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Long-term Annual and Seasonal Changes of Meta- and Protozooplankton in Lake Müggelsee (Berlin): Effects of Eutrophication, Grazing Activities, and the Impact of Predation

key words: zooplankton, Protozoa, herbivory, planktivory, fish, food web

Abstract

Annual changes of rotifers, copepods, cladocerans, the ciliate *Epistylis rotans,* and larvae of *Dreissena polymorpha* were analysed for the period 1908–1990. Though food resources increased 6–10 fold in the course of eutrophication, only rotifers and *Epistylis* increased accordingly. Probably as a result of increased predation pressure crustaceans increased only twice.
The seasonal pattern of metazoans and protozoans (flagellates, sarcodines, ciliates) were analysed for 12 and 3 years, resp. During winter and spring, large heterotrophic flagellates and ciliates dominated the zooplankton and were responsible for a pronounced – formerly underestimated – grazing pressure on phytoplankton. In early summer, metazoan filter-feeders were often able to cause a significant reduction of phyto- and protozooplankton. However, during some years, phytoplankton declined in the absence of a pronounced grazing pressure. Field data and experiments revealed that predators were able to regulate the density of cladocerans in early summer (mainly cyclopoids) and summer (mainly *Leptodora,* smelt and fish juveniles).

Contents

1. Introduction

Within this special issue on the limnology of Lake Müggelsee – a eutrophic, shallow, polymictic lake – this article is intended to describe the long-term changes of zooplankton as consumer and as prey of other organisms. Lake Müggelsee has already been sporadically investigated by limnologists for one hundred years, and quantitative data of zooplankton are available already from the first decade of this century.

Derived from palaeolimnological studies, artificial eutrophication experiments, and the comparison of abundance and species composition of lakes with different trophy it is known that zooplankton biomass generally increases with an increasing degree of eutrophication. These changes in biomass are accompanied by changes in species composition (cf. EINSLE 1983). Only a few studies are available (e. g. KIEFER 1973; WALZ *et al.* 1987; NAUWERCK 1991) which can document the long-term quantitative changes of zooplankton accompanied with the long-term effects of industrialisation and population growth in Europe for more than two or three decades. Data on metazooplankton of Lake Müggelsee have already been published at the end of the last century (HARTWIG 1897; ECKSTEIN 1895/96), when a large drinking water plant began to pump the surface water of Lake Müggelsee. The eutrophication process of the lake is well documented (cf. BARTHELMES 1978 b; BARTHELMES *et al.* 1978; WELLNER 1978; BEHRENDT *et al.* 1990). The most drastic changes in the ecosystem took place in the late 1960's and early 1970's, when the seston content increased several times and the submerged macrophytes completely disappeared. One aim of the present paper is to compare the results of an intensive study of zooplankton during the last 12 years with quantitative and qualitative investigations at the beginning of this century (VORKASTNER 1983). In such a long-term comparative study protozooplankters are - up to our knowledge - for the first time included. The comprehensive data set for phytoplankton and zooplankton gives an impression of the annual variations in trophic interactions, though the phytoplankton biomass stayed relatively stable. The results will be presented in several sections: metazooplankton (long-term changes, species list, seasonal changes), protozooplankton (long-term and seasonal changes), impact of metazoans and protozoans on phytoplankton and influence of planktivorous predators.

2. Material and Methods

Study area: Lake Müggelsee (Großer Müggelsee, Berlin) is a shallow (mean depth 4.9 m, max. depth 7.5 m), eutrophic and polymictic lake with an area of 7.2 km^2. The River Spree flows through the lake, the retention time of the water in Lake Müggelsee is about 40 days. For further details of the study area see BEHRENDT *et al.* (1990) and DRIESCHER *et al.*; (1993).

Zooplankton: Weekly (1987–1990) or biweekly (1979–86) samples were taken by means of a 5-l-Friedinger sampler. During the periods of icecover samples were taken sporadically. From 1979–1987 samples were collected at the deepest point in 1-m-intervals from the surface to the bottom (7 m, total 40 l), from 1988–1990 a mixed sample from 5 different points of the lake at different depths has been used (total 105 l) to take the vertical and horizontal inhomogeneities into account (for details of sampling see DRIESCHER *et al.,* 1993). 20–40 litres of water were filtered on a 50 µm mesh, resuspended in 100 ml lake water and fixed with formaldehyde (final concentration 4 %). The total sample was analysed for *Leptodora,* subsamples (by means of calibrated automatic pipettes) were analysed for the other zooplankters in counting chambers under a light microscope. Species determinations were mainly done according to FLÖSSNER (1972), KIEFER (1978) and KOSTE (1978). Crustacean biovolume was estimated using length-weight regressions published by BALUSHKINA & WINBERG (1979), BOTTRELL *et al.* (1976), MCCAULEY (in DOWNING & RIGLER 1984). When only dry weights were available, biovolumes were estimated using an assumed dry weight/wet weight relationship of 0.15. Formulas of RUTTNER-KOLISKO (1977) were modified according to actual length relationships of rotifers in Lake Müggelsee to determine rotifer biovolume.

Protozoans (heterotrophic flagellates, ciliates, rhizopods) were estimated by a life-counting technique under a light microscope on a temperated microscope table (cf. ARNDT & MATHES 1991). Unconcentrated samples were analysed in chambers of different size (2–10 µl; 50–100 µl; 400–800 µl; 2–10 ml). Biovolumes were calculated from measurements of dimensions of living animals and approximations to simple geometrical forms. Rare large protozoans were investigated in samples gently filtered on a 10 µm mesh sieve, generally fixed (Lugol's solution; mercury chloride) sedimented samples were analysed in addition.

Feeding experiments with metazooplankton: Studies on the food selection of older cyclopid stages regarding the predation on other metazooplankton was carried out using the presence/absence method. Experimental (cyclopoids enriched by light trapping and pipetting under a dissecting microscope) and control 1-l-bottles (3 parallels) were exposed *in situ* for 15 h on May 3rd, 1989. Metazooplankters were counted in subsamples from the beginning and at the end of the experiment.

Another experiment was carried out, where the hypothesis was tested that females of *Acanthocyclops robustus* (a common cyclopoid in Lake Müggelsee from spring till autumn) are not efficient predators on adult daphnids, but are able to use small soft-bodied neonates. Experimental (each with 2–3 *Acanthocyclops* females) and control vessels (10 ml, 3 paralleles) were alternatively supplied 4–6 hours old neonates of *Daphnia galeata* (body length 620 ± 58 µm), 1½ day old juveniles (898 ± 114 µm), or adult *D. galeata* (2145 ± 231 µm). All vessels were supplied with *Scenedesmus dimorphus* to prevent daphnids from starvation. No mortality of daphnids occurred in control vessels over the experimental period of 18 hours at 20 °C under dim light.

Feeding rates were determined according to PETERS (in DOWNING and RIGLER 1984). Food selection were calculated following JACOBS (1974).

Analysis of fish juveniles: 0+ fish were caught by a trawl net (opening about 14 m^2), which was tracked at a constant speed by a boat for 10 minutes. The end of the net had a mesh size of 1 mm. Juvenile fishes were fixed immediately after each catch in 4 % formaline. Fish guts were dissected under a stereomicroscope. Groups of ten gut contents were quantitatively analysed in plankton chambers under a microscope.

3. Results and Discussion

a. Long-term annual changes of metazooplankton

Earlier studies on zooplankton of Lake Müggelsee gave already some indication that the abundance of zooplankton increased with the eutrophication of the lake (VORKASTNER 1983, WELLNER 1978, MOTHES & KROCKER 1986). However, the interannual fluctuations in the small data sets were too large to give clear evidence for the changes in the abundance of zooplankton. Recently, a significant amount of zooplankton data have been added by KROCKER (1987). Today, we have a comprehensive data set for the last twelve years with 20–50 sampling dates each year. In Figure 1 a the annual means of zooplankton abundances (summarized for the period April–October, 95 % confidence limits are shown) are compared. Data from 1908–1935 were taken from VORKASTNER (1938), and data from 1976 from Wellner (1978). Zooplankton abundances for the period 1908–1934 (1935 was only sampled for the first half of the year) were significantly lower than for the period 1979–1990 ($p < 0.05$). Only *Dreissena*-larvae decreased significantly. The methods used for both data sets seem to be fairly well comparable. Since VORKASTNER counted even small algae, the mesh size of his plankton net should also have been in the size range of about 50 µm (most probably 44 µm as the standard net). The main difference between both samplings was that VORKASTNER used a plankton pump, which could have caused slight underestimations of large cyclopoids. According to the comparison of both data sets, rotifers increased their abundance about 6.1 fold, cladocerans about 2.0 fold and copepods about 2.4 fold. The 6 fold increase of rotifers (species composition did not change significantly) is in accordance with an increase of the seston content in the course of this century of about 5–10 fold (see Fig. 1 b, BEHRENDT *et al.* 1990) indicating a several fold increase in food concentration. Crustaceans, which are probably the most important predators of rotifers, increased only about twice. This may be explained by the fact that fish biomass increased several times (see Fig. 1 b, cf. BARTHELMES & WALDOW 1978, BEHRENDT *et al.* 1990). Crustaceans are the preferred food of planktivorous fish (see below), and thus, in contrast to the growth conditions for rotifers, predation pressure on crustaceans increased simultaneously with the

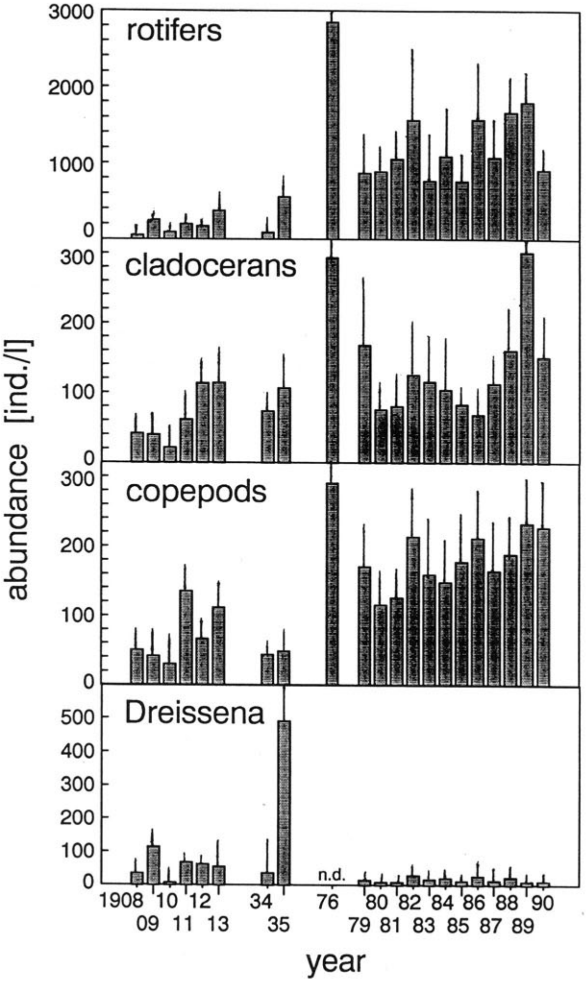

Figure 1 *a*. Long-term changes in the annual mean abundance (April–October) of rotifers, cladocerans, copepods and planktonic larvae of *Dreissena polymorpha* in Lake Müggelsee, Berlin. Data for the period 1908–1935 were taken from VORKASTNER (1938). The thin bars indicate the 95% confidence limits.

increase of food concentrations. A week point in this estimation of zooplankton changes is that all quantitative data available for comparison are based on abundances. Though it seems that the composition of dominant species did not change, the variation in grazing pressure may have caused changes in individual biomass of zooplankton.

The significant decrease of the abundance of *Dreissena* larvae to about one third of the values from the beginning of the century may be caused by a combination of several factors: 1) The volume of water of the River Spree flowing through Lake Müggelsee was reduced to one half, when a canal (Gosener Kanal) was opened in 1936; thus reducing the inflow of larvae from River Spree. 2) The biotope for adult *Dreissena* in Lake Müggelsee was significantly reduced due to high sedimentation rates, due to oxygen deficiency at the bottom, and due to a significant reduction of macrophytes during the last decades. 3) An increased fish stock since the 1950's may have caused higher predation pressure on larvae

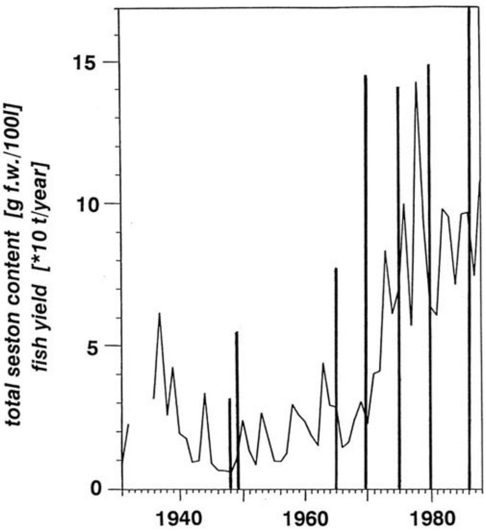

Figure 1 b. Long-term changes of total seston content (line) and fish production (bars) by the fishermen's co-operative Berlin Köpenick (modified after BEHRENDT *et al.* 1990).

by fish juveniles. 4) Waterfowls preying on adults of *Dreissena* seem to have increased in their population density in the past decade, esp. in winter (ARNDT, UNPUBL.). 5) Increased abundances of cyclopoids as potential predators (cf. ZANKAI 1984) may have caused higher predation pressure.

The data set for the zooplankton of Lake Müggelsee seems to be one of the few examples in literature, where the impact of industrialization and population growth in the course of nearly one century could be documented by quantitative plankton counts. Especially shallow lakes have seldom been investigated quantitatively for such a long period.

b. Species list of metazooplankton

The species which belong to the true zooplankton and which were found in the routine plankton samples were listed in Table 1. Typical benthic species were not included such as harpacticoids, ostracods, predominantly benthic cladocerans, insect larvae, or occasionally planktonic turbellarians etc. The lakes around Berlin are known for the coexistence of several forms of *Bosmina (Eubosmina)* (cf. LIEDER 1983 a). All three listed forms were morphologically clearly distincted and coexisted as productive forms of the zooplankton of Lake Müggelsee. In this relatively unstructured lake a large number of cyclopoid species coexist. The *strenuus-abyssorum* group and some planktonic rotifers (some synchaetids and trichocercids) were not separated into species. Most of the recorded zooplankton species are typical for eutrophic waters. Since the lake was naturally eutrophic (as a shallow lake with a large catchment area) already at the beginning of the century (today it is in a hypertrophic state), the composition of species did not change significantly during this century (cf. VORKASTNER 1938). However, one species, *Sida crystallina,* was never found in plankton samples during the last 12 years. The last record of this species was in 1958 (BARTHELMES 1978 a). *Sida* is known for oligo-mesotrophic waters. The possible extinction of this species may be a consequence of eutrophication. the calanoid copepod *Eurytemora velox* was reported by VORKASTNER but was not found in our plankton samples. Until the

Table 1. List of zooplankton species recorded in Lake Müggelsee 1979–1990 in our plankton samples

Rotatoria	
Brachionus angularis Gosse	XX
Brachionus calyciflorus Pallas	XX
Brachionus diversicornis (Daday)	X
Brachionus leydigi f. rotundus (Rousselet)	0
Brachionus urceolaris (O. F. M.)	X
Brachionus plicatilis (O. F. M.)	X
Keratella cochlearis (Gosse)	XXX
Keratella c. f. robusta (Lauterborn)	XXX
Keratella c. f. tecta (Lauterborn)	XXX
Keratella quadrata (O. F. M.)	XXX
Kellicottia longispina (Kellicott)	XX
Notholca acuminata (Ehrenberg)	X
Notholca labis Gosse	X
Notholca squamula (O. F. M.)	XX
Notholca foliacea (Ehrenberg)	0
Anuraeopsis fissa (Gosse)	XX
Euchlanis dilatata Ehrenberg	X
Trichocerca capucina Wierz. & Zach.	X
Trichocerca cylindrica (Imhof)	X
Trichocerca pusilla (Lauterborn)	XXX
Trichocerca similis (Wierzejski)	XXX
Trichocerca stylata (Gosse)	X
Trichocerca spp.	XX
Ascomorpha saltans Bartsch	XXX
Asplanchna priodonta Gosse	XXX
Asplanchna brightwelli (Gosse)	X
Synchaeta pectinata Ehrenberg	XX
Synchaeta oblonga Ehrenberg	XXX
Synchaeta tremula (O. F. M.)	XXX
Synchaeta t. kitina (Rousselet)	XXX
Synchaeta spp.	XX
Polyarthra dolichoptera Idelson	XX
Polyarthra vulgaris Carlin	XX
Polyarthra "vulgaris x *dolichoptera"*	XXX
Polyarthra spec.	X
Pompholyx sulcata (Hudson)	XXX
Filinia longiseta (Ehrenberg)	X
Filinia terminalis (Plate)	XX
Conochilus unicornis Rousselet	XX

Copepoda	
Eudiaptomus gracilis (Sars)	XXX
Eudiaptomus graciloides (Lilljeborg)	XX
Eucyclops serrulatus (Fischer)	X
Eucyclops macrurus (Sars)	X
Cyclops kolensis Lilljeborg	X
Cyclops vicinus Uljanin	XXX
Cyclops strenuus-abyssorum-Gruppe	XXX
Diacyclops bicuspidatus (Claus)	XX
Diacyclops b. limnobios Kiefer	X
Acanthocyclops robustus (Sars)	XXX
Mesocyclops leuckarti (Claus)	XXX
Thermocyclops crassus (Fischer)	XX
Thermocyclops oithonoides (Sars)	XX
Cyclops spec.	0

Cladocera	
Leptodora kindti (Focke)	XXX
Diaphanosoma brachyurum (Lievin)	XXX
Daphnia cucullata Sars	XXX
Daphnia galeata Sars	XXX
Daphnia hyalina Leydig	X
Daphnia longispina (O. F. M.)	X
Ceriodaphnia quadrangula (O. F. M.)	X
Bosmina longirostris (O. F. M.)	XXX
Bosmina (Eubosmina) coregoni coregoni Baird	XXX
Bosmina (Eub.) c. thersites (Poppe)	XXX
Bosmina (Eub.) longicornis berolinensis (Imhof)	XXX
Alona affinis (Leydig)	X
Chydorus sphaericus (O. F. M.)	XXX
Polyphemus pediculus L.	XX

Mollusca	
Dreissena polymorpha Pall. - larvae	XXX

(XXX ... dominant species, XX ... common species, X ... seldom occurring species, 0 ... single observation)

middle of this century this species was common in the plankton of Lake Müggelsee but was only seldom found in the middle of the 1980's (Lieder, pers. comm.).

c. Seasonal changes of metazooplankton

The seasonal changes in the biomass of rotifers, cladocerans and copepods are illustrated for the period 1979–1990 in Figure 2. Typically for Lake Müggelsee, rotifers reach their maximum biomass in spring (April/May). Most important rotifers during this time are the genera *Synchaeta, Polyarthra,* and *Keratella* and the species *Brachionus calyciflorus* and

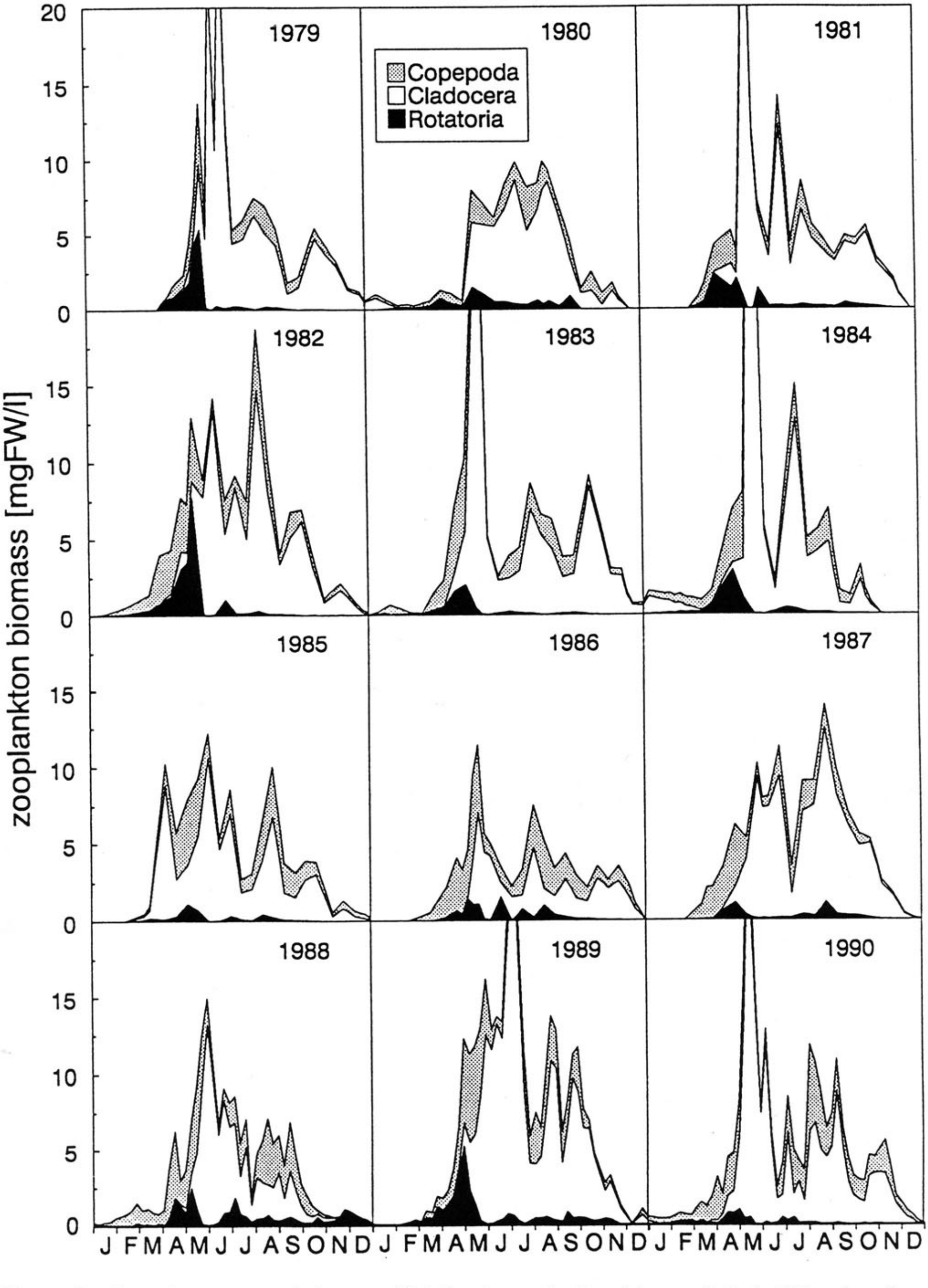

Figure 2. Long-term seasonal changes of total metazooplankton biomass in Lake Müggelsee from 1979 through 1990.

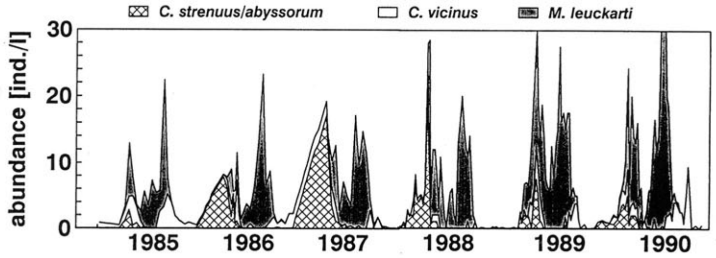

Figure 3. Long-term seasonal changes of the abundance of adult cyclopoids (*Cyclops strenuus/abyssorum, C. vicinus* and *Mesocyclops leuckarti*) in Lake Müggelsee from 1985 through 1990.

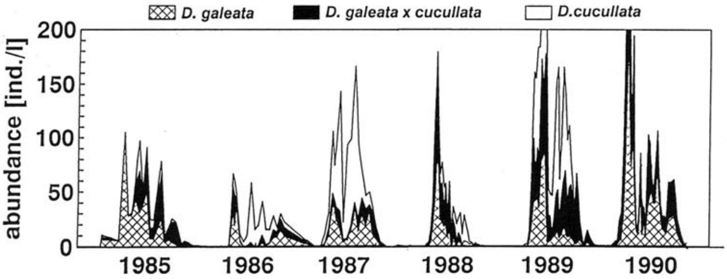

Figure 4. Long-term seasonal changes in the abundance of daphnids (*Daphnia galeata, D. cucullata* and hybrids of both species) in Lake Müggelsee from 1985 through 1990.

Asplanchna priodonta. During summer *Keratella cochlearis, Pompholyx sulcata, B. angularis, Ascomorpha saltans, Trichocerca similis* and *T. pusilla* are the dominant rotifers. Copepods are dominated by cyclopoids: *Cyclops strenuus-abyssorum* during winter, *C. vicinus* in spring and autumn and *Acanthocyclops robustus* and *Mesocyclops leuckarti* during summer. Though the general pattern occurs every year, there are significant annual changes in the contribution of each species (see Fig. 3). Cladocerans form the major part of zooplankton biomass. Daphnids were determined according to the criteria published by Flössner & Kraus (1986). Most important species are *Daphnia galeata, D. cucullata* and hybrids, *Bosmina longirostris* and two subspecies of *Bosmina (Eubosmina) coregoni* and one of *Bosmina (Eubosmina) longicornis.* Hybrids of *D. galeata* x *D. cucullata* were morphologically distinguished according to Flössner & Kraus (1986). Recent genetical investigations (Spaak pers. comm.) revealed that these morphological criteria allow a fairly good estimation of the abundance of each morph. Bosminids were not especially considered in this respect. Figure 4 shows the results of long-term investigations, which indicate that the relative abundance of each *Daphnia* form changes significantly from year to year and from season to season. *D. galeata, D. cucullata* and hybrids were dominant 1985, 1987 and 1989, resp. One of the reasons for the annual changes may be changes in predation pressure, since our analysis of gut contents of planktivorous fishes revealed always very low numbers of *D. cucullata* compared to other daphnids (see section 6), a phenomenon which is known also from other lakes (e. g. Lacroix *et al.* 1989, Nauwerck, pers. comm.). The coexistence of the closely related subspecies of *Bosmina (Eubosmina)* in Lake Müggelsee has already been well studied by Lieder (e. g. 1951, 1982, 1983 b). In Figure 5 we add to his qualitative material a set of quantitative data, which shows that during three successive years, each spring maximum was characterized by the dominance of another subspecies: 1988 *coregoni thersites,* 1989 *coregoni coregoni,* and 1990 *longicornis berolinensis.* Nevertheless, all subspecies coexisted in all three years in significant numbers. These quantitative data

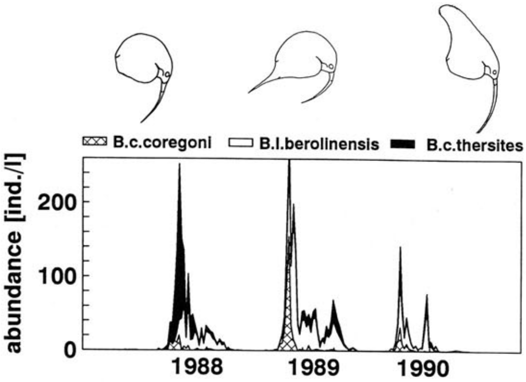

Figure 5. Seasonal changes of the abundance of three bosminids *(Bosmina [Eubosmina] coregoni coregoni, B. [E.] longicornis berolinensis, B. [E.] coregoni thersites)* in Lake Müggelsee from 1988 through 1990.

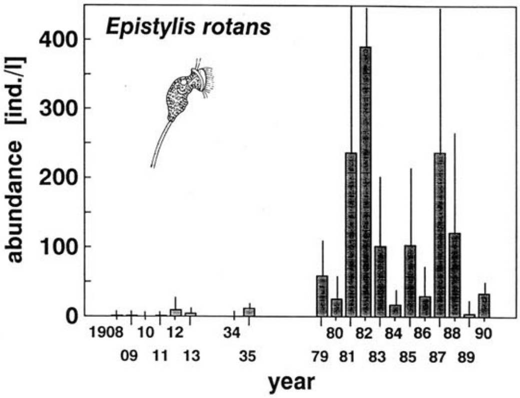

Figure 6. Long-term annual changes in the mean abundance (April–October) of the peritrichous ciliate *Epistylis rotans* in Lake Müggelsee, Berlin. Data for the period 1908–1935 from Vorkastner (1938). The thin bars indicate the 95 % confidence limits.

regarding the coexistence support the hypothesis that all three forms are separated regarding their niches in the ecosystem. The taxonomy of bosminids was followed the recent review by Lieder (in press).

Though the general development of zooplankton in the course of a year stayed the same in all 12 years summarized in Figure 2, there are not only differences in the dominance of species (see above), but there were considerable annual differences in total zooplankton biomass. The highest annual mean of rotifer biomass in 1989 (594 µg f.w./l) was about three times the biomass of the year 1990 (190 µg f.w./l). The highest cladoceran biomass occurred in 1989 (4408 µg f.w./l), the lowest 1980 (1364µg f.w./l). Copepods had the highest biomass 1986 (1455µg f.w./l) and the lowest 1979 (674 µg f.w./l). Up to now, these large differences in biomass cannot always be explained, they may be caused by the complex interactions of temperature, food conditions, predators and competitors (see also sections 3 e and 3 f).

d. Long-term and seasonal changes in protozooplankton

The knowledge on long-term changes of planktonic protozoans is very limited. The influence of eutrophication on protozooplankton has been estimated up to now from experiments with artificial eutrophication or from changes of protozooplankton biomass along eutrophication gradients (cf. BEAVER & CRISMAN 1989; BERNINGER *et al.* 1991; ARNDT 1991). In Lake Müggelsee, too, long-term quantitative studies on planktonic protozoans are nearly absent. However, there is one exception: VORKASTNER (1938) gave numbers of ciliates in his tables, and on p. 783 he stated that these ciliates were nearly exclusively the planktonic free-swimming peritrich *Epistylis spec.* Our comparative studies using different counting methods and fixatives revealed that VORKASTNER may have counted this species (which was certainly *E. rotans*) with the same efficiency as we did. Figure 6 illustrates the long-term changes of the abundance of *Epistylis* over a period of more than 80 years. Up to our knowledge such long-term changes have never been published for protozooplankters. The annual mean abundance (April–October) increased from about 3 ind./l in the eutrophic period 1908–1913 to 113 ind./l in the hypertrophic period 1979–1990. In the first period only one maximum in early summer was observed, whereas in the second period an additional maximum in late summer occured. This significant increase in the mean abundance of *Epistylis* can be explained in analogy to rotifers: food conditions improved several times for this nanophagous ciliate and on the other hand potential predators (esp. copepods, ARNDT *et al.* in prep.) increased their abundance only about twice. In addition, the formation of colonies and the ability to retract their stalk when in contact with potential predators may increase their survival rate. A similar increase in the mean abundance was observed for the tintinnid *Codonella cratera* which was "seldom" found during the period 1908–1913 (probably less than 5 ind./l) and occured in abundances up to several thousands per litre from 1979–1990. The annual differences in the mean abundance of *Epistylis* measured for the well investigated period from 1979–1990 were tremendous, though the biomass of phytoplankton (see Fig. 8) and bacteria (NIXDORF & ARNDT, 1993, this issue) varied only slightly. Such strong annual variations were not found for any metazooplankter in Lake Müggelsee. This indicates that special care is necessary when data sets for only one or two seasons are used for general conclusions regarding the importance of single protozooplankton taxa!

Comments on the protozooplankton biomass of Lake Müggelsee were already given elsewhere (ARNDT & MATHES 1991; ARNDT & NIXDORF 1991). Figure 7 gives a summary of monthly mean values (means of weekly samplings) of protozooplankton biomass compared with the biomass of metazooplankton. It is evident that about one fourth to one fifth of the zooplankton biovolume consists of protozoans. In winter and spring protozoans form regularly the major part of zooplankton biovolume. In spring the major part of protozoans are herbivores (ciliates and large heterotrophic flagellates) and replace metazoan herbivores during this time (see the following section). Due to the fact that the specific metabolic rates of protozoans were several times higher than those of metazoans (ARNDT 1992) protozoan activity may be comparable to that of metazoans. Direct comparisons to other studies are difficult, since only recently all components known to be of importance have been considered. The seasonal pattern is similar to the deep mesotrophic Lake Constance (cf. GELLER *et al.* 1991). The most interesting finding regarding the composition of protozoan biomass of Lake Müggelsee and other lakes was the significant contribution of large heterotrophic flagellates ($\geqq 15$ µm), which were formerly overlooked but which have to be considered now as a significant component of all limnetic pelagic ecosystems (cf. ARNDT & MATHES 1991). The same seems to be true for naked amoeba, which have very seldom been considered in plankton counts (since mostly fixed samples were investigated) but which should play a significant role at least for certain periods (cf. ARNDT 1993 b). Both groups together account for 10 to 70 per cent of protozoan biomass (see lower panel of

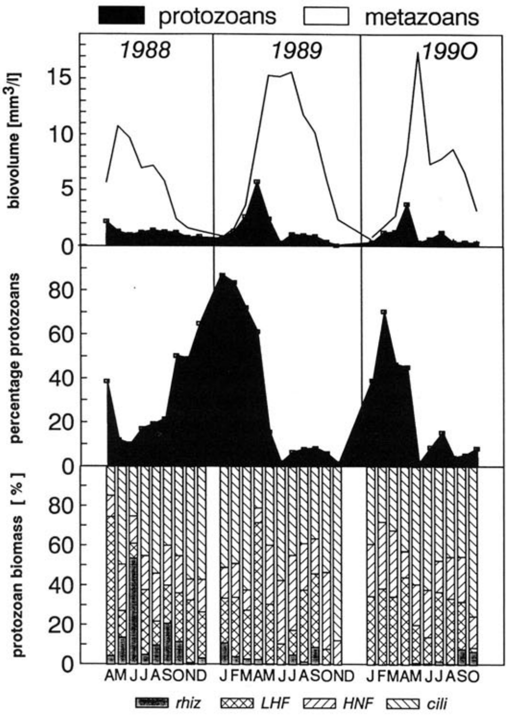

Figure 7. Seasonal changes of monthly mean values (weekly samplings) of protozooplankton in Lake Müggelsee, Berlin. Upper panel: biovolume of protozoans and metazoans; middle panel: relative contribution of protozoans to the total zooplankton biovolume. Lower panel: relative contribution of the different groups of protozooplankton (rhiz = heliozoans and naked amoebae, LHF = large (≧ 15 µm) heterotrophic flagellates, HNF = heterotrophic nanoflagellates; cili = ciliates) to the total protozooplankton biovolume.

Fig. 7). On an annual average, ciliates, heterotrophic nanoflagellates and large heterotrophic flagellates each contribute about one third to protozoan biomass. Annual changes in the activity of the microbial web may cause changes in the availability of nutrients for phytoplankters (cf. NIXDORF & ARNDT, 1993). During the clear-water phase in early summer protozoans are grazed down by metazoans (see section 39, ARNDT & NIXDORF 1991). Protozoans may contribute about 10 to 20 per cent to the food of metazoan filtrators (ARNDT 1993 a).

e. Metazoans and protozoans as significant grazers of phytoplankton

Clear-water phases: The long-term observations of phytoplankton and zooplankton biomass in the course of 12 successive years offer a good opportunity to compare the effect of metazoans on phytoplankton. The clear-water phase regularly appears in many lakes of the temperate zone in late spring at high metazooplankton densities. Quantitative studies of several lakes revealed that metazooplankton feeding (mainly cladocerans) is able to cause the decline of phytoplankton biomass (e. g. LAMPERT *et al.* 1986; LAMPERT 1988 a; LUECKE *et al.* 1990). Metazoan feeding is generally accepted as the main

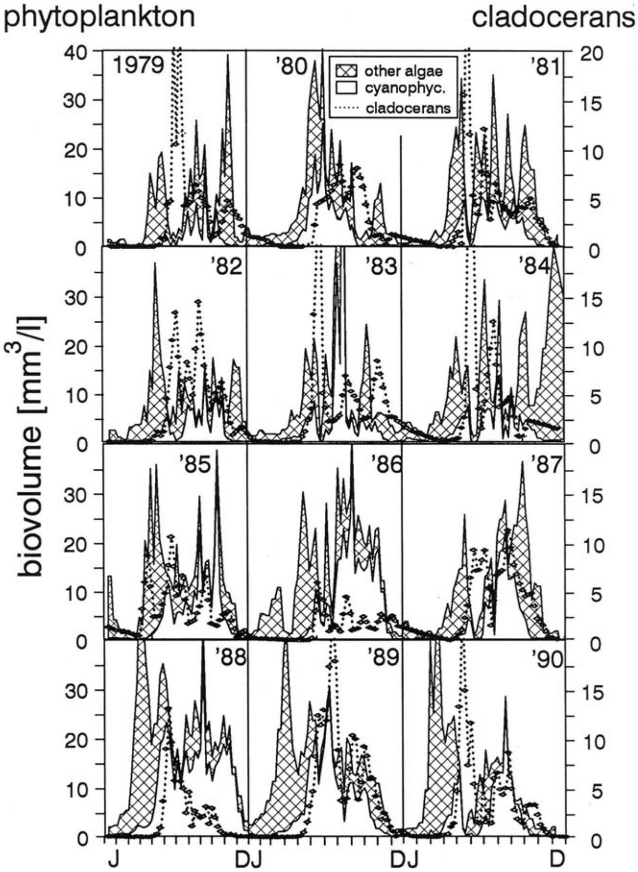

Figure 8. Comparison of the long-term seasonal changes of phytoplankton biovolume (white = filamentous blue-greens, hatched = other algae) with the biovolume of cladocerans (stippled line with rhombs) in Lake Müggelsee from 1979 through 1990.

cause for the late spring decline of phytoplankton (cf. SOMMER *et al.* 1986). This opinion is supported by most of the seasonal cycles of phytoplankton and cladoceran biomass in Lake Müggelsee (see Fig.8), too. However, there are some exceptions which indicate that other factors than cladoceran grazing may play an important role in addition:

1. In each year a significant decrease of algal biomass (blue-greens excluded) occurs irrespective of the biomass of zooplankton. In 1980, but especially in 1986, metazooplankton biomass was much to low to explain the reduction of phytoplankton by metazoan grazing.

2. In all years an exponential growth phase of algae occurs from January till March. In some years the exponential growth is continued until the grazing pressure by metazoans is effective (e. g. 1981, 1987), in most other years, however, a decline or a stagnation of algal growth occurred already at the end of March/beginning of April (e. g. 1979, 1984, 1986, 1988–90), at a time when metazoans have no significant effect on phytoplankton.

The dynamics of nutrients in Lake Müggelsee follow the typical seasonal pattern with maximum concentrations in autumn/winter and minimum concentrations in late spring e.g. KOZERSKI *et al.,* 1993). In some years dissolved reactive phosphorus is depleted up to two months prior to the maximum grazing pressure by metazoans (cf. NIXDORF & ARNDT, 1993). In stratified lakes, the clear-water phase and the maximum biomass of metazoans generally occur shortly after the establishment of stratification and the accompanied reduction of nutrient supply from the hypolimnion. In this case the effect of nutrient depletion and maximum grazing pressure are difficult to separate. In polymictic shallow waters, such as Lake Müggelsee, phytoplankton can exhaust the dissolved nutrients of the whole water column in contrast to the phytoplankton in deep lakes, where nutrients can steadily be supplied from deep waters and algae are partly in deep light limited strata. This may be one reason for the earlier decline or stagnation of phytoplankton in Lake Müggelsee. KÖHLER *et al.* (1993) found that the phytoplankton in River Spree (which has a similar species composition as Lake Müggelsee) shows a similar regular decline in late spring without the presence of metazooplankton filtrators. He interpreted the decline as a reaction of the phytoplankton community to changing environmental conditions (nutrient regime, water temperature), the grazing impact by the zoobenthic community and the change of the species composition from winter/spring species to summer species. This

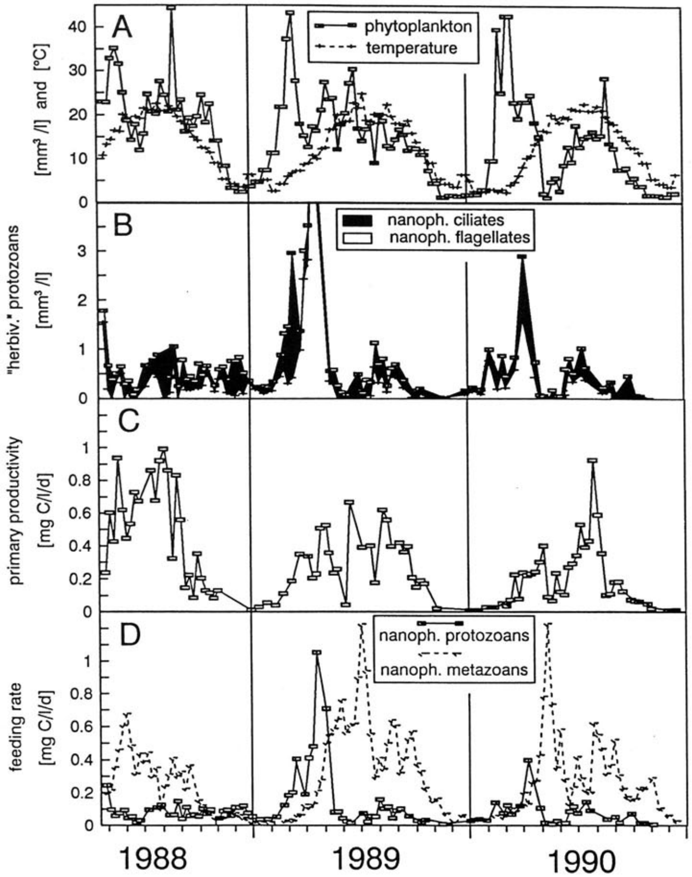

Figure 9. Estimated seasonal changes in the grazing impact on phytoplankton by nanophagous ("herbivorous") proto- and metazooplankters in Lake Müggelsee from April 1988 to December 1990. *A*: Phytoplankton biovolume and water temperature. *B*: Biovolume of nanophagous ciliates (black area) and flagellates (white area). *C*: Phytoplankton primary production. *D*: Estimated feeding rate of nanophagous protozoans and metazoans.

interpretation is supported by the results of VYHNALEK (1989) and his recent observations (VYHNALEK, pers. comm.), who found by means of different enclosure methods that most phytoplankters of a reservoir, which are typical for the spring bloom, show low growth rates just before the clear-water phase due to phosphorus limitation. Besides this physiological explanation for the decline of phytoplankton prior to the metazooplankton peak, protozoans - as another grazing loss factor - may be of importance.

Protozoans as phytoplankton consumers: As stated in the preceding section, protozoans compose at certain times the major part of the zooplankton biomass. The spring peak in March/April is produced mainly by protozoans feeding in the size range of < 1-20 µm. Algivorous heterotrophic flagellates have mostly been neglected in limnological studies of protozooplankton, therefore the biomass of potential herbivores among protozoans has been significantly underestimated (cf. ARNDT & MATHES 1991). Figure 9 summarizes the results of a comparison between the roughly estimated grazing pressure of nanophagous protozoans with that of nanophagous metazoans. The upper panel shows the seasonal change in phytoplankton biomass and water temperature. Panel *B* gives the biomass of nanophagous protozoans. These include all ciliates which were ≧ 20 µm in size and were not known to be typical feeders on bacteria (e. g. ciliates of the genus *Cyclidium* were excluded) and all heterotrophic flagellates which were ≧ 15 µm in size. All species of these large heterotrophic flagellates (LHF, and sometimes even smaller flagellates) were found to contain phytoplankton in their food vacuoles. Though recent investigations indicated that bacteria were also ingested by LHF, the major part of their food may consist of algae ranging from picoautotrophs to flagellates up to blue-green filaments and centric and pennate diatoms which have the same biovolume as the LHF (ARNDT unpubl.). To compare the impact on phytoplankton by protozoans with that by metazoans, the seasonal changes in primary production were confronted with the seasonal changes of the roughly estimated grazing pressure by protozoans and metazoans (Fig. 9 *C, D*). The consumption of nanophagous protozoans was roughly estimated by the following assumptions: dry weight of protozoans is 15 per cent of fresh weight (assuming a density of 1); 45 per cent of dry weight is carbon; grazing rate is 200 per cent of body carbon per day. The assumed grazing rate should be a minimum estimate since our production studies on ciliates and LHF in Lake Müggelsee revealed P/B-values in the range of 1-2 during spring (ARNDT in prep.). Dry weight to fresh weight ratios and carbon contents of nanophagous metazoans (all metazooplankters without Asplanchna and Leptodora) were derived from investigations of BEHRENDT (1990, rotifers: fresh weight [µg/ind] * 0.2 µg dw/µg fw * 0.45 µgC/ug dw; cladocerans: fw*0.12*0.45; copepods: fw*0.17*0.45). The food consumption of metazoans was roughly estimated assuming a ration of 80 per cent of the body carbon per day.

Though the calculation of zooplankton grazing rates are based on rough estimates, it is evident from Figure 9 (panel *C* & *D*) that zooplankton may have a significant impact on phytoplankton during the whole year with a maximum impact (by metazoans) during early summer. In 1989, protozoans should be responsible for about one third of the total algal losses due to grazing. During the other two years of investigation protozoan grazing my contribute about one quarter to one fifth to zooplankton grazing. During spring protozoans are the main phytoplankton grazers. At this time their grazing rates lie in the same range as the phytoplankton production. In 1989 and 1990 a significant decline in phytoplankton biomass occurred at the peak of protozoan grazing. In 1988 this decline occurred just before the study period, when at least ciliates had a maximum (cf. ARNDT & NIXDORF 1991). Though, the results need to be verified by field experiments on protozoan grazing, one can postulate already at this step of investigation that phytoplankton is under a strong grazing pressure already during the spring bloom. The effect of protozoan grazing on phytoplankton, however, may be different from that of metazoans regarding food selection and regarding nutrient recycling.

The spring peak of planktonic ciliates is a well-known phenomenon from various types of lakes (e. g. MÜLLER 1989, LAYBOURN-PARRY *et al.* 1990, SIMEK *et al.* 1990). Large heterotrophic flagellates have seldom been considered, however recent comparative studies of different types of lakes indicated that LHF, too, generally have their seasonal maximum in spring (MATHES pers. comm., ARNDT & MATHES 1991). Thus, it seems to be a general phenomenon that spring phytoplankton is under intensive grazing pressure by protozoans in temperate lakes, a phenomenon that has to be considered in future models regarding the seasonal successions of planktonic events in lakes.

f. Influence of planktivorous predators

Protozoans: Potential predators on protozooplankton are to be found among all groups of zooplankton, crustaceans (for review see STOECKER & CAPUZZO 1990), rotifers (for review see ARNDT 1993 a), and also among protozoans themselves (e. g. DOLAN & COATS 1991, ARNDT 1992). We have investigated the seasonal changes in the flux of matter through the microbial web (cf. NIXDORF & ARNDT, 1993, ARNDT 1990). During winter and spring protozoans are under significant grazing pressure by other protozoans and sometimes by cyclopoids and rotifers. In early summer metazoans *(Daphnia)* significantly depress protozoans via grazing (ARNDT & NIXDORF 1991). During summer planktonic crustaceans and sometimes protozoans are the most important consumers of protozooplankton production. The grazing pressure by metazoans on protozoans depends on the species composition of metazooplankton: filter-feeding crustaceans and rotifers select for small protozoans (heterotrophic flagellates, ciliates), whereas raptorially feeding crustaceans and rotifers strongly select for large ciliates (ARNDT, JÜRGENS & ZIMMERMANN 1992, in manus). At times, when metazoans are not significant predators, and thus large carnivorous/omnivorous protozoans have reduced mortality rates, they are (due to high growth rates compared to metazoans) able to function as regulators of protozoan density (ARNDT & NIXDORF 1991, ARNDT 1992). A detailed description of protozoan dynamics will be given elsewhere.

Rotifers: As may be derived from our analysis of gut contents and feeding experiments, main consumers of rotifer production in Lake Müggelsee are cyclopoids, *Asplanchna,* and to a less extent fish larvae, and *Leptodora kindti.* Large daphnids have also to be taken into account as effective grazers and predators by mechanical interference (e. g. BURNS & GILBERT 1986). Rotifers reach their biomass peak generally during the phytoplankton spring bloom and contribute only little to the total zooplankton biomass later in the year (see Fig. 2). The low biomass of rotifers during summer may be explained by the very high abundances of daphnids (esp. *Daphnia galeata,* see Fig. 4) by interference and exploitative competition (e. g. BURNS & GILBERT 1986), and by the high abundances of *Mesocyclops leuckarti* (in Fig.3 only abundances of adults are shown) and *Acanthocyclops robustus.* Both of these cyclopoid species are known as effective consumers of rotifers from other studies (e. g. MAIER 1990).

A more detailed analysis of a typical rotifer/crustacean succession in late spring (the time of the decline of rotifers) of 1989 indicates the complexity of interactions between rotifers and crustaceans during that time. The abundance of the most important metazooplankters are graphed in Figure 10 *(A). Keratella* and *Polyarthra* declined when *Asplanchna* and adult cyclopoids (as potential predators) peaked. The results of studies on food selection of older cyclopoid stages on other metazooplankton (presence/absence method) are shown in Figure 10 *(B).* Though cyclopoids selected for *Polyarthra,* a significant number of *Keratella* was consumed, too. Regarding the biomass eliminated by cyclopoids, *Polyarthra, Asplanchna* and cyclopoid nauplii formed the major part of their food. According to literature (see review by GILBERT 1980) *Asplanchna* may be a voracious predator on rotifers (esp.

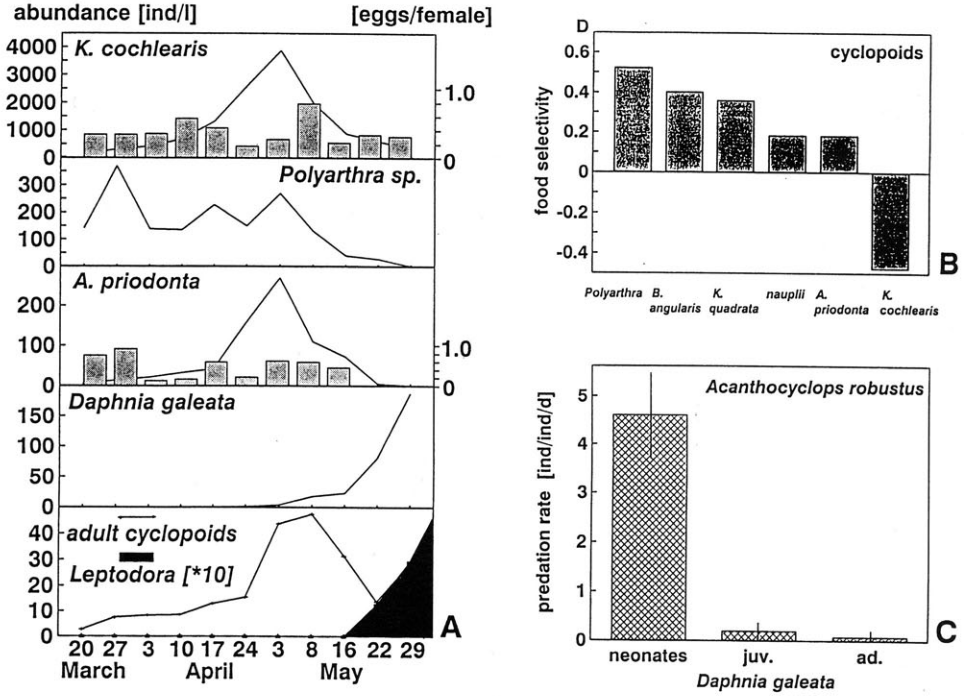

Figure 10. Impact of planktivorous ("carnivorous/omnivorous") metazoans in Lake Müggelsee in spring 1989.

A: Temporal changes in the abundance (columns = egg ratio) of *Keratella cochlearis, Polyarthra* sp., *Asplanchna priodonta, Daphnia galeata,* adult cyclopoids and *Leptodora kindti* (black area).

B: Food selectivity (index D according to JACOBS 1974) of older cyclopoid stages feeding on natural zooplankton at May 3rd, 1989.

C: Predation rate of females of *Acanthocyclops robustus* feeding on neonates, $1\frac{1}{2}$ day old juveniles and adults of *Daphnia galeata,* resp.

Keratella) on May 3rd. *Asplanchna* in turn and *Polyarthra* were then effectively reduced by cyclopoids. *Asplanchna* and *Keratella* (*Polyarthra* was not investigated) had still relatively high egg ratios at declining abundances. This indicates that predation should be a major cause of their decline. A comparable complex trophic relationship was found for similar species in an American lake by GILBERT & WILLIAMSON (1978). Cyclopoids (mainly *Cyclops vicinus*) declined in mid May for summer diapause. Later on *Daphnia* reached abundances which may have caused significant interference with rotifers.

According to the analysis of gut contents in 1990, *Leptodora* may have contributed to rotifer mortality, too. In guts of *Leptodora* we found remains of *Asplanchna* and in addition, but seldom, remains of *Keratella cochlearis, K. quadrata, Brachionus calyciflorus* and *B. angularis.* Regarding their biomass rotifers contributed only little to the total nutrition of *Leptodora.* Frequent occurrence of rotifers in guts corresponded to high abundances of rotifers in the plankton which is in agreement to BROWMAN *et al.* (1989), who concluded from their studies a relatively passive prey selection by *Leptodora.*

Fish juveniles could only occasionally contribute to rotifer mortality. Though rotifers are frequent food organisms found in guts of juvenile fish, regarding their biomass, rotifers composed only a negligible part of fish food in Lake Müggelsee.

Cladocerans: Gut content analysis of *Leptodora* and fish juveniles revealed – in agreement with most reports in literature – that cladocerans are the major food source of both groups. The activity of both groups of predators begins at the end of May and continues till the end of the year. The question arises, why daphnids do not reach higher abundances earlier in the year, when egg ratios are already high. *Lampert* (1978) already argued that cyclopoids should play a major role in suppression of daphnids in spring. However, most recent papers regarding feeding experiments with cyclopoids showed that daphnids are not very much affected by predation. In most of these studies up-grown daphnids of relatively large sizes and rigid carapaces were supplied as food. We tested the hypothesis that females of *Acanthocyclops robustus* (a common cyclopoid in Lake Müggelsee from spring till autumn) are not efficient predators on adult daphnids (see e. g. MAIER 1990), but are able to use small soft-bodied neonates. The results of the feeding experiments using neonates, juveniles and adult *Daphnia,* respectively, as a prey are shown in Figure 10 *(C).* Predation rates on adult *Daphnia* were not significantly different from zero. In all paralleles juveniles were grazed, the killed biomass was equal to about 22 % of the body weight of *Acanthocyclops* per day. But highest predation rates were found on neonates, predation rates were about 205 % of body weight per day. Among neonates those seemed to be prefered which were smaller than 650 μm. These results indicate that neonates of *Daphnia* are efficiently preyed by *Acanthocyclops* females. A few hours after extrusion out of the brood chamber, *Daphnia* seemed to be more and more protected against predation by cyclopoids. Additional experiments with other species are necessary. However, these results indicate that a suppression of daphnids by cyclopoids may be possible in spring. Conclusions from earlier feeding experiments using up-grown daphnids should be reevaluated. Cyclopoid predation could perhaps explain delayed *Daphnia* population maxima in many lakes.

The preying of *Leptodora* on *Daphnia* and other cladocerans is well-known (e. g. KARABIN 1974, CUMMINS *et al.* 1969; BROWMAN *et al.* 1989). In Figure 11 *(C)* the composition of the gut content of *Leptodora* (on a quantitative basis) in Lake Müggelsee is shown for 1990. *Leptodora* should contribute to the summer declines of cladocerans in June, July, and to the depressions in August and September. The results of the long-term analysis of the relationship between the biomass of *Leptodora* and other cladocerans are presented in Figure 12. If a daily ration of 20–40 % of the body weight of *Leptodora* is assumed (cf. KARABIN 1974, HERZIG & AUER 1990), a biomass of Leptodora that is similar to the biomass of cladocerans would drastically reduce the other cladocerans (assuming birth rates of about 0.3/d). And even a Leptodora biomass that is half the cladoceran biomass may be very effective, when the food selectivity and the impact by other predators on cladocerans would be considered in addition. From the results of long-term investigations it is evident that *Leptodora* is a very significant cladoceran predator during some years (e. g. 1982, 1984, 1985) but of only reduced importance during other years (e. g. 1980). The variable significance of *Leptodora* may be explained by changes in predation pressure on *Leptodora,* which is a preferred food item of juveniles of perch, smelt and pikeperch in Lake Müggelsee (KÖHLER unpubl.). Preliminary results of quantitative studies of planktivorous fish revealed significant interannual fluctuations in Lake Müggelsee (KÖHLER & FREDRICH unpubl.).

Leptodora fed preferentially on small daphnids (KÖHLER unpubl.), whereas fishes selected larger zooplankters – a well-known phenomenon (cf. KERFOOT & SIH 1987). Preliminary results regarding the planktivorous fish community obtained from trawl net fishing in the pelagic zone in spring/summer 1990 indicated that perch *(Perca fluviatilis)* hatched in April and dominated the 0+ community till the beginning of July. Perch fed only partly on *Daphnia,* thus allowing the *Daphnia* population to increase and to cause a clear-water phase in May. Smelt *(Osmerus eperlanus)* began to dominate the 0+ community in June/July. Smelt contributed significantly to the decline of *Daphnia* and *Leptodora*

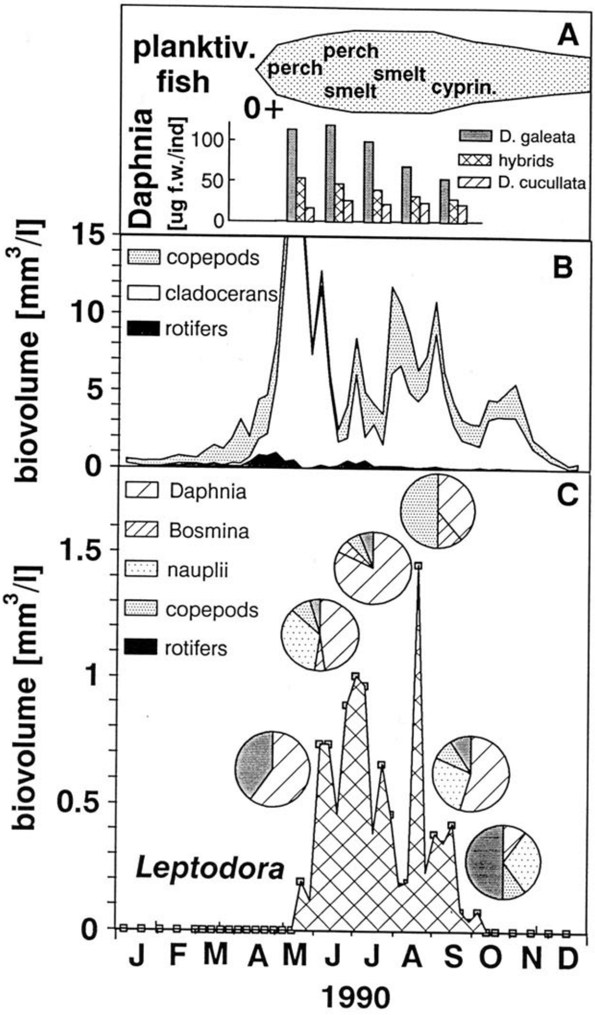

Figure 11. Seasonal dynamics of metazooplankton and planktivores in Lake Müggelsee in 1990. *A*: Semiquantitative estimation of the biomass of 0+ fish juveniles (dominant fish species are indicated). The monthly mean of the individual fresh weight of *Daphnia galeata,* hybrids, and *D. cucullata* are indicated.
B: seasonal changes of metazooplankton biovolume.
C: Seasonal changes of the biovolume of *Leptodora kindti.* Circles show the monthly mean composition of identifiable remains of food organisms of *Leptodora.*

during July 1990. In September cyprinids *(Abramis brama, Rutilus rutilus)*, which lived in the litoral zone from May till August 1990 and fed there on littoral *Bosmina* populations, occupied the pelagic region and may have contributed to the decrease of the cladoceran community in September. Much more quantitative data on planktivorous fish are necessary for a more detailed estimation of their grazing pressure on zooplankton.

A semiquantitative estimation of the seasonal changes in the grazing pressure by fish juveniles – presumably the quantitatively most important vertebrate planktivores in Lake Müggelsee – is given in Figure 11 (A). In the lower part of panel *A* the monthly mean body

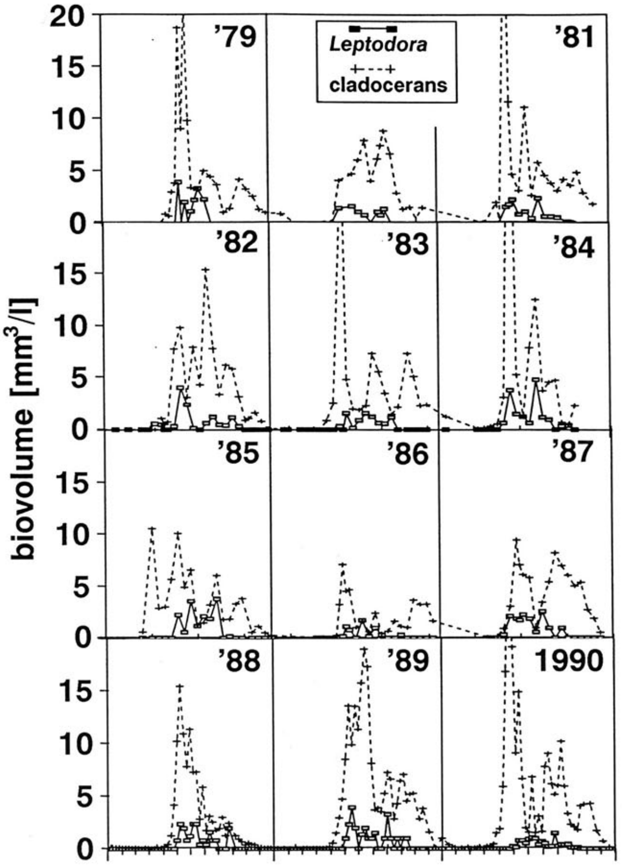

Figure 12. Comparison of the long-term seasonal changes of the biovolume of cladocerans (crosses) and *Leptodora kindti* (rectangles) in Lake Müggelsee from 1979 through 1990.

weights of *Daphnia galeata, Daphnia* hybrids and *D. cucullata* are illustrated. In the course of the summer a significant reduction in the body weight of the large *D. galeata* (the small *D. cucullata* did not change significantly) was observed. In September mean body weight of *Daphnia galeata* was only about one half the mean body weight in May. In September, all three daphnid groups had a nearly similar body weight. Many published field and laboratory observations from other lakes showed that visually feeding predators select for large zooplankters, whereas most invertebrate predators select for small organisms (e. g. KERFOOT & SIH 1987; KÖHLER *et al.* 1989). The increasing similarity of small body sizes of daphnids at the end of the summer 1990 may indicate that the impact of visually feeding predators should increase in the course of the year.

In Lake Müggelsee the predation pressure on *Daphnia* in spring should be mainly due to invertebrate predators (cyclopoids, *Leptodora*), early feeding stages of fish juveniles also select for the smaller zooplankters (KÖHLER, unpubl.) In June/July the impact of up-grown fish juveniles increased corresponding to size reductions in *D. galeata.* During this time the relative abundance of *D. cucullata,* which was much less consumed by fish juveniles (KÖHLER unpubl.), increased in several years (see Fig. 4). We observed significant annual differences in the biomass of planktivorous invertebrates (cyclopoids, *Leptodora*) and also the impact of planktivorous fish, esp. smelt, change significantly from year to year (Barthelmes & Waldow 1978, Köhler & Fredrich unpubl.). This may be one important reason for annual and seasonal changes in the absolute and relative abundance of *Daphnia* species and probably other zooplankters, which in turn may cause significant annual changes of phytoplankton. Fish populations appear to be much more variable from year to year in small shallow lakes than in large water bodies (cf. Oglesby 1977). In addition to the grazing pressure competition between the *Daphnia* species may play a certain role (cf. Lampert 1988 b).

Copepods: Cyclopoids are the major group of copepods in Lake Müggelsee. Their predators are nearly identical to those of cladocerans, however, the time course of predation is different. Cyclopoids are already present in high numbers during spring. At this time they are a major food source of 1+–3+ juveniles of perch and ruffle (Arndt unpubl.) and probably also of other fishes, but total predation pressure exerted by fishes during spring seems not to be able to control cyclopoids. According to our own experiments (e. g. Fig. 10 *B*) and the results by other authors (e. g. Brandl & Fernando 1978; Maier 1990; Zankai 1984; Adrian 1991) cyclopoids, esp. the dominant omnivorous forms in spring, may consume a significant part of their own nauplii. Generally at least two omnivorous cyclopoid species coexisted. In early summer cyclopoids, especially adult females, are heavily preyed by 0+ fish, especially perch, and later on by smelt. However, while the cyclopoid females were digested most of their eggs (up to certain stage of development) hatched in laboratory cultures after passing the digestive tract of cyprinids and percids (Arndt unpubl.). When the relative abundance of cyclopoids was high, *Leptodora* consumed significant numbers of nauplii and also copepodites and adult cyclopoids. The decline of the August peak 1990 (see Fig. 11 *B, C*) may be caused by *Leptodora* predation.

4. Conclusions

This paper was intended to summarize the present knowledge regarding the long-term annual and seasonal changes of proto- and metazooplankton of Lake Müggelsee. The long-term changes in the annual mean of zooplankton abundance clearly reflect the changes in the trophy of Lake Müggelsee which increased in the course of the last hundred years from a eutrophic to a hypertrophic level. In contrast to the general appearance of anoxic conditions in the course of lake eutrophication the polymictic shallow Lake Müggelsee is – except for the near-bottom-water during calm conditions at high temperatures – still well oxygenated over the whole water column. This may be a major reason, why the species composition did not change significantly. But the different groups of zooplankton changed regarding their abundance in a very different way. Rotifers and the ciliate *Epistylis* increased several times, whereas crustacean abundances were only doubled. We interpreted these differences by the influence of trophic relationships. In the second part of the paper we made an attempt to describe the trophic relationships in the plankton community. At least at this point we were confronted with the unsatisfactory situation (as it occurs in many field studies of trophic relationships) that analyses (including our own) were carried out not frequently enough or were not performed at the same time. Therefore, we had often to write in the subjunctive mood hopefully to stimulate more comprehensive studies especially on trophic relationships.

However, some results seem to be obvious:

1) Changes of biomass or abundance of single zooplankton groups in the course of eutrophication do not always reflect the changes in the trophy. Trophic relationships can have a significant effect on abundance (cf. rotifers/crustaceans).

2) In eutrophic systems which are generally expected to have low numbers of species, trophic relationships are, nevertheless, very complex. When Nilssen (1978) discussed the role of stability of eutrophic systems he was not aware of the fundamental role of phagotrophic protozoans at that time. Our results for Lake Müggelsee demonstrate that the phytoplankton (for bacteria it is shown in Nixdorf & Arndt, 1993) is grazed by a very different size spectrum of grazers: phagotrophic flagellates, ciliates, rotifers, and crustaceans. These groups are different enough in size to be each a potential food source of the larger groups. The resulting stability (supported by the fact that most species are omnivorous) in the general seasonal pattern of phytoplankton is reflected in Figures 2 and 8. In the case that large effective filter-feeding daphnids are not present (due to predators or low temperatures) ciliates or phagotrophic flagellates (which are in turn a food source of ciliates and cladocerans) act as phytoplankton grazers.

3) The detailed analysis of simultaneous investigations of phytoplankton and metazooplankton in the course of 12 successive years revealed, that metazoan grazing may be often responsible for the late spring algal decline. However, in some years phytoplankton declined without a notable grazing activity by metazooplankton. On the basis of this long-term data set it is evident that – though one factor may be dominant – other factors, too, can be of high significance (e. g. fast increases of water temperatures, nutrient depletions, short-term increases of sedimentation rates, or increased dark carbon losses, cf. Behrendt & Nixdorf 1991). Using grazing pressure by metazooplankton as the only cause of the occurrence of clear-water phases (at it is done in most recent papers) may lead to false or unsatisfactory conclusions.

4) The potentially high significance of protozoan herbivores had been overlooked in the traditional view of seasonal successions of planktonic events in lakes (cf. Sommer *et al.* 1986). According to our results from the shallow Lake Müggelsee, protozoans may be able to regulate the phytoplankton spring bloom. Estimated grazing rates sometimes exceeded phytoplankton production and a decline of phytoplankton biomass corresponding to peaks of protozoan abundances was observed before the clear-water phase. Laboratory experiments on the feeding rates of ciliates and phagotrophic flagellates (e. g. Müller 1991, Salbrechter & Arndt, in prep.) indicate that direct estimates of feeding rates support this conclusion. More detailed studies on protozoan herbivory will probably change our view on the regulation of the phytoplankton spring bloom in the near future.

5. Acknowledgement

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