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# Alternative blooming of *Aphanizomenon flos-aquae* or *Planktothrix agardhii* induced by the timing of the critical nitrogen:phosphorus ratio in hypertrophic riverine lakes

K. Teubner, R. Feyerabend, M. Henning, A. Nicklisch, P. Woitke and J.-G. Kohl

with 8 figures and 2 tables

Abstract: Großer Müggelsee and Langer See are limnologically similar but during an investigation from 1990 until 1993 marked differences were observed in the species that dominated during the summer blooms. Two distinct planktonic communities could be recognised, one dominated by "Planktothrix agardhii" and the other by "Aphanizomenon flos-aquae/Microcystis spp.". A sensitive moment for the differentiation of the plankton development to the one or the other cyanobacterial summer bloom was the time, when the total nitrogen to total phosphorus ratio (TN:TP ratio) dropped to a critical value of 16:1. In addition, the phytoplankton composition at the time when this ratio is reached is of decisive importance. Rapid growth of the N<sub>2</sub>-fixing A. flos-aquae was favoured at TN:TP<16:1 in both lakes, when the timing of the critical TN:TP ratio and low biomass of P. agardhii coincided (clear water phase). Throughout all the investigated years in Großer Müggelsee, the rapid growth of the heterocyst-forming cyanobacteria A. flos-aquae started at the time when TN:TP=16:1, even if this critical ratio was delayed by several weeks. However, if P. agardhii biovolume exceeded 6 mm<sup>3</sup> l<sup>-1</sup> at the time when the critical TN:TP ratio was reached, then the mass development of this cyanobacteria continued during summer and into autumn, whereas A. flos-aquae were only present in traces. Therefore, A. flos-aquae reached high biovolumes only when TN:TP<16:1, while the growth of P. agardhii seemed to be independent of seasonal variation of the TN:TP ratio. Differences between "P. agardhii" and "A. flos-aquae/Microcystis spp." dominated years were not restricted to cyanobacterial species, but were also seen in the diatom assemblages. A comparison, based on biovolumes of 15 dominant cyanobacteria and diatoms, showed that seasonal changes in phytoplankton in "P. agardhii"-years were more gradual than the drastic shifts observed in "A. flos-aquae/Microcystis spp."-years.

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## Introduction

Großer Müggelsee and Langer See belong to the same lowland river system of the River Spree and R. Dahme (Berlin). The two riverine lakes are similar in most of their limnological characteristics. Both are hypertrophic and have a similar range of phytoplankton species. However, the species that dominate in any given year can be quite different in the two lakes. In particular, the summer plankton can be dominated by either Aphanizomenon flos-aquae (Nostocales), which forms bundle-like colonies and also develops heterocysts for diazotrophic life, or alternatively by *Planktothrix* agardhii (Oscillatoriales), which occurs as single trichomes. Physiological and limnological aspects of the dominant phytoplankton communities have been discussed already (WUNDSCH 1940, TÄUSCHER 1981, VAN LIERE & MUR 1980, ZEVENBOOM & MUR 1980, ZEVENBOOM ET AL. 1982, HRBACEK 1984, KOHL et al. 1985, 1991, NIXDORF & HOEG 1993, TIPPMANN 1993). However, the timing and duration of nitrogen fixation by A. flos-aquae and its importance to the nitrogen budget in Müggelsee (DUDEL & KOHL 1991, 1992) needs further studies. So, the aim of this study was to investigate what factors determine the succession and subsequent dominance of important bloom-forming cyanobacterial species, in particular the influence of the nitrogen:phosphorus ratio, by comparing seasonal changes in two similar lakes from the same river system.

## Materials and methods

Großer Müggelsee and Langer See are lakes on the periphery of the city of Berlin. Basic limnological data characterising the two investigated lakes are summarised in Table 1. The hypertrophic state of both lakes is indicated by the total phosphorus and chlorophyll-*a* concentration for the June-September period according to FORSBERG & RYDING (1980). Integrated samples of the upper 2 m of water column were taken monthly from Großer Müggelsee in 1990-91 and from Langer See in 1990-92. A biweekly interval was followed for 1992-93 in Großer Müggelsee and 1993 in Langer See. These samples represent the whole water column or the mixed layer during temporary stratification.

Biovolume of phytoplankton was estimated according to the UTERMÖHL method (1958). However, the mean value of the normal or the log-normal distribution was selected for abundance distribution (single cells, filaments or number of colonies), depending on which fitted better. In the case of water blooms of *Microcystis*, the biovolume was estimated from counted colonies (biovolume of *Microcystis* species) compared with counts of single cells (total biovolume of *Microcystis*, REYNOLDS & JAWORSKI 1978, HUMPHRIES & WIDJAJA 1979).

Diatoms were prepared in a special gentle way to keep both thecae of each frustule together (TEUBNER 1995). This preparation technique allowed the measurement of the cell dimension in girdle view in addition to the valve diameter for different species and cell size. The calculation of biovolume of unicellular centric diatoms was based on a combination of biovolume estimates from valve-diameter size-classes in samples fixed with Lugol's solution and counts for species from permanent slides. Dead diatom cells were separately counted in the Lugol fixed samples and their share later eliminated from calculations from permanent slides.

lake	Großer Müggelsee	Langer See
maximum depth [m]	8	6.5
mean depth [m]	4.9	3.5
lake area [km <sup>2</sup> ]	7.3	1.53
retention time [days]	67.2	4.13
Secchi depth [m]	1.6	0.9
conductivity [mS m <sup>-1</sup> ,20°C]	61	59
total nitrogen [µmol l <sup>-1</sup> ]	89	106
total phosphorus [ $\mu$ mol l <sup>-1</sup> ]	6.2 (9.2*)	6.7 (8.7*)
soluble reactive silicon $[\mu mol l^{-1}]$	102	119
chlorophyll-a [ $\mu$ g l <sup>-1</sup> ]	52*	67*
total phytoplankton biovolume [mm <sup>3</sup> l <sup>-1</sup> ]	9.86	12.52
biovolume of cyanobacteria [%]	54	66
biovolume of diatoms [%]	36	27

**Table 1.** Morphometric, average physical, chemical and biological data of the investigated lakes (1990-93, \* averaged June-September, morphological data for Großer Müggelsee from DRIESCHER *et al.* 1993 and for Langer See from ANWAND 1973).

Taxonomic identification was carried out with a light microscope, using differential interference contrast, positive phase-contrast and epifluorescence techniques. In addition, scanning electron microscopy was used for diatoms. Besides standard determination keys, the following references were used for identification KOMÁREK & ETTL (1958), ANAGNOSTIDIS & KOMÁ-REK (1985, 1988), KOMÁREK & ANAGNOSTIDIS (1986, 1989), KOMÁREK (1991), KRAMMER & LANGE-BERTALOT (1991). Diatom species of the lakes are listed in TEUBNER (1997), cyanobacteria in TEUBNER (1996).

Cyanobacterial and diatom species were selected for multivariate statistical analyses, because these two algal groups were dominant (Table 1). Species that never exceeded 5% of total biovolume during the investigated period were excluded from principal component analysis (PCA). Step-wise species extraction was repeated with PCA until the first two components represented 50 % of total variance (15 species in Fig. 4). Total variance increased to 70% when species were further reduced to ten. Those species extracted by PCA were included in the hierarchical cluster analysis (HCA) but based on annual averaged data (10 species in Fig. 5).

Logarithmic data were standardized for multivariate statistical analyses using the computer program STATGRAPHICS plus 2.0 (STSC, inc. USA). PCA was based on a set of single data points (Fig. 4: 105 cases), HCA on annual average data (Fig. 5: 8 cases).

The total nitrogen and total phosphate were determined with slight modification according to LANGNER & HENDRIX (1982).

The zooplankton community was studied in the last two years of investigation in both lakes (1992-93). Zooplankton samples were taken with a Friedinger sampler, collected in a large vessel and sieved through 50  $\mu$ m plankton net. Zooplankton taxa were determined and enumerated in these enriched sample volumes. The biovolume of the cladocerans and copepods was ascertained from a volume-length-relation according to BABUSHKINA & VINBERG (1979).



**Fig. 1.** Seasonal changes in concentrations of total nitrogen (TN), total phosphorus (TP), biovolume of cyanobacteria and diatom species in Großer Müggelsee 1990-1993. a: both axis for TN and TP are scaled in the proportion of 16:1, so that the points where the lines in the graph intersect show the molar TN:TP-ratio of 16:1 (marked by arrows). b: cyanobacterial biovolume of *Limnothrix redekei* (Limred), *Planktothrix agardhii* (Plaaga), *Aphanizomenon gracile* (Aphgra), *A. flos-aquae* (Aphflo) and *Microcystis* spp. (Micspp). c: diatom biovolume of *Aulacoseira* spp. (Aulspp), species grouped according to Fig. 5 comprising *Stephano-discus hantzschii* (Stehan), *Cyclostephanos dubius* (Cstdub) and *Actinocyclus normanii* (Actnor), as well as *Stephanodiscus neoastraea* (Steneo) and the total biovolume of unicellular centric diatoms. The black and white bar at the bottom indicates the seasons: March-May (spring), June-August (summer), September-November (autumn), December-February (winter).

The arrangement for *in situ* grazing measurements followed the method of HANEY (1971), but in this study filamentous blue-greens from laboratory cultures were supplied as <sup>14</sup>C-labelled tracer algae. The grazing chamber was incubated in the lake for 10 min. and then the zooplankton was separated. The radioactivity in the total zooplankton and in  $4 \times 1$  ml from lake chamber water was determined by liquid scintillation measurement. The loss rate by grazing (grazing rate) was calculated from this data.

Specific net growth rates between sampling dates were calculated from phytoplankton biomass of lake and inflowing water and dilution rate by a mass balance equation. The vertical extinction of photosynthetically available radiation was measured by two spherical quantum sensors connected to a data logger (LI-193SA, LI-COR, Lincoln, Nebraska, USA).

Values of total incoming radiation (TIR) were kindly supplied by the Institute of Freshwater Ecology and Inland Fisheries Berlin. The effective light climate (RAMBERG, 1979) within the mixed layer and over the periods between sampling dates were calculated on the basis of TIR, the extinction coefficient and the mixing depth of the lakes according to RILEY (1957).

# Results

The phytoplankton of the hypertrophic lakes Großer Müggelsee and Langer See were dominated by cyanobacteria and diatom species which together made up 90-93% of the total biovolume (Table 1). The seasonal changes in nutrient concentrations and in biovolume of cyanobacteria and diatom species in Großer Müggelsee and Langer See from 1990 until 1993 are shown in Figs. 1 and 2. The structure of the winter/spring period of both lakes during all investigated years was similar (Fig. 4b). Diatoms dominated the phytoplankton during the spring peak. Species characteristic for the winter/spring period, such as Nitzschia acicularis W. SMITH, Fragilaria ulna (KÜTZ.) LANGE-BERTALOT, Stephanodiscus neoastraea HÅKANS-SON et HICKEL and S. hantzschii GRUNOW are shown in Fig. 4a for both lakes. Figs. 1c and 2c show that the spring biovolume of unicellular centric diatoms in Großer Müggelsee and Langer See were mainly composed of Stephanodiscus neoastraea and the species group Stephanodiscus hantzschii, Cyclostephanos dubius (FRICKE) ROUND and Actinocyclus normanii (Greg. ex GREV.) HUSTEDT (the three species were combined because of their close correlation in annual averages, Fig. 5a). Limnothrix redekei (VAN GOOR) MEFFERT is the most important cyanobacterial species in Großer Müggelsee and Langer See during winter/spring (Fig. 4a) often reaching 2-3 mm<sup>3</sup> l<sup>-1</sup>, because their biovolume peaks were restricted to early spring periods in the investigated years (Figs. 1b, 2b, 4b). However, at the time of the spring peak of *Limnothrix redekei*, also higher biovolumes of *P. agardhii* (GOM.) ANAGN. et KOM. developed contributing on average 6% to cyanobacterial biovolume in Großer Müggelsee and 20% in Langer See.

The molar ratio of total phosphorus to total nitrogen (TN:TP ratio) was always higher than 16:1 during spring development in both lakes, but was continually decreasing. Except for Großer Müggelsee in 1993, the TN:TP ratios always dropped to 16:1 at the end of May or early June in both lakes (dates are indicated by arrows in Figs. 1a and 2a). The change in phosphorus and nitrogen availability in shallow lakes is best reflected by their total values, since the loss (denitrification) and gain



Fig. 2. Same as Figs. 1a-c, but for Langer See.

processes (phosphate remobilization from sediment) are not always observed in the dissolved inorganic pools due to the efficient uptake systems of the phytoplankton under nutrient limitation.

Despite the similar structure of the phytoplankton community during early spring and the closeness in the timing of the switch from a period of prevailing P- to one of prevailing N-limitation (at the turning-point of TN:TP>16 to <16), a totally different summer plankton developed. Großer Müggelsee and Langer See differed significantly in their summer/autumn plankton, as shown in Fig. 4b. Accordingly the annual average phytoplankton biovolumes were also different. The similarity among the phytoplankton composition based on annual averages of all 4 years of both lakes is shown in the dendrogram of Fig. 5b.



**Fig. 3.** (a) Temperature of surface water (0,5 m depth); (b) total biovolume and percent of hyaline terminal cells and heterocysts of *A. flos-aquae* in Großer Müggelsee 1990-1993.

The annual average phytoplankton structure was similar in Großer Müggelsee during the period 1990-92 (Fig. 5b). In these first three years of observation the total biovolume of phytoplankton has regularly dropped from a spring maximum of around 11 mm<sup>3</sup> l<sup>-1</sup> to under 2 mm<sup>3</sup> l<sup>-1</sup> (clear water phase) at the time when the TN: TP approached 16:1 (Fig. 1).\_Immediately after TN:TP ratios fell short of 16:1, rapid growth of *A. flos-aquae* RALFS ex BORN. et FLAH. was initiated (arrows in Fig. 1 b). The biovolumes of heterocysts and hyaline terminal cells as percentages of the total biovolume of nostocal cyanobacteria are given in Fig. 3. Heterocysts never contributed more than 1.5 % in the first three years. The share of hyaline terminal cells was much higher attaining 12-15% in the summers of 1991-92 when water temperatures were above 23°C.

The summer blooms of *A. flos-aquae* were accompanied by mass development of chroococcal cyanobacterial species [*Microcystis aeruginosa* (KÜTZ.) KÜTZ., *M. flos-aquae* (KÜTZ), *M. ichtyoblabe* KÜTZ., *M. novacekii* (KOM.) COMP., *M. viridis* (A. BRAUN) LEMM., *M. wesenbergii* (KOM.) KOM.] and filamentous diatoms [*Aulacoseira ambigua* (GRUNOW) SIMONSEN, *A. granulata* (EHRENB.) SIMONSEN, *A. italica* (EHRENB.) SIMONSEN, Figs. 1, 4a].

A different phytoplankton structure was observed in Großer Müggelsee in 1993. In contrast to the previous summer periods, the surface water temperature did not



Fig. 4. Plot of the second versus the first principal component for the seasonal phytoplankton composition in the lakes Großer Müggelsee and Langer See. For clarity, the results of this principal component analyses are shown in two displays: a plot of the variables (a) and the corresponding plot of the distribution pattern of sample points (b); percent of total variance for the first two components: 33 % + 17 %. a: Correlation between biovolume of 15 dominant phytoplankton taxa; cyanobacteria: Aphgra-Aphanizomenon gracile, Aphflo-A. flos-aquae, Limred-Limnothrix redekei, Micaer-Microcystis aeruginosa/flos-aquae, Micvir-M. viridis, Plaaga-Planktothrix agardhii; diatoms: Actnor-Actinocyclus normanii, Aulspp-Aulacoseira spp., Cycrad-Cyclotella radiosa, Cstdub-Cyclostephanos dubius, Frauln-Fragilaria ulna, Nitaci-Nitzschia acicularis, Stehan-Stephanodiscus hantzschii, Stemin-S. minutulus/parvus, Steneo-S. neoastraea. b: Every symbol represents the species composition of phytoplankton in winter/spring or in summer/autumn in the two lakes (Großer Müggelsee (M): n=46, Langer See(L): n=59). Seasons labelled according to the value of the TN:TP ratio: for winter and spring TN:TP>16, for summer and autumn TN:TP  $\leq 16$  (compare to Figs. 1 and 2). The combination of single seasons is appropriate because of similar phytoplankton structure of winter/spring on the one and summer/autumn on the other side (TEUBNER 1996). Points are encircled to emphasise, that seasonal phytoplankton changes in "Planktothrix agardhii"-years were more gradual than the drastic shift observed in "Aphanizomenon flosaquae/Microcystis spp."-years. Because of the special phytoplankton situation in Langer See in summer/autumn 1993, sample points are differently labelled from the other points of the same season of this lake.

exceed 20°C (Fig. 3a). The TN:TP ratio did not drop to 16:1 until 2 August 1993 (arrow in Fig. 1a). This was a delay of 6 to 7 weeks when compared to the previous years. The development of *A. flos-aquae* was accordingly delayed and did not start until 2 August 1993 (Fig. 1b). In contrast to previous years, heterocysts developed a biovolume of about 5% during July, whereas the peak development of hyaline terminal cells coincided with the highest biovolumes, as previously observed, even if



**Fig. 5.** Dendrograms of hierarchical cluster analyses of biovolume of phytoplankton taxa (a) and phytoplankton composition in Langer See (L) and Großer Müggelsee (M) in the years 1990-1993 (b). a: cluster C<sub>a</sub> represents the structure of phytoplankton dominance of typical "*Aphanizomenon flos-aquae/Microcystis* spp." years, cluster C<sub>b</sub> that of "*Planktothrix agar-dhii*"-dominated plankton. b: Langer See 1990, 1992, 1993 were "*P. agardhii*" years, while Großer Müggelsee 1990-92 were typical "*A. flos-aquae/Microcystis* spp." years. Langer See 1991 and Großer Müggelsee (1993) were characterised as atypical "*A. flos-aquae/Microcystis* spp." years. The two dendrograms are based on the same data matrix of annual averages; method: squared euclidean distance, ward linkage. Abbreviations of species as in Fig. 4.

their relative amount in this cold and rainy summer period was much lower than of that of the hot summers two years before (Fig. 3, 1a, b). Also contrasting with previous years was the fact that the delayed summer development of *A. flos-aquae* was not accompanied by significant biovolumes of *Microcystis* spp. However, the period of growth of *Aulacoseira* spp. was unaffected and started in early June, as in the previous years (Figs 1b, c).

The summer plankton in Langer See was totally different from that of Großer Müggelsee, except for 1991 (Figs. 4b, 5b). In contrast to Großer Müggelsee, *P. agardhii* was already dominant when the TN:TP ratio approached 16:1(Fig. 2b). At this time the biovolume of *P. agardhii* had reached more than 6 mm<sup>3</sup> l<sup>-1</sup>, by 1992 it was more than 20 mm<sup>3</sup> l<sup>-1</sup>. A clear water phase was not observed. In these three years mass development of *P. agardhii* continued during summer and into autumn. Different from Großer Müggelsee, the summer blooms of this cyanobacteria were not accompanied by massive growth of other forms such as *Microcystis* and *Aulaco*-



Fig. 6. Relationship between molar TN:TP-ratio and biovolume of *Aphanizomenon flos-aquae* (Aphlo) and *Planktothrix agardhii* (Plaaga) respectively.

*seira* (Figs. 2b, c, 4a). Consequently the change in composition of phytoplankton from winter/spring to summer/autumn in Langer See was more gradual than the drastic shift observed in Großer Müggelsee (Fig. 4b).

The summer plankton of 1991 in Langer See was quite different from the other three years investigated (Figs. 4b, 5b). Similar to the situation in Großer Müggelsee, the spring biomass of total phytoplankton was very low ( $<0.2 \text{ mm}^3 \text{ l}^{-1}$ ) at the time when TN:TP was 16:1 (Fig. 2). The low biomass of *P. agardhii* was further diminished during the clear water phase and, thereafter, *A. flos-aquae* and accompanied species (*Microcystis* spp. and *Aulacoseira* spp.) increased in abundance.

Consequently whether "A. flos-aquae/Microcystis spp." or "P. agardhii" dominated summer plankton development was dependent on the qualitative and quantitative situation of the phytoplankton at the moment when the critical TN:TP ratio was approached. Low total biomass at the time of critical TN:TP ratio promoted the initialisation of rapid growth of A. flos-aquae. Higher biovolumes of more than 6 mm<sup>3</sup> l<sup>-1</sup> of P. agardhii at TN:TP=16:1 assisted in the establishment of that species. This implies that P. agardhii had already reached higher biovolumes at TN:TP ratios higher than 16 at the time when A. flos-aquae still remained below 1 mm<sup>3</sup> l<sup>-1</sup> (Fig. 6).

The population dynamics of zooplankton groups and algal classes for Langer See and Großer Müggelsee in 1992 and1993 are shown in Fig. 7. Although *P. agardhii* was steadily rising in abundance in Langer See during spring 1993, this does not imply that this alga was not grazed by zooplankton. The grazing loss rates amount to 0.17 ( $\pm$  0.16 SD) d<sup>-1</sup> for 16 measurements with radioactive labelled *P. agardhii* in the Langer See from May to July 1993. However, the high abundance of daphnids



**Fig. 7.** Dynamic of phyto- and zooplankton in Großer Müggelsee and Langer See in 1992-93 (zooplankton: Rotifers - *Asplanchna priodonta* was excluded).

could not control the large biomass of *P. agardhii* (Fig. 7). In Großer Müggelsee we have estimated a grazing loss rate as high as  $0.3 (\pm 0.15 \text{ SD}) \text{ d}^{-1}$  for 3 experiments in May 1993. Consequently, *P. agardhii* can be controlled by zooplankton at low abundance.

The impact of zooplankton on A. *flos-aquae* can be estimated by comparing the specific net growth rate of this species (result of lake-internal growth and losses, Table 2) and that of *P. agardhii* at the time before the clear water phase. Obviously, A. flos-aquae shows higher net growth rates indicating lower grazing losses at comparable low abundance of both species. Based on annual averages, Fig. 5a shows the preference of important species for the two alternative phytoplankton structures dominated by cyanobacteria. The dominance of "A. flos-aquae/Microcystis spp." (*M. aeruginosa*, *M. viridis*) were accompanied by *Aulacoseira* spp. and *Stephanodis*cus neoastraea, while higher biovolumes of P. agardhii were closely related to Aphanizomenon gracile, Stephanodiscus hantzschii, Cyclostephanos dubius and Actinocvclus normanii (compare Großer Müggelsee 1991-92 in Fig 1, Langer See 1990, 1992-93 in Fig. 2). Accordingly the seasonal dynamics of the centric diatoms in Großer Müggelsee indicate that Stephanodiscus neoastraea was dominant among the unicellular centric diatoms in the first three years with "typical" "A. flosaquae/Microcystis spp."-plankton, while the S. hantzschii-group was of greater importance during "atypical" plankton development in 1993 (Figs. 1b, c). The changes



**Fig. 8.** Secchi depth and effective light climate in Großer Müggelsee and Langer See. a: Relationship between concentrations of chlorophyll-*a* and Secchi depths in 1991-93. The broken line indicates 1,25m Secchi depth. Points for the "*P. agardhii*"-years (1990, 1992 and 1993) were differently labelled from that of the "*A. flos-aquae*"-year (1991) in Langer See. b: Effective light climate in 1992-93.

to the mass development of *Aulacoseira* spp. in years dominated by *A. flos-aquae* has already been mentioned above (Langer See 1991).

The relationship between the chlorophyll-a concentrations and Secchi depths in both lakes is shown in Fig. 8a. The Secchi depth was not related to chlorophyll-a concentration in Langer See. In years dominated by "P. agardhii", Secchi depths did not exceed 1.25m at 95% of the cases. Secchi depths was similar in Langer See during "P. agardhii"-years and the year of low biomass development of A. flos-aquae. Although data for 1991 fall within the range of the other years, transparency must have been slightly better during the A. flos-aquae year, because Secchi depths was never smaller than 65 cm (range: 65-125 cm), while it became as low as 40 cm during the P agardhii years (40-190 cm). In contrast the range of variation of Secchi depth in Großer Müggelsee was much greater (0.5-5m) and closer related to chlorophyll-a, which is due to the high population density of "A. flos-aquae/Microcystis spp." plankton. Nevertheless, the effective light climate was nearly the same during the summer-autumn periods of high phytoplankton biomass in both lakes (Fig. 8b), since the mean depth of Langer See is lower (Table 1). Light availability inferred from Secchi depth will be underestimated in "P. agardhii"-plankton in Langer See because pronounced light scattering by this alga leads to earlier vanishing of the Secchi disk when compared to lakes dominated by colonial forms such as A. flosaquae and Microcystis spp. (e.g. EDMONDSON 1980).

# Discussion

The importance of N:P ratios in phytoplankton has been investigated by several authors. The application of Redfield's ratio to freshwater systems has been discussed by RHEE & GOTHAM (1980) and HECKY *et al.* (1993). Variations of the N:P ratio in freshwaters have been related to the trophic level and catchment area of lakes (DOWNING & MCCAULY 1992), as well as to different phytoplankton assemblages (BEHRENDT 1990). The relative nutrient availability (TILMAN 1982) is of special importance for the seasonal development of blue green algae. It is well established, that low N:P ratios favour the dominance of cyanobacteria during summer (i. e. STEINBERG & HARTMANN 1988, THOMPSON & RHEE 1994), especially the nitrogen fixing species during the period of prevailing nitrogen limitation (i. e. TRIMBEE & HARRIS 1984, SOMMER *et al.* 1986).

Other studies reported the simultaneous presence of heterocystous and non-heterocystous cyanobacteria in eu- and hypertrophic lakes, with only one of the two dominant and the other negligible (i. e. ZEVENBOOM et al. 19982, summarised in SCHREURS 1992). Moreover, summer blooms of the oscillatorial species P. agardhii and the nostocal A. flos-aquae alternate in dominance in a single lake in different years or in limnological similar lakes of one river system, such as Großer Müggelsee and Langer See. Research into why one or the other filamentous cyanobacterial species dominates in summer blooms has been investigated by VAN LIERE & MUR (1980) and ZEVENBOOM & MUR (1980). Their chemostat experiments showed that A. flos-aquae and P. agardhii had the same maintenance requirement but the later was more competitive under low light availability. Strains of both species isolated from the Großer Müggelsee showed a maximum growth rate of 0.6 d<sup>-1</sup> and a halfsaturation constant of light limited growth of 0.4 (A. flos-aquae) or 0.3 MJ m<sup>-2</sup> d<sup>-1</sup> (P. agardhii) at a 12/12 hours photoperiod, 20° C, and nutrition with ammonium nitrate (SCHLANGSTEDT 1985, NICKLISCH & KOHL 1989, KOHL et al. 1989). The effective light climate was 0.8 MJ m<sup>-2</sup> d<sup>-1</sup> in the Langer See in 1992 and 0.5 MJ m<sup>-2</sup>

d<sup>-1</sup> in 1993 at the time when the TN:TP ratio reached to 16 (Figs.2 and 8b). A. flos-

period	net growth rate (d <sup>-1</sup> ) Aphanizomenon flos-aquae	net growth rate (d <sup>-1</sup> ) <i>Planktothrix agardhii</i>
16.3 29.3.	0.126	-0.116
30.3 12.4.	0.233	-0.018
13.4 26.4.	-0.002	-0.008
27.4 10.5.	0.171	0.035
11.5 24.5.	-0.286	-0.497

**Table 2.** Specific net growth rates of *Aphanizomenon flos-aquae* and *Planktothrix agardhii* in the Großer Müggelsee in spring 1992.

aquae could grow at a rate greater than  $0.3 \text{ d}^{-1}$  under the light availability in a well mixed water column. However, the wind-induced mixing is sometimes very low in summer and A. flos-aquae is able to move to their optimal light condition faster than P. agardhii because of the higher sedimentation and flotation velocities of the bundles (REYNOLDS 1989). The small difference in light-limited growth between the two species, therefore, can be further diminished. The grazing losses of the bundles of A. flos-aquae are also lower than that of the trichomes of P. agardhii. Therefore, both species should increase their population density under moderate light limitation and grazing pressure.

Of course, A. flos-aquae is the outstanding competitor under absolute nitrogen deficiency but P. agardhii also competes well under N-limitation (ZEVENBOOM & MUR 1980, NICKLISCH et al. 1991) and can survive long periods of N-deficiency (NICKLISCH 1994). However, both species are weak competitors under P-limitation (SOMMER 1985, NICKLISCH et al. 1991, NICKLISCH 1994). The hypertrophic river lakes like Großer Müggelsee show a moderate phosphate limitation of phytoplankton around the spring peak of diatoms (TIPPMANN 1993). The enhanced availability of phosphate later later in the year is seldom indicated by higher soluble reactive phosphate (SRP) concentrations since the recycled phosphate is rapidly consumed. However, the increase in total phosphate is a good indicator of improved phosphate availability. This increase is obvious if the populations of P. agardhii or A. flosaquae start to bloom (Figs. 1 and 2). The total phosphate is generally higher in Langer See, the diatoms become limited by silicate and, consequently, there remains enough phosphate for *P. agardhii* to start its mass development earlier in the year in Langer See compared with Müggelsee. This species achieves relatively high biomass levels that are not controlled by grazing, even in periods of high abundance of daphnids. Later on, SRP concentrations increase and return to non limiting levels. However, A. *flos-aquae* cannot invade the *P* agardhii blooms. The cause remains uncertain and should be studied experimentally.

In the Müggelsee, *P. agardhii* at low spring densities does not survive the strong grazing pressures by daphnids during the clear water phase. So, the available phosphate was thereafter used by *A. flos-aquae* that survived the clear water phase and which reached high abundance in 1990-92. In 1993 the weather was colder, the denitrification and the phosphate remobilisation were lower. All theses factors were reflected in a later decrease of the N:P ratio to 16:1 and a later increase of the abundance of *A. flos-aquae*, which is obviously favoured by the increase in total phosphate (phosphate remobilisation) (Fig. 1).

PICK & LEAN (1987) found the N:P ratio to be a poor indicator for N or P limitations or of growth rates of cyanobacterial plankton, at least for *P. agardhii* (PERS-SON 1981, ZEVENBOOM *et al.* 1982). However, the seasonal changes in TN:TP and in phytoplankton composition in our studies have indicated, that it is not only the TN:TP ratio of 16 which is significant for the progress to *P. agardhii* or *A. flosaquae* dominance, but also the phytoplankton composition at the time when the critical TN:TP ratio is reached. Rapid growth of the N2-fixing A. flos-aquae at TN :TP<16:1 was favoured in both lakes, when the timing of the critical TN:TP ratio and low biomass of P. agardhii coincided. This timing opened the window for mass development of A. flos-aquae. Throughout all the investigated years, the rapid growth of this heterocyst forming cyanobacteria started at the time when TN:TP= 16:1 in Großer Müggelsee, even if this critical ratio was delayed over several weeks as in 1993 (Fig. 1). Accordingly A. flos-aquae reached biovolumes greater than 1 mm<sup>3</sup> l<sup>-1</sup> only when TN:TP<16:1, while the growth of *P. agardhii* seemed to be independent from seasonal variation of the TN:TP ratio (Fig. 6). Because of the more drastic shift in seasonal change from spring to summer, the phytoplankton development was disrupted in Großer Müggelsee (Fig. 4b). This short-term dominance during annual phytoplankton development of A. flos-aquae and its accompanying cyanobacterial species characterises these species as summer bloom forms (e.g. REYNOLDS 1984). Contrasting with this, the more gradual change in composition of phytoplankton from winter/spring to summer/autumn in Langer See was in agreement with the long term dominance of *P. agardhii* (compare SCHREURS 1992).

The formation of heterocysts was not restricted to biomass peaks of A. flos-aquae in Großer Müggelsee (Fig. 3b) as found by JONES (1979), BAKER (1981) and ANA-GNOSTIDIS et al. (1988). However, it is known from Großer Müggelsee in 1982 and 1983 that only for some weeks during mass development do the nitrogen-fixing cyanobacteria make a significant contribution to the whole N-load of the lake (DUDEL & KOHL 1991, 1992). However, such frequency of heterocysts in populations of A. flos-aquae at times of good nitrogen availability in 1993 (up to 5 %, Fig. 3b) were not found in a cultured strain of this species (SCHLANGSTEDT 1985, KOHL et al. 1985).

In contrast to the heterocysts, the development of hyaline terminal cells was more closely related to peaks of biovolume and periods of high temperature (Fig. 3). It seems that especially during hot summers the relative amount of hyaline cells (ANA-GNOSTIDIS *et al.* 1988) was very high, about 10 to 15%. Ultrastructural investigations have shown, that the colourlessness of these cells is caused by large vacuoles (CMIECH *et al.* 1988). The importance of the high share of hyaline cells during hot summer periods is still unresolved.

The different cyanobacterial assemblages, the so called "P. agardhii" or according to WUNDSCH (1940) "H2S-Oscillatoria-lakes" and "A. flos-aquae/Microcystis spp." years are well known in hypertrophic shallow riverine lakes (e. g. KOHL *et al.* 1991, NIXDORF & HOEG 1993). In agreement with earlier comparisons on phytoplankton assemblages it was shown, that in years with a dominance of P. agardhii relatively high biovolumes of Aphanizomenon gracile coexisted, while the mass development of A. flos-aquae were accompanied by higher biovolumes of Microcystis species, such as M. aeruginosa and M. viridis (TÄUSCHER 1981, KOHL *et al.* 1985, ANA-GNOSTIDIS *et al.* 1988). In the present study biovolumes of the diatoms accompanying these cyanobacterial blooms have been investigated in detail. According to the annual averaged biovolumes *Stephanodiscus hantzschii*, *Cyclostephanos dubius* and *Actinocyclus normanii* were more closely related to "*P. agardhii*"-dominance, while *Aulacoseira* spp. and *Stephanodiscus neoastraea* were of greater importance in "*A. flos-aquae/Microcystis* spp." plankton (Figs. 4, 5, see also TEUBNER 1996, TEUBNER *et al.* 1996). Correspondingly, changes in cyanobacterial dominance or deviation from the typical blue-green years were not restricted to changes in cyanobacteria, but also included diatom taxa (Figs. 1, 2, 4) common in hyper- and eutrophic lakes (VAN DAM *et al.* 1994). This is of interest considering that diatoms contribute about 30% of total biovolume in addition to the 60% share of cyanobacteria in such shallow, hypertrophic lakes (Table 1).

The different flushing rates of the two lakes cannot be the decisive factor for the regulation of the different dominance structures of phytoplankton because the change was observed in both lakes but different years (KOHL *et al.* 1985, NIXDORF & HOEG 1993, TIPPMAN 1993, RÜCKER & KOHL 1994, TEUBNER 1996). Nevertheless, the residence time in Langer See was considerably longer during summer (up to 14 days) than the annual average of 4 days.

To conclude, the influence of the critical TN:TP ratio in favouring the development of *A. flos-aquae* (in the case of clear water phase) or prolongation of the dominance of *P. agardhii* does not necessarily have to be direct. Physiological indicators such as certain pigments and polyphosphate granules of cyanobacteria have indicated that limitations of N and P are species specific and, therefore, phytoplankton assemblages as a whole are rarely limited by one of these elements (TIPPMANN 1993, RÜCKER & KOHL 1994). The importance of N:P ratios for cyanobacteria must be seen in connection to other environmental variables such as light (discussed above) or temperature as has been reported from some experiments (e. g. KONOPKA & BROCK 1978, TILMAN *et al.* 1986). Moreover, other environmental and physiological factors can be important for the development and dominance of cyanobacterial plankton at the spring to summer transition (FOY 1983, DOKULIL & MAYER 1996).

Nevertheless, in this case, the time when the critical TN:TP ratio is reached is a sensitive moment for the differentiation of the plankton development in the one or the other cyanobacterial dominance. Therefore the time when the relative nutrient availability changed from preferential P to preferential N limitation is convenient for prediction of one of these alternative cyanobacterial dominance structures in summer plankton in shallow, hypertrophic, turbid riverine lakes.

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# References

- ANWAND, K. (1973): Gewässerverzeichnis der Seen- und Flußfischerei der Deutschen Demokratischen Republik. - 100 pp, Institut für Binnenfischerei Berlin-Friedrichshagen, Berlin.
- ANAGNOSTIDIS, K., ECONOMOU-AMILLI, A. & TAFAS, T. (1988): Aphanizomenon sp. from Lake Trichonis, Hellas (Greece) - A taxonomic consideration in relation to morphological and ecological parameters. - Arch. Hydrobiol. 80: 1-4 (50-53), 529-543.
- ANAGNOSTIDIS, K. & KOMÁREK, J. (1985): Modern approach to the classification system of cyanophytes 1. Introduction. Arch. Hydrobiol. **71**: 1-2(38,39), 291-302.
  - (1988): Modern approach to the classification system of cyanophytes 3. Oscillatoriales.
    Arch. Hydrobiol. 80: 1-4(50-53), 327-472.
- BABUSHKINA, E.W. & VINBERG, G.G. (1979): Dependence between length and body volume from planktonic cladocera. - In: VINBERG, G. G.: Laboratory and freshwater investigations about the biological fundamentals of the waters productivity (russ.) – 180 pp, AN SSSR, Zool. Inst. Leningrad.
- BAKER, K. K. (1981): Ecology and taxonomy of five natural populations of the genus *Aphanizomenon* Morren (Cyanophyceae). - Arch. Hydrobiol. **92**: 222-251.
- BEHRENDT, H. (1990): The chemical composition of phytoplankton and zooplankton in an eutrophic shallow lake. Arch. Hydrobiol. **118**: 129-145.
- CMIECH, H. A. GORDON, F. L. & REYNOLDS, C. S. (1988): Morphological and ultrastructural variability of planktonic Cyanophyceae in relation to seasonal periodicity. IV. *Aphanizomenon flos-aquae*: vegetative cells, heterocysts, akinetes. - Br. Phycol. J. 23: 239-250.
- DRIESCHER, E., BEHRENDT, H., SCHELLENBERGER, G. & STELLMACHER, R. (1993): Lake Müggelsee and its environment – Natural conditions and anthropogenic impacts. - Int. Rev. ges. Hydrobiol. 78: 327-343.
- DOKULIL, M. T. & MAYER, J. (1996): Population dynamics and photosynthetic rates of a *Cylindrospermopsis-Limnothrix* association in a highly eutrophic urban lake, Alte Donau, Vienna, Austria. - Algological Studies **83**: 179-195.
- DOWNING, J. A. & MCCAULEY, E. (1992): The nitrogen:phosphorus relationship in lakes. Limnol. Oceanogr. 37: 936-945.
- DUDEL, G. & KOHL, J.-G. (1991): Contribution of dinitrogen fixation and denitrification to the N-budget of a shallow lake. Verh. Internat. Verein. Limnol. 24: 884-888.
  - - (1992): The nitrogen budget of a shallow lake (Großer Müggelsee, Berlin). Int. Rev. ges. Hydrobiol. 77: 43-72.
- EDMONDSON, W. T. (1980): Secchi disk and chlorophyll. Limnol. Oceanogr. 25: 378-379.

- FORSBERG, C. & RYDING, S. O. (1980): Eutrophication parameters and trophic state indices in 30 waste-receiving Swedish lakes. Arch. Hydrobiol. **69**: 189-207.
- FOY, R. H. (1983): Interaction of temperature and light on the growth rates of two planktonic Oscillatoria species under a short photoperiod regime. - Br. Phycol. J. 18: 267-273.
- HANEY, J .F. (1971): An in situ method for measurement of zooplankton grazing rates. Limnol. Oceanogr. 16: 970-977.
- HECKY, R. E., CAMPBELL, P. & HENDZEL, L. L. (1993): The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. **38**: 709-724.
- HRBACEK, J. (1984): Contribution to the ecology of water-bloom forming blue-green algae Aphanizomenon flos-aquae and Microcystis aeruginosa. - Limnol. Oceanogr. 29: 1137-1140.
- HUMPHRIES, S. E. & WIDJAJA, F. (1979): A simple method for separating cells of *Microcystis* aeruginosa for counting. Br. Phycol. J. 14: 313-316.
- JONES, R. I. (1979): Notes on the growth and sporulation of a natural population of *Aphani*zomenon flos-aquae. - Hydrobiologia **61**: 55-58.
- KOHL, J.-G., DUDEL, G., HENZE, R., NICKLISCH, A., TEUBNER, K. & TIPPMANN, P. (1991):: Langzeittrends und multistabile Zustände im Phytoplankton eines polymiktischen Fluß-Sees (Großer Müggelsee, Berlin). - In: Erweiterte Zusammenfassung der Jahrestagung 1991 (30.9.-6.10.) in Mondsee (Deutsche Gesellschaft für Limnologie, ed.): 564 pp.
- KOHL, J.-G., DUDEL, G., SCHLANGSTEDT, M. & KÜHL, H. (1985): Zur morphologischen und ökologischen Abgrenzung von Aphanizomenon flos-aquae RALFS ex BORN. et FLAH. und A. gracile (LEMM.) LEMM. - Arch. Protistenkd. 130: 119-131.
- KOHL, J.-G., SCHLANGSTEDT, M. & DUDEL, G. (1989): Stabilization of growth during combined nitrogen starvation of the planktic blue-green alga *Anabaena solitaria* by dinitrogen fixation. - Arch. Hydrobiol. Beih. Ergebn. Limnol. 33: 457-464.
- KONOPKA, A. & BROCK, T. D. (1978): Effect of temperature on blue-green algae (Cyanobacteria) in lake Mendota. Appl. Environ. Microbiol.: **36**: 572-576.
- KOMÁREK, J. (1991): A review of water-bloom forming *Microcystis* species, with regard to populations from Japan. Algological Studies **64**: 115-127.
- KOMÁREK, J. & ANAGNOSTIDIS, K. (1986): Modern approach to the classification system of cyanophytes 2. Chroococcales. Arch. Hydrobiol., 73: 157-226.
  - (1989): Modern approach to the classification system of cyanophytes 4. Nostocales. -Arch. Hydrobiol. 82: 247-345.
- KOMÁREK, J. & ETTL, H. (1958): Algologische Studien. 359 pp. Verlag der Tschechoslowak. Akademie der Wissensch., Prag.
- KRAMMER, K. & LANGE-BERTALOT, H. (1991): Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. 576 pp. In: ETTL, H., GERLOFF, J., HEYNIG, H. & MOLLENHAUER, D. (eds.) Süßwasserflora von Mitteleuropa, Vol. 2, , Gustav Fischer Verlag, Stuttgart, New York.
- LANGNER, C.L. & HENDRIX, P.F. (1982): Evaluation of a persulphate digestion method for particulate nitrogen and phosphorus. Water Res. 16: 1451-1454.
- NICKLISCH, A. (1994): Does mortality by nitrogen deficiency influence the succession of *Lim-nothrix redekei* and *Planktothrix agardhii*? Verh. Internat. Verein. Limnol. **25**: 2214-2217.

- NICKLISCH, A. & KOHL, J.-G. (1989): The influence of light on the primary production of two planktic blue-green algae. Arch. Hydrobiol. Beih. Ergebn. Limnol. **33**: 451-455.
- NICKLISCH, A., ROLOFF, B. & RATSCH, A. (1991): Competition experiments with two planktic blue-green algae (Oscillatoriaceae). Verh. Internat. Verein. Limnol. 24: 889-892.
- NIXDORF, B. & HOEG, S. (1993): Phytoplankton community structure, succession and chlorophyll content in Lake Müggelsee from 1979 to 1990. - Int. Rev. ges. Hydrobiol. **78**: 359-377.
- PERSSON P.-E. (1981): Growth of *Oscillatoria agardhii* in a hypertrophic brackish water bay. - Annals Bot. Fennici **18**: 1-12.
- PICK, F. R. & LEAN, D. R. S (1987): The role of macronutrients (C, N, P) in controlling cyanobacterial dominance in temperate lakes. N.Z. J. Mar. Freshwater Res. 27: 425-434.
- RAMBERG, L. (1979): Relation between phytoplankton and light climate in two Swedish forest lakes. Int. Rev. ges. Hydrobiol. **64**: 749-782.
- REYNOLDS, C. S. (1984): Phytoplankton periodicity: The interactions of form, function and environmental variability. Freshwater Biol. 14: 111-142.
  - (1989): Physical determinants of phytoplankton succession. In: SOMMER, U. (ed.): Plankton Ecology, Succession in Plankton Communities. Springer, Berlin, New York. pp. 9-56.
- REYNOLDS, C. S. & JAWORSKI, G. H. M. (1978): Enumeration of natural *Microcystis* populations. - Br. Phycol. J. **13**: 269-277.
- RHEE, G.-Y. & GOTHAM, I. J. (1980): Optimum N:P ratios and coexistence of planktonic algae. J. Phycol. 16: 486-489.
- RILEY, G. A. (1957): Phytoplankton of the north central Sargasso Sea, 1950-1952. Limnol. Oceanogr. 2: 252-270.
- RÜCKER, J. & KOHL, J.-G. (1994): Indication of growth-limiting factors of planktonic cyanobacteria by application of microscope-photometry. - Verh. Internat. Verein. Limnol. 25: 2218-2220.
- SCHLANGSTEDT, M. (1985): Einfluß von Licht- und Stickstoffdargebot auf das Wachstum der N2-fixierenden Cyanophyceen Anabaena solitaria KLEB. und Aphanizomenon flos-aquae RALFS ex BORN. et FLAH. – Ph. D. Thesis, Humboldt-Universität zu Berlin, 119 pp.
- SCHREURS, H. (1992): Cyanobacterial dominance Relations to eutrophication and lake morphology, Academisch Proefschrift, Universiteit van Amsterdam.
- SOMMER, U. (1985): Comparison between steady state and non-steady competition: Experiments with natural phytoplankton. Limnol. Oceanogr. **30**: 335-346.
- SOMMER, U., GLIWICZ, Z. M., LAMPERT, W. & DUNCAN, A. (1986): The PEG-model of seasonal succession of planktonic events in fresh waters. - Arch. Hydrobiol. 106: 433-471.
- STEINBERG, C. E. W. & HARTMANN, H. M. (1988): Planktonic bloom-forming cyanobacteria and the eutrophication of lakes and rivers. Freshwater Biol. 20: 279-287.
- TÄUSCHER, L. (1981): Untersuchung zur Art- und Biozönosestruktur des Phytoplanktons des Großen Müggelsees (Berlin) unter Berücksichtigung produktions- und saprobiologischer Aspekte. Ph. D. Thesis, Humboldt-Universität zu Berlin, 141 pp.
- TEUBNER, K. (1995): A light microscopical investigation and multivariate statistical analyses of heterovalvar cells of *Cyclotella*-species (Bacillariophyceae) from lakes of the Berlin-Brandenburg region. Diatom Research **10**: 191-205.
  - (1996): Struktur und Dynamik des Phytoplanktons in Beziehung zur Hydrochemie und Hydrophysik der Gewässer: Eine multivariate statistische Analyse an ausgewählten Ge-

wässern der Region Berlin-Brandenburg. - Dissertation A, Humboldt-Universität zu Berlin, 232 pp.

- TEUBNER, K. (1997): Merkmalsvariabilität bei planktischen Diatomeen in Berlin-Brandenburger Gewässern. Nova Hedwigia 65: 233-250.
- TEUBNER, K., HAAKE, H., WOITKE, P. & KOHL, J.-G. (1996): Die Beziehung zwischen der Artenzusammensetzung und der Jahresdynamik des Phytoplanktons und der Hydrochemie in 11 Gewässern in Berlin-Brandenburg. In: Erweiterte Zusammenfassung der Jahrestagung 1995 (24.9.-29.9) in Berlin (Deutsche Gesellschaft für Limnologie, ed.): 707 pp.
- THOMPSON, P.-A. & RHEE, G.-Y. (1994): Phytoplankton responses to eutrophication. Arch. Hydrobiol. Beih. Ergebn. Limnol. **42**: 126-166.
- TIPPMANN, P. (1993): Zur Bedeutung der Nährstofflimitation für die saisonalen Phytoplanktonsukzessionen in zwei eutrophen Flußseen. – Ph. D. Thesis, Humboldt-Universität Berlin, 107 pp.
- TILMAN, D. (1982): Resource competition and community structure. 296 pp. In: Monographs in Population Biology 17, (R. M. May, ed.), Princeton University Press, Princeton (New Jersey).
- TILMAN, D., KIESLING, R. STERNER, R. KILHAM, S. S. & JOHNSON, F. A. (1986): Green, bluegreen and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. - Arch. Hydrobiol. 106: 473-485.
- TRIMBEE, A. M. & HARRIS, G. P. (1984): Phytoplankton population dynamics of a small reservoir: Effect of intermittent mixing on phytoplankton succession and the growth of bluegreen algae. - J. Plankton Res. 6: 699-713.
- UTERMÖHL, H. (1958): Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. -Mitt. int. Verein. theor. angew. Limnolog. 9: 1-38.
- VAN DAM, H., MERTENS, A. & SINKELDAM, J. (1994): A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. - Neth. J. Aquatic Ecol. 28: 117-133.
- VAN LIERE, L. & MUR, L. R. (1980): Occurrence of *Oscillatoria agardhii* and some related species, a survey. Develop. Hydrobiol. **2**: 67-77.
- WUNDSCH, H. (1940): Beiträge zur Fischereibiologie märkischer Seen. VI. Die Entwicklung eines besonderen Seentypus (H2S-Oscillatorienseen) im Fluß-Seengebiet der Spree und Havel und seine Bedeutung für die fischereibiologischen Bedingungen in dieser Region. -Z. Fischerei 38: 444-658.
- ZEVENBOOM, W. & MUR, L. R. (1980): N2-fixing cyanobacteria: Why they do not become dominant in Dutch, hypertrophic lakes. Develop. Hydrobiol. 2: 123-130.
- ZEVENBOOM, W. DE VAATE, A. B.& MUR, L. R. (1982): Assessment of factors limiting growth rate of *Oscillatoria agardhii* in hypertrophic lake Wolderwijd, 1978, by use of physiological indicators. Limnol. Oceanogr. **27**: 39-52.

# Alternative blooming of *Aphanizomenon flos-aquae* or *Planktothrix agardhii* induced by the timing of the critical nitrogen: phosphorus ratio in hypertrophic riverine lakes

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with 8 figures and 2 tables

Abstract: Großer Müggelsee and Langer See are limnologically similar but during an investigation from 1990 until 1993 marked differences were observed in the species that dominated during the summer blooms. Two distinct planktonic communities could be recognised, one dominated by "Planktothrix agardhii" and the other by "Aphanizomenon flos-aquae/Microcystis spp.". A sensitive moment for the differentiation of the plankton development to the one or the other cyanobacterial summer bloom was the time, when the total nitrogen to total phosphorus ratio (TN: TP ratio) dropped to a critical value of 16:1. In addition, the phytoplankton composition at the time when this ratio is reached is of decisive importance. Rapid growth of the N2-fixing A. flos-aquae was favoured at TN: TP < 16:1 in both lakes, when the timing of the critical TN : TP ratio and low biomass of P. agardhii coincided (clear water phase). Throughout all the investigated years in Großer Müggelsee, the rapid growth of the heterocyst-forming cyanobacteria A. flos-aquae started at the time when TN: TP = 16: 1, even if this critical ratio was delayed by several weeks. However, if P. agardhii biovolume exceeded 6 mm<sup>3</sup> l<sup>-1</sup> at the time when the critical TN: TP ratio was reached, then the mass development of this cyanobacteria continued during summer and into autumn, whereas A. flos-aquae were only present in traces. Therefore, A. flos-aquae reached high biovolumes only when TN: TP < 16:1, while the growth of P. agardhii seemed to be independent of seasonal variation of the TN : TP ratio. Differences between "P. agardhii" and "A. flos-aquae/Microcystis spp." dominated years were not restricted to cyanobacterial species, but were also seen in the diatom assemblages. A comparison, based on biovolumes of 15 dominant cyanobacteria and diatoms, showed that seasonal changes in phytoplankton in "P. agardhii"-years were more gradual than the drastic shifts obersved in "A. flos-aquae/Microcystis spp."-years.

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## Introduction

Großer Müggelsee and Langer See belong to the same lowland river system of the River Spree and R. Dahme (Berlin). The two riverine lakes are similar in most of their limnological characteristics. Both are hypertrophic and have a similar range of phytoplankton species. However, the species that dominate in any given year can be quite different in the two lakes. In particular, the summer plankton can be dominated by either Aphanizomenon flos-aquae (Nostocales), which forms bundle-like colonies and also develops heterocysts for diazotrophic life, or alternatively by Planktothrix agardhii (Oscillatoriales), which occurs as single trichomes. Physiological and limnological aspects of the dominant phytoplankton communities have been discussed already (WUNDSCH 1940, TÄUSCHER 1981, VAN LIERE & MUR 1980, ZEVENBOOM & MUR 1980, ZEVENBOOM et al. 1982, HRBACEK 1984, KOHL et al. 1985, 1991, NIXDORF & HOEG 1993, TIPPMANN 1993). However, the timing and duration of nitrogen fixation by A. flos-aquae and its importance to the nitrogen budget in Müggelsee (DUDEL & KOHL 1991, 1992) needs further studies. So, the aim of this study was to investigate what factors determine the succession and subsequent dominance of important bloom-forming cyanobacterial species, in particular the influence of the nitrogen: phosphorus ratio, by comparing seasonal changes in two similar lakes from the same river system.

#### Materials and methods

Großer Müggelsee and Langer See are lakes on the periphery of the city of Berlin. Basic limnological data characterising the two investigated lakes are summarised in Table 1. The hypertrophic state of both lakes is indicated by the total phosphorus and chlorophyll-a concentration for the June-September period according to FORSBERG & RYDING (1980). Integrated samples of the upper 2 m of the water column were taken monthly from Großer Müggelsee in 1990–91 and from Langer See in 1990–92. A biweekly interval was followed for 1992–93 in Großer Müggelsee and 1993 in Langer See. These samples represent the whole water column or the mixed layer during temporary stratification.

Biovolume of phytoplankton was estimated according to the method of UTERMÖHL (1958). However, the mean value of the normal or the log-normal distribution was selected for abundance distribution (single cells, filaments or number of colonies), depending on which fitted better. In the case of water blooms of *Microcystis*, the biovolume was estimated from counted colonies (biovolume of *Microcystis* species) compared with counts of single cells (total biovolume of *Microcystis*, REYNOLDS & JAWORSKI 1978, HUMPHRIES & WIDJAJA 1979).

Diatoms were prepared in a special gentle way to keep both thecae of each frustule together (TEUBNER 1995). This preparation technique allowed the measurement of the cell dimension in girdle view in addition to the valve diameter for different species and cell size. The calculation of biovolume of unicellular centric diatoms was based on a combination of biovolume estimates from valve-diameter size-classes in samples fixed with Lugol's solution and counts for species from permanent slides. Dead diatom cells were separately counted in the Lugol fixed samples and their share later eliminated from calculations from permanent slides.

Table 1. Morphometric, average physical, chemical and biological data of the investigated
lakes (1990-93, *averaged June-September, morphological data for Großer Müggelsee from
DRIESCHER et al. 1993 and for Langer See from ANWAND 1973).

lake	Großer Müggelsee	Langer See	
maximum depth [m]	8	6.5	
mean depth [m]	4.9	3.5	
lake area [km <sup>2</sup> ]	7.3	1.53	
retention time [days]	67.2	4.13	
Secchi depth [m]	1.6	0.9	
conductivity $[mSm^{-1}, 20 \degree C]$	61	59	
total nitrogen $[\mu mol l^{-1}]$	89	106	
total phosphorus $[\mu mol 1^{-1}]$	6.2 (9.2*)	6.7 (8.7*)	
soluble reactive silicon $[\mu mol 1^{-1}]$	102	119	
chlorophyll-a $[\mu mol l^{-1}]$	52*	67*	
total phytoplankton biovolume $[mm^3 l^{-1}]$	9.86	12.52	
biovolume of cyanobacteria [%]	54	66	
biovolume of diatoms [%]	36	27	

Taxonomic identification was carried out with a light microscope, using differential interference contrast, positive phase-contrast and epifluorescence techniques. In addition, scanning electron microscopy was used for diatoms. Besides standard determination keys, the following references were used for identification KOMÁREK & ETTL (1958), ANAGNOSTIDIS & KOMÁ-REK (1985, 1988), KOMÁREK & ANAGNOSTIDIS (1986, 1989), KOMÁREK (1991), KRAMMER & LANGE-BERTALOT (1991). Diatom species of the lakes are listed in TEUBNER (1997), cyanobacteria in TEUBNER (1996).

Cyanobacterial and diatom species were selected for multivariate statistical analyses, because these two algal groups were dominant (Table 1). Species that never exceeded 5% of total biovolume during the investigated period were excluded from principal component analysis (PCA). Step-wise species extraction was repeated with PCA until the first two components represented 50% of total variance (15 species in Fig. 4). Total variance increased to 70% when species were further reduced to ten. Those species extracted by PCA were included in the hierarchical cluster analysis (HCA) but based on annual averaged data (10 species in Fig. 5).

Logarithmic data were standardized for multivariate statistical analyses using the computer program STATGRAPHICS plus 2.0 (STSC, inc. USA). PCA was based on a set of single data points (Fig. 4: 105 cases), HCA on annual average data (Fig. 5: 8 cases).

Total nitrogen and total posphorus were determined with slight modification according to LANGNER & HENDRIX (1982).

The zooplankton community was studied in the last two years of investigation in both lakes (1992–93). Zooplankton samples were taken with a Friedinger sampler, collected in a large vessel and sieved through 50 µm plankton net. Zooplankton taxa were determined and enumerated in these enriched sample volumes. The biovolume of the cladocerans and copepods was ascertained from a volume-length-relation according to BALUSHKINA & VINBERG (1979).



Fig. 1. Seasonal changes in concentrations of total nitrogen (TN), total phosphorus (TP), biovolume of cyanobacteria and diatom species in Großer Müggelsee 1990–1993 a: both axis for TN and TP are scaled in the proportion of 16:1, so that the points where the lines in the graph intersect show the molar TN: TP-ratio of 16:1 (marked by arrows). b: cyanobacterial biovolume of *Limnothrix redekei* (Limred), *Planktothrix agardhii* (Plaaga), *Aphanizomenon* gracile (Aphgra), A. flos-aquae (Aphflo) and Microcystis spp. (Micspp). c: diatom biovolume of Aulacoseira spp. (Aulspp), species grouped according to Fig. 5 comprising Stephanodiscus hantzschii (Stehan), Cyclostephanos dubius (Cstdub) and Actinocyclus normanii (Actnor), as well as Stephanodiscus neoastraea (Steneo) and the total biovolume of unicellular centric diatoms. The black and white bar at the bottom indicates the seasons: March-May (spring), June-August (summer), September-November (autumn), December-February (winter).

The arrangement for in situ grazing measurements followed the method of HANEY (1971), but in this study filamentous blue-greens from laboratory cultures were supplied as <sup>14</sup>C-labelled tracer algae. The grazing chamber was incubated in the lake for 10 min. and then the

zooplankton was separated. The radioactivity in the total zooplankton, and in  $4 \times 1$  ml from lake chamber water was determined by liquid scintillation measurement. The loss rate by grazing (grazing rate) was calculated from this data.

Specific net growth rates between sampling dates were calculated from phytoplankton biomass of lake and inflowing water and dilution rate by a mass balance equation. The vertical extinction of photosynthetically available radiation was measured by two spherical quantum sensors connected to a data logger (LI-193SA, LI-COR, Lincoln, Nebraska, USA).

Values of total incoming radiation (TIR) were kindly supplied by the Institute of Freshwater Ecology and Inland Fisheries Berlin. The effective light climate (RAMBERG 1979) within the mixed layer and over the periods between sampling dates were calculated on the basis of TIR, the extinction coefficient and the mixing depth of the lakes according to RILEY (1957).

#### Results

The phytoplankton of the hypertrophic lakes Großer Müggelsee and Langer See were dominated by cyanobacteria and diatom species which together made up 90-93% of the total biovolume (Table 1). The seasonal changes in nutrient concentrations and in biovolume of cyanobacteria and diatom species in Großer Müggelsee and Langer See from 1990 until 1993 are shown in Figs. 1 and 2. The structure of the winter/spring period of both lakes during all investigated years was similar (Fig. 4b). Diatoms dominated the phytoplankton during the spring peak. Species characteristic for the winter/spring period, such as Nitzschia acicularis W. SMITH, Fragilaria ulna (KÜTZ.) LANGE-BERTALOT, Stephanodiscus neoastraea HAKANS-SON et HICKEL and S. hantzschii GRUNOW are shown in Fig. 4a for both lakes. Figs. 1c and 2c show that the spring biovolume of unicellular centric diatoms in Großer Müggelsee and Langer See was mainly composed of Stephanodiscus neoastraea and the species group Stephanodiscus hantzschii, Cyclostephanos dubius (FRICKE) ROUND and Actinocyclus normanii (GREG. ex GREV.) HUSTEDT (the three species were combined because of their close correlation in annual average, Fig. 5a). Limnothrix redekei (VAN GOOR) MEFFERT is the most important cyanobacterial species in Großer Müggelsee and Langer See during winter/spring (Fig. 4a) often reaching 2-3 mm<sup>3</sup>l<sup>-1</sup>, because their biovolume peaks were restricted to early spring periods in the investigated years (Figs. 1b, 2b, 4b). However, at the time of the spring peak of Limnothrix redekei, also higher biovolumes of P. agardhii (GOM.) ANAGN. et KOM. developed contributing on average 6% to cyanobacterial biovolume in Großer Müggelsee and 20% in Langer See.

The molar ratio of total phosphorus to total nitrogen (TN: TP ratio) was always higher than 16:1 during spring development in both lakes, but was continually decreasing. Except for Großer Müggelsee in 1993, the TN: TP ratios always dropped to 16:1 at the end of May or early June in both lakes (dates are indicated by arrows in Figs. 1a and 2a). The change in phosphorus and nitrogen availability in shallow lakes is best reflected by their total values, since the loss (denitrification) and gain



Fig. 2. Same as Figs. 1 a-c, but for Langer See.

processes (phosphate remobilization from sediment) are not always observed in the dissolved inorganic pools due to the efficient uptake systems of the phytoplankton under nutrient limitation.

Despite the similar structure of the phytoplankton community during early spring and the closeness in the timing of the switch from a period of prevailing P- to one of prevailing N-limitation (at the turning-point of TN: TP>16 to <16), a totally different summer plankton developed. Großer Müggelsee and Langer See differed significantly in their summer/autumn plankton, as shown in Fig. 4b. Accordingly, the annual average phytoplankton biovolumes were also different. The similarity among the phytoplankton composition based on annual averages of all 4 years of both lakes is shown in the dendrogram of Fig. 5b.



Fig. 3. (a) Temperature of surface water (0.5 m depth); (b) total biovolume and percent of hyaline terminal cells and heterocysts of *A. flos-aquae* in Großer Müggelsee 1990–1993.

The annual average phytoplankton structure was similar in Großer Müggelsee during the period 1990–92 (Fig. 5b). In these first three years of observation the total biovolume of phytoplankton has regularly dropped from a spring maximum of around  $11 \text{ mm}^3 \text{ I}^{-1}$  to under  $2 \text{ mm}^3 \text{ I}^{-1}$  (clear water phase) at the time when the TN: TP approached 16:1 (Fig. 1). Immediately after TN:TP ratios fell short of 16:1, rapid growth of *A. flos-aquae* RALFS ex BORN et FLAH. was initiated (arrows in Fig. 1b). The biovolumes of heterocysts and hyaline terminal cells as percentages of the total biovolume of nostocal cyanobacteria are given in Fig. 3. Heterocysts never contributed more than 1.5% in the first three years. The share of hyaline terminal cells was much higher attaining 12–15% in the summers of 1991–92 when water temperatures were above 23 °C.

The summer blooms of *A. flos-aquae* were accompanied by mass development of chroococcal cyanobacterial species [*Microcystis aeruginosa* (KÜTZ.) KÜTZ., *M. flos-aquae* (KÜTZ.), *M. ichtyoblabe* ÜTZ., *M. novacekii* (KOM.) COMP., *M. viridis* (A. BRAUN) LEMM., *M. wesenbergii* (KOM.) KOM.] and filamentous diatoms [*Aulaco-seira ambigua* (GRUNOW) SIMONSEN, *A. granulata* (EHRENB.) SIMONSEN, *A. italica* (EHRENB.) SIMONSEN, Figs. 1, 4a].

A different phytoplankton structure was observed in Großer Müggelsee in 1993. In contrast to the previous summer periods, the surface water temperature did not



Fig. 4. Plot of the second versus the first principal component for the seasonal phytoplankton composition in the lakes Großer Müggelsee and Langer See. For clarity, the results of this principal component analyses are shown in two displays: a plot of the variables (a) and the corresponding plot of the distribution pattern of sample points (b); percent of total variance for the first two components:  $33\% \pm 17\%$ . a: Correlation between biovolume of 15 dominant phytoplankton taxa; cyanobacteria: Aphgra-Aphanizomenon gracile, Aphflo-A. flos-aquae, Limred-Limnothrix redekei, Micaer-Microcystis aeruginosa/flos-aquae, Micvir-M. viridis, Plaaga-Planktothrix agardhii; diatoms: Actnor-Actinocyclus normanii, Aulspp-Aulacoseira spp., Cycrad-Cyclotella radiosa, Cstdub-Cyclostephanos dubius, Frauln-Fragilaria ulna, Nitaci-Nitzschia acicularis, Stehan-Stephanodiscus hantzschii, Stemin-S. minutulus/parvus, Steneo-S. neoastraea. b: Every symbol represents the species composition of phytoplankton in winter/spring or in summer/autumn in the two lakes (Großer Müggelsee (M): n = 46, Langer See (L): n = 59). Seasons labelled according to the value of the TN : TP ratio: for winter and spring TN: TP  $\leq$  16, for summer and autumn TN: TP  $\leq$  16 (compare to Figs. 1 and 2). The combination of single seasons is appropriate because of similar phytoplankton structure of winter/spring on the one and summer/autumn on the other side (TEUBNER 1996). Points are encircled to emphasise, that seasonal phytoplankton changes in "Planktothrix agardhii"-years were more gradual than the drastic shift observed in "Aphanizomenon flosaquae/Microcystis spp."-years. Because of the special phytoplankton situation in Langer See in summer/autumn 1993, sample points are differently labeled from the other points of the same season of this lake.

exceed 20 °C (Fig. 3a). The TN: TP ratio did not drop to 16:1 until 2<sup>nd</sup> August 1993 (arrow in Fig. 1a). This was a delay of 6 to 7 weeks when compared to the previous years. The development of *A. flos-aquae* was accordingly delayed and did not start until 2<sup>nd</sup> August 1993 (Fig. 1b). In contrast to previous years, heterocysts developed a biovolume of about 5% during July, whereas the peak development of hyaline terminal cells coincided with the highest biovolumes, as previously observed, even if



Fig. 5. Dendrograms of hierarchical cluster analyses of biovolume of phytoplankton taxa (a) and phytoplankton composition in Langer See (L) and Großer Müggelsee (M) in the years 1990–1993 (b). a: cluster C<sub>a</sub> represents the structure of phytoplankton dominance of typical "Aphanizomenon flos-aquae/Microcystis spp." years, cluster C<sub>b</sub> that of "Planktothrix agardhii"-dominated plankton. b: Langer See 1990, 1992, 1993 were "P. agardhii" years, while Großer Müggelsee 1990–92 were typical "A. flos-aquae/Microcystis spp." years. Langer See 1991 and Großer Müggelsee (1993) were characterised as atypical "A. flos-aquae/Microcystis spp." years. The two dendrograms are based on the same data matrix of annual averages; method: squared euclidean distance, ward linkage. Abbreviations of species as in Fig. 4.

their relative amount in this cold and rainy summer period was much lower than of that of the hot summers two years before (Fig. 3, 1a, b). Also contrasting with previous years was the fact that the delayed summer development of *A. flos-aquae* was not accompanied by significant biovolumes of *Microcystis* spp. However, the period of growth of *Aulacoseira* spp. was unaffected and started in early June, as in the previous years (Figs. 1b, c).

The summer plankton in Langer See was totally different from that of Großer Müggelsee, except for 1991 (Figs. 4b, 5b). In contrast to Großer Müggelsee, *P. agardhii* was already dominant when the TN: TP ratio approached 16:1 (Fig. 2b). At this time the biovolume of *P. agardhii* had reached more than  $6 \text{ mm}^3 \text{ I}^{-1}$ , by 1992 it was more than  $20 \text{ mm}^3 \text{ I}^{-1}$ . A clear water phase was not observed. In these three years mass development of *P. agardhii* continued during summer and into autumn. Different from Großer Müggelsee, the summer blooms of this cyanobacteria were not accompanied by massive growth of other forms such as *Microcystis* and *Aulaco*-



Fig. 6. Relationship between molar TN: TP-ratio and biovolume of *Aphanizomenon flos-aquaz (Aphflo)* and *Planktothrix agardhii* (Plaaga) respectively.

*seira* (Figs. 2b, c, 4a). consequently the change in composition of phytoplankton from winter/spring to summer/autumn in Langer See was more gradual than the drastic shift observed in Großer Müggelsee (Fig. 4b).

The summer plankton of 1991 in Langer See was quite different from the other three years investigated (Figs. 4b, 5b). Similar to the situation in Großer Müggelsee, the spring biomass of total phytoplankton was very low ( $<0.2 \text{ mm}^3 \text{ l}^{-1}$ ) at the time when TN: TP was 16:1 (Fig. 2). The low biomass of *P. agardhii* was further diminished during the clear water phase and, thereafter, *A. flos-aquae* and accompanied species (*Microcystis* spp. and *Aulacoseira* spp.) increased in abundance.

Consequently, whether "A. flos-aquae/Microcystis spp." or "P. agardhii" dominated summer plankton development was dependent on the qualitative and quantitative situation of the phytoplankton at the moment when the critical TN: TP ratio was approached. Low total biomass at the time of critical TN: TP ratio promoted the initialisation of rapid growth of A. flos-aquae. Higher biovolumes of more than  $6 \text{ mm}^3 \text{l}^{-1}$  of P. agardhii at TN: TP = 16:1 assisted in the establishment of that species. This implies that P. agardhii had already reached higher biovolumes at TN : TP ratios higher than 16 at the time when A. flos-aquae still remained below 1 mm<sup>3</sup> l<sup>-1</sup> (Fig. 6).

The population dynamics of zooplankton groups and algal classes for Langer See and Großer Müggelsee in 1992 and 1993 are shown in Fig. 7. Although *P. agardhii* was steadily rising in abundance in Langer See during spring 1993, this does not imply that this alga was not grazed by zooplankton. The grazing loss rates amount to 0.17 ( $\pm$ 0.16 SD)d<sup>-1</sup> for 16 measurements with radioactive labelled *P. agardhii* in the Langer See from May to July 1993. However, the high abundance of daphnids



**Fig. 7.** Dynamic of phyto- and zooplankton in Großer Müggelsee and Langer See in 1992–93 (zooplankton: Rotifers – *Asplanchna priodonta* was excluded).

could not control the large biomass of *P. agardhii* (Fig. 7). In Großer Müggelsee we have estimated a grazing loss rate as high as 0.3 ( $\pm$ 0.15 SD) d<sup>-1</sup> for 3 experiments in May 1993. Consequently, *P. agardhii* can be controlled by zooplankton at low abundance.

The impact of zooplankton on A. flos-aquae can be estimated by comparing the specific net growth rate of this species (result of lake-internal growth and losses, Table 2) and that of *P. agardhii* at the time before the clear water phase. Obviously, A. flos-aquae shows higher net growth rates indicating lower grazing losses at comparable low abundance of both species. Based on annual averages, Fig. 5a shows the preference of important species for the two alternative phytoplankton structures dominated by cyanobacteria. The dominance of "A. flos-aquae/Microcystis spp." (M. aeruginosa, M. viridis) were accompanied by Aulacoseira spp. and Stephanodiscus neoastraea, while higher biovolumes of P. agardhii were closely related to Aphanizomenon gracile, Stephanodiscus hantzschii, Cyclostephanos dubius and Actinocyclus normanii (compare Großer Müggelsee 1991-92 in Fig. 1, Langer See 1990, 1992-93 in Fig. 2). Accordingly, the seasonal dynamics of the centric diatoms in Großer Müggelsee indicate that Stephanodiscus neoastraea was dominant among the unicellular centric diatoms in the first three years with "typical" "A. flosaquae/Microcystis spp."-plankton, while the S. hantzschii-group was of greater importance during "atypical" plankton development in 1993 (Figs. 1b, c). The changes



**Fig. 8.** Secchi depth and effective light climate in Großer Müggelsee and Langer See. a: Relationship between concentrations of chlorophyll-a and Secchi depths in 1991–93. The broken line indicates 1.25 m Secchi depth. Points for the "*P. agardhii*"-years (1990, 1992 and 1993) were differently labeled from that of the "*A. flos-aquae*"-year (1991) in Langer See. b: Effective light climate in 1992–93.

to the mass development of *Aulacoseira* spp. in years dominated by *A. flos-aquae* has already been mentioned above (Langer See 1991).

The relationship between the chlorophyll-a concentrations and Secchi depths in both lakes is shown in Fig. 8a. Secchi depth was not related to chlorophyll-a concentration in Langer See. In years dominated by "P. agardhii", Secchi depths did not exceed 1.25 m at 95% of the cases. Secchi depths was similar in Langer See during "P. agardhii"-years and the year of low biomass development of A. flos-aquae. Although data for 1991 fall within the range of the other years, transparency must have been slightly better during the A. flos-aquae year, because Secchi depths was never smaller than 65 cm (range: 65-125 cm), while it became as low as 40 cm during the P. agardhii years (40-190 cm). In contrast the range of variation of Secchi depth in Großer Müggelsee was much greater (0.5-5 m) and closer related to chlorophyll-a, which is due to the high population density of "A. flos-aquae/Microcystis spp." plankton. Nevertheless, the effective light climate was nearly the same during the summer-autumn periods of high phytoplankton biomass in both lakes (Fig. 8b), since the mean depth of Langer See is lower (Table 1). Light availability inferred from Secchi depth will be underestimated in "P. agardhii"-plankton in Langer See because pronounced light scattering by this alga leads to earlier vanishing of the Secchi disk when compared to lakes dominated by colonial forms such as A. flosaquae and Microcystis spp. (e.g. EDMONDSON 1980).

#### Discussion

The importance of N:P ratios in phytoplankton has been investigated by several authors. The application of Redfield's ratio to freshwater systems has been discussed by RHEE & GOTHAM (1980) and HECKY et al. (1993). Variations of the N:P ratio in freshwaters have been related to the trophic level and catchment area of lakes (DOWNING & MCCAULY 1992), as well as to different phytoplankton assemblages (BEHRENDT 1990). The relative nutrient availability (TILMAN 1982) is of special importance for the seasonal development of blue green algae. It is well established, that low N:P ratios favour the dominance of cyanobacteria during summer (i.e. STEINBERG & HARTMANN 1988, THOMPSON & RHEE 1994), especially the nitrogen fixing species during the period of prevailing nitrogen limitation (i.e. TRIMBEE & HARRIS 1984, SOMMER et al. 1986).

Other studies reported the simultaneous presence of heterocystous and non-heterocystous cyanobacteria in eu- and hypertrophic lakes, with only one of the two dominant and the other negligible (i.e. ZEVENBOOM et al. 1982, summarised in SCHREURS 1992). Moreover, summer blooms of the oscillatorial species P. agardhii and the nostocal A. flos-aquae alternate in dominance in a single lake in different years or in limnological similar lakes of one river system, such as Großer Müggelsee and Langer See. Research into why one or the other filamentous cyanobacterial species dominates summer blooms has been carried out by VAN LIERE & MUR (1980) and ZEVENBOOM & MUR (1980). Their chemostat experiments showed that A. flos-aquae and P. agardhii had the same maintenance requirement but the later was more competitive under low light availability. Strains of both species isolated from the Großer Müggelsee showed a maximum growth rate of  $0.6 d^{-1}$  and a halfsaturation constant of light limited growth of 0.4 (A. flos-aquae) or 0.3 MJ m<sup>-2</sup> d<sup>-1</sup> (P. agardhii) at a 12/12 hours photoperiod, 20°C, and nutrition with ammonium nitrate (SCHLANGSTEDT 1985, NICKLISCH & KOHL 1989, KOHL et al. 1989). The effective light climate was 0.8 MJ m<sup>-2</sup> d<sup>-1</sup> in the Langer See in 1992 and 0.5 MJ m<sup>-2</sup> d<sup>-1</sup> in 1993 at the time when the TN: TP ratio reached 16 (Figs. 2 and 8b). A. flos-

period	net growth rate (d <sup>-1</sup> ) Aphanizomenon flos-aquae	net growth rate (d <sup>-1</sup> ) Planktothrix agardhii	
16.329.3.	0.126	-0.116	-
30.312.4.	0.233	-0.018	
13.426.4.	-0.002	-0.008	
27.410.5.	0.171	0.035	
11.5.–24.5.	-0.286	-0.497	

Table 2. Specific net growth rates of *Aphanizomenon flos-aquae* and *Planktothrix agardhii* in the Großer Müggelsee in spring 1992.

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aquae could grow at a rate greater than  $0.3 d^{-1}$  under the light availability in a well mixed water column. However, the wind-induced mixing is sometimes very low in summer and *A. flos-aquae* is able to move to their optimal light condition faster than *P. agardhii* because of the higher sedimentation and flotation velocities of the bundles (REYNOLDS 1989). The small difference in light-limited growth between the two species, therefore, can be further diminished. The grazing losses of the bundles of *A. flos-aqua* are also lower than that of the trichomes of *P. agardhii*. Therefore, both species should increase their population density under moderate light limitation and grazing pressure.

Of course, A. flos-aquae is the outstanding competitor under absolute nitrogen deficiency but P. agardhii also competes well under N-limitation (ZEVENBOOM & MUR 1980, NICKLISCH et al. 1991) and can survive long periods of N-deficiency (NICKLISCH 1994). However, both species are weak competitors under P-limitation (SOMMER 1985, NICKLISCH et al. 1991, NICKLISCH 1994). The hypertropic river lakes like Großer Müggelsee show a moderate phosphate limitation of phytoplankton around the spring peak of diatoms (TIPPMANN 1993). The enhanced availability of phosphate later in the year is seldom indicated by higher soluble reactive phosphate (SRP) concentrations since the recycled phosphate is rapidly consumed. However, the increase in total phosphorus is a good indicator of improved phosphate availability. This increase is obvious if the populations of P. agardhii or A. flosaquae start to bloom (Figs. 1 and 2). Total phosphorus is generally higher in Langer See, the diatoms become limited by silicate and, consequently, there remains enough phosphate for P. agardhii to start its mass development earlier in the year in Langer See compared with Müggelsee. This species achieves relatively high biomass levels that are not controlled by grazing, even in periods of high abundance of daphnids. Later on, SRP concentrations increase and return to non limiting levels. However, A. flos-aquae cannot invade the P. agardhii blooms. The cause remains uncertain and should be studied experimentally.

In the Müggelsee, *P. agardhii* at low spring densities does not survive the strong grazing pressures by daphnids during the clear water phase. So, the available phosphate was thereafter used by *A. flos-aquae* that survived the clear water phase and which reached high abundance in 1990-92. In 1993 the weather was colder, the denitrification and the phosphate remobilisation were lower. All these factors were reflected in a later decrease of the N:P ratio to 16:1 and a later increase of the abundance of *A. flos-aquae*, which is obviously favoured by the increase in total phosphorus (phosphate remobilisation) (Fig. 1).

PICK & LEAN (1987) found the N: P ratio to be a poor indicator for N or P limitations or of growth rates of cyanobacterial plankton, at least for *P. agardhii* (PERS-SON 1981, ZEVENBOOM et al. 1982). However, the seasonal changes in TN: TP and in phytoplankton composition in our study have indicated, that it is not only the TN : TP ratio of 16 which is significant for the progress to *P. agardhii* or *A. flosaquae* dominance, but also the phytoplankton composition at the time when the

critical TN: TP ratio is reached. Rapid growth of the N2-fixing A. flos-aquae at TN :TP < 16:1 was favoured in both lakes, when the timing of the critical TN:TP ratio and low biomass of P. agardhii coincided. This timing opened the window for mass development of A. flos-aquae. Throughout all the investigated years, the rapid growth of this heterocyst forming cyanobacteria started at the time when TN: TP = 16:1 in Großer Müggelsee, even if this critical ratio was delayed over several weeks as in 1993 (Fig. 1). Accordingly, A. flos-aquae reached biovolumes greater than  $1 \text{ mm}^3 \text{l}^{-1}$  only when TN: TP<16:1, while the growth of *P. agardhii* seemed to be independent from seasonal variation of the TN: TP ratio (Fig. 6). Because of the more drastic shift in seasonal change from spring to summer, the phytoplankton development was disrupted in Großer Müggelsee (Fig. 4b). The short-term dominance during annual phytoplankton development of A. flos-aquae and its accompanying cyanobacterial species characterises these species as summer bloom forms (e.g. REYNOLDS 1984). Contrasting with this, the more gradual change in composition of phytoplankton from winter/spring to summer/autumn in Langer See was in agreement with the long term dominance of P. agardhii (compare SCHREURS 1992).

The formation of heterocysts was not restricted to biomass peaks of A. flos-aquae in Großer Müggelsee (Fig. 3b) as found by JONES (1979), BAKER (1981) and ANA-GNOSTIDIS et al. (1988). Nevertheless, it is known from Großer Müggelsee in 1982 and 1983 that only for some weeks during mass development do the nitrogen-fixing cyanobacteria make a significant contribution to the whole N-load of the lake (DUDEL & KOHL 1991, 1992). However, high frequency of heterocysts in populations of A. flos-aquae at times of good nitrogen availability in 1993 (up to 5%, Fig. 3b) were not found in a cultured strain of this species (SCHLANGSTEDT 1985, KOHL et al. 1985).

In contrast to the heterocysts, the development of hyaline terminal cells was more closely related to peaks of biovolume and periods of high temperature (Fig. 3). It seems that especially during hot summers the relative amount of hyaline cells (ANA-GNOSTIDIS et al. 1988) was very high, about 10 to 15%. Ultrastructural investigations have shown, that the colourlessness of these cells is caused by large vacuoles (CMIECH et al. 1988). The importance of the high share of hyaline cells during hot summer periods is still unresolved.

The different cyanobacterial assemblages, the so called "P. agardhii" or according to WUNDSCH (1940) "H<sub>2</sub>S-Oscillatoria-lakes" and "A. flos-aquae/Microcystis spp." years are well known in hypertrophic shallow riverine lakes (e.g. KOHL et al. 1991, NIXDORF & HOEG 1993). In agreement with earlier comparisons on phytoplankton assemblages it was shown, that in years with a dominance of P. agardhii relatively high biovolumes of Aphanizomenon gracile coexisted, while the mass development of A. flos-aquae were accompanied by higher biovolumes of Microcystis species, such as M. aeruginosa and M. viridis (TÄUSCHER 1981, KOHL et al. 1985, ANA-GNOSTIDIS et al. 1988). In the present study biovolumes of the diatoms accompanying these cyanobacterial blooms have been investigated in detail. According to

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the annual averaged biovolumes *Stephanodiscus hantzschii*, *Cyclostephanos dubius* and *Actinocyclus normanii* were more closely related to "*P. agardhii*"-dominance, while *Aulacoseira* spp. and *Stephanodiscus neoastraea* were of greater importance in "*A. flos-aquae/Microcystis* spp." plankton (Figs. 4, 5, see also TEUBNER 1996, TEUBNER et al. 1996). Correspondingly, changes in cyanobacterial dominance or deviation from the typical blue-green years were not restricted to changes in cyanobacteria, but also included diatom taxa (Figs. 1, 2, 4) common in hyper- and eutrophic lakes (VAN DAM et al. 1994). This is of interest considering that diatoms contribute about 30% of total biovolume in addition to the 60% share of cyanobacteria in such shallow, hypertrophic lakes (Table 1).

The different flushing rates of the two lakes cannot be the decisive factor for the regulation of the different dominance structures of phytoplankton because the change was observed in both lakes but different years (KOHL et al. 1985, NIXDORF & HOEG 1993, TIPPMAN 1993, RÜCKER & KOHL 1994, TEUBNER 1996). Nevertheless, the residence time in Langer See was considerably longer during summer (up to 14 days) than the annual average of 4 days.

To conclude, the influence of the critical TN:TP ratio in favouring the development of *A. flos-aquae* (in the case of clear water phase) or prolongation of the dominance of *P. agardhii* does not necessarily have to be direct. Physiological indicators such as certain pigments and polyphosphate granules of cyanobacteria have indicated that limitations of N and P are species specific and, therefore, phytoplankton assemblages as a whole are rarely limited by one of these elements (TIPPMANN 1993, RÜCKER & KOHL 1994). The importance of N:P ratios for cyanobacteria must be seen in connection to other environmental variables such as light (discussed above) or temperature as has been reported from some experiments (e.g. KONOPKA & BROCK 1978, TILMAN et al. 1986). Moreover, other environmental and physiological factors can be important for the development and dominance of cyanobacterial plankton at the spring to summer transition (FOY 1983, DOKULIL & MAYER 1996).

Nevertheless, in this case, the time when the critical TN: TP ratio is reached is a sensitive moment for the differentiation of the plankton development in the one or the other cyanobacterial dominance. Therefore the time when the relative nutrient availability changed from preferential P to preferential N limitation is convenient for prediction of one of these alternative cyanobacterial dominance structures in summer plankton in shallow, hypertrophic, turbid riverine lakes.

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#### References

- ANWAND, K. (1973): Gewässerverzeichnis der Seen- und Flußfischerei der Deutschen Demokratischen Republik. – 100 pp., Institut für Binnenfischerei Berlin-Friedrichshagen, Berlin.
- ANAGNOSTIDIS, K. ECONOMOU-AMILLI, A. & TAFAS, T. (1988): Aphanizomenon sp. from Lake Trichonis, Hellas (Greece) – A taxonomic consideration in relation to morphological and ecological parameters. – Arch. Hydrobiol. 80: 1–4 (50–53), 529–543.
- ANAGNOSTIDIS, K. & KOMÁREK J. (1985): Modern approach to the classification system of cyanophytes – 1. Introduction. – Arch. Hydrobiol. 71: 1–2(38, 39), 291–302.
- ANAGNOSTIDIS, K., ECONOMOU-AMILLI, A. & TAFAS, T. (1988): Aphanizomenon sp. from Lake Trichonis, Hellas (Greece) – A taxonomic consideration in relation to morphological and ecological parameters. – Arch. Hydrobiol. 80: 1–4 (50–53), 529–543.
- --(1988): Modern approach to the classification system of cyanophytes 3. Oscillatoriales.
  Arch. Hydrobiol. 80: 1-4(50-53), 327-472.
- BALUSHKINA, E.W. & VINBERG, G.G. (1979): Dependence between length and body volume from planktonic cladocera. – In: VINBERG, G.G.: Laboratory and freshwater investigations about the biological fundamentals of the waters productivity (russ.) – 180 pp, AN SSSR, Zool. Inst. Leningrad.
- BAKER, K.K. (1981): Ecology and taxonomy of five natural populations of the genus *Aphanizomenon* Morren (Cyanophyceae). Arch Hydrobiol. **92**: 222–251.
- BEHRENDT, H. (1990): The chemical composition of phytoplankton and zooplankton in an eutrophic shallow lake. Arch. Hydrobiol. 118: 129–145.
- CMIECH, H.A. GORDON, F.L. & REYNOLDS, C.S. (1988): Morphological and ultrastructural variability of planktonic Cyanophyceae in relation to seasonal periodicity. IV. Aphanizomenon flos-aquae: vegetative cells, heterocysts, akinetes. - Br. Phycol. J. 23: 239-250.
- DRIESCHER, E., BEHRENDT, H., SCHELLENBERGER, G. & STELLMACHER, R. (1993): Lake Müggelsee and its environment – Natural conditions and anthropogenic impacts. – Int. Rev. ges. Hydrobiol. 78: 327–343.
- DOKULIL, M.T. & MAYER, J. (1996): Population dynamics and photosynthetic rates of a Cylindrospermopsis-Limnothrix association in a highly eutrophic urban lake, Alte Donau, Vienna, Austria. – Algological Studies 83: 179–195.
- DOWNING, J.A. & MCCAULEY, E. (1992): The nitrogen: phosphorus relationship in lakes. Limnol. Oceanogr. 37: 936-945.
- DUDEL, G. & KOHL, J.-G. (1991): Contribution of dinitrogen fixation and denitrification to the N-budget of a shallow lake. – Verh. Internat. Verein. Limnol. 24: 884–888.
- -- (1992): The nitrogen budget of a shallow lake (Großer Müggelsee, Berlin). Int. Rev. ges. Hydrobiol. 77: 43-72.
- EDMONDSON, W.T. (1980): Secchi disk and chlorophyll. Limnol. Oceanogr. 25: 278-379.

#### 342 K. Teubner et al.

- FORSBERG, C. & RYDING S.O. (1980): Eutrophication parameters and trophic state indices in 30 waste-receiving Swedish lakes. Arch. Hydrobiol. 69: 189–207.
- FOY, R.H. (1983): Interaction of temperature and light on the growth rates of two planktonic Oscillatoria species under a short photoperiod regime. – Br. Phycol. J. 18: 267–273.
- HANEY, J.F. (1971): An in situ method for measurement of zooplankton grazing rates. Limnol. Oceanogr. 16: 970–977.
- HECKY, R.E., CAMPBELL, P. & HENDZEL, L.L. (1993): The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. 38: 709–724.
- HRBACEK, J. (1984): Contribution to the ecology of water-bloom forming blue-green algae Aphanizomenon flos-aquae and Microcystis aeruginosa. – Limnol. Oceanogr. 29: 1137– 1140.
- HUMPHRIES, S.E. & WIDJAJA, F. (1979): A simple method for separating cells of *Microcystis* aeruginosa for counting. Br. Phycol. J. 14: 313–316.
- JONES R.I. (1979): Notes on the growth and sporulation of a natural population of *Aphanizomenon flos-aquae*. Hydrobiologia 61: 55-58.
- KOHL, J.-G., DUDEL, G., HENZE, R., NICKLISCH, A., TEUBNER, K. & TIPPMANN, P. (1991): Langzeittrends und multistabile Zustände im Phytoplankton eines polymiktischen Fluß-Sees (Großer Müggelsee, Berlin). – In: Erweiterte Zusammenfassungen der Jahrestagung 1991 (30.9.–6.10.) in Mondsee (Deutsche Gesellschaft für Limnologie, ed.): 564 pp.
- KOHL, J.-G., DUDEL, G., SCHLANGSTEDT, M. & KÜHL, H. (1985): Zur morphologischen und ökologischen Abgrenzung von Aphanizomenon flos-aquae RALFS ex BORN. et FLAH. und A. gracile (LEMM.) LEMM. – Arch. Protistenkd. 130: 119–131.
- KOHL, J.-G., SCHLANGSTEDT, M. & DUDEL, G. (1989): Stabilization of growth during combined nitrogen starvation of the planktic blue-green alga *Anabaena solitaria* by dinitrogen fixation. – Arch. Hydrobiol. Beih. Ergebn. Limnol. 33: 457–464.
- KONOPKA, A. & BROCK, T.D. (1978): Effect of temperature on blue-green algae (Cyanobacteria) in lake Mendota. Appl. Environ. Microbiol. 36: 582–576.
- KOMÁREK, J. (1991): A review of water-bloom forming *Microcystis* species, with regard to populations from Japan. Algological Studies 64: 115-127.
- KOMÁREK, J. & ANAGNOSTIDIS, K. (1986): Modern approach to the classification system of cyanophytes – 2. Chroococcales. – Arch. Hydrobiol. 73: 157–226.
- --(1989): Modern approach to the classification system of cyanophytes 4. Nostocales. Arch. Hydrobiol. 82: 247-345.
- KOMÁREK, J. & ETTL, H. (1958): Algologische Studien. 359 pp. Verlag der Tschechoslowak. Akademie der Wissensch., Prag.
- KRAMMER, K. & LANGE-BERTALOT, H. 81991): Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. 576 pp. In: ETTL, H., GERLOFF, J., HEYNIG, H. & MOLLENHAUER, D. (eds.): Süßwasserflora von Mitteleuropa, Vol. 2, Gustav Fischer Verlag, Stuttgart, New York.
- LANGNER, C.L. & HENDRIX, P.F. (1982): Evaluation of a persulphate digestion method for particulate nitrogen and phosphorus. – Water Res. 16: 1451–1454.
- NICKLISCH, A. (1994): Does mortality by nitrogen deficiency influence the succession of *Lim-nothrix redekei* and *Planktothrix agardhii?* Verh. Internat. Verein. Limnol. 25: 2214–2217.

- NICKLISCH, A. & KOHL, J.-G. (1989): The influence of light on the primary production of two planktic blue-green algae. Arch. Hydrobiol. Beih. Ergebn. Limnol. 33: 451–455.
- NICKLISCH, A., ROLOFF, B. & RATSCH, A. (1991): Competition experiments with two planktic blue-green algae (Oscillatoriaceae). – Verh. Internat. Verein. Limnol. 24: 889–892.
- NIXDORF, B. & HOEG, S. (1993): Phytoplankton community structure, succession and chlorophyll content in Lake Müggelsee from 1979 to 1990. – Int. Rev. ges. Hydrobiol. 78: 359– 377.
- PERSSON, P.-E. (1981): Growth of *Oscillatoria agardhii* in a hypertrophic brackish water bay. - Ann. Bot. Fennici 18: 1-12.
- PICK, F.R. & LEAN, D.R.S. (1987): The role of macronutrients (C, N, P) in controlling cyanobacterial dominance in temperate lakes. – N.Z.J. Mar. Freshwater Res. 27: 425–434.
- RAMBERG, L. (1979): Relation between phytoplankton and light climate in two Swedish forest lakes. – Int. Rev. ges. Hydrobiol. 64: 749–782.
- REYNOLDS, C.S. (1984): Phytoplankton periodicity: The interactions of form, function and environmental variability. Freshwater Biol. 14: 111–142.
- (1989): Physical determinants of phytoplankton succession. In: SOMMER, U. (ed.): Plankton Ecology, Succession in Plankton Communities. Springer, Berlin, New York. pp. 9-56.
- REYNOLDS, C.S. & JAWORSKI, G.H.M. (1978): Enumeration of natural *Microcystis* populations. - Br. Phycol. J. 13: 269–277.
- RHEE, G.-Y. & GOTHAM, I.J. (1980): Optimum N: P ratios and coexistence of planktonic algae. J. Phycol. 16: 486–489.
- RILEY, G.A. (1957): Phytoplankton of the north central Sargasso Sea, 1950–1952. Limnol. Oceanogr. 2: 252–270.
- RÜCKER, J. & KOHL, J.-G. (1994): Indication of growth-limiting factors of planktonic cyanobacteria by application of microscope-photometry. – Verh. Internat. Verein. Limnol. 25: 2218–2220.
- SCHLANGSTEDT, M. (1985): Einfluß von Licht- und Stickstoffdargebot auf das Wachstum der N2-fixierenden Cyanophyceen Anabaena solitaria KLEB. und Aphanizomenon flos-aquae RALFS ex BORN. et FLAH. – Ph. D. Thesis, Humboldt-Universität Berlin, 119 pp.
- SCHREURS, H. (1992): Cyanobacterial dominance Relations to eutrophication and lake morphology, Academisch Proefschrift, Universiteit van Amsterdam.
- SOMMER, U. (1985): Comparison between steady state and non-steady competition: Experiments with natural phytoplankton. – Limnol. Oceanogr. 30: 335–346.
- SOMMER, U., GLIWICZ, Z.M., LAMPERT, W. & DUNCAN, A. (1986): The PEG-model of seasonal succession of planktonic events in fresh waters. – Arch. Hydrobiol. 106: 433–471.
- STEINBERG, C.E.W. & HARTMANN, H.M. (1988): Planktonic bloom-forming cyanobacteria and the eutrophication of lakes and rivers. – Freshwater Biol. 20: 279–287.
- TÄUSCHER, L. (1981): Untersuchung zur Art- und Biozönosestruktur des Phytoplanktons des Großen Müggelsees (Berlin) unter Berücksichtigung produktions- und saprobiologischer Aspekte. – Ph. D. Thesis, Humboldt-Universität Berlin, 141 pp.
- TEUBNER, K. (1995): A light microscopical investigation and multivariate statistical analyses of heterovalvar cells of *Cyclotella*-species (Bacillariophyceae) from lakes of the Berlin-Brandenburg region. Diatom. Res. **10**: 191–205.
- (1996): Struktur und Dynamik des Phytoplanktons in Beziehung zur Hydrochemie und Hydrophysik der Gewässer: Eine multivariate statistische Analyse an ausgewählten Ge-

wässern der Region Berlin-Brandenburg. – Ph. D. Thesis, Humboldt-Universität Berlin, 232 pp.

3

- TEUBNER, K. (1997): Merkmalsvariabilität bei planktischen Diatomeen in Berlin-Brandenburger Gewässern. Nova Hedwigia 65: 233–250.
- TEUBNER, K., HAAKE, H., WOITKE, P. & KOHL, J.-G. (1996): Die Beziehung zwischen der Artenzusammensetzung und der Jahresdynamik des Phytoplanktons und der Hydrochemie in 11 Gewässern in Berlin-Brandenburg. – In: Erweiterte Zusammenfassung der Jahrestagung 1995 (24.9–29.9) in Berlin (Deutsche Gesellschaft für Limnologie, ed.): 707 pp.
- THOMPSON, P.-A. & RHEE, G.-Y. (1994): Phytoplankton responses to eutrophication. Arch. Hydrobiol. Beih. Ergebn. Limnol. 42: 126–166.
- TIPPMANN, P. 81993): Zur Bedeutung der Nährstofflimitation für die saisonalen Phytoplanktonsukzessionen in zwei eutrophen Flußsee. – Ph. D. Thesis, Humboldt-Universität Berlin, 107 pp.
- TILMAN, d. 81982): Resource competition and community structure. 296 pp. In: Monographs in Population Biology 17, (R.M. May, ed.), Princeton University Press, Princeton (New Yersey).
- TILMAN, D., KIESLING, R., STERNER, R., KILHAM, S.S. & JOHNSON, F.A. (1986): Green, bluegreen and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. – Arch. Hydrobiol. 106: 473–485.
- TRIMBEE, A.M. & HARRIS, G.P: (1984): Phytoplankton population dynamics of a small reservoir: Effect of intermittent mixing on phytoplankton succession and the growth of bluegreen algae. – J. Plankton Res. 6: 699–713.
- UTERMÖHL, H. (1958): Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt. Internat. Verein. Limnol. 9: 1–38.
- VAN DAM, H., MERTENS, A. & SINKELDAM, J. (1994): A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. – Neth. J. Aquatic Ecol. 28: 117– 133.
- VAN LIERE, L. & MUR, L.R. (1980): Occurrence of Oscillatoria agardhii and some related species, a survey. Develop. Hydrobiol. 2: 67–77.
- WUNDSCH, H. (1940): Beiträge zur Fischereibiologie märkischer Seen. VI. Die Entwicklung eines besonderen Seentypus (H<sub>2</sub>S-Oscillatorienseen) im Fluß-Seengebiet der Spree und Havel und seine Bedeutung für die fischereibiologischen Bedingungen in dieser Region. – Z. Fischerei **38**: 444–658.
- ZEVENBOOM, W. & MUR, L.R. (1980): N<sub>2</sub>-fixing cyanobacteria: Why they do not become dominant in Dutch, hypertrophic lakes. Develop. Hydrobiol. 2: 123–130.
- ZEVENBOOM, W., DE VAATE, A.B. & MUR, L.R. (1982): Assessment of factors limiting growth rate of Oscillatoria agardhii in hypertrophic lake Wolderwijd, 1978, by use of physiological indicators. – Limnol. Oceanogr. 27: 39–52.