrichs with regard to the trophy.

Changes in the composition of total protozooplankton biomass

The composition of protozoan biomass was relatively similar during spring and summer when comparing lakes of the same trophy (Fig. 6). Generally, the percentage of large heterotrophic flagellates was higher during spring, whereas the relative contribution of ciliates was higher during summer. Predominantly algivorous LHF (chrysomonads and dinoflagellates) and ciliates (oligotrichs) prevailed during spring, while a more diverse protozoan community with respect to functional groups (bacterivorous, omnivorous and predatory protozoans) was established during summer.

A significant increase of biovolumes with increasing lake trophy was recorded for all protozoan groups, except for sarcodines, during spring (Fig. 6). Despite the significant differences in lake trophy (*e.g.* Secchi depth varied from more than 3 m in mesotrophic lakes to about 0.2 m in polytrophic lakes) and the considerable changes in total protozooplankton biomass, there was no clear trend in the relative contribution of each protozoan group. Heterotrophic nanoflagellates composed about 22% of protozoan biomass in mesotrophic lakes during spring, and their contribution decreased to about 7% in polytrophic lakes (summer values ranged between 7-22%). This group was the only one which showed a trend at least for the spring values. The contribution of large heterotrophic flagellates ranged between 29-59% and 8-40% of protozooplankton biomass during spring and summer, respectively. Sarcodines composed between 0-0.8% and 0.1-4.5% of protozooplankton biomass during spring and summer, respectively. Ciliates were, beside large flagellates, the most important group composing protozooplankton biomass (30-59% during spring, about 48-68% during summer).

Relationship between protozooplankton and phytoplankton biomass

The plot of values of zooplankton biovolume/phytoplankton biovolume for the single lakes shows the high variability of the data set (Fig. 7). The increases in protozoan biovolume seem to reach a plateau at high lake trophy as indicated by the stippled line connecting mean values of lakes in the different classes of trophy. The analysis by linear regressions between the biomass of different protozoan groups and the biomass of phytoplankton (log-transformed data) during spring are shown in Figure 8. The slopes of regression lines for total protozoans, HNF, LHF, and ciliates were significantly different from zero (F-test, $p < 0.005$; Table II). Metazoan biovolume showed only a slight though not significant increase with increases in phytoplankton biovolume. The slopes of LHF, ciliates and total protozoans were not significantly different from each other (t-test, $p > 0.10$), whereas the slope of HNF was significantly lower than that of each of the other protozoans (t-test, $p < 0.001$). The analysis by regressions between zooplankton biovolumes and the chlorophyll *a* values (log-transformed data) revealed similar data as for the phytoplankton biovolume (Table II). The regressions between protozoan biovolume and phytoplankton biovolume explained about 40% of the variability of HNF and LHF, and explained 60% and 70% of the variability of values of ciliates and total protozoans, respectively.

Discussion

Data on the contribution of total protozooplankton (including ciliates, sarcodines, and nano- and microflagellates) to total zooplankton biovolume (including metazoans and protozoans) is available only from very few lakes. In the mesotrophic Lake
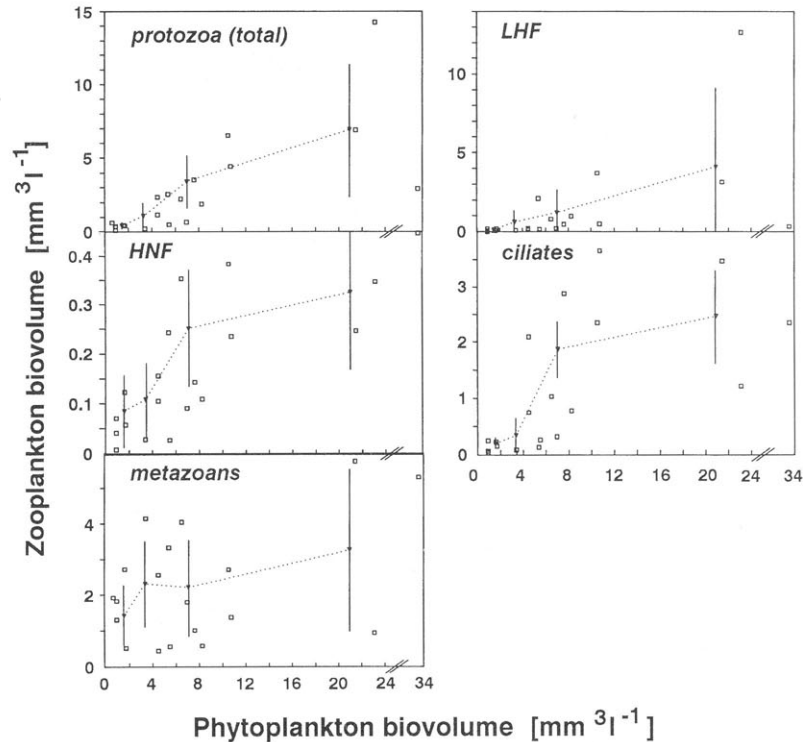
Fig. 7. Relationships between biovolume of protozooplankton groups or metazooplankton and the phytoplankton biovolume during spring sampling. Rectangles represent the data for each lake. The stippled line connects the mean values (± SE) for groups of lakes defined in Table I.

Constance, Geller *et al.* (1991) estimated that protozoans contribute about 9% of the annual mean zooplankton carbon (excluding large heterotrophic flagellates). In the epi- and hypolimnion of the mesotrophic, alpine Lake Mondsee the contribution of protozoans to total zooplankton biomass was about 40% on annual average (Salbrechter and Arndt, 1994, this issue). In a eutrophic lake (Müggelsee, Berlin) the contribution of protozoans to total zooplankton biovolume ranged from 2% in the clear-water phase, 10% during summer, 50-60% during spring and up to 90% during winter (Arndt *et al.*, 1993). In the Mecklenburgian lakes, one fifth of the zooplankton biomass in mesotrophic lakes was due to protozoans, whereas in the polytrophic lakes more than one half of the biomass was due to protozoans (Fig. 3). During winter the importance of protozoans in these lakes seemed to be even higher (*cf.* Mathes, 1992). The restriction of sampling to the epilimnion in this study may have underestimated metazoan biomass. However, most of the lakes were shallow (Table I) and epilimnion samples comprised the major part or the whole water column especially in most of the highly eutrophic and polytrophic lakes.

Fig. 8. Regression lines relating the biovolume (mm^3 m^{-3}, log-transformed values) of different zooplankton groups to corresponding data of phytoplankton biovolume (mm^3 m^{-3}, log-transformed values) in Mecklenburgian lakes during spring (see also Table II).
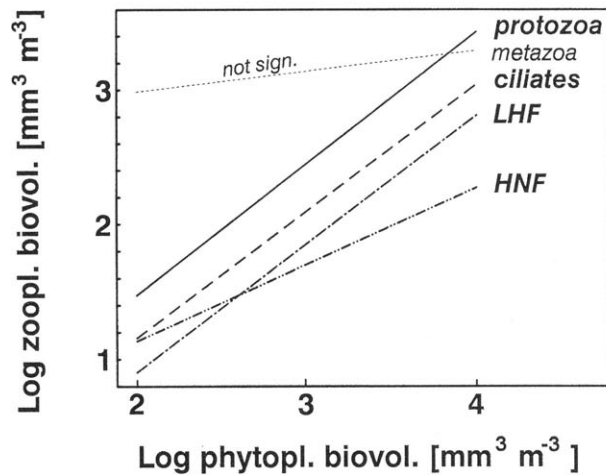

TABLE II. – Regression models relating protozoan and metazoan biovolume (mm^3 m^{-3}, log-transformed values) to corresponding data of phytoplankton biovolume (mm^3 m^{-3}, log-transformed values) and chlorophyll a (g m^{-3}, log-transformed values) in Mecklenburgian lakes during spring.

Dependent variable	N	R^2	F-ratio	Model P	Slope (SE)	T-value	Const.
	Independent	variable:	phytoplankton	biovolume			
HNF	19	0.39	11.0	0.004	0.569 (0.171)	3.32	-0.001
LHF	19	0.40	11.6	0.003	0.952 (0.280)	3.40	-0.997
Ciliates	19	0.60	25.0	<0.001	0.938 (0.188)	5.00	-0.715
Protozoans	19	0.69	38.4	<0.001	0.974 (0.157)	6.20	-0.470
Metazoans	19	0.05	0.9	0.36	0.152 (0.161)	0.94	2.681
Total zoopl.	19	0.55	20.8	<0.001	0.506 (0.111)	4.56	1.716
	Independent	variable:	chlorophyll a				
HNF	19	0.26	6.0	0.025	0.709 (0.289)	2.45	-0.874
LHF	19	0.41	11.7	0.003	1.458 (0.427)	3.41	-3.590
Ciliates	19	0.57	22.9	<0.001	1.408 (0.294)	4.78	-3.149
Protozoans	19	0.61	27.0	<0.001	1.401 (0.270)	5.20	-2.745
Metazoans	19	0.08	1.4	0.26	0.293 (0.244)	1.20	2.019
total zoopl.	19	0.56	21.7	<0.001	0.780 (0.168)	4.65	0.316

The comparative study of different lakes revealed that one third, sometimes up to one half, of the protozoan biomass consisted of heterotrophic flagellates, which were larger than the so-called nanoflagellates. Nanoflagellates are generally counted in fixed samples after staining with fluorochromes (*cf.* Caron, 1983). This procedure leads to a considerable underestimation of large flagellates ($\geq$ 15 µm), since their relative abundance is very low. In addition, large and delicate chrysomonads are difficult to detect, since disruption of cells may occur during fixation and filtration (Arndt, unpubl.). Most of these large heterotrophic flagellates seem to be predominantly herbivores (*cf.* Nauwerck, 1963; Arndt and Mathes, 1991). Large

heterotrophic flagellates are already known as a significant component of marine protozooplankton (*e.g.* Smetacek, 1981; Hansen, 1991), and recent investigations in the hypereutrophic Lake Müggelsee (Berlin, *cf.* Arndt *et al.*, 1993) indicated that LHF may be the most important grazers on phytoplankton during the spring bloom.

There are only few quantitative data on planktonic sarcodines. During the investigations of the Mecklenburgian lakes, heliozoans were occasionally very abundant. Peak abundances of planktonic heliozoans may exert a significant grazing pressure on other components of the planktivore community especially on moving organisms such as flagellates and ciliates (*cf.* Sandon, 1932). Their sporadic occurrence (sometimes in considerable biomasses) seems to be a typical phenomenon in lakes (*e.g.* Rainer, 1968; Laybourn-Parry *et al.*, 1990; Arndt, 1993b). The sporadic occurrence of sarcodines is supported by their ability to populate the planktonic habitat within short periods of time: many naked amoebae have the ability to form floating or flagellated stages; many sarcodines can form gas vacuoles/bubbles and produce fat droplets while populating the pelagial; rapid excystment and encystment may occur (for review see Arndt, 1993b). Thus, the sporadic sampling during this study was not adequate to analyse the relationship between the sarcodines biovolume and lake trophy.

The composition of ciliates in the investigated lakes is similar to that reported from other lakes (*e.g.* Laybourn-Parry *et al.*, 1990; Müller *et al.*, 1991). Our comparative studies of lakes of different trophy did however not confirm the results of Beaver and Crisman (1982) for Florida lakes, who found an increasing importance of small size classes of ciliates (bacterivorous forms) along a trophic gradient leading to eutrophy. Beaver and Crisman (1982) interpreted their results as a response of nanociliates (< 20 μm) to increasing concentrations of bacteria. In their studies, nanociliates were mainly composed of bacterivorous scuticociliates. In the Mecklenburgian lakes, however, prostomatid ciliates, which are known to comprise also important algivorous ciliates (Müller, 1991), composed a significant part of the nanociliate group. Further, the relative contribution of oligotrichs did not decrease significantly with increasing trophy. Much more taxonomic work has to be done about the quantitative composition of protozooplankton (*cf.* Foissner, 1994) to clarify whether there are significant changes in the species composition of lakes of different trophy.

Seasonally, the composition of protozooplankton in the Mecklenburgian lakes changed from dominance of preferentially algivorous ciliates and flagellates during spring to a more diverse protozoan community during summer including a significant part of bacterivorous and omnivorous species. The different responses during spring and summer may be related to the different quality of phytoplankton with edible algae (cryptomonads, diatoms) prevailing during spring and large forms and colonies (in some lakes cyanobacteria) prevailing during summer. A comparison of the size structure of flagellates and ciliates (see Fig. 4) revealed that the mean body size during spring was larger than during summer, probably as a result of low grazing pressure by metazoans in spring, whereas small forms may grow fast enough to tolerate the metazoans' grazing pressure during summer. The carbon flux through the microbial food web in German Lowland lakes may differ significantly between spring and summer as was shown for hypereutrophic Lake Müggelsee (Arndt, 1990). During

spring, algae and small protozoans were mainly consumed by protozoans which in turn were eaten by raptorially feeding metazoans. During summer, filter-feeding metazoans were the major consumers of algae and protozoans. Similar changes in the carbon flux were described for the deep mesotrophic Lake Constance (Weisse *et al.*, 1990; Weisse, 1991). Metazoans may exert a significant grazing pressure on protozooplankton, crustaceans seem to be more important predators on protozoans than rotifers (for reviews see Stoecker and Capuzzo, 1990; Arndt, 1993a; Jürgens, this issue). In our study the metazoan biomass did not significantly increase with increasing levels of trophy. Furthermore, rotifers composed half of metazoan biomass in polytrophic lakes. This reduced top-down effect may explain why large ciliates could establish high biomasses in polytrophic lakes (*cf.* Fig. 4). It may be that the fish community in the lakes regulated the grazing pressure of metazoans on protozoans (Christoffersen *et al.*, 1993; Köthe and Benndorf, 1994), but only little is known regarding the fish stock in the different lakes investigated during this study.

The analysis of the response of protozoans to changes in phytoplankton biomass may reveal a resonable estimate of the influence of trophy on protozooplankton. The most pronounced response to increasing phytoplankton biovolume was that of large heterotrophic flagellates and ciliates (Table II, Figs. 7-8). This is not surprising, since members of both protozoan groups seemed to be predominant algivores during our study. Little is known with respect to LHF response to trophy, however, the positive response of ciliate biomass to increases in lake trophy are a well-known phenomenon (*e.g.* Pace, 1986; Beaver and Crisman, 1989). The positive response of heterotrophic nanoflagellates to trophy is in agreement with the results of Berninger *et al.* (1991) and Gasol and Vaqué (1993). During the present study most HNF were probably bacterivores. Thus, the positive response of HNF may have mainly been an indirect effect as a result of increases in the abundance of bacteria which are known to increase with an increase in trophy (*e.g.* Cole *et al.*, 1988; Tzaras and Pick, 1994, this issue). The slope of the regression of HNF biomass *vs.* phytoplankton biomass was significantly lower than that of either ciliates or LHF. This may be explained by a reduction of bacteria due to other grazers at more eutrophic conditions (*e.g.* higher concentrations of microfiltrating rotifers). Since total biomasses of metazoans did not increase significantly with an increase in trophy, maybe that ciliates and LHF exerted a significant grazing impact on HNF during the present study. This idea is supported by dilution experiments which have indicated that ciliates may prey on HNF in Lake Constance (Weisse, 1991) and by size-fractionation experiments which showed that the presence of ciliates and LHF caused a significant reduction of the growth rate of HNF in Lake Müggelsee (Berlin; *cf.* Arndt, 1990; Arndt and Nixdorf, 1991). The recent review given by Gasol and Vaqué (1993) indicated that there is generally a relatively weak response of HNF abundance to trophy in eutrophic systems. This was confirmed by recent studies of Tzaras and Pick (1994, this issue).

Since the major aim of this investigation was to estimate the influence of trophy and phytoplankton biomass on protozooplankton biomass and composition, the analysis of data was restricted to the epilimnion. Thus, high abundances of protozoans (*e.g.* ciliates) which may occur in the less oxygenated or anoxic hypolimnion or in the

metalimnion of some lakes (*cf.* Bark, 1985; Lavrentyev and Maslevtsov, 1988) were not considered in this study. Though care was taken to analyse samples from the different lakes during the same period of the seasonal succession (during spring phytoplankton bloom and during summer stratification), sampling only once per season may be partly responsible for the high variability of protozoan biomass.

Conclusions

The biomass of all protozoan groups was significantly correlated with the phytoplankton biomass. However, the strength of the response by the protozoan groups was different. Large heterotrophic flagellates showed the strongest response and composed one third to one half of total protozooplankton biomass. This observation underlines the importance of this protozoan group when analysing the influence of the trophy on the relative importance of microbial processes. In contrast to protozooplankton, metazooplankton did not show a significant relationship to lake trophy. The relative contribution of protozoans increased with the increase of trophy from about one fifth of total zooplankton biomass in mesotrophic lakes to about one half of zooplankton biomass in polytrophic lakes. In addition, it has to be considered that protozoans have generally much higher metabolic rates than metazoans. It is known from other studies of oligotrophic (*e.g.* Pace, 1986) and eutrophic lakes (Karabin, 1985) that there is only a relatively low response of metazoan biomass to lake trophy. In addition, the relative contribution of "inefficient" metazoan micro-filtrators such as *Bosmina* and rotifers seems to increase with increasing trophy (Karabin, 1985; Riemann and Christoffersen, 1993). The present investigations that included lakes from the upper range of trophy, give evidence for the hypothesis that the relative importance of the microbial food web compared to that of the grazer food chain is increasing along a gradient leading to eutrophy. This would confirm the results by Riemann and Christoffersen (1993). The idea that the increasing importance of picoplankton along a gradient leading to oligotrophy may cause an increasing importance of the microbial web (*e.g.* Porter *et al.*, 1988) may overlook the high importance of waste produced by metazoan feeding (*e.g.* Lampert, 1978) which fuels the microbial food web under eutrophic conditions (Güde, 1988; Jumars *et al.*, 1989; Arndt *et al.*, 1992).

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