Verh. Internat. Verein. Limnol.	24	879–883	Stuttgart, März 1991

Spring clear-water phase in a eutrophic lake: Control by herbivorous zooplankton enhanced by grazing on components of the microbial web

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Introduction

Metazooplankters are known as important regulators of the density and composition of phytoplankton in lakes (Sommer et al. 1986). At high densities of zooplankton the transparency of even highly eutrophic waters can increase significantly and sometimes so-called clear-water phases can occur. Up to now this phenomenon is mainly explained by limitations of phytoplankton growth due to direct interactions such as grazing by metazooplankton (mainly crustaceans) and exhaustion of dissolved nutrients by the phytoplankton itself. However, during the last years the knowledge regarding the activity and biomass of bacteria and protozoans (e.g. Pace & Orcutt 1981, Güde 1988, Arndt et al. 1990) in limnetic pelagic ecosystems has much increased, and it seems very probable that in many lakes the metabolic activity of planktonic protozoans is comparable to that of metazooplankton. From this point of view, the interactions should be much more complex than the simplified assumptions of most ecosystem models calculating nutrient remineralization as a function of metazooplankton feeding. It is known that protozoans act as significant contributors to nutrient remineralization in aquatic ecosystems (e.g. Caron et al. 1988, Jürgens & Güde 1990). Unfortunately, only very few data sets are available from limnetic ecosystems including all microbial components (bacteria, heterotrophic flagellates, ciliates, rhizopods).

In Lake Müggelsee (Berlin) we found an apparent minimum of microbial components at the time of the biomass peak of metazooplankters in early summer. A similar phenomenon has also been reported from some other ecosystems (Güde 1988, Arndt 1986). This gave rise to our investigations on the direct grazing impact of metazoans on microbial components as important nutrient remineralizers. As a result of our field studies a modified concept of interactions in the pelagic zone of lakes considering the contribution of microbial components is presented.

Material and methods

The investigations were carried out in Lake Müggelsee (Berlin), a polymictic shallow eutrophic lake with an area of 7.2 km^2 and a mean depth of 4.9 m. For routine sampling of all components subsamples were taken from an integrated sample of the mixed surface layer in weekly to biweekly intervals at 8–9 a.m. (105 l from 21 stations at different depths according to the depth profile of the lake). With a few exceptions the lake was always mixed down to the bottom. Phytoplankton were fixed with acid Lugols' solution and counted under an inverted microscope by the Utermöhl-method. Bacteria were fixed with particle-free formaldehyde (2 %) and filtered and counted (after prestaining with acridine-orange) on black Nuclepore filters (pore size 0.2 μm) under an epifluorescence microscope according to Hobbie et al. (1977). Protozoans were counted using a minute live-counting technique under a light microscope (cf. Dale & Burkill 1982, Güde 1986) on a temperated microscopic table. Unconcentrated samples were analysed in chambers of different size (10 μl, 50 μl, 400 μl, 2–10 ml). Differentiation regarding autotrophy and heterotrophy of flagellates were done by means of epifluorescence microscopy (cf. Davis & Sieburth 1982). Lifecounting has some considerable advantages, especially under highly eutrophic conditions, compared to the analysis of fixed samples stained with fluorochromes which is widely used in marine biology: exclusion of biases from fixation, storage and concentration; possible registration of behaviour and the size of organisms as well as counts of protozoans present at very different concentration. For our purposes the advantages outweighed the disadvantages (counting only immediately after sampling, only a short time for observation of living animals). The mesozooplankton biomass was estimated from formalin-fixed (4 %) net samples (20 or 40 l, > 44 μm) using species-specific length/weight-regressions (Downing & Rigler 1984). Biovolumes of the other biological components were calculated from measurements of dimensions and approximations to simple geometrical forms. Heterotrophic flagellates and small ciliates (< 30 μm) have been considered quantitatively only since April 1988.

The grazing impact by mesozooplankton on the protozoan community was investigated by means of the size-fractionation-technique. Two 1 l-glass-bottles were filled with the biotope water from the integrated sample

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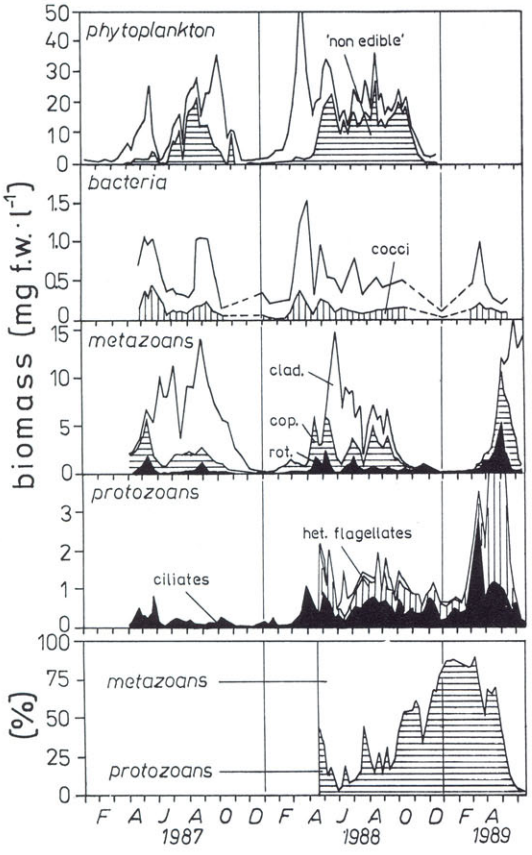

Fig. 1. Seasonal changes in the biomass of phytoplankton ('non-edible' means filamentous forms), bacteria, metazoans (separated for rotifers, copepods and cladocerans), and protozoans in Lake Müggelsee (upper 4 panels) and the seasonal changes in the percentage of protozooplankton biomass within the total zooplankton biomass from April 1988 through June 1989 (lower panel).

without any manipulation, and two bottles were filled with biotope-water after filtration through a 28 μm-sieve. Concentrations of protozoans were determined at the beginning and after an incubation *in situ* for 12 to 48 hours. The mortality of protozoans caused by the presence of mesozooplankton was calculated from the difference in the growth rate in the presence and absence of mesozooplankton assuming an exponential growth of protozoans being the same under both conditions (cf. Gilbert 1989). *Codonella cratera* did never show growth under enclosure conditions, hence this species was excluded from calculations. 36 different experiments were carried out.

Results

Seasonal successions of biological components

The seasonal changes in the biomass of the plankton of Lake Müggelsee are shown in Fig. 1. The phytoplankton succession represents the general pattern as decribed for eutrophic lakes (Sommer et al. 1986). In early spring, cryptophyceans dominate followed by diatoms. At high densities of mesozooplankton the abundance of 'edible' algae decreases significantly in May/June, but in some years filamentous blue-greens are still present (1988, 1989) so that transparency does not decrease to a clear-water phase. From summer till autumn, blue-greens *(Aphanizomenon, Oscillatoria)* dominate, and diatoms generally appear again in late autumn (see also Hoeg 1983). The planktonic bacteria show much less variability in biomass. From low winter values biomass rises after the first phytoplankton bloom and decreases at high concentrations of protozoans and rotifers in April and at maximum concentrations of filter-feeding crustaceans in May/June. During summer, no clear pattern of changes in bacterial biomass could be observed. The decline in late autumn cannot well be described by our data set, but its timing seems to be governed by the autumn bloom of phytoplankton. The percentage of attached bacteria was relatively low ($< 10-20\,\%$) and did not change considerably in the course of a year. On an annual basis the bacterial production is about one quarter of primary production (Nixdorf 1990, Nixdorf unpubl.).

The spring zooplankton is composed of rotifers (*Synchaeta, Polyarthra,* and brachionids) and cyclopoids *(C. vicinus, Mesocyclops leuckarti)* (see also Krocker 1987). Predatory feeding of cyclopoids and *Asplanchna* may be the reason for a reduced development of rotifers. In May, daphnids *(D. galeata, D. cucullata)* build up the major biomass peak. Their grazing activity can be responsible for a significant reduction of phytoplankton biomass (Behrendt & Nixdorf, this volume). During summer the zooplankton composition is changed more to smaller crustaceans (e.g. *Bosmina, Chydorus)* representing the main characteristics of the PEG-model (cf. Sommer et al. 1986). The protozooplankton of Lake Müggelsee comprises three major groups: ciliates, heterotrophic flagellates and rhizopods. Two groups of them, large heterotrophic flagellates ($\geq 15\,\mu$m) and naked amoebae, which have formerly obviously been overlooked in protozooplankton investigations of lakes can contribute significantly to the protozooplankton

biomass of Lake Müggelsee (ARNDT in prep.). The contribution of protozoans to total zooplankton biomass (Fig. 1, lower panel) changes considerably in the course of the year with highest values (90 %) during winter, lowest values in May/June (2 %) and moderate values (20 %) during summer. Though the overall importance of protozoans in winter and spring is clear, their contribution to nutrient mineralization should also be significant during summer considering their several times higher productivity compared to metazoans. Growth rate estimations under *in situ* conditions excluding predators revealed doubling times ranging from up to $2\,d^{-1}$ for large ciliates (> 30 µm) and large flagellates (≥ 15 µm) up to $3\,d^{-1}$ for small ciliates and $7\,d^{-1}$ for nanoflagellates (ARNDT unpubl.).

Mortality of protozoans caused by mesozooplankters

When looking at the graphs in Fig. 1, there seems to exist a paradoxon: those components which are most productive, bacteria and protozoans, show the most equalized level of biomass in the course of the year. For bacteria this phenomenon is already known, though the reasons are not fully cleared up (GÜDE 1990). Highly productive nanoflagellates are able to control bacterial growth (e.g. GÜDE 1986). In addition mesozooplankters and ciliates should play a significant role (RIEMANN & SONDERGAARD 1987, GÜDE 1988). In Lake Müggelsee protozoan biomass is in the same range as bacterial biomass making close interactions between these components very probable. However, regarding the fate of protozoan production only sporadic investigations are to find in literature indicating that mesozooplankters should be able to consume protozoans (e.g. PORTER et al. 1979) field investigations are rare (e.g. GILBERT 1989, ARNDT et al. 1989).

Though, our enclosure-experiments may be suffered from bottle-effects and underestimations of protozoan death rates due to grazers (large protozoans) left in the control flasks which can grow up in the absence of mesozooplankton (see below), the investigations give an impression about the impact of mesozooplankton. The death rates of protozoans induced by interference with mesozooplankton were separated for large ciliates (> 30 µm body length, e.g. large oligotrichs, gymnostomes), small ciliates (e.g. small oligotrichs, scuticociliates), heterotrophic nanoflagellates

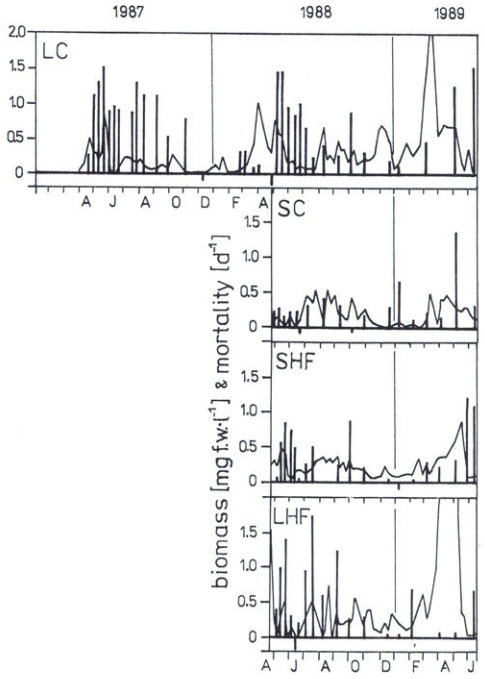

Fig. 2. Seasonal changes in the biomass and the mortality, induced by interference with metazoans (size-fractionation technique), of large ciliates (> 30 µm body length, LC), small ciliates (SC), small heterotrophic flagellates (< 15 µm, SHF) and large heterotrophic flagellates (LHF), resp.

(< 15 µm, e.g. monads, bodonids, choanoflagellates), and large heterotrophic flagellates (e.g. chrysomonads, colourless dinoflagellates) and compared to the seasonal changes in their biomass in the field (Fig. 2). The following main results can be derived: 1) All protozoan components are exposed to significant grazing pressure by mesozooplankters. 2) Larger ciliates and larger flagellates are more affected by mesozooplankton than smaller ones. 3) There seem to exist seasonal changes in grazing pressure with highest values at the mesozooplankton maximum and lowest values during winter. 4) Sometimes, we recorded negative death rates indicating some kind of promotion when mesozooplankton is present.

Coming back to the title of our paper, what does the mesozooplankton peak in May/June mean for the microbial components, we can conclude that the observed minimum of microbes at that time is the result of intensive grazing pressure by metazoans. Often more than 100 % of protozoan

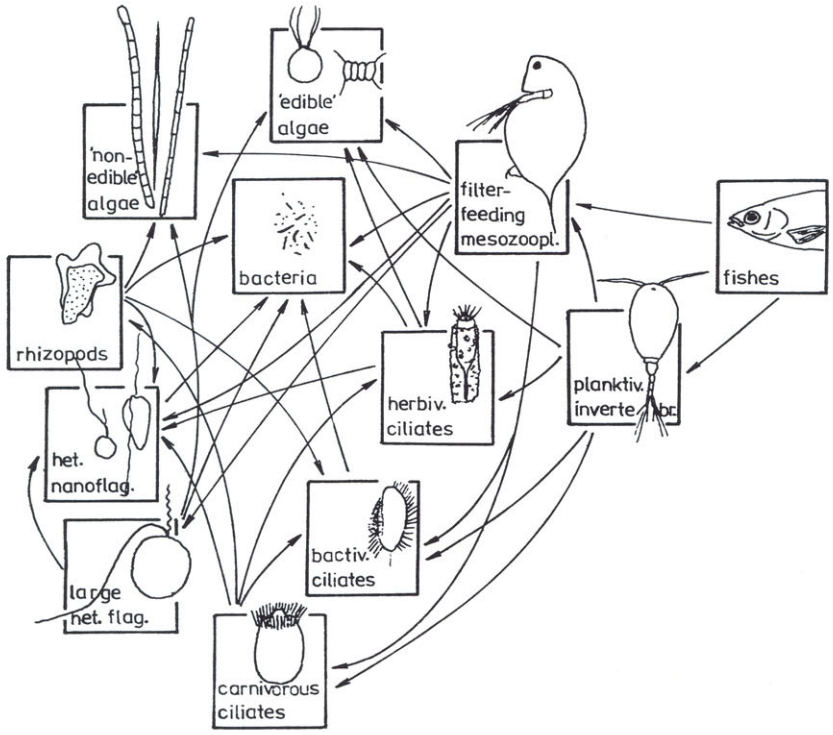

Fig. 3. Feeding interactions in the plankton of Lake Müggelsee derived from grazing experiments or analysis of food vacuoles and gut contents (ARNDT unpubl.).

production (control flasks) were eliminated by metazoans. However, during other seasons mesozooplankton seems to have more a regulating effect via controlling predatory protozoans. This is underlined by observations of high growth rates of small ciliates and nanoflagellates grown in biotope-water filtered through a 5- or 10 μm-sieve compared to those grown in water filtered only through a 28 μm-sieve. In the latter omnivorous ciliates like *Monodinium* and *Strobilidium velox* grew up (ARNDT unpubl.).

Our results offer an explanation for the seasonal occurrence of larger protozoans which are restricted to those phases when mesozooplankters are of reduced importance (winter, spring). Many ciliates have developed special swimming patterns (cf. FENCHEL 1987) which may be explained – with the high grazing pressure in mind – also as escape reactions analogueous to mesozooplankton.

Conclusions

According to our preliminary results the mesozooplankton at its highest densities in early summer may not only have a direct effect on phytoplankton via grazing. Including microbial activities, the succession of planktonic events may be characterized as follows: In early summer, the spring phytoplankton community with relatively low grazing pressure and high, nutrient recycling changes to an intensively grazed phytoplankton community and grazed components of the microbial recycling (esp. protozoans). By this way, nutrient deficiency in the water column should be increased (cf. GÜDE 1988). Then, in summer, a phytoplankton community is established under moderate grazing pressure accompanied by intensive microbial recycling. During winter and early spring, protozoans seem to be the most important zooplankton component. During this time not only ciliates, but also large heterotrophic flagellates may significantly contribute to phytoplankton mortality. These large flagellates have mostly been overlooked in limnological research (cf. SUTTLE et al. 1986). In Lake Müggelsee their biomass was as high as that of nanoflagellates, they often consumed algae of the 'non-edible' fraction of phytoplankton (ARNDT in prep.). Fig. 3 summarizes our qualitative investigations regarding the food spectrum of the planktonic animals. It is evident that the term 'herbivores' gets more and more insufficient to describe the incorporation of the complex microbial web into the pelagic food web which contains all the basic

components of marine ecosystems (cf. PORTER et al. 1985). Much work has to be done to get a knowledge about the quantitative importance of the interactions within this enlarged food web in limnetic ecosystems.

Acknowledgements

We are very thankful to all of our colleagues from the laboratory at Lake Müggelsee for valueable discussions and help in the field work. Especially, we acknowledge the skilled counting of mesozooplankton by MARIA KROCKER and phytoplankton by SIGRIED HOEG.

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