

Seasonal successions and trophic relations between phytoplankton, zooplankton, ciliate and bacteria in a hypertrophic shallow lake in Vienna, Austria

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Key words: eutrophication, trophic relations, filamentous cyanobacteria, ciliates, zooplankton, bacteria

Abstract

Alte Donau nowadays is an eutrophic urban lake within the city of Vienna. Increasing nutrient concentrations and massive blooms of cyanobacteria mainly caused by *Limnothrix redekei* Van Goor and *Cylindrospermopsis raciborskii* (Wolsz.) Seenayya et Subba Raju were recently registered. As a consequence Secchi depth was significantly reduced especially during the summer season (minimum: 0.25 m). An investigation including water chemistry, phytoplankton, macrophytes, and sediment was initiated in 1993 and extended to metazooplankton, ciliates and bacteria in 1994. The first half of the year 1994 was characterised by relatively clear water and a high diversity of the phytoplankton composition due to flushing of the lake with water of better quality by the end of 1993. Ciliates and metazooplankton held about 10% of the total biomass of all the investigated trophic levels. The vanishing of the remaining macrophytes enlarged the nutrient supply during summer 1994 and favoured the development of cyanobacteria. The high water temperatures which excluded certain zooplankton species, and the inedibility of the filaments further increased the dominance of cyanobacteria. In November, when the algal bloom finally ceased, the highest bacterial numbers of the investigation period occurred. Thereafter, other algal groups, bacteria and metazooplankton gained more importance.

Interactions are possible because of close overlap in space and time due to the turbulent mixed conditions of the water body and the change from the macrophyte dominated to the algal dominated stable state. Planned restoration measures must aim to re-establish the previous macrophyte dominated clear-water stage.

Introduction

The open water zone of lakes are characterised by complex interactions. Community interactions in pelagic food webs are affected by small- to large scale physical, chemical and biological processes, are trophically dynamic and are governed by nutrient limitation, competition, predation and other ecological forces (Carpenter, 1988). In shallow waters, trophic level interactions are complicated by detrital pathways and influences from the sediments (Herzig, 1979). Community structure, biomass, and production are influenced by both producers and consumers which function simulta-

neously. If bottom up effects by producers or top down control by consumers dominate is largely a function of the trophic level of the lake (McQueen et al., 1986).

In this paper we describe the seasonal development of phytoplankton, algal picoplankton, bacteria, ciliates and metazooplankton from a shallow hypertrophic urban lake in 1994 and try to elucidate some of the interactions between food web components.

Table 1. Morphometric data for Alte Donau.

| | |
|------------------------------|--|
| Altitude | 157 m a.s.l. |
| Area | 1.583 km ² |
| Volume | 3.697 × 10 ⁶ m ³ |
| Maximum depth | 6.8 m |
| Mean depth | 2.33 m |
| Min. theoret. retention time | 20 days |

Site description

Alte Donau, formerly the main course of the River Danube, was formed as an ox-bow lake in the years 1870–1875 when the river has been regulated. Today, Alte Donau is a shallow lake with no superficial connection with the river, fed only by subterranean flow from the ground-water and precipitation. Location and morphometry are indicated in Figure 1. Morphometric data are summarised in Table 1. As an urban lake, Alte Donau is of high recreational importance.

In the past, Alte Donau was always characterised by clear water, concentrations of chlorophyll *a* below 5 µg l⁻¹, and a domination of various macrophytes covering almost the whole area. In 1992, a remarkable decline of the macrophytes was observed leaving only remnants of *Charophyceae*-stands. The massive growth of phytoplankton at the same time caused a significant reduction of the Secchi-depth to less than 0.25 m during the summer season. This shift to a new stable state (Dokulil & Janauer, 1995) was caused by altered hydrological conditions which resulted in an increase in the water level by 0.4 m and largely reduced level fluctuations (Donabaum et al., 1996).

Limnological investigations, including macrophytes, phytoplankton, water chemistry and sediment chemistry, were initiated in 1993 to develop restoration measures. The project was extended to include metazooplankton, rotifers, ciliates and bacteria in 1994.

As an immediate short-term improvement of water quality, about half of the lake water was drained in December 1993 and replaced with water of better quality from the nearby Neue Donau (Figure 1).

Methods

The investigation period was from April to November 1994. During the summer season the samples were taken at fortnight intervals, while in October and November samples were taken monthly. Because of the nar-

row and shallow connection between the two basins of Alte Donau and the irregular morphometry in the south (Figure 1), three sampling stations were selected in the southern basin, two in the northern basin. Bacteria were investigated only at one station in each basin.

Previous results from 1993 indicated that vertical differences were negligible. Therefore integrated water samples for chemical analysis and phytoplankton biomass were taken with an acrylic plastic tube from the top 2 m. In addition, near-bottom water was collected with a Schindler sampler. Standard analytical techniques were used for all the chemical and physical variables.

Samples for the phytoplankton enumeration were fixed with Lugol's solution. Quantification of the phytoplankton was carried out with an inverted microscope (NIKON). About 400 individuals of the dominating species were counted (Utermöhl, 1958).

Lengths and widths of phytoplankton, zooplankton and ciliates were measured using an image analysing system (Lucia M., NIKON) to determine mean biovolumes. For calculating the cell volumes of phytoplankton and ciliates cell shapes were approximated by simple geometric forms.

Abundance and biomass of algal picoplankton and bacteria were investigated at two sites of Alte Donau. Samples were collected from four depths in the northern basin and from two depths in the southern basin. Depending on season, 10 to 50 ml of water were fixed with formaldehyde solution (4% f.c.) and stored at 4 °C. Cells were counted by their fluorescence with an excitation at 515 nm–565 nm and at 1250 × magnification. Cell size of picocyanobacteria was measured and average cell volume was calculated and converted to carbon assuming a conversion factor of 200 fg C mm⁻³ (Weisse, 1991). Carbon biomass was estimated by multiplying the average cell carbon content with the total algal picoplankton cell counts.

For bacterial numbers and biomass 10 ml samples were fixed with buffered formaldehyde solution (4% f.c.; pH=8) in sterile 20 ml plastic scintillation vials and stored at 4 °C in the refrigerator prior to the microscopic examination. Bacteria were counted and their cell volumes measured according to the method of Hobbie et al. (1977). Bacterial carbon biomass was calculated by converting cell volumes (CV) into cellular carbon content (CC) using the allometric relation of Norland (1993), where the CC (in f.w. C cell⁻¹) amounts to 120 CV^{0.72}. The average CC was then multiplied by the total number of bacteria.

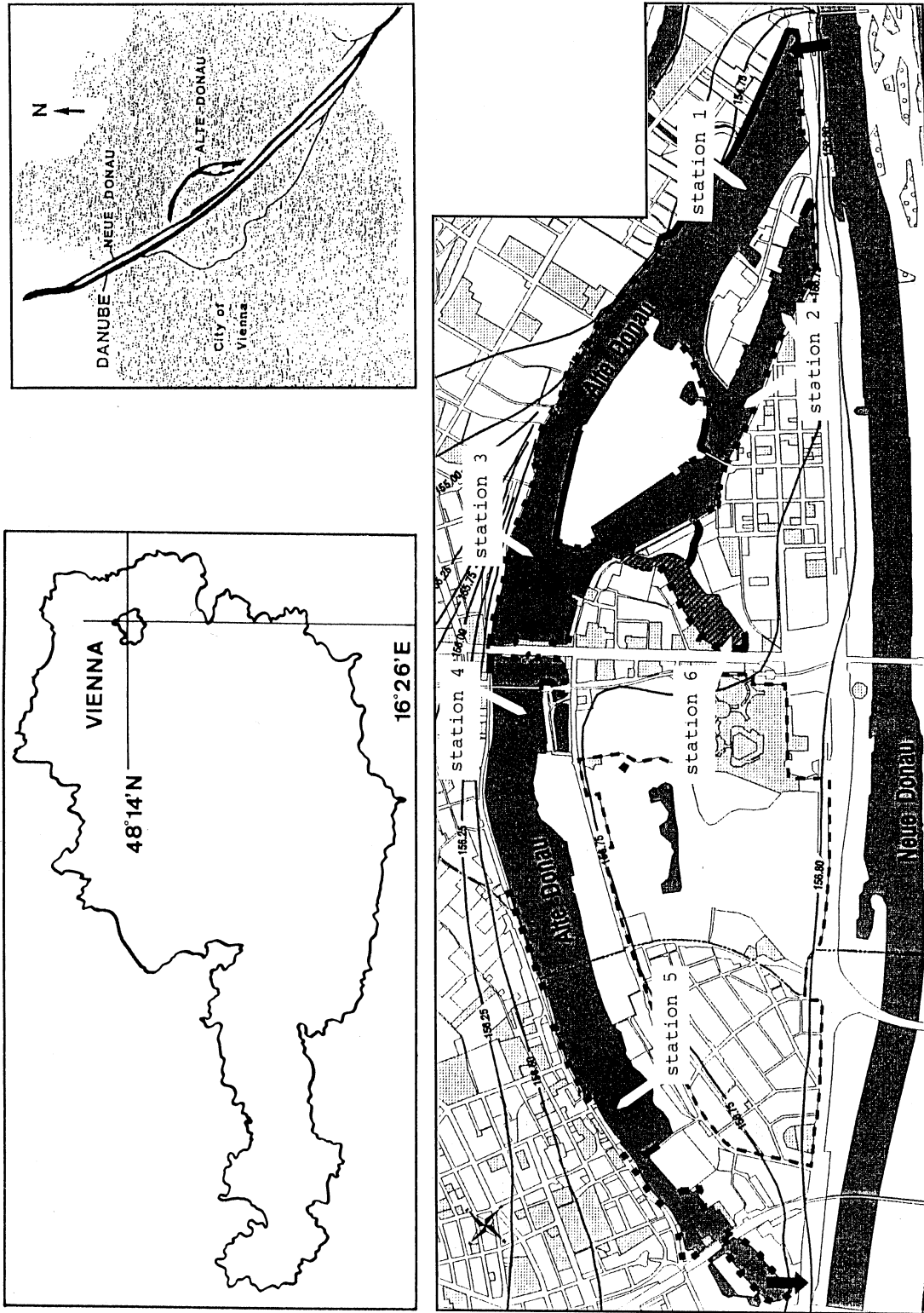


Figure 1. Map of Austria, location of Alte Donau in Vienna and map of the study site with sampling stations.

The metazooplankton and ciliates samples were taken with a 51 Schindler sampler from three different depths (surface, middle, bottom) to account for vertical inhomogeneities and then combined to an integrated sample. For the metazooplankton, the whole water volume (15 l) was filtered through a net of 44 μm mesh size, resuspended in 50 ml lake water and fixed with formaldehyde (4% f.c.). Subsamples were analysed by the Utermöhl method under an inverted microscope (Utermöhl, 1958). Crustacean biovolumes were estimated using length/weight regressions published by McCauley (1984) and Bottrell et al. (1976) assuming a dry weight/wet weight ratio of 0.15. Rotifer biovolumes were calculated using measurements of all three dimensions according to Ruttner-Kolisko (1977).

Unconcentrated subsamples were fixed with Bouin's fluid as described by Skibbe (1994) respectively with Lugol's solution for the Ciliates. One litre of untreated water was taken for living examination. The quantitative protargol stain (QPS) and living observation were used for the taxonomical identification based on publications of Kahl (1930–1935), Krainer (1988), Foissner et al. (1991, 1992 & 1994) and Foissner (1994). The applied techniques generally allowed the identification of ciliates to genera, in some cases to species. Ciliate abundances were determined using protargol preparations described in detail by Skibbe (1994). An obvious shrinkage of stained ciliates was noticed due to the protargol preparation. Therefore calculated cell volumes were multiplied with a correcting factor of 0.4 (Jerome et al., 1993). Conversion to fresh weight (F.W.) assumed a specific density of one for all species.

Results

Physical and chemical variables

Concentrations of total phosphorus (TP) total nitrogen (TN) and chlorophyll *a* increased significantly from 1987 to 1994 while Secchi-depth decreased correspondingly. Concentrations of soluble reactive phosphorus (SRP) were sometimes below detection limits during the summer of 1994 and oxygen depletion occurred at times near the sediment. Flushing Alte Donau with water of better quality in December 1993 resulted in increased Secchi-depth, lower chlorophyll *a* and lower nutrient concentrations during the first half of 1994, and greater variability between basins (Table 2).

Phytoplankton

The filamentous cyanobacteria *Limnothrix redekei* and *Cylindrospermopsis raciborskii* were first detected in 1992 and dominated the phytoplankton from May to November 1993 (Dokulil & Mayer, 1996). As a result of the flushing of Alte Donau in December 1993, phytoplankton species composition was significantly altered in the first half of 1994. Diatoms, represented by *Fragilaria ulna* var. *acus* (Kützing) Lange-Bertalot and centric diatoms (*Cyclotella* spp., *Stephanodiscus* spp.) as well as Chrysophytes (*Dinobryon* ssp.) became more prominent and cyanobacterial contribution became largely suppressed (Figure 2). Green algae, such as *Tetraedron minimum* (A. Br.) Hansg., *Scenedesmus quadricauda* (Turp.) Bréb and *Scenedesmus acuminatus* (Lag.) Chod., gained importance in June/July. Despite of low abundance, the dinoflagellates *Ceratium hirundinella* (O. F. Müller) Dujardin, *Glenodinium* ssp., and *Peridinium* ssp. contributed significantly to total biomass.

Phytoplankton biomass ranged from 4.22 mg l⁻¹ to 53.92 mg l⁻¹ in the northern basin and from 4.85 mg l⁻¹ to 60.87 mg l⁻¹ in the southern basin. Although cyanobacterial contribution in April/May was greater in the southern basin when compared to the northern basin, total algal biomass remained below 10 mg l⁻¹ until mid-July. More green algae developed in the northern part and biomass started to increase by mid-June (Figure 2).

Limnothrix redekei and *Cylindrospermopsis raciborskii* began to increase exponentially in both basins in August. These species formed algal blooms during September and early October when maximal development of both total phytoplankton and cyanobacterial biomass was reached.

Algal picoplankton

Cell numbers of algal picoplankton ranged from 0.5×10^8 (2.9.94) to more than 30×10^8 cells l⁻¹ (13.7.94). A first maximum was observed in May and a larger one in July, when small colonies were the dominating picoalgal forms. Thereafter numbers of algal picoplankton decreased rapidly to minimum values in late summer. During autumn and winter the determination of cell densities was not possible due to high amounts of detritus in the water column. The fluctuation of the biomass of the algal picoplankton followed the pattern of the cell numbers, with maximum values

Table 2. Annual mean values and ranges for selected variables for the years 1987, 1993 and 1994. For 1994 values are shown for both basins. n.d. = not determined.

| Variable (unit) | 1987 | 1993 | 1994 | |
|--|------------|-----------------|-----------------|-----------------|
| | | | southern basin | northern basin |
| Secchi-depth (m) | 1.65 | 0.4 (0.3-0.5) | 0.7 (0.25-1.90) | 0.8 (0.25-1.80) |
| pH-value | n.d. | n.d. | 8.4 (7.52-9.14) | 8.5 (7.9-9.32) |
| Oxygen (mg l^{-1}) | n.d. | 8.5 (0-14.8) | 8.1 (5.2-14.4) | 7.8 (4.1-14.3) |
| SRP ($\mu\text{g l}^{-1}$) | n.d. | n.d. | 3 (0-22) | 4 (0-16) |
| Total phosphorus ($\mu\text{g l}^{-1}$) | 35 (25-50) | 55 (23-131) | 67 (24-98) | 86 (41-145) |
| Total nitrogen (mg l^{-1}) | 0.56 | 1.96 (0.5-7.76) | 1.7 (0.49-2.28) | 1.8 (0.62-4.25) |
| DOC (mg l^{-1}) | n.d. | n.d. | 5.9 (3.15-9.61) | 6.0 (3.9-8.59) |
| Chlorophyll- <i>a</i> ($\mu\text{g l}^{-1}$) | 5 | 41 (6-102) | 40 (1-114) | 52 (10-143) |

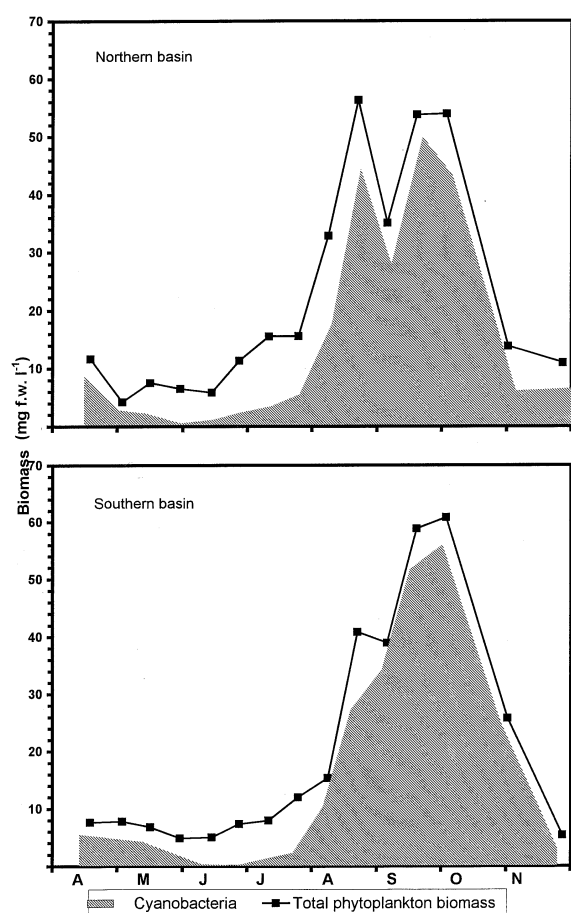


Figure 2. Seasonal development of total phytoplankton and cyanobacterial biomass in the northern basin (upper panel) and southern basin (lower panel).

of about $100 \mu\text{g C l}^{-1}$ in July and minimum values of less than $10 \mu\text{g C l}^{-1}$ in late summer (Figure 3).

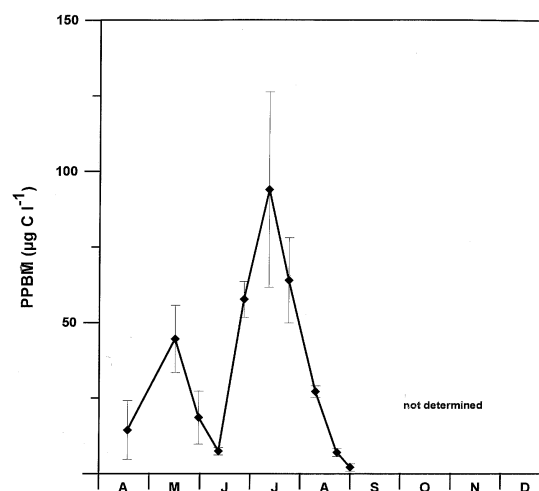


Figure 3. Seasonal development of picoplanktonic biomass (PPBM) in $\mu\text{g C l}^{-1}$; bars represent standard deviations of six measurements at different depths.

Heterotrophic bacterioplankton

At both sampling sites bacterial numbers continuously increased from densities of about 15×10^9 in early spring to an average maximum in December of 15×10^9 cells l^{-1} . A significant difference between the two basins of Alte Donau were registered in the beginning of May, when bacterial numbers in the northern basin were about 2.5 times higher than in the southern basin. Bacterial biomass varied between 30 and $115 \mu\text{g C l}^{-1}$ steadily increasing towards the end of the year (Figure 4).

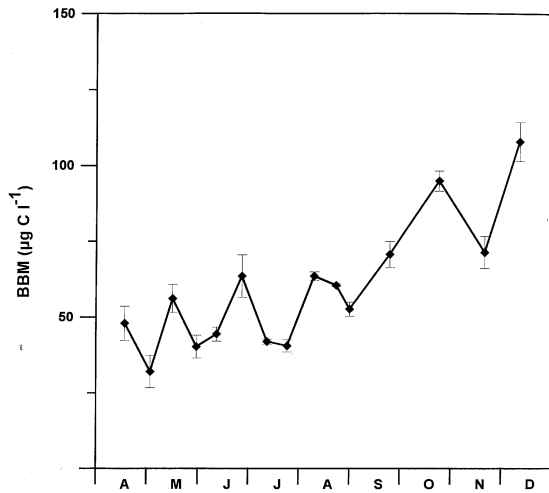


Figure 4. Seasonal variation of bacterial biomass (BBM); values are given in $\mu\text{g C l}^{-1}$; bars represent standard deviations of six measurements at different depths.

Ciliates

Cell abundance ranged from 9 to 135 ind. ml^{-1} during the sampling period. The mean ciliate number was 54 ind. ml^{-1} in the northern basin and 46 ind. ml^{-1} in the southern basin. There were no significant differences in the mean abundance between the southern and the northern basin. In both basins the highest abundances were found at the end of June after a smaller peak in the first days of May. However, seasonal succession differed between basins. A second peak developed in the northern basin in early autumn, whereas cell abundances were decreasing in the southern part.

Biomass ranged from a minimum of 58 mg to a maximum of 2472 mg F.W. m^{-3} . The mean value was 323 mg in the northern basin and 367 mg F.W. m^{-3} in the southern basin. Similar like abundance, ciliate biomass was different in the two basins. The peak value in the southern basin at the beginning of May was mainly caused by the large prostomatid *Bursellopsis spumosa* (Schmidt) Corrliss. After this species decreased, haptorids strongly contributed to total ciliate biomass (Figure 5). In the northern basin ciliates of the group Hymenostomata significantly contributed to total biomass at the beginning of May (Figure 5). During the rest of the year biomass values of both basins were very similar with an exception in the northern basin in early autumn. This biomass peak corresponded with higher abundances of the Oligotrichida at that time (Figure 5).

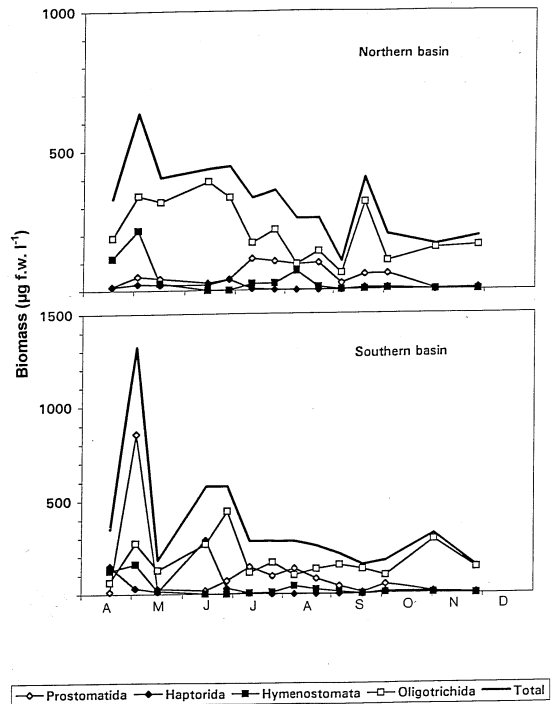


Figure 5. Seasonal development of total biomass of the ciliates and the four most important groups in the northern basin (upper panel) and in the southern basin (lower panel).

Genera of the Oligotrichida (*Halteria* spp., *Strobilidium* spp., *Pelagostrombidium* spp.) were the dominant components of ciliate plankton both in numbers and biomass during the whole sampling period. Their percentage share ranged from 61% to 63%. Second in importance were the prostomatids *Urotricha* spp., *Coleps* spp. and *Balanion* sp. (16%–18%). During summer, small hymenostomes (*Cyclidium* spp., Scuticociliata) became important to total ciliate abundance with relative contributions of about 12%. Haptorids (especially *Askenasia* spp., *Mesodinium* sp. and *Monodinium* sp.) were relatively abundant only until the end of July. Peritrichs and other ciliate groups were not abundant in the plankton during the investigated period (relative abundances <2%).

Metazooplankton and rotifers

The seasonal changes in biomass of rotifers, cladocerans and copepods are shown in Figure 6. The seasonal development of metazooplankton was very similar in the northern and southern basin, with maximum biomass of copepods in summer. Rotifers reached high

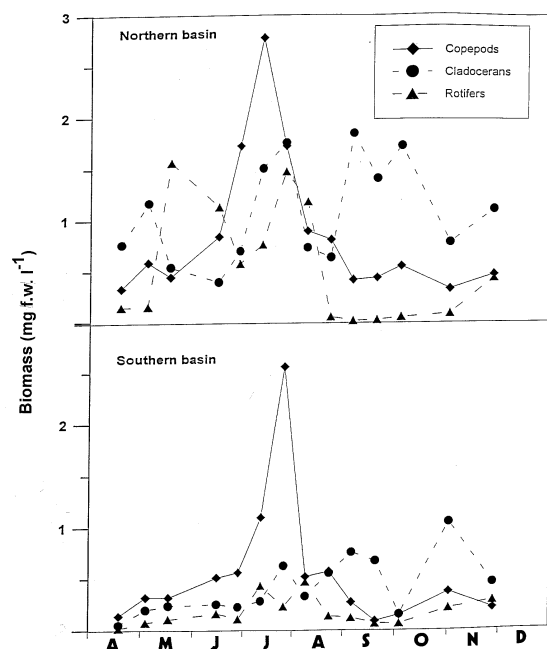


Figure 6. Seasonal development of the metazooplankton and rotifer biomass in the northern basin (upper panel) and in the southern basin (lower panel).

biomass in May and August, cladocerans increased in autumn. Although the seasonal changes were similar, the annual mean for total zooplankton differed between the northern (1425 ind. l^{-1} ; $1236 \text{ g l F.W. l}^{-1}$) and southern basin (3511 ind. l^{-1} ; $3462 \mu\text{g F.W. l}^{-1}$).

Metazooplankton was dominated by cyclopoid copepods, which contributed 44% in the northern and 25% in the southern basin to the biomass. The herbivorous calanoid copepod *Eudiaptomus gracilis* (Sars) gains in significance during winter time. The most important cladoceran species was *Eubosmina coregoni* Baird (60% of number). With numbers up to 1000 individuals per litre, this was the dominating species at the end of the investigated period in both basins. *Daphnia cucullata* Sars and *Chydorus sphaericus* (O. F. Müller) got important during spring and summer.

The seasonal cycle of rotifers showed two development peaks in the southern basin. The first was composed of a very diverse spring community, while the summer maximum consisted only of one species. In the northern basin, a real spring maximum could not be observed but in both basins the reduced development of rotifers in summer appeared at the same time when cyclopoids were dominant. The rotifer fauna consisted

of 31 species. Mainly the genera *Brachionus*, *Keratella* and *Polyarthra* were responsible for the obtained densities. Among the registered rotifers the abundant species belong to the group of unselective microfiltrators and have to be taken into account as important herbivores.

Discussion

The phytoplankton composition, especially the bloom of filamentous cyanobacteria in the second half of the year is an indication of the eutrophic to hypertrophic state of Alte Donau. *Cylindrospermopsis raciborskii* is adapted to low light conditions, is able to fix atmospheric nitrogen (Lampert & Sommer, 1993) and can store phosphorus through luxury uptake (Zaiss, 1985). However, filamentous algae are less edible than more smaller cells. The feeding pressure from metazooplankton is therefore negligible (Kurmayer, unpubl. data) and does not significantly influence the development of the cyanobacteria.

Bacterial numbers are comparable with the abundance in other eutrophic waters (e.g. Chrost & Faust, 1983; Riemann & Søndergaard, 1986). Biomass seems to be somewhat influenced by ciliate and metazooplankton grazing. The increase in bacterial numbers during the second half of the year may be a reaction to better food supply due to the expected release of easily utilisable dissolved organic matter during the phytoplankton bloom and after its breakdown.

The high number of different ciliate species (27) found during the investigation and the annual mean abundance of 57 640 individuals are characteristic features of eutrophic waters. In late summer, when the highest nutrient concentrations were measured and algae blooms occurred, Hymenostomata of the genus *Cyclidium* sp. appeared indicating an increase of the trophic situation. The decline of ciliate biomass in the second half year seems to be a result of the change in the spectrum of food particles because of the altered phytoplankton composition (Pfister, 1995). However, ciliates can feed on fine particulate detritus (Posch, 1995).

The species composition of metazooplankton also indicates the eutrophic state. The high abundances of cyclopoid copepods (*Thermocyclops*) and the low numbers of calanoid copepods (*Eudiaptomus gracilis*) are characteristic for waters with increased eutrophication (Gliwicz, 1969). The high contribution of cladocerans (McNaught, 1975) to metazooplankton

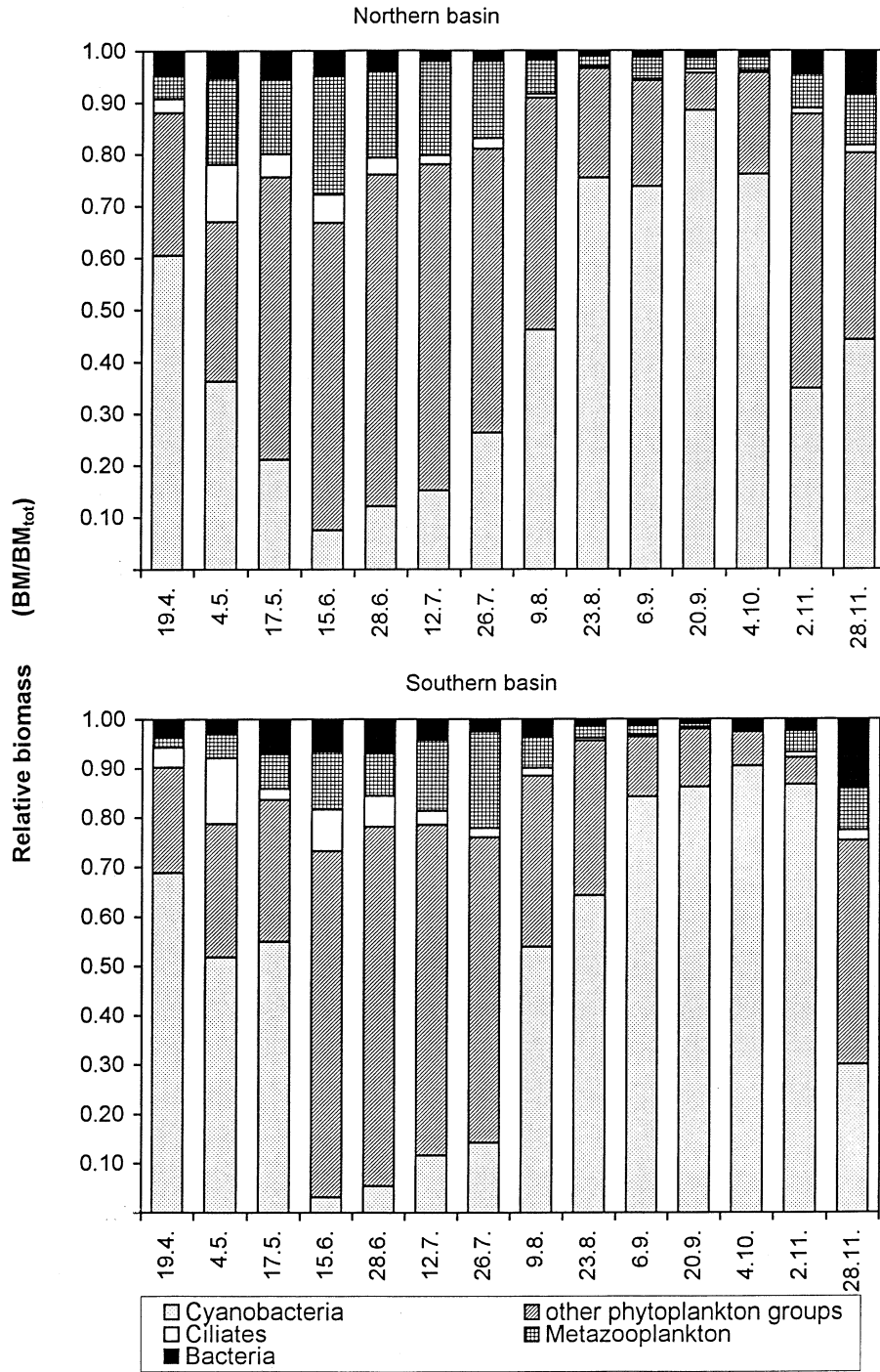


Figure 7. Seasonality of the relative biomass proportion of all investigated trophic levels in the northern basin (upper panel) and in the southern basin (lower panel).

abundance and biomass also associated with nutrient enrichment has been recorded at all sampling stations. Rotifers, like *Brachionus angularis*, *B. calyciflorus*, *Anureopsis* sp and *Filinia longiseta* as well as the cladocera *Daphnia cucullata* are indicators for eutrophic conditions. The high abundance of small cladocerans (*Eubosmina coregoni*) compared to big daphnids (*Daphnia cucullata*) is in agreement with literature, that small cladocerans are favoured through eutrophication (Beaver & Crisman, 1982). The feeding pressure of planktivorous fish seems to be responsible for that, as unpublished preliminary data suggest.

The algal feeding zooplankton and the ciliates had a significantly higher biomass in the southern basin. Feeding pressure on the edible phytoplankton species must have been therefore stronger in the southern basin than in the northern basin.

As a consequence of flushing the Alte Donau with water of better quality in December 1993, good light conditions in early spring lower nutrient concentrations and a mixed phytoplankton assemblage retarded cyanobacterial development. High water temperatures favoured growth of cyanobacteria in summer. At the same time, zooplankton biomass decreased (Figure 7) because of the shift in food supply to domination of inedible algae and water temperatures which are too high for certain species. The phytoplankton biomass gains importance during summer and amounts to almost 100% of the total biomass of all investigated trophic levels in September and October (Figure 7). Because of this shift in food supply more bacteria feeding daphnids and ciliates appeared.

In both basins the ciliates peaked in May and in June. The predatory *Bursellopsis spumosa* together with the metazooplankton caused high feeding pressure on ciliates. As a consequence, ciliate biomass declined. A second peak was observed in the northern basin at the end of September which might be an outcome of better food supply, possibly by fine particulate detritus (Posch, 1995; Posch & Arndt, 1996).

In autumn, the structure of the zooplankton community is characterised by the high abundance of cyanobacteria and increasing bacterial numbers. Large filter feeders, inhibited by filamentous inedible algae, gained significance (Gliwicz, 1977). Abundance and biomass of metazooplankton is dominated by *Eubosmina coregoni*, which is believed to be a 'low efficiency bacteria feeder' by Geller & Müller (1981). The available food composition, with bacteria as main food source, and the handicap of big filamentous cyanobacteria (length of the filaments between 70

and 400 μm) for other zooplankton species, offered best requirements for *Eubosmina coregoni*.

Rotifers and nauplii played an important role as herbivorous components in spring and early summer, when the phytoplankton community was composed of smaller forms (e.g. chlorococcal green algae, centric diatoms). Microfiltrators like *Keratella* spp. and *Brachionus* sp. feeding on particles in the range of 0.5 to 20 μm , including detritus and bacteria (Pourriot, 1977), had high abundance in spring and contributed to the decline of the algal biomass. *Polyarthra* sp. building large peak values in May, prefers food in a somewhat larger size range from 1–40 μm (Bogdan et al., 1980; Bogdan & Gilbert, 1987).

To summarise, physico-chemical structuring forces of the environment, such as underwater light conditions and temperature, are mainly responsible for the seasonal succession and the growth of phytoplankton species. Bacterial numbers are controlled by the availability of organic substances and affected by predation of ciliates and rotifers. Bacterial availability as food, algal composition and predation imposed by zooplankton are factors structuring the ciliate assemblage. The metazooplankton community is largely structured by food supply from algae and bacteria and the feeding pressure by planktivorous fish.

All these interactions are possible because of close overlap in space and time due to the turbulent mixed conditions of the water body and the change from the macrophyte dominated to the algal dominated stable state (Dokulil & Janauer, 1995). Any restoration measures must aim to re-establish the previous macrophyte dominated clear-water stage.

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