

**Teubner, K. 2000. Synchronised changes of planktonic cyanobacterial and diatom assemblages in North German waters reduce seasonality to two principal periods. Arch. Hydrobiol., Spec. Issues Advanc. Limnol. 55: 565-580.**

*This copy is for private use only and allows to search for words in the document. It is aimed as a preview of the published article and might contain all the content of the print version as you are free to check by a download from the publisher. For reference use the citation above.*



## **Synchronised changes of planktonic cyanobacterial and diatom assemblages in North German waters reduce seasonality to two principal periods**

Katrin Teubner

**with 9 figures**

---

**Abstract:** The seasonal dynamics of cyanobacterial and diatom assemblages in 11 water bodies along a meso- to hypertrophic gradient were compared. The cyanobacterial and diatom communities are characterised according to representative species of each algal class, selected by data reduction following principal component analyses and discriminant analysis. The cyanobacterial and diatom assemblages of the four seasons show different similarities in their species composition. In this respect the assemblages of the four seasons can be distinguished as only two different periods: winter/spring and summer/autumn. Species show a preference of growth either in the period of winter/spring (*Limnothrix redekei*, *Nitzschia acicularis*, *Stephanodiscus neoastraea*) or of summer/autumn (*Aphanizomenon flos-aquae*, several species of *Microcystis* and *Anabaena*, *Planktothrix agardhii*, *Aulacoseira granulata/italica/ambigua*, *Actinocyclus normanii*). The significant compositional changes for both algal classes during the transition from spring to summer and from autumn to spring were discussed in relation to synchronised seasonal variations of TN:TP ratios.

---

### **Introduction**

Seasonality is one of the most studied topics in phytoplankton research (e. g. REYNOLDS 1984, SOMMER et al. 1986, POULÍČKOVÁ 1993, SEIP & REYNOLDS 1995) Multivariate statistical methods have been used on several occasions, e. g. principal component analysis by BARTELL et al. (1995) and canonical correspondence analysis by STEVENSON & WHITE (1995).

A central problem in the seasonality of phytoplankton is the timing of the compositional changes. The aim of this study is to compare these changes of species in assemblages of Cyanobacteria (Cyanoprokaryota, KOMÁREK & ANAGNOSTIDIS 1999) with changes in diatom species composition. The comparison of seasonality of these two algal assemblages is interesting because of different season mass-development as well as of different macronutrient requirements. This paper presents a multi-system study with a focus on dominant seasonal patterns in phytoplankton assemblages that are beyond the system level.

---

**Author's address:** Katrin Teubner, Institute of Limnology Austrian Academy of Sciences, A-5310 Mondsee, [katrin.teubner@oeaw.ac.at](mailto:katrin.teubner@oeaw.ac.at)

## Materials and methods

Samples were taken from 8 lakes in Berlin-Brandenburg in Germany. Langer See (LANS), Großer Müggelsee (MUES), Flakensee (FLAS), Kiessee (KIES) and Krumme Lake (KRUL) are lakes on the periphery of the city of Berlin. In addition the inlet waters of some flushed river lakes were sampled (inlet of Großer Müggelsee (MUEZ) and Flakensee (Woltersdorfer Schleuse, FLZW, Löcknitz FLZL). Parsteiner See (PARS), Rosinsee (ROSS) and Großer Plagesee (GPLA) are part of the biosphere reserve "Schorfheide-Chorin" in Brandenburg, in the north of Berlin (location in Fig. 1).

Integrated samples were taken monthly from the 11 waters from 1990-91. This sampling frequency was continued for Langer See, Kiessee, Rosinsee and Parsteiner See in 1992. A biweekly interval was followed in Großer Müggelsee and Flakensee including the inlet waters (MUEZ, FLZL, FLZW) in 1992-93. All samples represented the epilimnetic mixed layer. Maximum depth and lake area, mean total phosphorus, total nitrogen, soluble reactive silica, conductivity and secchi depth for the investigated lakes are tabulated in TEUBNER 1995 and 1997.

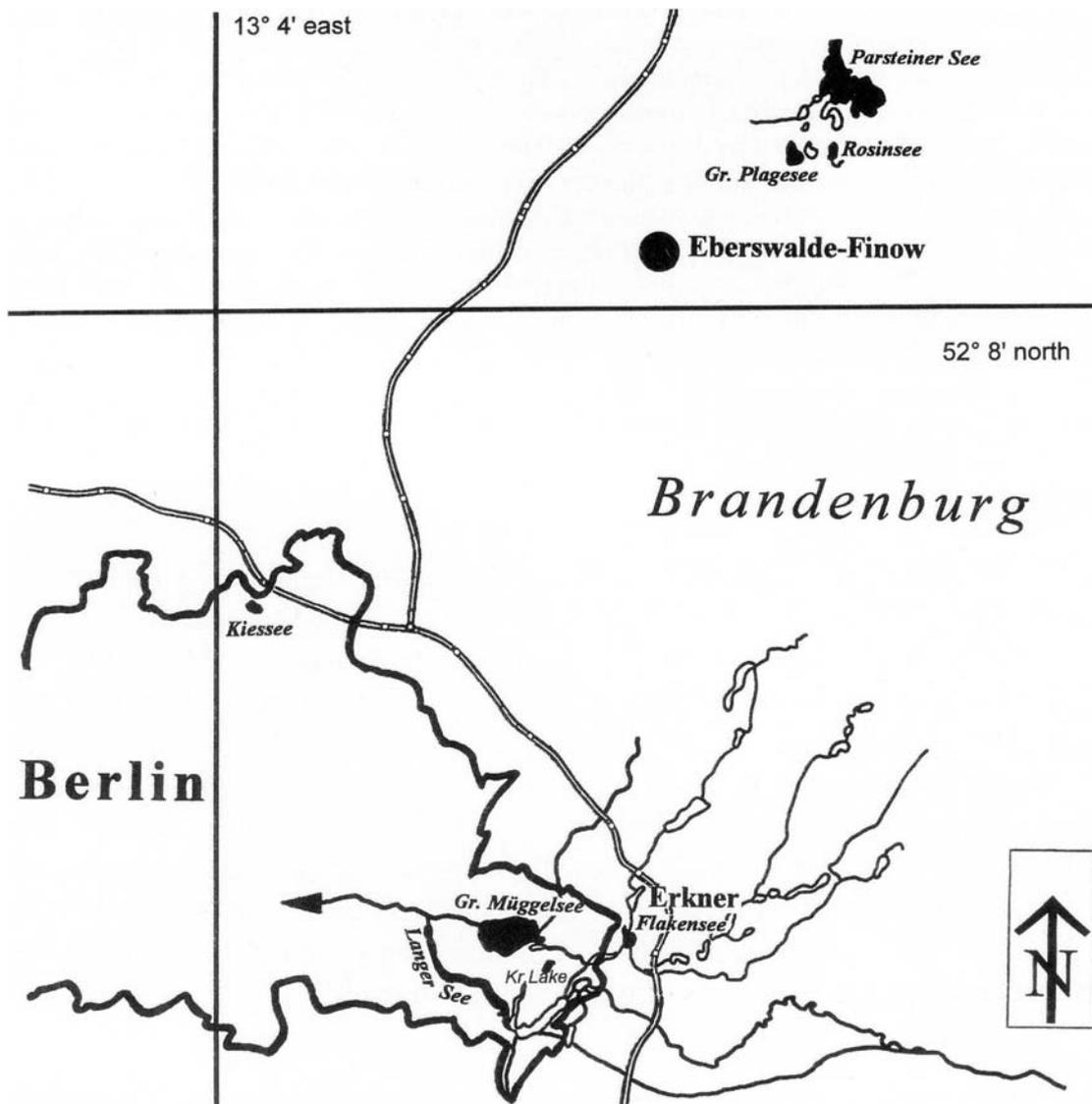


Fig. 1. Location of investigated waters in Berlin and Brandenburg.

Biovolume of phytoplankton was estimated according to the UTERMÖHL method (1958). 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. Diatoms were prepared in a special gentle way to keep both valves 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 sizes. For the biovolume estimation of unicellular centric diatom species the counts of each sample fixed with Lugol's solution were combined with counts from a permanent slide. For taxonomic details of diatoms in the 11 waters refer to TEUBNER 1997, for Cyanobacteria to TEUBNER 1996. Figs. 3-7 are based on seasonal averages: (spring: March-May, summer: June-August, autumn: September-November, winter: December-February).

Algal species never exceeding 5% of total biovolume during the investigated period were not included in principal component analysis (PCA). Stepwise species extraction was repeated in PCA until the first three components represented more than 60% of total variance. In this way the 17 cyanobacterial species were reduced to the 10 most representative species, similarly diatom species were reduced from 22 to 10 (extracted species are shown in Fig. 3, cases: n=129 seasonal averages).

During the stepwise reduction of species in PCA, their dominance in different waters as well as seasons was considered, because data were seasonal averages of the phytoplankton of the 11 waters. In order to show the seasonality, however, points were labelled only according to seasons (Fig. 3). These 10 extracted cyanobacterial and diatom species were the basis for discriminant analysis (DA), but further reductions were done in order to show those species which exhibited most seasonal difference in mass development (forward selection method). All multivariate analyses were based on the relative biovolume of the species, to take account of a dataset with widely varying total biovolumes of phytoplankton (Fig. 2b, cyanobacterial and diatom species were related to the total biovolume of their respective algal class).

Logarithmic data were standardised for multivariate statistical analyses (HENRION et al. 1988, HENRION & HENRION 1995) using the computer program Statgraphics plus 2.0 (STSC, inc. USA).

Triangular diagrams (Fig. 8) based on long term seasonal averages were created in Grapher for Windows 4.0, Golden Software, Inc. Each point indicates a seasonal TN:TP:SRSi ratio of a water and represents the sum of the concentrations equal to 100% (TN+TP+SRSi=100). The corners of the triangle represent the concentration of one element only (100%) and the absence of the remaining two nutrients. The line TN:TP=16:1 (bold line in Fig. 8) from a SRSi-corner to an intersection point on the TN:TP-axis indicate the constant TN:TP ratio of 16:1 at variable SRSi. In analogy, the dashed lines indicate a constant TN:TP ratio at variable SRSi concentrations for a single water. Because of the relatively small amount of TP in comparison to SRSi and TN, points for the original data set fall close to the SRSi:TN axis (see also the amount of sums of TN, TP and SRSi in text legend of Fig. 8). For clearer presentation of the points within the area the concentrations were normalised by the relation of the concentration

of an element to its sum over the entire data set ( $C_{\text{norm}} = \frac{100 C}{\sum_{i=1}^n C_i}$ ). As a result, points representing seasonal TN<sub>norm</sub>:TP<sub>norm</sub>:SRSi<sub>norm</sub> ratios become more scattered and are easier to distinguish, but TN:TP:SRSi ratios can not be read directly. It is, however, possible to recalculate these ratios. The intersection point of the bold line TN:TP=16:1 on the TN:TP axis is given by following calculation:

from  $SRSi=0$  and  $TN:TP=16:1$  is  $TN_{norm}+TP_{norm}+SRSi_{norm} = 0.4309+0.3758+0 = 1.1148 = 100\% = 39.38 + 60.62 + 0$  ( $TN_{norm} = \frac{100*16}{3644.62} = 0.4390$  and  $TP_{norm} = \frac{100*1}{147.98} = 0.3758$ , sums of TN and TP over the entire data set see legend of Fig. 8). The intersection point of the line indicating  $TN:TP=16:1$  on the TN-TP-axis is therefore 39.38:60.62 (TN scaling is from left to right and the TP scaling from right to left on the TN-TP-axis). For further complex calculations in normalised triangular diagrams refer to TEUBNER (1996).

## Results

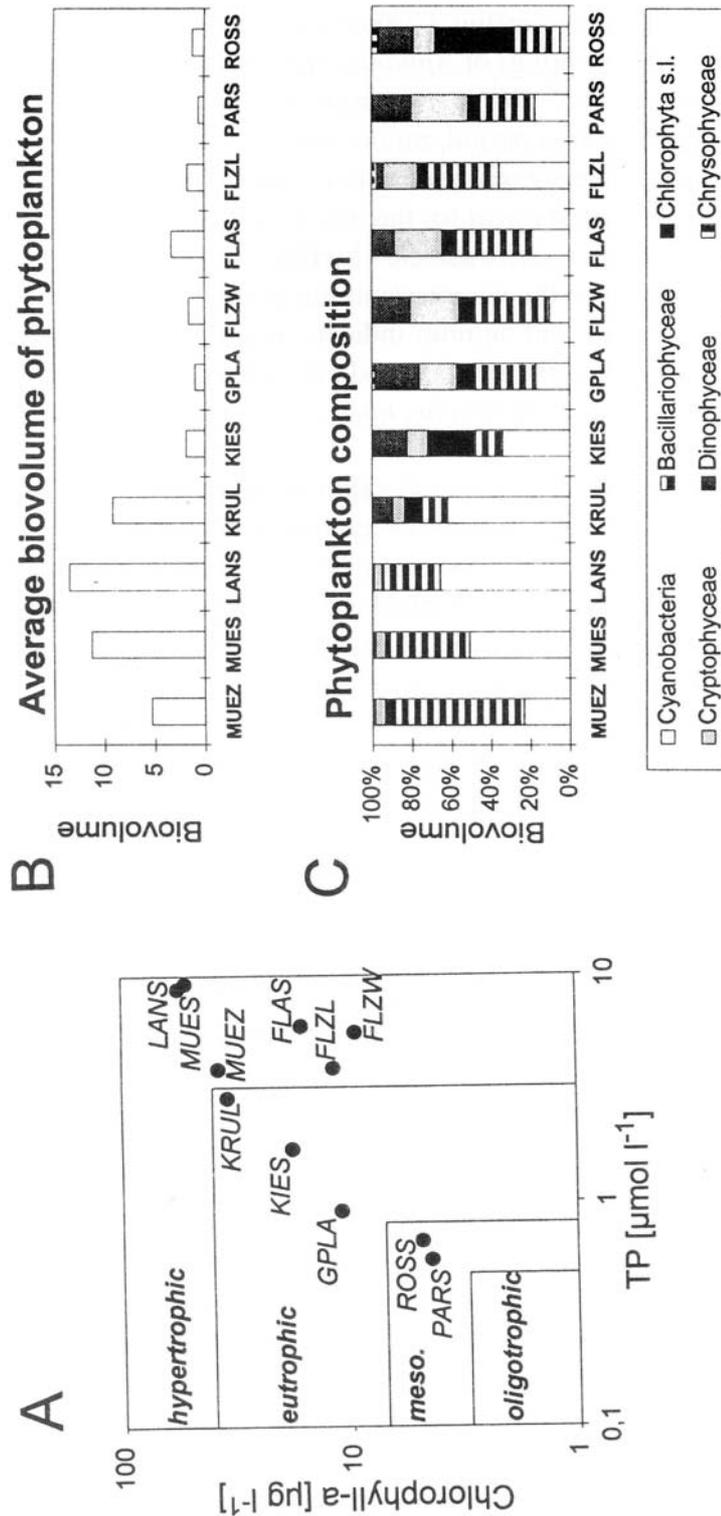
The trophic levels of the investigated waters ranged from meso- to hypertrophic, but the majority are hypertrophic (Fig. 2 a). Großer Müggelsee and Langer See are riverine lakes with high concentrations of chlorophyll- $\alpha$ . The hypertrophic, flushed Flakensee is characterised by higher conductivity in comparison to other soft waters (highest average conductivity of about 121 mS m<sup>-1</sup> in FLZW). The deepest lakes are the mesotrophic Parsteiner See and Rosinsee (the deepest lake is PARS with the maximum depth of 27 m). Krumme Lake and Großer Plagesee are eutrophied dystrophic lakes.

Except for one lake (ROSS) the diatoms and cyanobacteria contributed at least 50% to the long term averages of the total phytoplankton in the investigated waters (Fig. 2c). In the hypertrophic riverine lakes (LANS, MUES, MUEZ), however, the biovolume of these two algal classes reached levels of about 90%. Details in seasonal species composition in these two algal assemblages are shown in Fig. 3. The plot of species (see vector plot) and the two plots showing the seasonal distribution pattern could be overlaid because these were results of a single PCA for cyanobacteria and diatoms respectively. In respect of cyanobacteria a high share of biovolume of *Limnothrix redekei*, *Aphanizomenon gracile* and *Planktothrix agardhii* were indicated for spring and winter, whereas *Aphanizomenon flos-aquae*, several species of *Microcystis*, *Anabaena* and *Planktolyngbya subtilis* (*Lyngbya limnetica*) were prominent in summer and autumn. (Points representing winter and spring are mainly close to vectors of Limred, Aphgra and Plaaga, whereas points for summer and autumn close to the vectors of the remaining species). Seasonal differences in diatom assemblages were mainly indicated by higher share of *Nitzschia acicularis* and related species in winter and spring, but of *Aulacoseira* spp. and *Actinocyclus normanii* in summer and autumn. For both algal classes, the points of winter corresponded with those of spring, whereas points for summer corresponded with autumn (see trendlines for better visualisation). Nevertheless the sets of winter-spring and summer-autumn points partly overlapped each other on the plane of the first and second principal component. This overlapping is mainly due to the fact that phytoplankton differ not only because of different seasonality but also of different lake types. Among the 20 species of both algal classes 7 cyanobacterial and 4 diatom species were selected by DA showing to the greatest possible extend differences in seasonal biovolume development (Fig. 4D and 5D). *Limnothrix redekei* is the only cyanobacterium of the 7 species characterised as typical spring and winter species (see high value of classification coefficients for spring and winter in comparison to summer and autumn in Fig. 4D). For the remaining six cyanobacteria, the highest shares of biovolume were indicated both for summer and autumn. This is expressed in Fig. 6 as the relative percentage biovolumes of three summer/autumn species versus *Limnothrix redekei*,

the reference species for winter/spring. Cyanobacterial assemblages often consisted of either *Limnothrix redekei* (winter, spring) or *Aphanizomenon flos-aquae* and *Planktolybia subtilis* respectively (summer, autumn). While the major biovolume peaks for *Planktothrix agardhii* occurred in the summer/autumn period, minor peaks were also present in winter/spring (See also the closer relation to *Limnothrix redekei* in comparison to the other summer/autumn species in Fig. 3). Thus, a species typical for the one period is not necessarily absent in the other. Correspondingly, the diatom species selected by DA show either a preference for mass development in winter/spring or in summer/autumn period. The higher coefficients for spring and winter than for summer and autumn indicate *Stephanodiscus neoastraea* and *Nitzschia acicularis* as typical winter/spring species, and, in contrast, *Aulacoseira* spp. (*A. granulata*, *A. ambigua* and *A. italica*) and *Actinocyclus normanii* as summer/autumn species (Fig. 5D, in correspondence with Fig. 7).

The success rate for predictions of membership of the grouping variable's categories (= four seasons) using the discriminant functions developed in this analysis is indicated in Fig. 4C and 5C. In the case of cyanobacteria, for example, 58.82% of the assemblages measured in spring were correctly classified as spring phytoplankton. Nevertheless most of the incorrectly classified cases of spring phytoplankton were classified as winter (26.47%), whereas only 11.76% and 2.94% as summer and autumn respectively. For all other seasons of cyanobacterial and diatom assemblages the highest percentage of the cases were also correctly classified. It is, however, easily shown that the highest percentage of the incorrectly classified cases were predicted for the membership in the successive season (except for summer diatoms: highest number of incorrectly classified cases are membership in winter and the remaining high number as autumn). Therefore many cases of spring were also classified as winter and vice versa, cases of summer as autumn and vice versa. This strong overlapping between the two successive seasons is the main reason for the relative low overall success rate of 60.47% for cyanobacteria and 50.39% for diatoms. This correspondence is visualised by close arrangement of centroids of winter and spring or summer and autumn, but the gap between winter/spring and summer/autumn along the first discriminant axis which accounted a very high percentage of variance in seasonal cyanobacterial (85%, Fig. 4A) and diatom assemblages (90%, Fig. 5A). Thus the results of PCA and DA have show, that, for both algal classes, the species composition in winter and spring as well in summer and autumn are similar, but quiet different between winter/spring and summer/autumn period (Fig. 3 to 5).

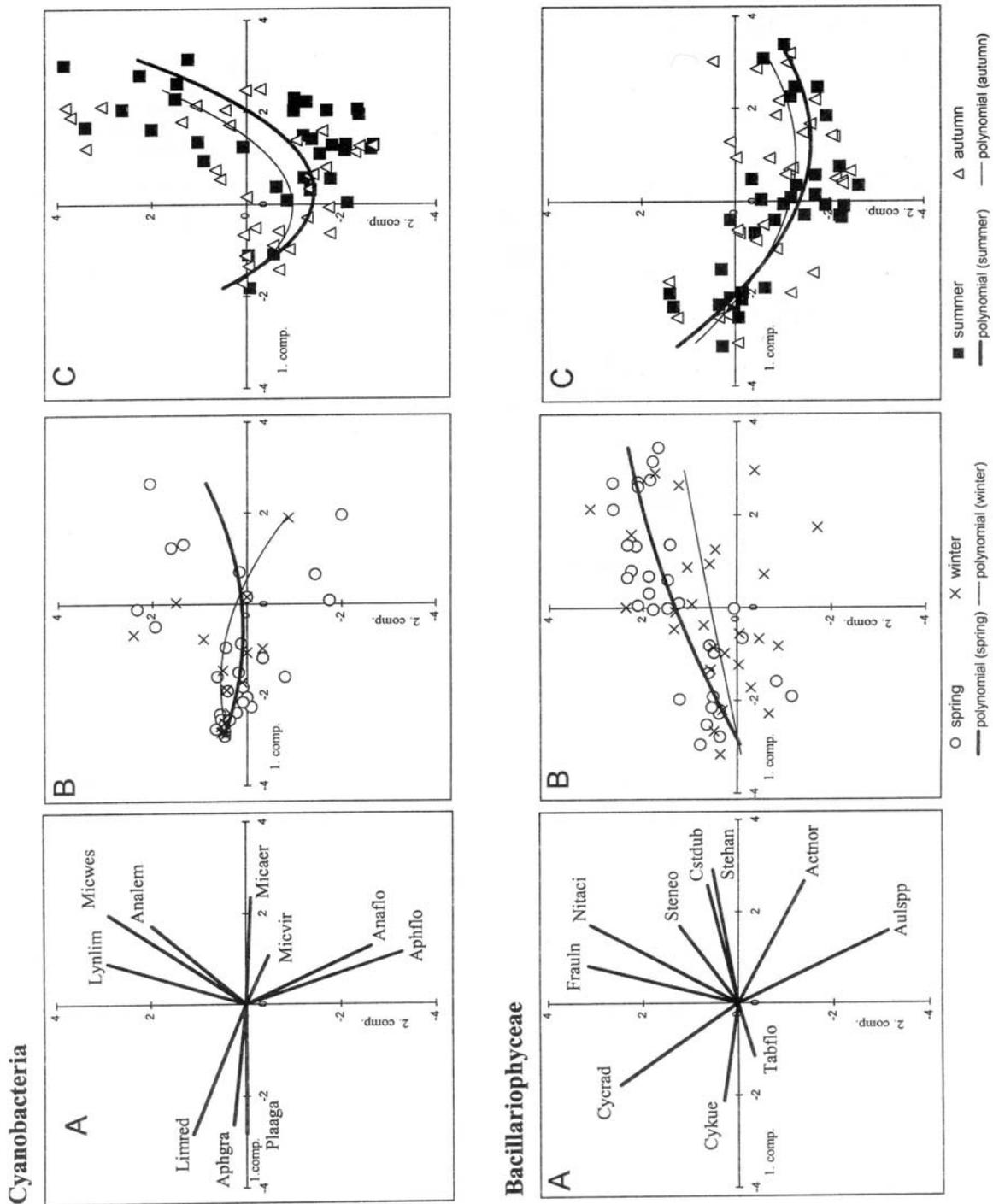
The seasonal changes of the ratio of macronutrient elements for single waters are shown in Fig. 8 (normalised TN:TN:SRSi ratios, see methods). Each point for a season represents the ratios of TN:TP, SRSi:TN and SRSi:TP in proportion to each other and therefore the nutrient situation for siliceous and non-siliceous algae are shown at the same time. It is possible to separate the points of winter and spring from that of summer and autumn by a line of a constant TN:TP ratio (dashed lines in the 11 triangular diagrams). This indicates, that high ratios were measured in spring and winter (points on leftside of the dashed line) and low in summer and autumn (points on rightside of the dashed line) in proportion to various SRSi concentrations in every water. In the case of the hypertrophic riverine lakes Langer See (LANS) and Großer Müggelsee (MUES) the TN:TP ratios changed from winter/spring to summer/autumn even at the critical molar ratio of 16:1 (TN:TP=16:1 see bold line). Different trends for the investigated lakes, however, are shown with respect to SRSi concentrations in relation to TN:TP. The tendency of higher SRSi concentrations occurs during summer/autumn e.g. for the Kiesesee (KIES) and dimictic mesotrophic lakes Parsteiner See (PARS) and Rosinsee (ROSS),



**Fig 2.** Overview of the limnology of the 11 investigated waters. **A:** Relationship between chlorophyll- $\alpha$  and total phosphorus concentration in the 11 waters. Trophic levels are indicated by the averaged data of the June-September period according to FORSBERG & RYDING (1980). **B:** Long term averages (1990-1993 for MUES, MUEZ and FLAS, all others 1990-92) of total biovolume of phytoplankton [ $\text{mm}^3 \text{l}^{-1}$ ]. **C:** Same as **B**, but showing percentage distribution of algal classes. For abbreviations identifying water bodies see Methods.

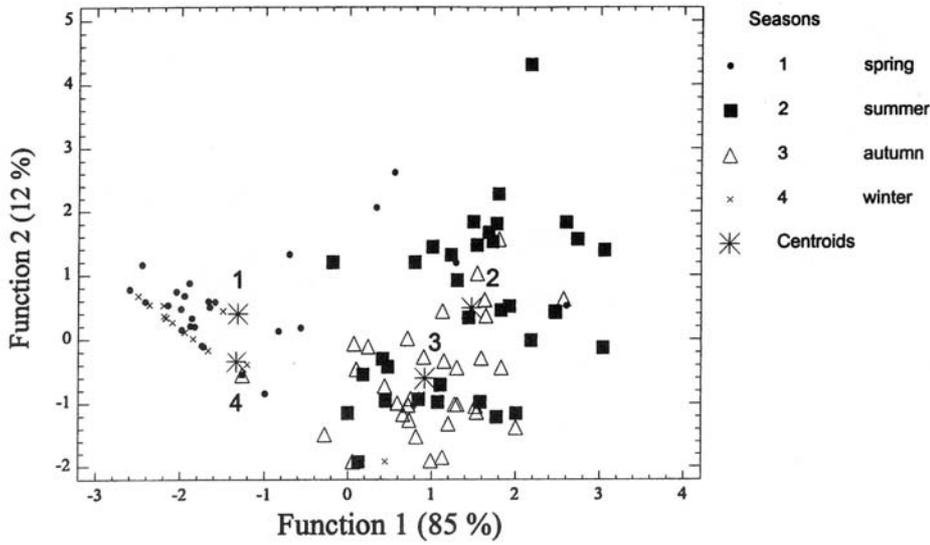
**Fig. 3.** (Continuation)

**Micwes-***M. wesenbergii*, **Plaaga-***Planktothrix agardhii*; for diatoms: **Aulsp-***Aulacoseira* spp. (*A. granulata*, *A. ambigua* and *A. italica*), **Actnor-***Actinocyclus normanii*, **Cyckue-***Cyclotella kuetzingiana/ocellata/comensis*, **Cygrad-***C. radiosa*, **Cstdub-***Cyclostephanos dubius*, **Frauln-***Fragilaria ulna*, **Nitaci-***Nitzschia acicularis*, **Stehan-***Stephanodiscus hantzschii*, **Steneo-***S. neoastraea*, **Tabflo-***Tabellaria flocculosa*.



**Fig. 3.** Plot of the second versus the first principal component for seasonal cyanobacterial and diatom assemblages. For clarity the results are shown in 3 displays: species are shown as vectors in **A**, seasons as points for winter/spring in **B** and summer/autumn in **C**. The fitted polynomials shall visualise the correspondence between winter and spring as well as summer and autumn. Total variance for the first two components: 28% + 19% = 47% for cyanobacteria, 32% + 18% = 50% for diatoms. Abbreviations for cyanobacterial species: **Anaflor**-*Anabaena flos-aquae*, **Analem**-*Anabaena lemmermannii*, **Aphflo**-*Aphanizomenon flos-aquae*, **Aphgra**-*A. gracile*, **Limred**-*Limnithrix redekei*, **Lynlim**-*Planktolyngbya subtilis* (Syn.: *Lynbya limnetica*), **Micaer**-*Microcystis aeruginosa* incl. *M. flos-aquae*, **Micvir**-*M. viridis*,

**A Plot of Discriminant Functions incl. Cyanobacteria**



Discriminant Function	Eigenvalue	Canonical Correlation	Functions Derived	Chi-Square	DF	P-Value
1	1,67412	0,79123	1	153,0994	21	0,0000
2	0,232954	0,43467	2	32,6057	12	0,0011
3	0,0583976	0,23489	3	6,9526	5	0,2242

**C Classification Table**

Actual season	Group Size	Predicted season			
		1	2	3	4
1	34	20 ( 58,82%)	4 ( 11,76%)	1 ( 2,94%)	9 ( 26,47%)
2	34	1 ( 2,94%)	22 ( 64,71%)	10 ( 29,41%)	1 ( 2,94%)
3	34	0 ( 0,00%)	7 ( 20,59%)	24 ( 70,59%)	3 ( 8,82%)
4	27	10 ( 37,04%)	0 ( 0,00%)	5 ( 18,52%)	12 ( 44,44%)

Percent of cases correctly classified: 60,47%

**D Classification Function Coefficients for season**

	1	2	3	4
Micaer	0,358821	1,32211	1,24687	0,261807
Limred	1,23049	-0,267462	-0,378044	0,60694
Lymlim	0,215528	1,68396	1,92193	0,322085
Plaaga	0,368931	1,2704	1,37929	0,712095
Anaflo	0,322699	1,49954	0,362604	0,0457291
Analem	1,21398	2,48237	1,468	0,700518
Aphflo	0,639861	1,67969	1,71606	0,424252
CONSTANT	-3,80758	-7,21481	-5,6659	-2,82046

during winter/spring or autumn/winter in the flushed hypertrophic Flakensee (FLAS) and Großer Müggelsee (MUES).

## Discussion

The mass development of cyanobacteria at the onset of summer were discussed in relation to low nitrogen:phosphorus ratios, high water temperatures and light regimes in well mixed water columns in shallow lakes and stratified deep lakes (e. g. VAN LIER & MUR 1980, ZEVENBOOM & MUR 1980, SOMMER et al. 1986, KOHL et al. 1989, DUDEL & KOHL 1991, STEINBERG & HARTMANN 1988, SCHREURS 1992, NICKLISCH 1994, DOKULIL & TEUBNER 1999). Correspondingly most of the cyanobacteria in the investigated lakes (several species of *Microcystis* and *Anabaena*, *Aphanizomenon flos-aquae*) were characterised as typical summer/autumn species (see also REYNOLDS 1984, TRIMBEE & HARRIS 1984, HECKY et al. 1986). A very close relationship between cyanobacterial summer bloom and nitrogen:phosphorus ratio could be detected for these hypertrophic riverine lakes (TEUBNER et al. 1999). The development in either the „*Planktothrix agardhii*“ or the „*Aphanizomenon flos aquae*/*Microcystis* spp.“ was induced by the timing of critical nitrogen:phosphorus ratio (TN:TP=16:1). *Limnothrix redekei* was the only typical winter/spring species of cyanobacteria as noted by MEFFERT (1975). The spring growth of *L. redekei* is related to light adaptation in turbid turbulent water columns (NICKLISCH & KOHL 1989) and low temperature requirements (FOY 1983). In contrast to cyanobacteria the number of diatoms species was more uniform in the winter/spring or summer/autumn period. The growth preference of *Nitzschia acicularis* in winter/spring corresponds with the low light requirement (KOHL & GIERSDORF 1991). The highest value of classification function coefficients was found for *Aulacoseira granulata/ambigua/italica* for summer, and for *Actinocyclus normanii* for autumn. This corresponds with the description for *Aulacoseira granulata* as a species which starts mass development in summer (REYNOLDS 1984, HECKY et al. 1986, DAVEY 1987, POULÍCKOVÁ 1993), whereas *Actinocyclus normanii* is described as a more typical autumn species (KISS et al. 1990).

The underlying idea of this paper, however, was the comparison of compositional changes between cyanobacterial and diatom assemblages. Since the highest percentage of cases for each season was correctly classified, the specificity of cyanobacterial and diatom assemblages for the four single seasons cannot therefore be completely ignored. More interestingly, however, is the correspondence between the seasons taking account the similar phytoplankton composition in winter and spring or summer and autumn. In view of only two different periods

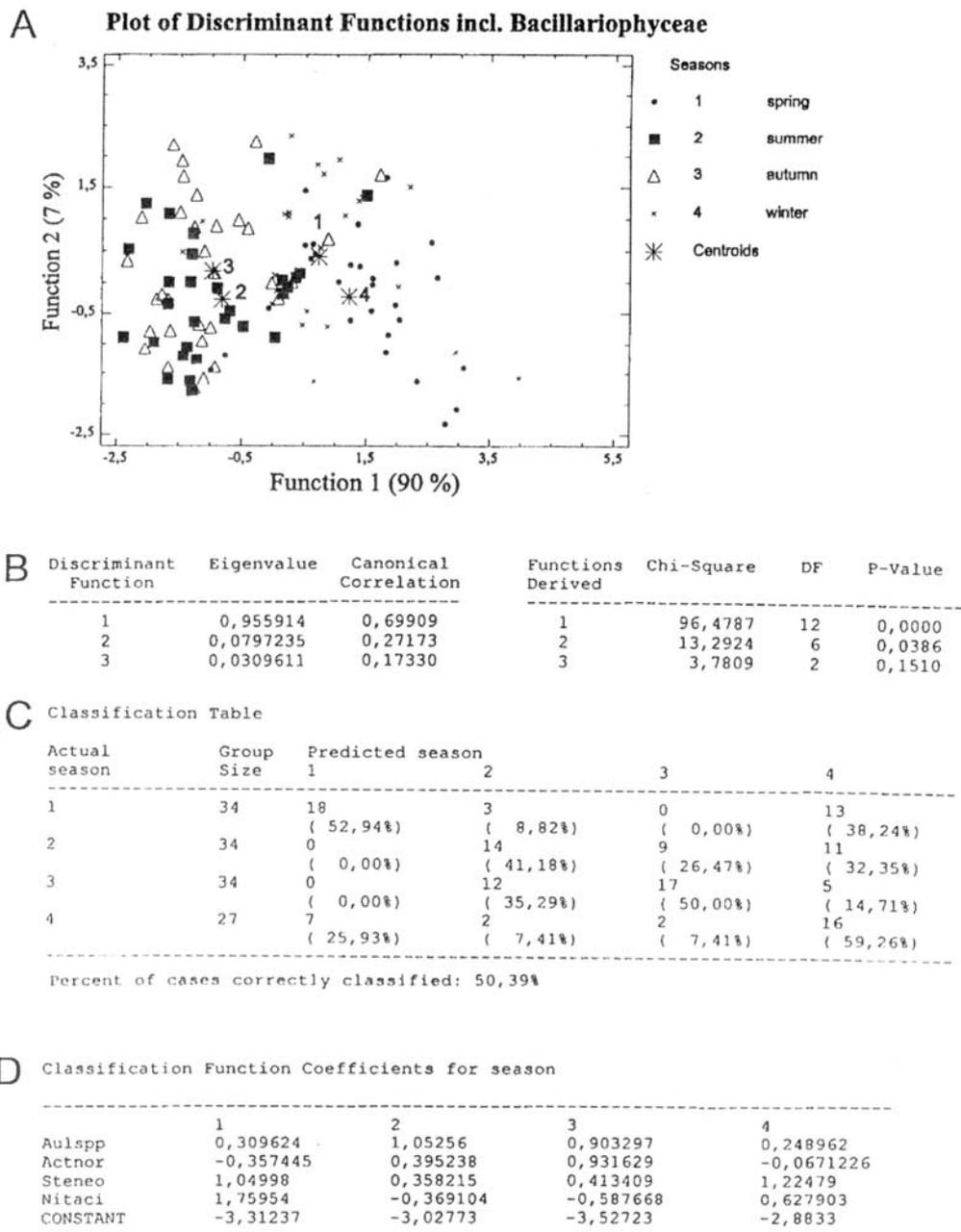
---

**Fig. 4.** Discriminant analysis for the four seasonal cyanobacterial assemblages. **A:** Plot of the second versus the first discriminant function for seasons of cyanobacterial assemblages (percentage of variance accounted for by each discriminant function). **B:** Statistics of the three discriminant functions: eigenvalue, canonical correlation, chi-square, degrees of freedom and probability levels. **C:** Classification table: indication of success rate for predictions of membership of the grouping variable's categories (=four seasons) using the discriminant functions developed in this analysis. **D:** Classification function coefficients of cyanobacterial species for the four seasons (Fisher's linear discriminant function coefficients). The higher coefficients for spring and winter than for summer and autumn indicate *Limnothrix redekei* (Limred) as typical winter/spring species, contrasting with, for example, *Aphanizomenon flos-aquae* (Aphflo) as summer/autumn species.

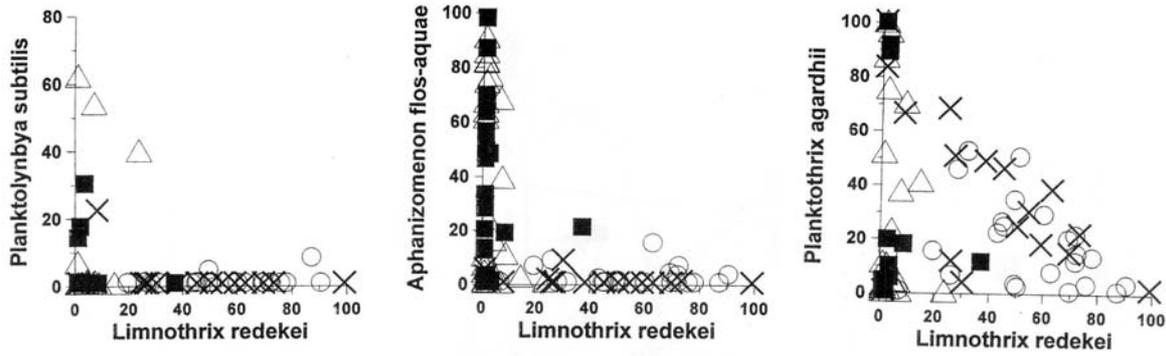
Using the forward selection method, the number of 10 cyanobacterial species (see Fig. 3) was reduced to 7. Abbreviations of species see Fig. 3. Labels 1-4 for seasons in **C** and **D** are shown in legend in **A**.

## Erratum

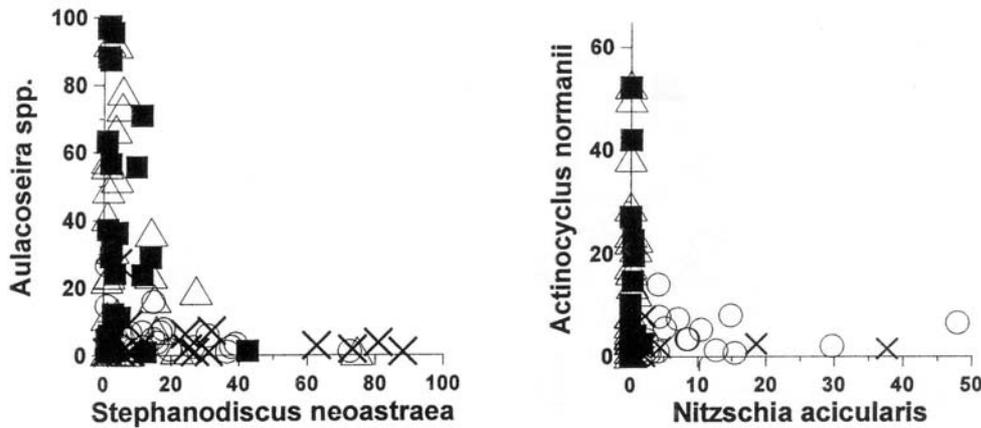
Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **55**, Limnology and Lake Management 2000+  
 TEUBNER, K.: Synchronised changes of planktonic cyanobacterial and diatom assemblages in  
 North German waters reduce seasonality to two principal periods  
 Figure 5 was changed by mistake. The correct figure:



**Fig. 5.** Same as Fig. 4, but for diatoms. **D:** Using the forward selection method the number of 10 diatom species (see Fig. 3) was reduced to 4.

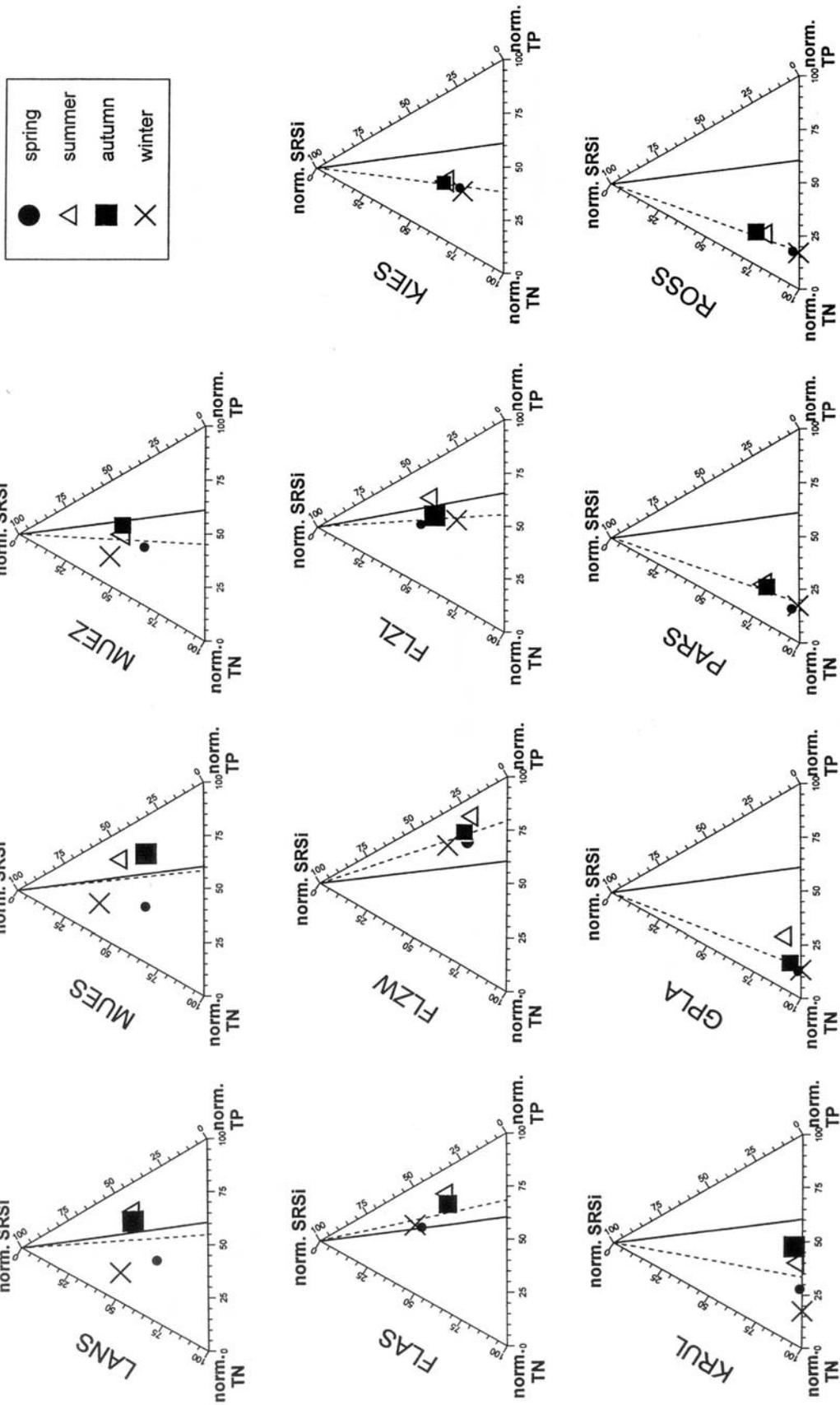


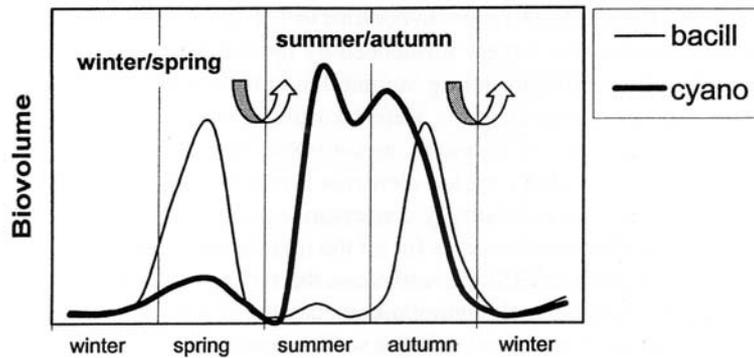
**Fig. 6.** Contribution of biovolume to total of Cyanobacteria (%) of *Planktolyngbya subtilis*, *Aphanizomenon flos-aquae* and *Planktothrix agardhii* (summer/autumn species) versus *Limnithrix redekei* (reference species for winter/spring period, see Fig. 4D) in different seasons.



**Fig. 7.** Contribution of biovolume to total of Bacillariophyceae (%) of *Aulacoseira* spp. and *Actinocyclus normanii* (summer/autumn species) versus *Stephanodiscus neoastraea* and *Nitzschia acicularis* (winter/spring species) in different seasons (seasonality of species see coefficients in Fig. 5 D, *Aulacoseira* species see text legend for Fig. 3).

per year, (winter/spring and summer/autumn) the overall success rate using the DA would be increased from 60% to 88% for cyanobacterial and from 50% to 82% for the diatom assemblages. This indicates that the compositional changes for cyanobacteria and diatoms in the investigated lakes were synchronised (see arrows in scheme in Fig. 9). Significant compositional changes for both algal classes occurred only twice a year: during the transition from spring to summer and from autumn to winter. Therefore, for both algal classes, species composition always changed at transitions from turnover to more stable stratified conditions. The species composition from winter will continue until spring, that of summer until autumn. In summer/autumn the species composition of both algal groups remains stable, but diatom biomass fluctuates throughout the summer and peaks in autumn in contrast to cyanobacteria. Correspondingly, individual cyanobacterial and diatom species showed a preference for either the winter/spring or summer/autumn periods, but never for a combination of periods e.g. spring/summer and autumn/winter.





**Fig. 9.** Scheme for seasonal dynamic of diatoms and cyanobacteria. The arrows indicate the changes in species composition for both algal classes, cyanobacteria and diatoms. From the point of species composition the four seasons can be distinguished as only two different periods: winter/spring and summer/autumn.

The close correspondence of compositional change of cyanobacteria with diatoms is not surprising in view of the fact that the majority of the investigated lakes are shallow. Minor peaks of diatom biovolumes during the summer blooms of cyanobacteria were more the rule than the exception as previously mentioned. This is analogous to mass development of diatoms in other shallow lakes over the whole year (e. g. Neusiedler See DOKULIL 1984, DOKULIL & PADISÁK 1993). For mainly deep, stratified lakes, however, heavy blooms of diatoms were described as restricted to spring and autumn (SOMMER et al. 1986, POULÍKOVÁ 1993). The deepest lake in the investigated data set is the Parsteiner See (maximum depth: 27 m). The overall success rate for a correct classification in the two distinct periods for this lake (cyanobacteria: 91%, diatoms: 100%) is in the same range of the riverine lakes, like Großer Müggelsee (maximum depth: 7.5 m, overall success rate for cyanobacteria: 88%, for diatoms: 94%). Therefore the distinction of species composition in winter/spring and summer/autumn is consistent for both the shallow polymictic and the deep dimictic lakes in the present data set.

The seasonal dynamic of TN:TP:SRSi indicated that the TN:TP ratios were synchronised with the compositional changes in phytoplankton communities. In all investigated lake types similar composed assemblages of diatoms and cyanobacteria grew in winter/spring under conditions of higher TN:TP ratios, while distinctive summer/autumn assemblages grew

**Fig. 8.** Triangular diagrams for seasonal changes of normalised TN:TP:SRSi ratios. The normalisation was based on the data set including all long term seasonal averages of the 11 waters, but for clarity the results are separately shown for each location. Points on the bold lines indicate the constant molar ratio of TN:TP=16:1 at variable concentrations of SRSi. Points on the left side of this line indicate a ratio TN:TP>16:1, to the right side TN:TP<16:1. Points on the left side of the dashed line show higher TN:TP ratios than compared with points on the right side (for details see Methods).

Data bases:

$$\text{normalised concentration} = C_{\text{norm}} = \frac{100 C}{\sum_{i=1}^n C_i}; \quad \sum_{i=1}^n \text{TN}_i = 3644.62, \quad \sum_{i=1}^n \text{TP}_i = 147.98, \quad \sum_{i=1}^n \text{SRSi}_i = 2463.16,$$

calculation of the point of intersection for line for TN:TP=16:1 on the TN-TP axis (see Methods).

under comparatively lower TN:TP ratios. In contrast to TN:TP, the dynamic of SRSi in relation to the two macroelements was largely influenced by hydrological and morphometric differences. Higher SRSi concentration during summer/autumn in proportion to TN and TP and lower concentration during winter/spring were measured only in lakes with longer retention time like Rosinsee, Parsteiner See (dimictic, mesotrophic lakes) and Kiessee (gravel pit lake). The seasonal trends of the rapidly cycled elements P and N is therefore in all investigated lakes comparable, in contrast to relatively conservative Si, which is recycled at longer intervals. A general trend of nutrient dynamic for all investigated lakes were consequently only detected for TN:TP, but not for SRSi. Nevertheless, the synchronisation of seasonal variations of TN:TP with seasonal changes of phytoplankton, cannot be reduced to the causal relationship (nutrient source for algal growth) but must be seen in a wider context.

## Conclusion

In meso- to hypertrophic, shallow and moderately deep lakes of the North German region seasonal changes in species composition in cyanobacterial assemblages corresponded to those of diatoms. The seasonal composition of planctonic cyanobacterial and diatom assemblages can be distinguished by two different periods: winter/spring and summer/autumn. For both algal classes, therefore significant compositional changes were recognisable only two times a year, during the transition from spring to summer and from autumn to winter. These compositional changes of phytoplankton were synchronised to seasonal variations of the TN:TP ratios.

## Acknowledgement

Sampling and chemical analysis (1990-91) were done in co-operation between the Department of Ecology at Humboldt-University (HUB, guided by Prof. J.-G. Kohl) and the Department of Limnology at Technical University of Berlin (guided by Prof. Rippl) during a research venture on regional limnology. Studies from 1992-94 were supported by a project by the Bundesministerium für Forschung und Technologie at the HUB (BEO 339400 A). I am grateful to Mrs. Wachsmuth (HUB) for phytoplankton counts from Langer See 1993 and assistance in diatom preparation. I also thank Prof. M. T. Dokulil for critical reviewing the manuscript and Dr. Steven Lowry for English corrections.

## References

- BARTELL, S.M., ALLEN, T.F.H. & KOONCE, J.F. (1978): An assessment of principal component analysis for description of phytoplankton periodicity in Lake Wingra. - *Phycologia* **17**, 1-11.
- DAVEY, M.C. (1987): Seasonal variation in the filament morphology of the freshwater diatom *Melosira granulata* (Ehrenb.) Ralfs. - *Freshwat. Biol.* **18**: 5-16.
- DOKULIL, M. (1984): Assessment of components controlling phytoplankton photosynthesis and bacterioplankton production in a shallow, alkaline, turbid lake (Neusiedlersee, Austria). - *Internat. Rev. ges. Hydrobiol.* **69**: 679-727.
- DOKULIL, M. & PADISÁK, J. (1993): Langfristige (1968 -1990) und jahreszeitliche Dynamik der planktischen Diatomeen im Neusiedler See. - In: BFB-Bericht 79, 5-11; Biologisches Forschungsinst. für Burgenland, Illmitz.
- DOKULIL, M.T. & TEUBNER, K. (1999): Cyanobacterial dominance in eutrophic lakes. Causes-Consequences-Solutions. - *J. Lake Science China*, in press.

- DUDEL, G. & KOHL, J.-G. (1991): Contribution of dinitrogen fixation and denitrification to the N-budget of shallow lake. - Verh. Internat. Verein. Limnol. **24**: 884-888.
- 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.
- HECKY, R.E., KLING, H.J. & BRUNSKILL, G.J. (1986): Seasonality of phytoplankton in relation to silicon cycling and interstitial water circulation in large, shallow lakes of Central Canada. - Hydrobiologia **138**: 117-126.
- HENRION, G., HENRION, A. & HENRION, R. (1988): Beispiele zur Datenanalyse mit Basic-Programmen. - 1-363; Deutscher Verlag der Wissenschaften, Berlin.
- HENRION, R. & HENRION, G. (1995): Multivariate Datenanalyse. Methodik und Anwendung in der Chemie und verwandten Gebieten. - 1-261; Springer-Verlag, Berlin-Heidelberg-New York-London-Paris-Tokyo-Hong Kong-Barcelona-Budapest.
- KISS, K.T., Le Cohu, R., Coste, M., Genkal, S.I. & Houk, V. (1990): *Actinocyclus normanii* (Bacillariophyceae), in some rivers and lakes in Europe. Morphological examinations and quantitative relations. - Ouvrage dédié à H. Germain: 111-123.
- KOHL, J.-G. & GIERSDORF, K. (1991): Competition ability of two planktic diatoms under different vertical light gradients, mixing-depth and -frequencies: An experimental approach. - Verh. Internat. Verein. Limnol. **24**: 2652-2656.
- KOHL, J.-G., SCHLANGENSTEDT, 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.
- KOMÁREK, J. & ANAGNOSTIDIS, K. (1999): Cyanoprokaryota. 1. Teil Chroococcales. - In: Süßwasserflora von Mitteleuropa. - 1-548; Gustav Fischer, Jena.
- MEFFERT, M.-E. (1975): Analysis of the population dynamics of *Oscillatoria redekei* van Goor in Lake Edeberg. - Verh. Internat. Verein. Limnol. **19**: 2682-2688.
- NICKLISCH, A. (1994): Does mortality by nitrogen deficiency influence the succession of *Limnothrix 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.
- POULÍCKOVÁ, A. (1993): Ecological study of seasonal maxima of centric diatoms. - Algol. Stud. **68**: 85-106.
- REYNOLDS, C.S. (1984): Phytoplankton periodicity: The interactions of form, function and environmental variability. - Freshwat. Biol. **14**: 111-142.
- SCHREURS, H. (1992): Cyanobacterial dominance - relations to eutrophication and lake morphology. - Academisch Proefschrift, Universiteit van Amsterdam.
- SEIP, K. L. & REYNOLDS, C. S. (1995): Phytoplankton functional attributes along trophic gradient and season. - Limnol. Oceanogr. **40**: 589-597.
- 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. - Freshwat. Biol. **20**: 279-287.
- Stevenson, R.J. & White, K.D. (1995): A comparison of natural and human determinants of phytoplankton communities in the Kentucky River basin, USA. - Hydrobiologia **297**: 201-216.
- 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 Gewässern der Region Berlin-Brandenburg. - Ph. D. Thesis, Humboldt-Universität zu Berlin, 1-232.

- (1997): Merkmalsvariabilität bei planktischen Diatomeen in Berlin-Brandenburger Gewässern. - *Nova Hedwigia* **65**: 233-250.
- TEUBNER, K., FEYERABEND, R., HENNING, M., NICKLISCH, A., WOITKE, P. & KOHL, J.-G. (1999): Alternative blooming of *Aphanizomenon flos-aquae* or *Planktothrix agardhii* induced by the timing of the critical nitrogen:phosphorus ratio in hypertrophic riverine lakes. - *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **54**: 325-344.
- 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 blue-green algae. - *J. Plankton Res.* **6**: 699-713.
- UTERMÖHL, H. (1958): Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. - *Mitt. int. Verein. Limnol.* **9**: 1-38.
- VAN LIERE, L. & MUR, L.R. (1980): Occurrence of *Oscillatoria agardhii* and some related species, a survey. - *Developments in Hydrobiology* **2**: 67-77.
- ZEVENBOOM, W. & MUR, L.R. (1980): N<sub>2</sub>-fixing cyanobacteria: Why they do not become dominant in Dutch, hypertrophic lakes. - *Developments in Hydrobiology* **2**: 123-130.

## Synchronised changes of planktonic cyanobacterial and diatom assemblages in North German waters reduce seasonality to two principal periods

Katrin Teubner

with 9 figures

---

**Abstract:** The seasonal dynamics of cyanobacterial and diatom assemblages in 11 water bodies along a meso- to hypertrophic gradient were compared. The cyanobacterial and diatom communities are characterised according to representative species of each algal class, selected by data reduction following principal component analyses and discriminant analysis. The cyanobacterial and diatom assemblages of the four seasons show different similarities in their species composition. In this respect the assemblages of the four seasons can be distinguished as only two different periods: winter/spring and summer/autumn. Species show a preference of growth either in the period of winter/spring (*Limnothrix redekei*, *Nitzschia acicularis*, *Stephanodiscus neoastraea*) or of summer/autumn (*Aphanizomenon flos-aquae*, several species of *Microcystis* and *Anabaena*, *Planktothrix agardhii*, *Aulacoseira granulata/italica/ambigua*, *Actinocyclus normanii*). The significant compositional changes for both algal classes during the transition from spring to summer and from autumn to spring were discussed in relation to synchronised seasonal variations of TN:TP ratios.

---

### Introduction

Seasonality is one of the most studied topics in phytoplankton research (e.g. REYNOLDS 1984, SOMMER et al. 1986, POULÍCKOVÁ 1993, SEIP & REYNOLDS 1995) Multivariate statistical methods have been used on several occasions, e.g. principal component analysis by BARTELL et al. (1995) and canonical correspondence analysis by STEVENSON & WHITE (1995).

A central problem in the seasonality of phytoplankton is the timing of the compositional changes. The aim of this study is to compare these changes of species in assemblages of Cyanobacteria (Cyanoprokaryota, KOMÁREK & ANAGNOSTIDIS 1999) with changes in diatom species composition. The comparison of seasonality of these two algal assemblages is interesting because of different seasonal mass-development as well as their different macronutrient requirements. This paper presents a multi-system study with a focus on dominant seasonal patterns in phytoplankton assemblages beyond the system level.

---

**Author's address:** Katrin Teubner, Institute of Limnology Austrian Academy of Sciences, A-5310 Mondsee, katrin.teubner@oeaw.ac.at

## Materials and methods

Samples were taken from 8 lakes in Berlin-Brandenburg in Germany. Langer See (LANS), Großer Müggelsee (MUES), Flakensee (FLAS), Kiessee (KIES) and Krumme Lake (KRUL) are lakes on the periphery of the city of Berlin. In addition the inlet waters of some flushed river lakes were sampled (inlet of Großer Müggelsee (MUEZ) and Flakensee (Woltersdorfer Schleuse, FLZW, Löcknitz FLZL). Parsteiner See (PARS), Rosinsee (ROSS) and Großer Plagesee (GPLA) are part of the biosphere reserve "Schorfheide-Chorin" in Brandenburg, in the north of Berlin (location in Fig. 1).

Integrated samples were taken monthly from the 11 waters from 1990-91. This sampling frequency was continued for Langer See, Kiessee, Rosinsee and Parsteiner See in 1992. A biweekly interval was followed in Großer Müggelsee and Flakensee including the inlet waters (MUEZ, FLZL, FLZW) in 1992-93. All samples represented the epilimnetic mixed layer. Maximum depth and lake area, mean total phosphorus, total nitrogen, soluble reactive silica, conductivity and Secchi depth for the investigated lakes are tabulated in TEUBNER 1995 and 1997.

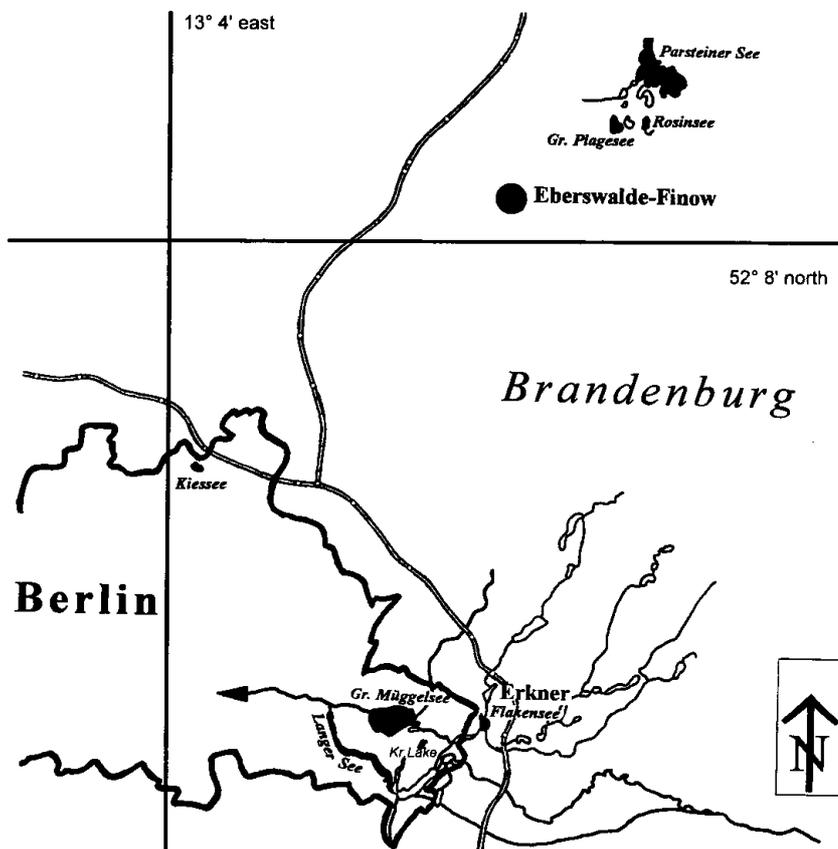


Fig. 1. Location of investigated waters in Berlin and Brandenburg.

Biovolume of phytoplankton was estimated according to the UTERMÖHL method (1958). 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. Diatoms were prepared in a special gentle way to keep both valves 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 sizes. For the biovolume estimation of unicellular centric diatom species, the counts of each sample fixed with Lugol's solution were combined with counts from a permanent slide. For taxonomic details of diatoms in the 11 waters refer to TEUBNER 1997 and for Cyanobacteria to TEUBNER 1996. Figs. 3-7 are based on seasonal averages: (spring: March-May, summer: June-August, autumn: September-November, winter: December-February).

Algal species never exceeding 5% of total biovolume during the investigated period were not included in principal component analysis (PCA). Stepwise species extraction was repeated in PCA until the first three components represented more than 60% of total variance. In this way the 17 cyanobacterial species were reduced to the 10 most representative species, similarly diatom species were reduced from 22 to 10 (extracted species are shown in Fig. 3, cases: n=129 seasonal averages).

During the stepwise reduction of species in PCA, their dominance in different waters as well as seasons was considered, because data were seasonal averages of the phytoplankton of the 11 waters. In order to show the seasonality, however, points were labelled only according to seasons (Fig. 3). These 10 extracted cyanobacterial and diatom species were the basis for discriminant analysis (DA), but further reductions were done in order to show those species which exhibited most seasonal difference in mass development (forward selection method). All multivariate analyses were based on the relative biovolume of the species, to take account of a dataset with widely varying total biovolumes of phytoplankton (Fig. 2b, cyanobacterial and diatom species were related to the total biovolume of their respective algal class).

Logarithmic data were standardised for multivariate statistical analyses (HENRION et al. 1988, HENRION & HENRION 1995) using the computer program Statgraphics plus 2.0 (STSC, inc. USA).

Triangular diagrams (Fig. 8) based on long term seasonal averages were created in Grapher for Windows 4.0, Golden Software, Inc. Each point indicates a seasonal TN:TP:SRSi ratio of a water and represents the sum of the concentrations equal to 100% (TN+TP+SRSi=100). The corners of the triangle represent the concentration of one element only (100%) and the absence of the remaining two nutrients. The line TN:TP=16:1 (bold line in Fig. 8) from a SRSi-corner to an intersection point on the TN:TP-axis indicates the constant TN:TP ratio of 16:1 at variable SRSi. By analogy, the dashed lines indicate a constant TN:TP ratio at variable SRSi concentrations for a single water. Because of the relatively small amount of TP in comparison to SRSi and TN, points for the original data set fall close to the SRSi:TN axis (see also the amount of sums of TN, TP and SRSi in text legend of Fig. 8). For clearer presentation of the points within the area the concentrations were normalised by the relation of the concentration of an element to its sum over the entire data set ( $C_{\text{norm}} = \frac{100 C}{\sum_{i=1}^n C_i}$ ). As a result, points repre-

senting seasonal TN<sub>norm</sub>:TP<sub>norm</sub>:SRSi<sub>norm</sub> ratios become more scattered and are easier to distinguish, but TN:TP:SRSi ratios cannot be read directly. It is, however, possible to recalculate these ratios. The intersection point of the bold line TN:TP = 16:1 on the TN:TP axis is given by following calculation:

from  $SRSi=0$  and  $TN:TP=16:1$  is  $TN_{norm}+TP_{norm}+SRSi_{norm}=0.4309+0.3758+0=1.1148=100\%=39.38+60.62+0$  ( $TN_{norm}=\frac{100 \cdot 16}{3644.62}=0.4390$  and  $TP_{norm}=\frac{100 \cdot 1}{147.98}=0.3758$ , sums of TN and TP over the entire data set, see legend of Fig. 8). The intersection point of the line indicating  $TN:TP=16:1$  on the TN-TP-axis is therefore 39.38:60.62 (TN scaling is from left to right and the TP scaling from right to left on the TN-TP-axis). For further complex calculations in normalised triangular diagrams refer to TEUBNER (1996).

## Results

The trophic levels of the investigated waters ranged from meso- to hypertrophic, but the majority are hypertrophic (Fig. 2a). Großer Müggelsee and Langer See are riverine lakes with high concentrations of chlorophyll- $\alpha$ . The hypertrophic, flushed Flakensee is characterised by higher conductivity in comparison to other soft waters (highest average conductivity of about  $121 \text{ mS m}^{-1}$  in FLZW). The deepest lakes are the mesotrophic Parsteiner See and Rosinsee (the deepest lake is PARS with a maximum depth of 27 m). Krumme Lake and Großer Plagesee are eutrophied, dystrophic lakes.

Except for one lake (ROSS), the diatoms and cyanobacteria contributed at least 50% to the long term averages of the total phytoplankton in the investigated waters (Fig. 2c). In the hypertrophic riverine lakes (LANS, MUES, MUEZ), however, the biovolume of these two algal classes reached levels of about 90%. Details of seasonal species composition in these two algal assemblages are shown in Fig. 3. The plot of species (see vector plot) and the two plots showing the seasonal distribution pattern could be overlaid because these were results of a single PCA for cyanobacteria and diatoms respectively. In respect to cyanobacteria, a high share of biovolume of *Limnothrix redekei*, *Aphanizomenon gracile* and *Planktothrix agardhii* was indicated for spring and winter, whereas *Aphanizomenon flos-aquae*, several species of *Microcystis*, *Anabaena* and *Planktolyngbya subtilis* (*Lyngbya limnetica*) were prominent in summer and autumn. (Points representing winter and spring are mainly close to vectors of Limred, Aphgra and Plaaga, whereas points for summer and autumn are close to the vectors of the remaining species). Seasonal differences in diatom assemblages were mainly indicated by higher share of *Nitzschia acicularis* and related species in winter and spring, but of *Aulacoseira* spp. and *Actinocyclus normanii* in summer and autumn. For both algal classes, the points of winter corresponded with those of spring, whereas points for summer corresponded with autumn (see trendlines for better visualisation). Nevertheless the sets of winter-spring and summer-autumn points partly overlapped each other on the plane of the first and second principal component. This overlapping is mainly due to the fact that phytoplankton differ not only because of different seasonality but also of different lake types. Among the 20 species of both algal classes, 7 cyanobacterial and 4 diatom species were selected by DA showing to the greatest possible extent differences in seasonal biovolume development (Fig. 4D and 5D). *Limnothrix redekei* is the only cyanobacterium of the 7 species characterised as a typical spring and winter species (see high value of classification coefficients for spring and winter in comparison to summer and autumn in Fig. 4D). For the remaining six cyanobacteria, the highest shares of biovolume were indicated both for summer and autumn. This is expressed in Fig. 6 as the relative percentage biovolumes of three summer/autumn species versus *Limnothrix redekei*,

the reference species for winter/spring. Cyanobacterial assemblages often consisted of either *Limnothrix redekei* (winter, spring) or *Aphanizomenon flos-aquae* and *Planktolybia subtilis* respectively (summer, autumn). While the major biovolume peaks for *Planktothrix agardhii* occurred in the summer/autumn period, minor peaks were also present in winter/spring. (See also the closer relation to *Limnothrix redekei* in comparison to the other summer/autumn species in Fig. 3). Thus, a species typical for the one period is not necessarily absent in the other. Correspondingly, the diatom species selected by DA show either a preference for mass development in winter/spring or in the summer/autumn period. The higher coefficients for spring and winter than for summer and autumn indicate *Stephanodiscus neoastraea* and *Nitzschia acicularis* as typical winter/spring species, and, in contrast, *Aulacoseira* spp. (*A. granulata*, *A. ambigua* and *A. italica*) and *Actinocyclus normanii* as summer/autumn species (Fig. 5D, in correspondence with Fig. 7).

The success rate for predicting of membership of the grouping variable's categories (= four seasons) using the discriminant functions developed in this analysis is indicated in Fig. 4C and 5C. For example, in the case of cyanobacteria, 58.82% of the assemblages measured in spring were correctly classified as spring phytoplankton. Nevertheless, most of the incorrectly classified cases of spring phytoplankton were classified as winter (26.47%), whereas only 11.76% and 2.94% as summer and autumn respectively. For all other seasons of cyanobacterial and diatom assemblages, the highest percentage of the cases were also correctly classified. It is, however, easily shown that the highest percentage of the incorrectly classified cases were predicted for the membership in the successive season (except for summer diatoms: highest number of incorrectly classified cases are membership in winter and the remaining high number as autumn). Therefore many cases of spring were also classified as winter and vice versa, cases of summer as autumn and vice versa. This strong overlapping between the two successive seasons is the main reason for the relative low overall success rate of 60.47% for cyanobacteria and 50.39% for diatoms. This correspondence is visualised by close arrangement of centroids of winter and spring or summer and autumn, but the gap between winter/spring and summer/autumn along the first discriminant axis which accounted for a very high percentage of variance in seasonal cyanobacterial (85%, Fig. 4A) and diatom assemblages (90%, Fig. 5A). Thus the results of PCA and DA show, that, for both algal classes, the species composition in winter and spring as well in summer and autumn are similar, but quite different between winter/spring and summer/autumn periods (Figs. 3 to 5).

The seasonal changes of the ratio of macronutrient elements for single waters are shown in Fig. 8 (normalised TN:TP:SRSi ratios, see methods). Each point for a season represents the ratios of TN:TP, SRSi:TN and SRSi:TP in proportion to each other and therefore the nutrient situation for siliceous and non-siliceous algae are shown at the same time. It is possible to separate the points of winter and spring from that of summer and autumn by a line of a constant TN:TP ratio (dashed lines in the 11 triangular diagrams). This indicates, that high ratios were measured in spring and winter (points on leftside of the dashed line) and low in summer and autumn (points on rightside of the dashed line) in proportion to various SRSi concentrations in every water. In the case of the hypertrophic riverine lakes Langer See (LANS) and Großer Müggelsee (MUES) the TN:TP ratios changed from winter/spring to summer/autumn even at the critical molar ratio of 16:1 (TN:TP=16:1 see bold line). Different trends for the investigated lakes, however, are shown with respect to SRSi concentrations in relation to TN:TP. The tendency of higher SRSi concentrations occurs during summer/autumn e.g. for the Kiese (KIES) and dimictic mesotrophic lakes Parsteiner See (PARS) and Rosinsee (ROSS),

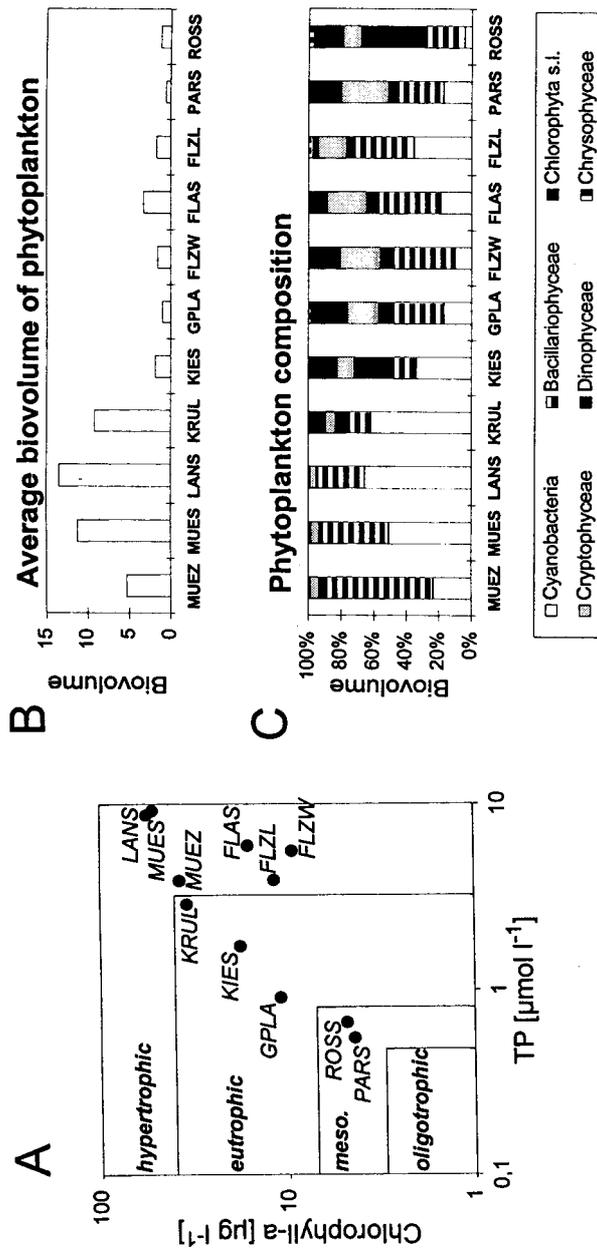
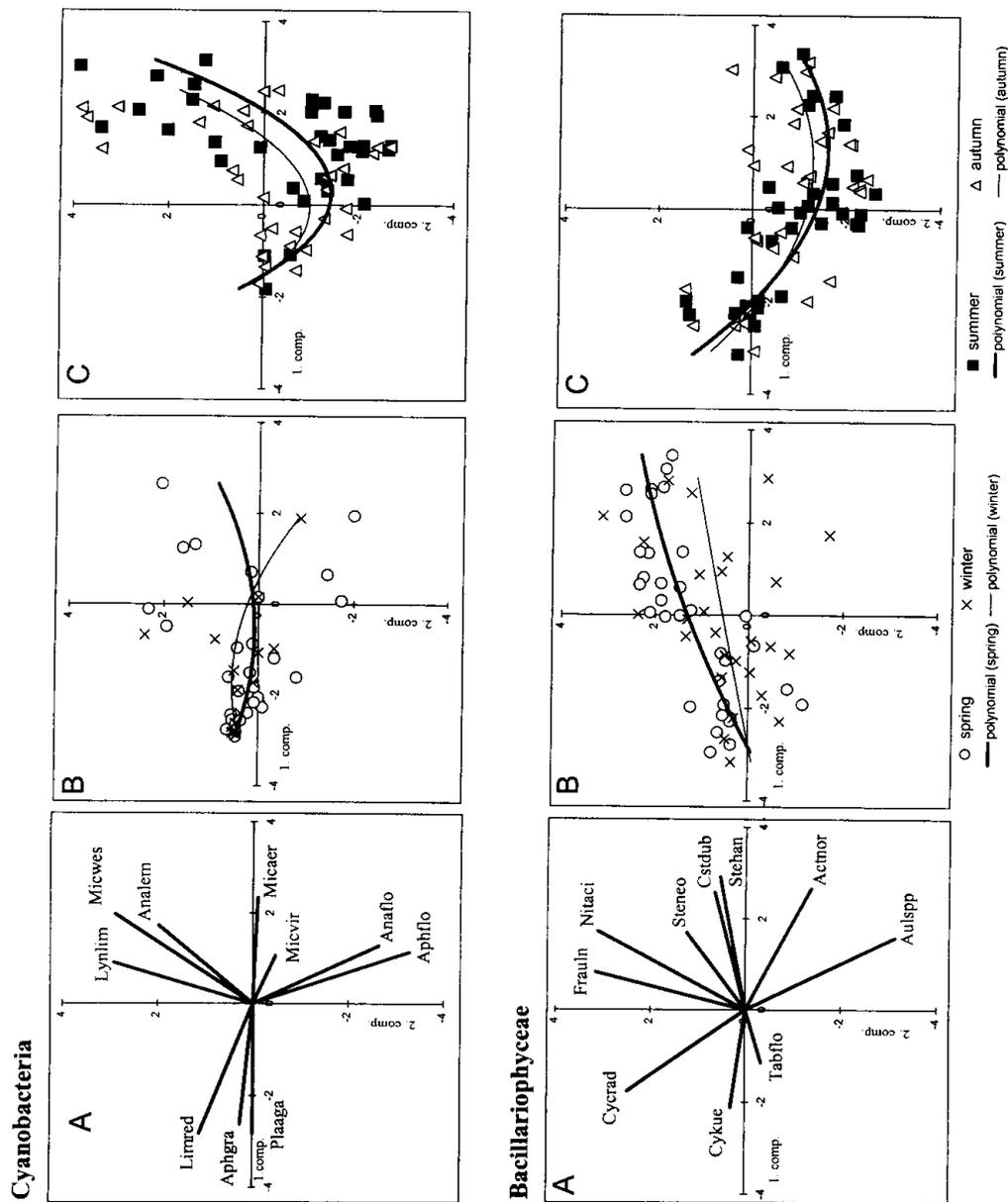


Fig. 2. Overview of the limnology of the 11 investigated waters. **A**: Relationship between chlorophyll-*a* and total phosphorus concentration in the 11 waters. Trophic levels are indicated by the averaged data of the June-September period according to FORSBERG & RYDING (1980). **B**: Long term averages (1990-1993 for MUES, MUEZ and FLAS, all others 1990-92) of total biovolume of phytoplankton [ $\text{mm}^3 \text{l}^{-1}$ ]. **C**: Same as B, but showing percentage distribution of algal classes. For abbreviations identifying water bodies see Methods.

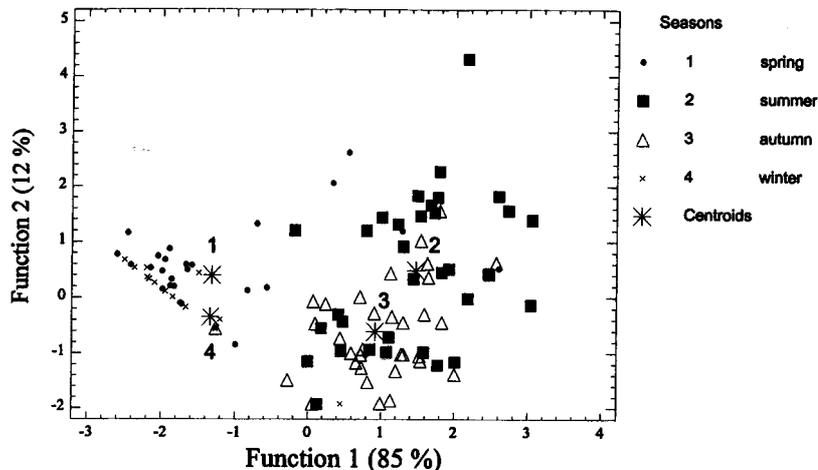
Fig. 3. (Continuation)

**Micwes**-*M. wesenbergii*, **Plaaga**-*Planktothrix agardhii*; for diatoms: **Aulspp**-*Aulacoseira* spp. (*A. granulata*, *A. ambigua* and *A. italica*), **Actnor**-*Actinocyclus normanii*, **Cyckue**-*Cyclotella kuetzingiana/ocellata/comensis*, **Cygrad**-*C. radiosa*, **Cstdub**-*Cyclostephanos dubius*, **Frauln**-*Fragilaria ulna*, **Nitaci**-*Nitzschia acicularis*, **Stehan**-*Stephanodiscus hantzschii*, **Steneo**-*S. neoastraea*, **Tabflo**-*Tabellaria flocculosa*.



**Fig. 3.** Plot of the second versus the first principal component for seasonal cyanobacterial and diatom assemblages. For clarity the results are shown in 3 displays: species are shown as vectors in **A**, seasons as points for winter/spring in **B** and summer/autumn in **C**. The fitted polynomials shall visualise the correspondence between winter/spring as well as summer and autumn. Total variance for the first two components:  $28\% + 19\% = 47\%$  for cyanobacteria,  $32\% + 18\% = 50\%$  for diatoms. Abbreviations for cyanobacterial species: **Anaflo**-*Anabaena flos-aquae*, **Analem**-*Anabaena lemmermannii*, **Aphflo**-*Aphanizomenon flos-aquae*, **Aphgra**-*A. gracile*, **Limred**-*Limnothrix redekei*, **Lynlim**-*Planktolyngbya subtilis* (Syn.: *Lynbya limnetica*), **Micaer**-*Microcystis aeruginosa* incl. *M. flos-aquae*, **Micvir**-*M. viridis*,

**A Plot of Discriminant Functions incl. Cyanobacteria**



Discriminant Function	Eigenvalue	Canonical Correlation	Functions Derived	Chi-Square	DF	P-Value
1	1,67412	0,79123	1	153,0994	21	0,0000
2	0,232954	0,43467	2	32,6057	12	0,0011
3	0,0583976	0,23489	3	6,9526	5	0,2242

**C Classification Table**

Actual season	Group Size	Predicted season			
		1	2	3	4
1	34	20 ( 58,82%)	4 ( 11,76%)	1 ( 2,94%)	9 ( 26,47%)
2	34	1 ( 2,94%)	22 ( 64,71%)	10 ( 29,41%)	1 ( 2,94%)
3	34	0 ( 0,00%)	7 ( 20,59%)	24 ( 70,59%)	3 ( 8,82%)
4	27	10 ( 37,04%)	0 ( 0,00%)	5 ( 18,52%)	12 ( 44,44%)

Percent of cases correctly classified: 60,47%

**D Classification Function Coefficients for season**

	1	2	3	4
Micaer	0,358821	1,32211	1,24687	0,261807
Limred	1,23049	-0,267462	-0,378044	0,60694
Lymlim	0,215528	1,68396	1,92193	0,322085
Plaaga	0,368931	1,2704	1,37929	0,712095
Anaflo	0,322699	1,49954	0,362604	0,0457291
Analem	1,21398	2,48237	1,468	0,700518
Aphflo	0,639861	1,67969	1,71606	0,424252
CONSTANT	-3,80758	-7,21481	-5,6659	-2,82046

during winter/spring or autumn/winter in the flushed, hypertrophic Flakensee (FLAS) and Großer Müggelsee (MUES).

## Discussion

The mass development of cyanobacteria at the onset of summer was discussed in relation to low nitrogen:phosphorus ratios, high water temperatures and light regimes in well mixed water columns in shallow lakes and stratified deep lakes (e. g. VAN LIER & MUR 1980, ZEVENBOOM & MUR 1980, SOMMER et al. 1986, KOHL et al. 1989, DUDEL & KOHL 1991, STEINBERG & HARTMANN 1988, SCHREURS 1992, NICKLISCH 1994, DOKULIL & TEUBNER 1999). Correspondingly most of the cyanobacteria in the investigated lakes (several species of *Microcystis* and *Anabaena*, *Aphanizomenon flos-aquae*) were characterised as typical summer/autumn species (see also REYNOLDS 1984, TRIMBEE & HARRIS 1984, HECKY et al. 1986). A very close relationship between cyanobacterial summer blooms and nitrogen:phosphorus ratios could be detected for these hypertrophic riverine lakes (TEUBNER et al. 1999). The development in either the "*Planktothrix agardhii*" or the "*Aphanizomenon flos aquae*/*Microcystis* spp." was induced by the timing of the critical nitrogen:phosphorus ratio (TN:TP= 16:1). *Limnothrix redekei* was the only typical winter/spring species of cyanobacteria as noted by MEFFERT (1975). The spring growth of *L. redekei* is related to light adaptation in turbid turbulent water columns (NICKLISCH & KOHL 1989) and low temperature requirements (FOY 1983).

In contrast to cyanobacteria, the number of diatom species was more uniform in the winter/spring and summer/autumn periods. The growth preference of *Nitzschia acicularis* in winter/spring corresponds with the low light requirement (KOHL & GIERSDORF 1991). The highest value of classification function coefficients were found for *Aulacoseira granulata/ambigua/italica* for summer, and for *Actinocyclus normanii* for autumn. This corresponds with the description for *Aulacoseira granulata* as a species which starts mass development in summer (REYNOLDS 1984, HECKY et al. 1986, DAVEY 1987, POULČKOVÁ 1993), whereas *Actinocyclus normanii* is described as a more typical autumn species (KISS et al. 1990).

The underlying idea of this paper, however, was to compare the compositional changes between cyanobacterial and diatom assemblages. Since the highest percentage of cases for each season was correctly classified, the specificity of cyanobacterial and diatom assemblages for the four single seasons cannot therefore be completely ignored. More interestingly, however, is the correspondence between the seasons taking account the similar phytoplankton composition in winter and spring or summer and autumn. In view of only two different periods

**Fig. 4.** Discriminant analysis for the four seasonal cyanobacterial assemblages. **A:** Plot of the second versus the first discriminant function for seasons of cyanobacterial assemblages (percentage of variance accounted for by each discriminant function). **B:** Statistics of the three discriminant functions: eigenvalue, canonical correlation, chi-square, degrees of freedom and probability levels. **C:** Classification table: indication of success rate for predictions of membership of the grouping variable's categories (=four seasons) using the discriminant functions developed in this analysis. **D:** Classification function coefficients of cyanobacterial species for the four seasons (Fisher's linear discriminant function coefficients). The higher coefficients for spring and winter than for summer and autumn indicate *Limnothrix redekei* (Limred) as typical winter/spring species, contrasting with, for example, *Aphanizomenon flos-aquae* (Aphflo) as summer/autumn species.

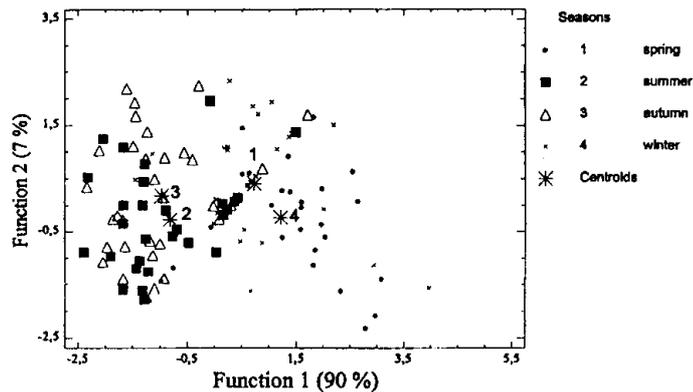
Using the forward selection method, the number of 10 cyanobacterial species (Fig. 3) was reduced to 7. Abbreviations of species see Fig. 3. Labels 1-4 for seasons in **C** and **D** are shown in legend in **A**.

## Erratum

Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **55**, Limnology and Lake Management 2000+  
TEUBNER, K.: Synchronised changes of planktonic cyanobacterial and diatom assemblages in  
North German waters reduce seasonality to two principal periods

Figure 5 was changed by mistake. The correct figure:

### A Plot of Discriminant Functions incl. Bacillariophyceae



Discriminant Function	Eigenvalue	Canonical Correlation	Functions Derived	Chi-Square	DF	P-Value
1	0,955914	0,69909	1	96,4787	12	0,0000
2	0,0797235	0,27173	2	13,2924	6	0,0386
3	0,0309611	0,17330	3	3,7809	2	0,1510

### C Classification Table

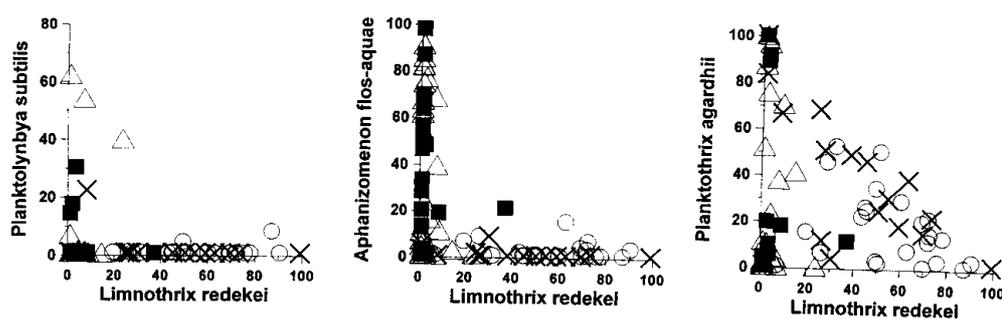
Actual season	Group Size	Predicted season			
		1	2	3	4
1	34	18 ( 52,94%)	3 ( 8,82%)	0 ( 0,00%)	13 ( 38,24%)
2	34	0 ( 0,00%)	14 ( 41,18%)	9 ( 26,47%)	11 ( 32,35%)
3	34	0 ( 0,00%)	12 ( 35,29%)	17 ( 50,00%)	5 ( 14,71%)
4	27	7 ( 25,93%)	2 ( 7,41%)	2 ( 7,41%)	16 ( 59,26%)

Percent of cases correctly classified: 50,39%

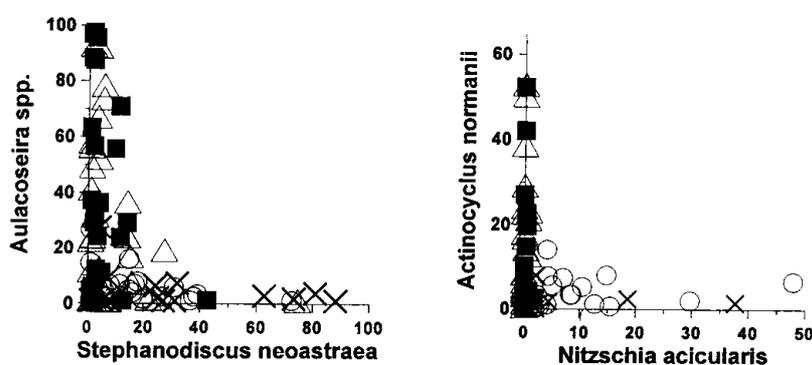
### D Classification Function Coefficients for season

	1	2	3	4
Aulspp	0,309624	1,05256	0,903297	0,248962
Actnor	-0,357445	0,395238	0,931629	-0,0671226
Steneo	1,04998	0,358215	0,413409	1,22479
Nitaci	1,75954	-0,369104	-0,587668	0,627903
CONSTANT	-3,31237	-3,02773	-3,52723	-2,8833

**Fig. 5.** Same as Fig. 4, but for diatoms. **D:** Using the forward selection method the number of 10 diatom species (Fig. 3) was reduced to 4.

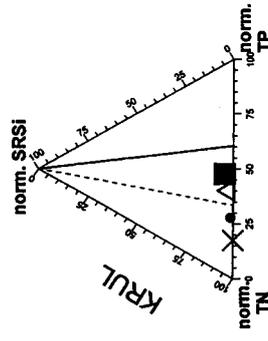
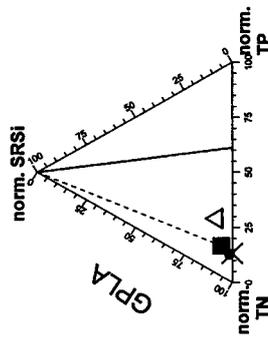
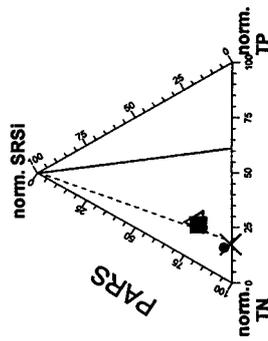
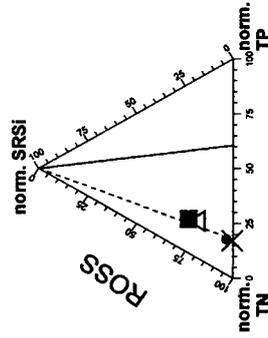
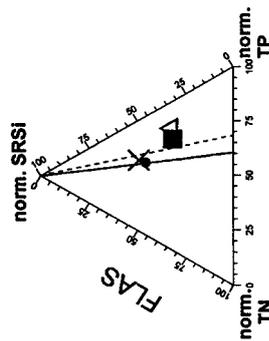
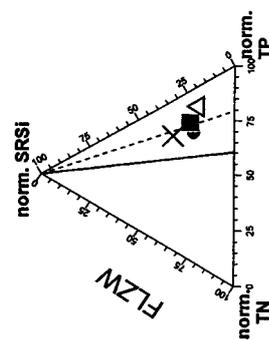
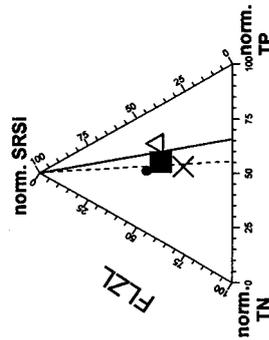
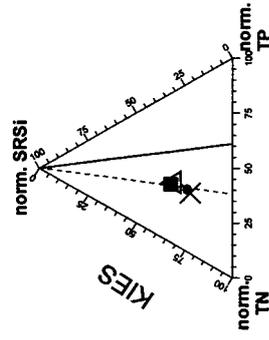
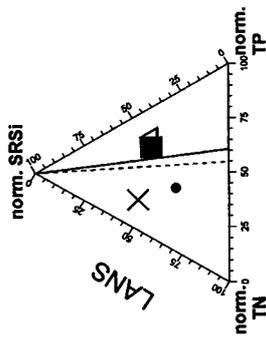
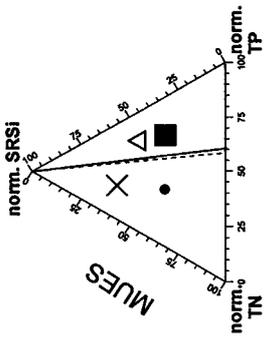
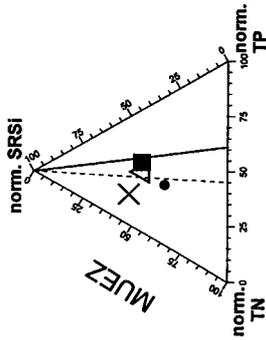
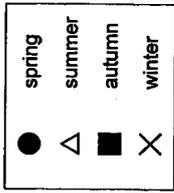


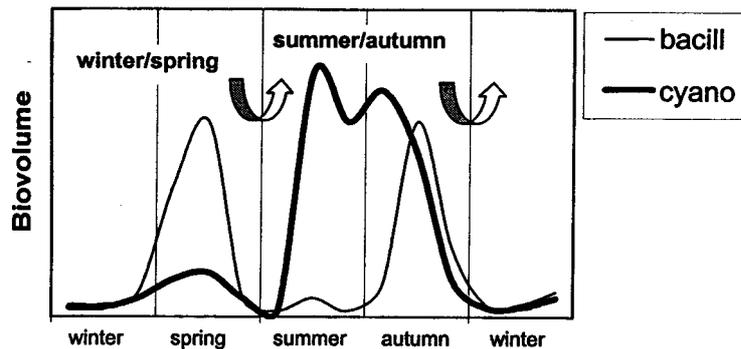
**Fig. 6.** Contribution of biovolume to total of Cyanobacteria (%) of *Planktolyngbya subtilis*, *Aphanizomenon flos-aquae* and *Planktothrix agardhii* (summer/autumn species) versus *Limnothrix redekei* (reference species for winter/spring period, Fig. 4D) in different seasons.



**Fig. 7.** Contribution of biovolume to total of Bacillariophyceae (%) of *Aulacoseira* spp. and *Actinocyclus normanii* (summer/autumn species) versus *Stephanodiscus neoastrea* and *Nitzschia acicularis* (winter/spring species) in different seasons (for seasonality of species, see coefficients in Fig. 5D, for *Aulacoseira* species see legend for Fig. 3).

per year (winter/spring and summer/autumn) the overall success rate using the DA would be increased from 60% to 88% for cyanobacterial and from 50% to 82% for the diatom assemblages. This indicates that the compositional changes for cyanobacteria and diatoms in the investigated lakes were synchronised (see arrows in scheme in Fig. 9). Significant compositional changes for both algal classes occurred only twice a year: during the transition from spring to summer and from autumn to winter. Therefore, for both algal classes, species composition always changed at transitions from turnover to more stable stratified conditions. The species composition in winter is maintained until spring, that of summer until autumn. In summer/autumn, the species composition of both algal groups remains stable, but diatom biomass fluctuates throughout the summer and peaks in autumn in contrast to cyanobacteria. Correspondingly, individual cyanobacterial and diatom species showed a preference for either the winter/spring or summer/autumn periods, but never for a combination of other periods e.g. spring/summer and autumn/winter.





**Fig. 9.** Scheme for seasonal dynamic of diatoms and cyanobacteria. The arrows indicate the changes in species composition for both algal classes, cyanobacteria and diatoms. From the point of species composition the four seasons can be distinguished as only two different periods: winter/spring and summer/autumn.

The close correspondence of compositional change of cyanobacteria with diatoms is not surprising in view of the fact that the majority of the investigated lakes are shallow. Minor peaks of diatom biovolumes during the summer blooms of cyanobacteria were more the rule than the exception as previously mentioned. This is analogous to mass development of diatoms in other shallow lakes over the whole year (e. g. Neusiedler See, DOKULIL 1984, DOKULIL & PADISÁK 1993). For mainly deep, stratified lakes, however, heavy blooms of diatoms were described as restricted to spring and autumn (SOMMER et al. 1986, POULÍCKOVÁ 1993). The deepest lake in the investigated data set is the Parsteiner See (maximum depth: 27 m). The overall success rate for a correct classification in the two distinct periods for this lake (cyanobacteria: 91%, diatoms: 100%) is in the same range as for the riverine lakes, e.g. Großer Müggelsee (maximum depth: 7.5 m, overall success rate for cyanobacteria: 88%, for diatoms: 94%). Therefore the distinction of species composition in winter/spring and summer/autumn is consistent for both the shallow polymictic and the deep dimictic lakes in the present data set.

The seasonal dynamics of TN:TP:SRSi indicated that the TN:TP ratios were synchronised with the compositional changes of phytoplankton communities. In all the investigated lake types, similar constituted assemblages of diatoms and cyanobacteria grew in winter/spring under conditions of higher TN:TP ratios, while distinctive summer/autumn assemblages grew

**Fig. 8.** Triangular diagrams for seasonal changes of normalised TN:TP:SRSi ratios. The normalisation was based on the data set including all long term seasonal averages of the 11 waters, but for clarity the results are separately shown for each location. Points on the bold lines indicate the constant molar ratio of TN:TP=16:1 at variable concentrations of SRSi. Points to the left side of this line indicate a ratio TN:TP>16:1, to the right side, TN:TP<16:1. Points on the left side of the dashed line show higher TN:TP ratios compared with points on the right side (for details see Methods).

Data bases:

$$\text{normalised concentration} = C_{\text{norm}} = \frac{100 C}{\sum_{i=1}^n C_i} ; \sum_{i=1}^n \text{TN}_i = 3644.62, \sum_{i=1}^n \text{TP}_i = 147.98, \sum_{i=1}^n \text{SRSi}_i = 2463.16,$$

calculation of the point of intersection for line for TN:TP=16:1 on the TN-TP axis (see Methods).

under comparatively lower TN:TP ratios. In contrast to TN:TP, the dynamic of SRSi in relation to the two macrolelements was largely influenced by hydrological and morphometric differences. Higher SRSi concentration during summer/autumn in proportion to TN and TP and lower concentration during winter/spring were measured only in lakes with longer retention time like Rosinsee, Parsteiner See (dimictic, mesotrophic lakes) and Kiessee (gravel pit lake). The seasonal trends of the rapidly cycled elements P and N are therefore in all investigated lakes comparable, in contrast to relatively conservative Si, which is recycled at longer intervals. A general trend of nutrient dynamics for all the investigated lakes was consequently only detected for TN:TP, but not for SRSi. Nevertheless, the synchronisation of seasonal variations of TN:TP with seasonal changes of phytoplankton, cannot be reduced to a causal relationship (nutrient sources for algal growth) but must be seen in a wider context.

## Conclusion

In meso- to hypertrophic, shallow and moderately deep lakes of the North German region seasonal changes in species composition in cyanobacterial assemblages corresponded to those of diatoms. The seasonal composition of planctonic cyanobacterial and diatom assemblages can be distinguished by two different periods: winter/spring and summer/autumn. For both algal classes, therefore significant compositional changes were recognisable only two times a year, during the transition from spring to summer and from autumn to winter. These compositional changes of phytoplankton were synchronised with seasonal variations of the TN:TP ratios.

## Acknowledgement

Sampling and chemical analysis (1990-91) were done in co-operation between the Department of Ecology at Humboldt-University (HUB, headed by Prof. J.-G. Kohl) and the Department of Limnology at Technical University of Berlin (headed by Prof. W. Rippl) during a research project on regional limnology. Studies from 1992-94 were supported by a project of the Bundesministerium für Forschung und Technologie at the HUB (BEO 339400 A). I am grateful to Mrs. Wachsmuth (HUB) for phytoplankton counts from Langer See 1993 and assistance in diatom preparation. I also thank Prof. M.T. Dokulil for critical reviewing the manuscript and Dr. Steven Lowry for English corrections.

## References

- BARTELL, S.M., ALLEN, T.F.H. & KOONCE, J.F. (1978): An assessment of principal component analysis for description of phytoplankton periodicity in Lake Wingra. – *Phycologia* **17**: 1-11.
- DAVEY, M.C. (1987): Seasonal variation in the filament morphology of the freshwater diatom *Melosira granulata* (Ehrenb.) Ralfs. – *Freshwat. Biol.* **18**: 5-16.
- DOKULIL, M. (1984): Assessment of components controlling phytoplankton photosynthesis and bacterioplankton production in a shallow, alkaline, turbid lake (Neusiedlersee, Austria). – *Internat. Rev. ges. Hydrobiol.* **69**: 679-727.
- DOKULIL, M. & PADISÁK, J. (1993): Langfristige (1968 -1990) und jahreszeitliche Dynamik der planktischen Diatomeen im Neusiedler See. – In: *BFB-Bericht* 79, 5-11; Biologisches Forschungsinst. für Burgenland, Illmitz.
- DOKULIL, M.T. & TEUBNER, K. (1999): Cyanobacterial dominance in eutrophic lakes. Causes-Consequences-Solutions. – *J. Lake Science China*, in press.

- DUDEL, G. & KOHL, J.-G. (1991): Contribution of dinitrogen fixation and denitrification to the N-budget of shallow lake. – Verh. Internat. Verein. Limnol. **24**: 884-888.
- 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.
- HECKY, R.E., KLING, H.J. & BRUNSKILL, G.J. (1986): Seasonality of phytoplankton in relation to silicon cycling and interstitial water circulation in large, shallow lakes of Central Canada. – Hydrobiologia **138**: 117-126.
- HENRION, G., HENRION, A. & HENRION, R. (1988): Beispiele zur Datenanalyse mit Basic-Programmen. – 1-363; Dt. Verl. der Wissensch., Berlin.
- HENRION, R. & HENRION, G. (1995): Multivariate Datenanalyse. Methodik und Anwendung in der Chemie und verwandten Gebieten. – 1-261; Springer-Verlag, Berlin-Heidelberg-New York-London-Paris-Tokyo-Hong Kong-Barcelona-Budapest.
- KISS, K.T., LE COHU, R., COSTE, M., GENKAL, S.I. & HOUK, V. (1990): *Actinocyclus normanii* (Bacillariophyceae), in some rivers and lakes in Europe. Morphological examinations and quantitative relations. – Ouvrage dédié à H. Germain: 111-123.
- KOHL, J.-G. & GIERSDORF, K. (1991): Competition ability of two planktic diatoms under different vertical light gradients, mixing-depth and -frequencies: An experimental approach. – Verh. Internat. Verein. Limnol. **24**: 2652-2656.
- KOHL, J.-G., SCHLANGENSTEDT, 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.
- KOMÁREK, J. & ANAGNOSTIDIS, K. (1999): Cyanoprokaryota. 1. Teil Chroococcales. – In: Süßwasserflora von Mitteleuropa. – 1-548; Gustav Fischer, Jena.
- MEFFERT, M.-E. (1975): Analysis of the population dynamics of *Oscillatoria redekei* van Goor in Lake Edeberg. – Verh. Internat. Verein. Limnol. **19**: 2682-2688.
- NICKLISCH, A. (1994): Does mortality by nitrogen deficiency influence the succession of *Limnothrix 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.
- POULICKOVÁ, A. (1993): Ecological study of seasonal maxima of centric diatoms. – Algal. Stud. **68**: 85-106.
- REYNOLDS, C. S. (1984): Phytoplankton periodicity: The interactions of form, function and environmental variability. – Freshwat. Biol. **14**: 111-142.
- SCHREURS, H. (1992): Cyanobacterial dominance – relations to eutrophication and lake morphology. – Academisch Proefschrift, Universiteit van Amsterdam.
- SEIP, K.L. & REYNOLDS, C. S. (1995): Phytoplankton functional attributes along trophic gradient and season. – Limnol. Oceanogr. **40**: 589-597.
- 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. – Freshwat. Biol. **20**: 279-287.
- STEVENSON, R.J. & WHITE, K.D. (1995): A comparison of natural and human determinants of phytoplankton communities in the Kentucky River basin, USA. – Hydrobiologia **297**: 201-216.
- 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 Gewässern der Region Berlin-Brandenburg. – Ph. D. Thesis, Humboldt-Universität zu Berlin, 1-232.
- (1997): Merkmalsvariabilität bei planktischen Diatomeen in Berlin-Brandenburger Gewässern. – Nova Hedwigia **65**: 233-250.

- TEUBNER K., FEYERABEND, R., HENNING, M., NICKLISCH, A., WOITKE, P. & KOHL, J.-G. (1999): Alternative blooming of *Aphanizomenon flos-aquae* or *Planktothrix agardhii* induced by the timing of the critical nitrogen:phosphorus ratio in hypertrophic riverine lakes. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **54**: 325-344.
- 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 blue-green algae. – J. Plankton Res. **6**: 699-713.
- UTERMÖHL, H. (1958): Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. – Mitt. int. Verein. Limnol. **9**: 1-38.
- VAN LIERE, L. & MUR, L.R. (1980): Occurrence of *Oscillatoria agardhii* and some related species, a survey. – Developments in Hydrobiology **2**: 67-77.
- ZEVENBOOM, W. & MUR, L.R. (1980): N<sub>2</sub>-fixing cyanobacteria: Why they do not become dominant in Dutch, hypertrophic lakes. – Developments in Hydrobiology **2**: 123-130.