

## Seasonal and interannual variability of picocyanobacteria in Lake Constance (1987-1997)

Ursula Gaedke and Thomas Weisse

with 4 figures

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**Abstract:** The ecology of chroococcoid picocyanobacteria was studied from 1987 to 1997 in large, deep, mesotrophic Lake Constance in relation to various abiotic and biotic factors that may influence their population dynamics. Picocyanobacteria dominated the autotrophic picoplankton (APP) numerically in this lake at all depths and times. Their abundances did not respond unequivocally to the decline of wintery phosphorus concentrations by a factor of 2.5 during the decade of investigation. They showed a recurrent seasonal pattern with peaks in spring and late summer, interspersed by a pronounced minimum during and after the clear-water phase around June. The magnitude, timing, and number of peaks and troughs which varied interannually could in part be related to weather conditions or the impact of other plankton groups. Larger phytoplankton and picocyanobacteria exhibited a distinct and predictable response to the vertical mixing intensity during early spring. Except for 1993, picocyanobacteria and larger phytoplankton decreased simultaneously during the mass development of daphnids in late May or June which gave rise to the clear-water phase. As the daphnid development depends more strongly on surface water temperature than on vertical mixing intensity, an early onset of stratification may imply a longer spring development which contributed to a higher seasonal average of picocyanobacterial abundances in 1989-1991. The decline in picocyanobacteria around the clear-water phase was often more pronounced and lasted longer than did the decline in larger algae. The rate of decrease may be related to daphnid abundance, however, no such relationship existed in respect to its duration. Summer peaks of picocyanobacteria were recorded despite the presence of relatively high densities of daphnids. We conclude that with the exception of the clear-water phase grazing control by nano- and microzooplankton may be more important for controlling picocyanobacterial numbers than is grazing by daphnids. Picocyanobacteria declined in autumn prior to or concomitant with larger algae without any obvious relationship to phytoplankton biovolume or the extent of vertical mixing within the uppermost 20 m. The as yet unexplained variation in the population dynamics of picocyanobacteria points to the significance of species-specific protist grazing and to shifts in picocyanobacterial species composition which should be tackled in future studies.

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**Authors' addresses:** U. Gaedke, Limnological Institute, University of Konstanz, D-78457 Konstanz, Germany. – T. Weisse, Max-Planck-Institute for Limnology, P.O. Box 165, D-24302 Plön, Germany. Present address: Institut für Limnologie der Österreichischen Akademie der Wissenschaften, Gaisberg 116, A-5310 Mondsee. E-mail: thomas.weisse@oeaw.ac.at

## Introduction

The smallest unicellular algae within the size range of picoplankton (0.2-2.0  $\mu\text{m}$ ; SIEBURTH et al. 1978) are ubiquitous components of lakes and oceans (STOCKNER & ANTIA 1986). They are composed of photoautotrophic picocyanobacteria and, in the ocean only, prochlorophytes (CHISHOLM et al. 1988) and there are generally fewer eukaryotes of various taxonomic algal classes. Although their cell numbers seem to increase slightly along a gradient leading to eutrophy, the relative significance of the autotrophic picoplankton (APP) is highest in pristine (ultra)oligotrophic waters where picocyanobacteria may dominate primary production (FOGG 1986, PORTER et al. 1988, WEISSE 1993).

Cell numbers, biomass, primary production, and seasonal dynamics of APP have been studied intensively in the Überlinger See, the northwest basin of Upper Lake Constance, since 1987 (WEISSE 1988, WEISSE & KENTER 1991, WEISSE & SCHWEIZER 1991, ROLINSKI 1992, SCHWEIZER 1993). Pigment composition and the genetic diversity of various picocyanobacterial isolates from the lake have been investigated by ERNST and colleagues (ERNST 1991, ERNST et al. 1992, 1995, 1996, POSTIUS et al. 1996). The ecology of colonial cyanobacteria which functionally do not belong to the picoplankton has been summarized by ERNST (1990). Colonial cyanobacteria are, however, relatively unimportant in Lake Constance, contributing less than 10% to the total annual phytoplankton biomass (ERNST 1990, SOMMER et al. 1993, GAEDKE 1998a).

We report long-term records of picocyanobacterial cell numbers (1987-97) and aim to identify mechanisms which may be responsible for their observed seasonal dynamics and interannual variability. Among abiotic factors, we considered the impact of nutrient supply and direct and indirect effects of changing meteorological conditions. From 1987 to 1997, total phosphorus (TP) concentrations measured during winter mixing decreased from about 57 to 18  $\mu\text{g/l}$  (GÜDE et al. 1998). As a consequence, the spatio-temporal window of nutrient depletion increased during the growing season. In 1987 and 1988, average concentrations of soluble reactive phosphorus (SRP) in the illuminated uppermost 8 m of the water column varied between less than 3 and 3-10  $\mu\text{g/l}$  throughout the summer. In contrast, during most recent years, SRP remained consistently below 3  $\mu\text{g/l}$  after the onset of spring algal growth around April until October/November (GAEDKE 1998a, her Fig. 1, GÜDE et al. 1998). Phosphorus was identified as the most limiting nutrient of phytoplankton growth in Lake Constance throughout the season (e.g., SOMMER 1987, GAEDKE 1998a). Measurements of internal algal C:P-quotas conducted in 1995 (HOCHSTÄDTER 1997) clearly indicate nutrient depletion of phytoplankton during summer.

We then examined the impact of vertical mixing intensity on picocyanobacterial abundances in the spring because it greatly influences the dynamics of eukaryotic phytoplankton in the lake (GAEDKE et al. 1998a). Mixing intensity was estimated using a hydrodynamical simulation model (OLLINGER & BÄUERLE 1998) and was directly related to weather conditions which greatly varied during the study period (GAEDKE et al. 1998b). We also briefly evaluated the impact of winter and spring weather conditions on plankton development in summer.

Among biotic factors, we investigated the potential impact of grazing by *Daphnia* on the population dynamics of picocyanobacteria in late spring and summer. In contrast to numerous larger phytoplankton species, the overall net effect of daphnids on the total abundance of picocyanobacteria seems unpredictable and may vary during each season and interannually. At

their population peak around June, daphnids are of utmost importance to the energy flow in the planktonic food web of Lake Constance controlling population sizes of all plankton groups including bacteria, algae, and heterotrophic protists (GAEDKE & STRAILE 1994, 1998). So far, the grazing control of picocyanobacterial abundance by *Daphnia* has not been explored in detail. Daphnids may exert a direct adverse effect on picocyanobacteria as they fall into the prey size range of daphnids in Lake Constance (KNISELY & GELLER 1986, HANSEN et al. 1994). However, daphnids may also release picocyanobacteria from predation by grazing or outcompeting other picoalgal predators such as flagellates and ciliates. Furthermore, grazing of daphnids on larger phytoplankton improves the underwater light climate and grazing activities enhance nutrient recycling which may benefit picocyanobacterial growth. Finally limitations arise from considering only a bulk parameter such as picocyanobacterial cell numbers rather than looking at shifts in species composition that could not be accounted for in the present investigation.

## Methods

Upper Lake Constance (in German: Bodensee-Obersee) is a large (472 km<sup>2</sup>) and deep ( $z_{\text{mean}}=101$  m,  $z_{\text{max}}=253$  m) lake on the northern fringe of the Alps. The population dynamics of picocyanobacteria were studied from 1987-1997 at the routine sampling station of the Limnological Institute Konstanz located at the deepest site (147 m) of the Überlinger See, a northwestern arm of Upper Lake Constance. Sampling was conducted at depths from 0 to 20 m. An initial survey performed from March 1987 until December 1988 revealed that APP cell numbers were constantly low at depths greater than 20 m (WEISSE & SCHWEIZER 1991). Water bottle samples were taken weekly or every two weeks during the growing season (March through November) and occasionally every three to four weeks during winter. Annual means were calculated by interpolating results if the sampling interval was longer than one week. Sampling has been described in detail by WEISSE (1988) and WEISSE & MÜLLER (1998).

Samples were immediately fixed aboard ship with formalin (final concentration 1.5 % vol.) and stored in the dark at 4 °C until they were concentrated onto 0.2 µm Nuclepore filters and counted using epifluorescence microscopy. Picocyanobacteria were differentiated from eukaryotic picoplankton based upon their epifluorescent characteristics under green and blue excitation (WEISSE 1988, WEISSE & KENTER 1991, MACISAAC & STOCKNER 1993). Phycocyanin-rich cyanobacteria were characterized by their orange-red fluorescence under green and their yellow-orange fluorescence under blue excitation. Phycocyanin-rich cyanobacteria and picoeukaryotes appeared purple-red or red at both green and blue excitation. They were differentiated from each other based upon the presence or absence of a chloroplast. Since eukaryote cell numbers were constantly low, i.e., usually less than 5 % of the total APP abundance at all depths and times, during the first year of observation (see also SCHWEIZER 1993 for the years 1988-1990), we have used green excitation only in the routine counting since 1988. Cell numbers presented in this study therefore represent picocyanobacteria only.

Samples of larger phytoplankton and daphnids were obtained at least with the same sampling frequency as APP. Phytoplankton was counted with the Utermöhl technique and cell counts were converted to biovolume using fixed cell volumes (for details see GAEDKE 1998a). Daphnid biomass was obtained from the number of individuals observed in vertical

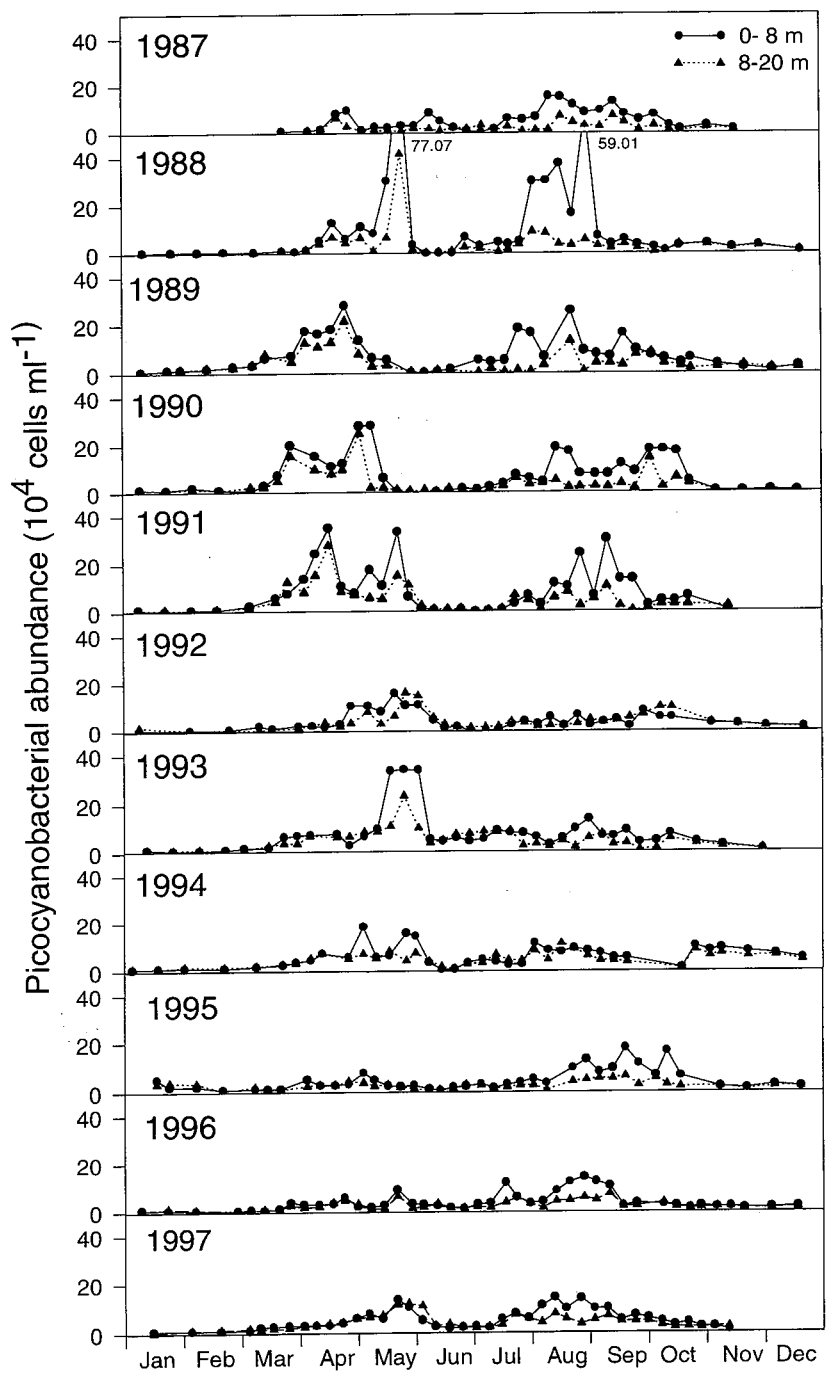


Fig. 1. Abundance of picocyanobacteria from 1987 through 1997.

hauls from the depth of 140 m to the surface with a Clarke-Bumpus sampler and length-weight relationships established for Lake Constance (for details see STRAILE & GELLER 1998).

The turbulence in the water column and the vertical mixing intensities were evaluated in detail with a one-dimensional hydrodynamical  $k$ - $\epsilon$  simulation model for the years 1979-95 (OLLINGER & BÄUERLE 1998 and unpubl.;  $k$  stands for the turbulent kinetic energy and  $\epsilon$  for its dissipation). In order to quantify the losses imposed by vertical mixing on autotrophic plankton, three different water layers were defined ranging from 0-8, 8-20, and 20-100 m. Algal growth in Lake Constance is often not light-limited within the uppermost 8 m, whereas a threshold of 20 m was chosen because a positive net photosynthesis is hardly found below this depth (HÄSE et al. 1998). The hydrodynamical model was used to estimate the daily proportion of a passive tracer (e.g. plankton cells) which is transferred by mixing from the uppermost water layer (layer 1) to the water layer 20-100 m (layer 3) (GAEDKE et al. 1998a). This proportion is called  $p_{13}$ . Values of  $p_{13}$  close to zero indicate that plankton cells residing in the euphotic zone are largely safe from being mixed below 20 m and vice versa, values of  $p_{13}$  of 0.5 imply that half of the population in the depth of 0-8 m would be lost per day to the deep, dark water layer in the depth of 20-100 m.

## Results

At first sight, population dynamics of picocyanobacteria in Lake Constance showed a recurrent seasonal pattern. Peaks occurred in spring and late summer-fall, minima in winter and during the clear-water phase (LAMPERT & SCHÖBER 1978) between the end of May and early July (Fig. 1). Overall, picocyanobacterial numbers ranged from less than  $0.01$ – $77 \times 10^4$  cells/ml. This overall pattern is blurred by interannual variability. Remarkable deviations were the spring peaks in 1987, 1995, and 1996 which were less pronounced than during the other years (Fig. 1). In 1993, no distinct minimum was recorded around May/June, and picocyanobacterial abundance constantly remained above  $4 \times 10^4$  cells/ml in spring and summer. Summer peaks were most pronounced in 1988-91 (Fig. 1).

The annual average of picocyanobacterial biovolume at the depth of 0-20 m ranged from  $0.31 \text{ cm}^3/\text{m}^2$  in 1996 to  $0.61 \text{ cm}^3/\text{m}^2$  in 1991. An average cell volume of  $0.57 \mu\text{m}^3$  was assumed (WEISSE & KENTER 1991). The seasonal (March-November) mean of picocyanobacterial cell numbers varied interannually by a factor of 3.6 in the uppermost 8 m and 2.8-fold at 8-20 m and 0-20 m (Fig. 2). The 11-year average of the seasonal abundance at 0-8 m was almost twice as high ( $7.6 \pm 2.7$  [SD]  $\times 10^4$  cells/ml) as at the depth of 8-20 m ( $4.3 \pm 1.3$  [SD]  $\times 10^4$  cells/ml). When all data were included, no significant trend emerged between picocyanobacterial abundance and the year of investigation. This statement holds equally true when averaging the entire year or just the period of most severe phosphorus deficiency from May to October (GAEDKE & SCHWEIZER 1993, GAEDKE 1998 a). When the first year of observation (1987) is omitted, however, picocyanobacterial cell numbers decreased significantly in near-surface waters from 1988 through 1997 ( $R^2=0.82$ ,  $P<0.01$ , least-squares linear regression). For the same period, this decline was also significant ( $R^2=0.52$ ,  $P<0.05$ ) for values integrated over the 0-20 m water column, but not at the depth of 8-20 m ( $R^2=0.13$ ). Similar results were obtained when regressing abundances against TP-concentrations during winter mixing. Regarding average densities at the depth of 0-20 m in June, July, August, or September separately, no

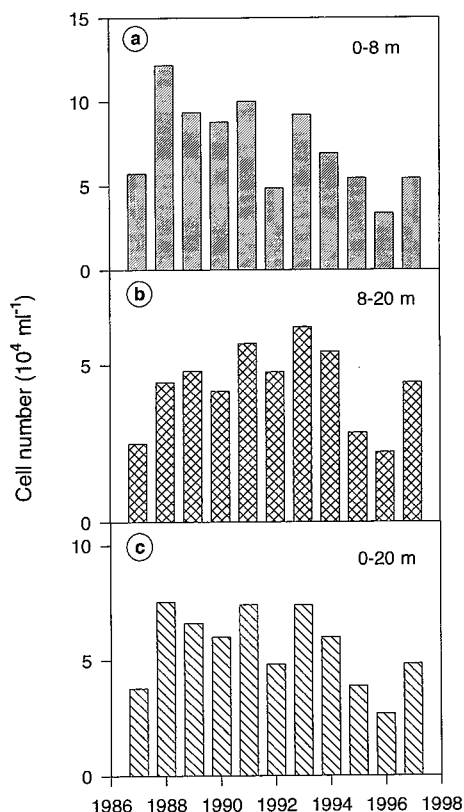
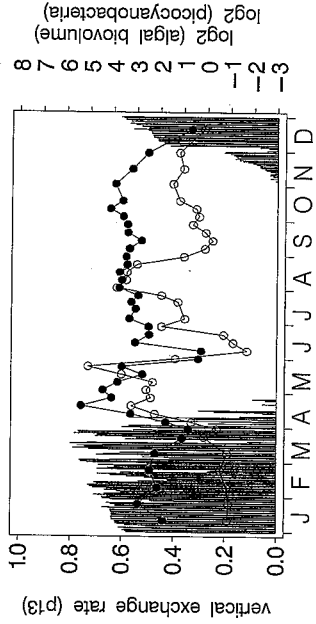


Fig. 2. Average seasonal (March–November) concentration of picocyanobacteria.

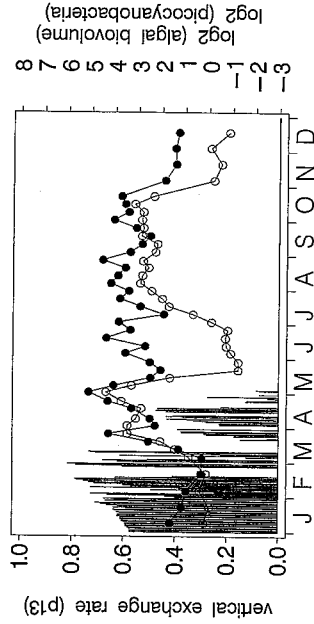
relationships were found between picocyanobacterial abundance and the year of investigation (1987–1996).

Each year in early spring, picocyanobacteria exhibited dynamics and net population increases that were similar to those of larger phytoplankton (Fig. 3). This covariation is most likely caused by the impact of vertical mixing intensity. The latter determines the mean light intensity to which individual algal cells were exposed during the past hours and days, and influences the potential for growth of autotrophic plankton during this time of the year in deep Lake Constance. As already established for larger phytoplankton (GAEDKE et al. 1998a), there was obviously a close relationship between the onset of spring growth of picocyanobacteria and the vertical exchange rate ' $p_{13}$ ' (Fig. 3). This coefficient quantifies the proportion of cells which is theoretically mixed from the uppermost 0–8 m below the depth of 20 m per day. Values of  $p_{13}$  depend on the power of the density stratification to prevent wind-induced turbulence to be dispersed towards greater depths (OLLINGER & BAUERLE 1998). They are always small at low wind speeds. At higher wind speeds, exchange rates depend on the strength of stratification. Picocyanobacterial abundances hardly increased before values of  $p_{13}$  were low for a consecutive period of at least a few days, i.e., until only a minor fraction of the population at the depth of 0–8 m was transferred into the dysphotic zone below 20 m. The comparison between the temporal development of picocyanobacterial

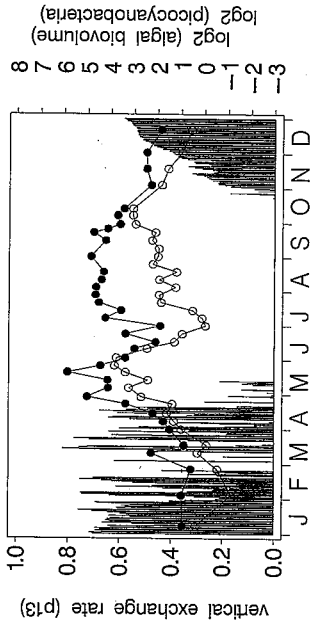
1988



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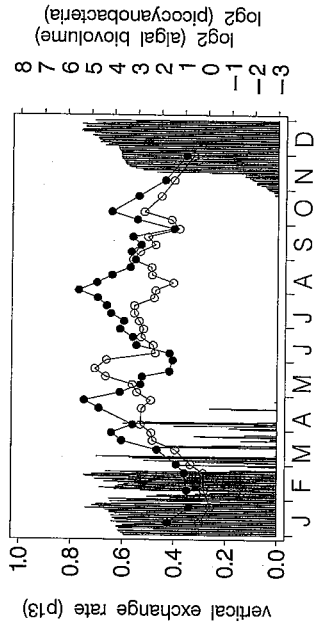


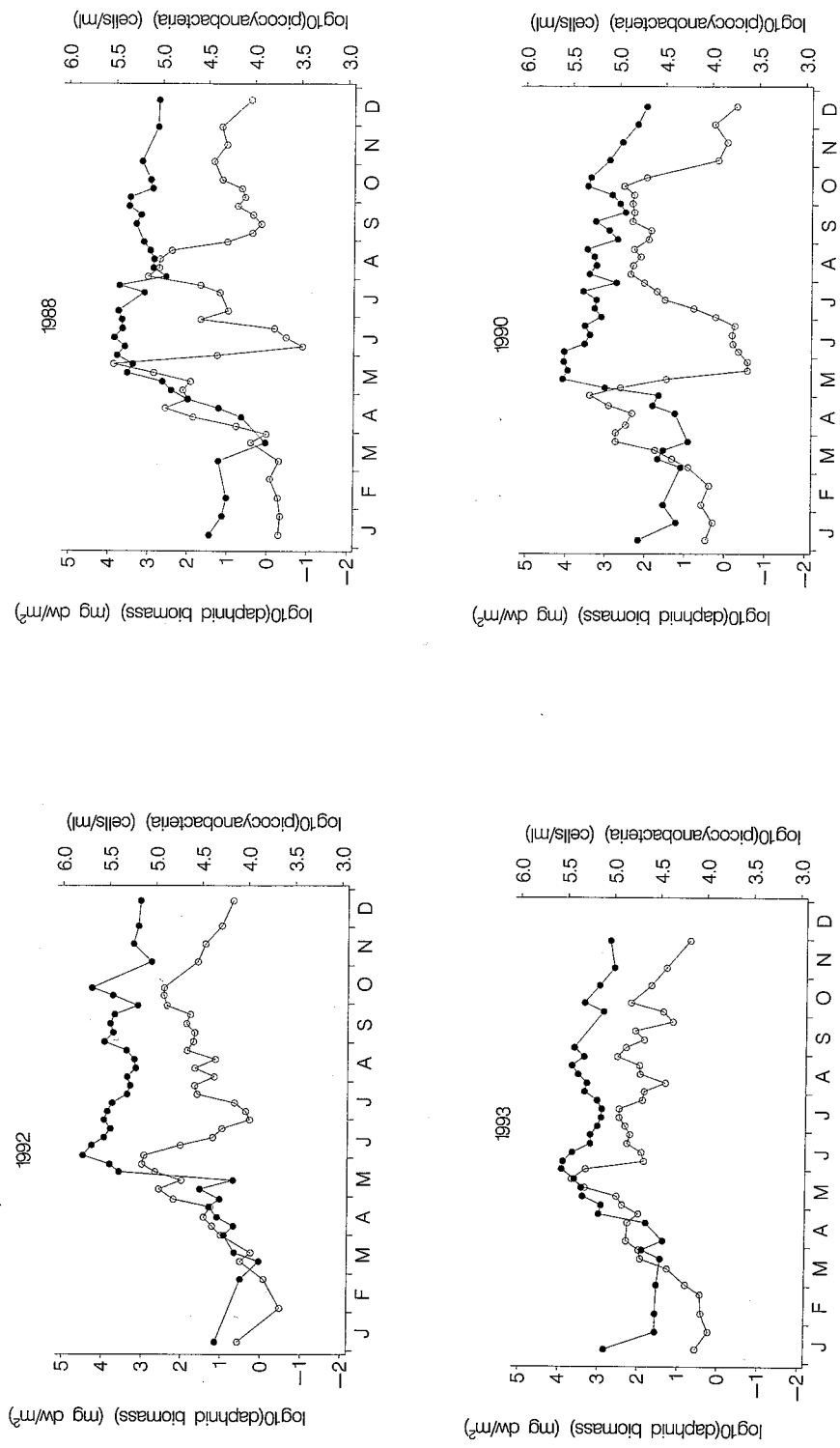
Fig. 3. Temporal development of the vertical mixing intensity, the phytoplankton biovolume, and the abundance of picocyanobacteria. The vertical mixing intensity is quantified as the proportion  $p_{13}$  of cells which is theoretically mixed from the uppermost 0.8 m below the depth of 20 m per day (OLLINGER & BÄUERLE, 1998, GAEDKE et al. 1998a).  $p_{13}$  is represented by vertical needles for each day, i.e., gaps between needles indicate values close to zero for the respective day(s). For the upper 20 m of the water column, the abundance of picocyanobacteria (open circles, cells times  $10^4$  per ml) and the biovolume of larger phytoplankton (full dots,  $\text{cm}^3/\text{m}^2$ ) is given on a  $\log_2$  scale in order to show the relative change of standing stocks. In 1990, values of  $p_{13}$  are lacking from August, 5 onwards.

abundance and  $p_{13}$  was complicated by the relatively low sampling frequency of the former as compared to the potentially high rate of change of  $p_{13}$ . The lines connecting individual sampling points in Figures 3 and 4 reflect only the net change in abundances during this time interval, but not the true variability. A low rate of change may hide the occurrence of a pronounced increase and subsequent decrease (cf. GAEDKE et al. 1998). The interannual differences in weather conditions cause marked differences in the spring mixing regime between years (Fig. 3). For example, the early onset of vernal growth in 1989-1991 (Fig. 1) can be attributed to an early stabilization of the water column (Fig. 3) after exceptionally mild winters especially in 1989 and 1990. In 1993 and 1994, the termination of mixing below 20 m did not immediately result in a further increase in picocyanobacterial densities as was observed for larger algae during April. No relationship was found between the interannual variability in the spring development of picocyanobacteria and that of daphnids (e.g. Fig. 4).

Except for 1993, picocyanobacteria decreased largely concomitant with larger phytoplankton during the clear-water phase (Fig. 3). Low densities of picocyanobacteria prevailed for a longer period of time than did the low densities of larger phytoplankton. In numerous years (1987, 1989, 1991, 1994, and 1995), minimum densities of picocyanobacteria were observed later than those of other algae. Summer blooms of picocyanobacteria were more pronounced in 1988-1991 than during the other years (Fig. 1). During these years, summer biovolume of larger phytoplankton was lower than in the previous and subsequent years (GAEDKE 1998a). This statement holds especially true for 1988 when maximum densities of picocyanobacteria were recorded (Figs. 1, 3). In addition to this inverse trend between the extent of summer peaks of picocyanobacteria and those of larger phytoplankton, no consistent patterns were identified when comparing their respective temporal courses in summer. In some years, picocyanobacteria blooms developed although the biovolume of larger algae was high, whereas in others inverse patterns were found. In autumn, picocyanobacteria declined prior (e.g., 1987, 1988, and 1989) or concomitant (e.g., 1990, 1992, and 1993) to larger phytoplankton (e.g. Fig. 3).

The largely coherent decrease in all autotrophs during the clear-water phase suggests that they are all subject to severe grazing pressure which is predominantly exerted by daphnids during most years. Only in 1987 did picocyanobacteria decrease later than did the larger algae during the weakly expressed clear-water phase. This year was characterized by an exceptionally high density of rotifers in May/June (HOCHSTÄDTER 1997) and a retarded daphnid development most probably owing to low spring temperatures (GAEDKE et al. 1998a). The decrease in picocyanobacteria in early July coincided with maximum daphnid abundances. In 1993, however, picocyanobacterial abundance increased during the first two weeks of low phytoplankton biomass at the onset of the clear-water phase (Fig. 3) when daphnid levels were already high (1-3 gDW/m<sup>2</sup>; Fig. 4). Picocyanobacterial numbers remained consistently at a fairly high level throughout summer and autumn 1993 without obvious covariation with daphnids or larger phytoplankton (Figs. 3, 4). Furthermore, picocyanobacterial abundance increased again during several summers (1987, 1988, 1989, 1991, and 1994) in spite of high daphnid biomass exceeding 1 gDW/m<sup>2</sup>, data for 1987, 1989, and 1994 not shown). In 1988, the early break-down of the summer peak of picocyanobacteria coincided with an increase in daphnid abundance.





**Fig. 4.** Temporal development of the abundance of picocyanobacteria (open circle, cells/ml on a  $\log_{10}$  scale) and of the biomass of daphnids (full dots,  $\text{mgDW/m}^2$  on a  $\log_{10}$  scale).

## Discussion

### Interannual variation versus permanent shifts in the seasonal course of picocyanobacteria from 1987 through 1997

The ongoing decrease of winterly phosphorus concentrations in Lake Constance by a factor of 3–4 since the late 1970's affected both eukaryotic phytoplankton biomass and species composition (GAEDKE 1998a, KÜMMERLIN 1998). It motivated a search for potential responses of picocyanobacteria during the 11-year study. Average abundances and seasonal patterns of picocyanobacteria did vary interannually, but did not exhibit trends unambiguously related to reduced phosphorus levels. Picocyanobacterial abundances are not necessarily impacted by a reduction in P-levels to such an extent because they seem to be generally well adapted to low P-concentrations (SØNDERGAARD 1991, WEHR 1991, TAKAMURA & NOJIRI 1994). WEHR (1991) demonstrated experimentally that *Synechococcus* sp. were never P-limited in Calder Lake, New York, even though SRP-concentrations in the epilimnion were usually below 1.5 µg/l during summer.

The lack of an unambiguous response of the average seasonal abundance of picocyanobacteria or their seasonal dynamics to re-oligotrophication is in accordance with findings from other plankton groups in Lake Constance. In summer, phytoplankton biovolume and taxonomic composition (GAEDKE 1998a) as well as total chlorophyll concentrations and primary production (HÄSE et al. 1998) did respond to reduced P-concentrations when the entire period of decreasing phosphorus concentrations is considered, i.e., from 1979 onwards. However, only a few trends clearly related to declining nutrient concentrations were found when looking at the period from 1987 until 1996 which matches approximately with the period for which picocyanobacterial cell numbers are available. All groups of pelagic organisms responded at the individual or species level at least as sensitively as at the community level (GAEDKE 1998b). Shifts in the species composition of picocyanobacteria might have occurred during the study period, but remained undetected in our routine cell counts. Using restriction fragment length polymorphism (RFLP) analyses of the DNA of various picocyanobacterial isolates from Lake Constance, ERNST and colleagues (1995) found large genetic diversity among *Synechococcus* spp. and suggested seasonal succession among picocyanobacteria in this lake. Furthermore, it is difficult to discern the impact of reduced P-concentrations on the abundance of picocyanobacteria because other external factors influencing planktonic population dynamics (e.g. weather conditions) also varied considerably during the period of investigation.

In recent years, spring peaks of picocyanobacteria were less pronounced than during the first half of the study period except for 1987. The year 1987 was characterized by unusually cold winter and spring temperatures, and surface irradiances were well below the long-term average in spring and early summer 1987 (GAEDKE et al. 1998b). A possible reason for less pronounced spring growth of picocyanobacteria during more recent years is that SRP-concentrations were depleted below 3 µg/l shortly after the onset of the vernal bloom of autotrophs. Recent laboratory experiments performed with two different *Synechococcus* sp. isolates from Lake Constance and the minute eukaryote *Chlorella minutissima* revealed that the latter was the superior competitor when relatively high initial phosphorus levels became rapidly depleted by the growing algae (NAISMITH 1997). Both *Synechococcus* strains were less able to store nutrients than were the eukaryotic algae. In contrast to summer averages, algal biovolume and total chlorophyll concentrations in late spring did not yet decline significantly in Lake

Constance during its re-oligotrophication (HÄSE et al. 1998, STÜBER & GAEDKE, unpubl.). Picocyanobacteria might have suffered from enhanced competition for phosphorus with eukaryotic algae during spring in most recent years.

Most years with a strong development of picocyanobacteria during spring were also characterized by an unusually early onset of stratification. The significance of such hydrodynamical processes for both the timing and the extent of phytoplankton and picocyanobacterial spring development was shown by relating population dynamics of autotrophs to estimates of the vertical mixing intensity derived from a hydrodynamical model (OLLINGER & BÄUERLE 1998) (Fig. 3). Mixing intensity was of outstanding importance for autotrophic net growth in spring in deep Lake Constance. However, not all ups and downs of autotrophs during spring can be explained in terms of mixing. In early March 1990 and in March-April 1992, picocyanobacterial standing stocks increased although estimates of losses by vertical mixing were fairly high (Fig. 3). The most pronounced spring bloom of picocyanobacteria was observed in 1988. This year was marked by permanently high mixing intensities throughout March caused by cold, windy, and cloudy weather conditions and a sudden decrease in the vertical mixing intensity in April (Fig. 3) which was caused by calm, sunny, and warm weather (GAEDKE et al. 1998b). Hence, growth conditions of autotrophs changed suddenly from adverse to favourable. This may have caused the exceptionally pronounced bloom of all autotrophs since grazers are less able to control their prey under such non-equilibrium conditions which favour mismatches between predator and prey.

Summer peaks recorded during the last six years were less pronounced than during four (1988-1991) of the five initial years. There are two explanations that are probably interrelated that may account for this observation. First, in contrast to previous and subsequent years, no distinct summer algal blooms were recorded in 1988-1990 (GAEDKE 1998a). In summer 1991, a brief, but pronounced bloom of *Fragilaria crotonensis* occurred prior to the picocyanobacteria bloom, but otherwise summer phytoplankton biovolume was low. The inverse pattern of picocyanobacterial and larger phytoplankton biomass in summer with high values of picocyanobacteria and low ones of larger algae in 1988-1991 and vice versa during other years may partially explain why summer chlorophyll concentrations varied less than phytoplankton biovolume (GAEDKE 1998a). The decrease in algal summer blooms during the eighties was related to enforced P-depletion, whereas the re-occurrence of more distinct phytoplankton peaks in late summer is partially attributable to algal species which may exploit alternative phosphorus sources by mixotrophy or vertical migration (GAEDKE 1998a). The more pronounced development of picocyanobacteria during summers when larger phytoplankton did not develop strongly as well may challenge the notion that picocyanobacteria are the superior competitors for inorganic nutrients at low concentrations (SØNDERGAARD 1991, WEHR 1991, TAKAMURA & NOJIRI 1994). Enhanced P-limitation of large phytoplankton owing to a picocyanobacterial bloom is feasible in principle. However, in Lake Constance, the summer biovolume of picocyanobacteria remained an order of magnitude lower than that of larger phytoplankton.

A second potential reason for the deviation in the summer development of autotrophs in 1988-1991 from other years is that the years 1989-1991 are characterized by exceptionally early water column stabilization in spring. In 1988, there was an extremely rapid ceasing of deep vertical mixing (see above) (GAEDKE et al. 1998a). These processes affect plankton dynamics in spring, but may also be relevant in summer. For example, summer daphnid biomass is lower (STRAILE & GAEDKE, subm.) and survival of planktivorous fish larvae is

higher (ECKMANN et al. 1988) when water temperatures rise early in spring. This, in turn, may influence the autotrophic plankton.

### The role of grazers for controlling picocyanobacterial population dynamics

In an earlier study conducted in 1987, WEISSE (1988) demonstrated experimentally that population dynamics of APP which include the dominant picocyanobacteria were largely controlled by nano- and microzooplankton grazing during the period when the lake was stratified. Assuming theoretical clearance rates, MÜLLER et al. (1991) further pointed to the potential significance of ciliates as picoplankton grazers, especially during summer. Nano-sized ciliates and heterotrophic flagellates were identified as the primary picoplankton grazers, which is in accordance with recent experimental findings using cultured organisms from Lake Constance (MÜLLER 1996) and elsewhere (PERNTHALER et al. 1996, ŠIMEK et al. 1995, 1997). These studies showed that protozoan grazing on picocyanobacteria is species-specific. Recent grazing experiments conducted in our laboratory using several heterotrophic nanoflagellate species and various *Synechococcus* spp. strains further elaborated on this finding (ASSMANN, in prep.). The same *Synechococcus* strain was positively selected by some flagellate species but discarded by others. Selection for or against *Synechococcus* strains was neither based on size nor pigment type alone (phycoerythrin-rich vs. phycocyanin-rich).

Grazing by protists and microzooplankton should become relatively unimportant when daphnids reach high biomasses and may structure the whole microbial community by their intense grazing from "above" (STOCKNER & PORTER 1988, PACE et al. 1990). Our observations suggest that the impact of daphnids on total picocyanobacterial abundance varied strongly, both seasonally and interannually. From 1988-1994, daphnids reached biomasses of more than 3 gDW/m<sup>2</sup> during May and/or June and, except for 1993, picocyanobacteria declined by one or two orders of magnitude during this time (Fig. 4). Less pronounced reductions in picocyanobacterial cell numbers were observed in 1987 when daphnids developed very late in the season and in 1995 and 1996 when maximum abundance of daphnids was lower than in previous years (STRAILE & GELLER 1998, STRAILE, unpubl.). During these years, less expressed spring peaks contributed the lower rates of change in picocyanobacteria around the clear-water phase (Fig. 1). The seasonally variable relationship between the temporal development of daphnids and picocyanobacteria is in accordance with evaluations of the effect of daphnids on certain size ranges of plankton organisms in Lake Constance (GAEDKE & STRAILE 1998), and findings from other lakes (STOCKNER & PORTER 1988, STERNER 1989, PACE et al. 1990, VAQUÉ & PACE 1992, WEISSE 1993). The per capita grazing of daphnids may not be constant throughout the season. It is likely to be reduced in summer since the daphnid populations then dominated by *Daphnia hyalina* perform extended vertical migration at this time (GELLER 1986). This implies that daphnids graze only at night on picocyanobacteria in the euphotic zone. Similar to the grazing impact of protists on picocyanobacteria, a deeper understanding of the direct and indirect effects of daphnids on picocyanobacteria demands an improved knowledge of species-specific interactions.

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