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Cyanobacterial dominance in lakes

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Abstract

Cyanobacterial dominance in lakes has received much attention in the past because of frequent bloom formation in lakes of higher trophic levels. In this paper, underlying mechanisms of cyanobacterial dominance are analyzed and discussed using both original and literature data from various shallow mixed and deep stratifying lakes from temperate and (sub)tropical regions. Examples include all four ecotypes of cyanobacteria sensu Mur et al. (1993), because their behavior in the water column is entirely different. Colony forming species (*Microcystis*) are exemplified from the large shallow Tai Hu, China. Data from a shallow urban lake, Alte Donau in Austria are used to characterize well mixed species (*Cylindrospermopsis*), while stratifying species (*Planktothrix*) are analyzed from the deep alpine lake Mondsee. Nitrogen fixing species (*Aphanizomenon*) are typified from a shallow river-run lake in Germany. Factors causing the dominance of one or the other group are often difficult to reveal because several interacting factors are usually involved which are not necessarily the same in different environments. Strategies for restoration, therefore, depend on both the cyanobacterial species involved and the specific causing situation. Some uncertainty about the success of correctives, however, will remain due to the stochastic nature of the events and pathways leading to cyanobacterial blooms. Truly integrated research programs are required to generate predictive models capable of quantifying key variables at appropriate spatial and temporal scales.

Introduction

The phytoplankton of many lakes, especially those of higher trophic levels, is dominated by large, colony-forming species of cyanobacteria (formerly referred to as blue-green algae) such as *Microcystis, Planktothrix, Limnothrix, Anabaena*, or *Aphanizomenon.* Permanent cyanobacterial dominance is, therefore, regarded as the ultimate phase of eutrophication occurring world-wide (e.g. Robarts, 1985; Jones, 1994; Pizzolon et al., 1999). Despite considerable research summarized in Schreurs (1992), the reasons for such outbreaks largely remain unclear. Excessive abundance or ‘blooming’ of cyanobacteria generally has detrimental effects on the domestic, industrial and recreational uses of water bodies and is in many cases a direct motivation for restoration measures.

Because of their success and ubiquity in freshwater systems, cyanobacteria are probably the best studied group of phytoplanktonic micro-organisms (Stanier & Cohen-Bazire, 1977; Bryant, 1994). Several of their prokaryotic properties such as gas-vesicles, low CO_2/high pH optimum and nitrogen-fixation bear special ecological significance. These and further molecular characteristics of cyanobacteria are described in more detail in Schreurs (1992), Mur et al. (1993) and Bryant (1994).

Not all features are present in all cyanobacterial forms. The extent to which certain characteristics are expressed is dependent on the form and the size of the organism. For instance, the formation of colonies or aggregates is of decisive importance for the physiology and behavior of cyanobacteria.

In practice, the planktonic cyanobacteria can be divided into four ecotypes according to their behavior in the water column (Schreurs, 1992; Mur et al., 1993):

1. Species able to fix N_2 (e.g. *Aphanizomenon flos-aquae, Cylindrospermopsis raciborskii*).
2. Stratifying species (e.g. *Planktothrix rubescens*). This ecotype flourishes in a certain ‘optimal’

depth, usually the metalimnion, because of the ability to fine-tune their buoyancy regulation. They grow in solitary filaments (Reynolds, 1987).

3. Turbulent species (e.g. *Limnothrix redekei, Planktothrix agardhii*). This group is usually well-mixed in the epilimnion. Species do not fix N_2, and are not stratifying or migrating.
4. Colony or aggregate forming species (e.g. *Microcystis* and *Aphanizomenon*). Daily excursions through the epilimnion possible because of their large unit size (Humphries & Lyne, 1988; Kromkamp & Walsby, 1990).

Some species may be classified into several of the above mentioned groups (e.g. *Aphanizomenon flos-aquae*) which can fix nitrogen, may form aggregates or thrive in mixed conditions. Moreover, it can stratify as solitary filaments (Konopka, 1989). In some cases, further differentiation is possible based on detailed physiological information. Among the turbulent species, *Limnothrix redekei* can be differentiated from *Planktothrix agardhii* by their appearance in different seasons (Teubner, 1996, 2000) due to temperature and light preferences (Foy et al., 1976; Niklisch & Kohl, 1989).

This review summarizes the causes and consequences of cyanobacterial dominance based on examples from all four ecotypes. Solutions are presented to reduce eutrophication and bloom-forming cyanobacterial species.

Causes of cyanobacterial dominance

When lakes become more eutrophic, the diversity of the phytoplankton assemblage decreases ultimately leading to the dominance of cyanobacteria. Bloom formation may result in surface scums, producing unpleasant taste and odors, and are an unsatisfactory food source for many organisms in the food-web (Andersen, 1997). Although it is clear that the increased input of nutrients is the prime cause of the heavy selective pressure on the phytoplankton, it is the system as a whole which determines the final result of this process (Smith et al., 1987). Besides nutrients, the morphology of lakes is of decisive importance for cyanobacterial development. According to Schreurs (1992), long-term dominance by filamentous species is related to shallow lake depth, while colony forming species are more commonly dominating in deeper lakes.

Hypotheses to explain the success of cyanobacteria are several and include the following:

1. Elevated temperatures as the cause of increased abundance of cyanobacteria especially during summer because of their, in general, higher temperature optima compared to other algal groups. This belief has been substantiated by many authors both in the field and experimentally (e.g. Jackson, 1964; Tilman & Kiesling, 1984; McQueen & Lean, 1987; Robarts & Zohary, 1987).
2. Low light-energy requirements of cyanobacteria as the steering factor for bloom formation derived largely from physiological studies of individual species (e.g. Zevenboom & Mur, 1980; Niklisch & Kohl, 1989; Schreurs, 1992).
3. Superior uptake kinetics for inorganic carbon (low CO_2/high pH-hypothesis) was postulated to be responsible for cyanobacterial dominance by King (1970) and Shapiro (1984, 1990). In lakes of low alkalinity, carbon dioxide availability did not initiate blue-green maxima but was largely responsible for their maintenance (Shapiro, 1997).
4. Low TN/TP-ratios are beneficial for both nitrogen and non-nitrogen fixing species of cyanobacteria formalized by Smith (1983) and substantiated or disregarded by several authors. In some cases, it is the timing when the critical ratio is reached rather than the ratio itself which is important for the dominance of one or another species (Teubner et al., 1997).
5. The inorganic nitrogen hypothesis suggests that the forms and amounts of inorganic nitrogen favor different algal groups. Non-N-fixing cyanobacteria are favored by ammonium-nitrogen, while eukaryotic phytoplankton develops when nitrate-nitrogen is the main N-component present. Scarcity of nitrogen induces nitrogen-fixation and hence favors the development of species capable to fix molecular nitrogen (Blomquist et al., 1994). For a detailed discussion of the inorganic nitrogen hypothesis, refer to Hyenstrand et al. (1998).
6. Cyanobacteria migrating from the sediment to the water column gain competitive advantage by storage of internal phosphorus reserves (Pettersson et al., 1993).
7. Cyanobacteria have higher requirements for trace elements compared with eukaryotic phytoplankton as reviewed by Reuter & Petersen (1987).
8. The buoyancy hypothesis is related to forms, which bear gas-vesicles, such as *Microcystis* and

Planktothrix, and are therefore able to use water column stability as a resource (review by Reynolds et al., 1987). They can either accumulate at some intermediate depth where conditions favour them or rise to the water surface where light and carbon dioxide are available. Other cyanobacteria, such as *Limnothrix* or *Aphanizomenon*, are more dependent on higher turbulence (Dokulil & Mayer, 1996; Teubner, 1996).

9. The minimization of mortality through an immunity to grazing by zooplankton has been hypothesized by Porter (1973) and substantiated by field and laboratory observations (e.g. Burns, 1987; Haney, 1987; Lampert, 1987).
10. Suppression of the growth of other algae through the excretion of organic compounds (Murphy et al., 1976; Keating, 1978).
11. Toxin production by toxigenic strains of cyanobacteria affecting natural grazers and other aquatic biota (Lindholm et al., 1989). Species of the genera *Oscillatoria* and *Anabaena* are among the most distributed toxin producers in eutrophicated freshwaters (Berg et al., 1986).

Further factors important for blue-green dominance are the recruitment from the sediments (Trimbee & Harris, 1984), oxygen depletion in the water column and anoxic conditions at the sediment–water interface (Trimbee & Prepas, 1988), and the structure and composition of fish populations (Fott et al., 1980).

Rarely will a single factor be responsible for the mass appearance of cyanobacteria but a combination of several of them, including hydrodynamic effects may influence their dominance (e.g. Spencer & King, 1989; Dokulil & Mayer, 1996). Accumulating data indicate that food-web dynamics involving stoichiometric feedback mechanisms appear to be of crucial importance (Elser, 1999). The occurrence of cyanobacterial blooms can thus be viewed as a probabilistic event ultimately dependent on highly complex non-linear food web interactions subject to chaotic dynamics (Andersen, 1997; Elser, 1999). Interaction of factors in such catastrophic systems leads to hysteresis in its response to control variables. Dominance of cyanobacteria can, therefore, be an alternative stable state of the algal community in lakes (Scheffer et al., 1997).

Discussion of factors affecting cyanobacterial dominance

The production of high persistent concentrations of biomass is closely linked with eutrophication of lakes. Associated with the dominance of cyanobacteria are several negative effects, such as reduced transparency, decreased biodiversity, elevated primary production and the potential occurrence of oxygen depletion, which may result in massive fish kills, odor and taste compounds, as well as production of toxins (Reynolds, 1991). Cyanobacterial toxins pose a severe potential health hazard causing anything from skin irritation to sublethal intoxication and maybe most harmful through chronic uptake with drinking water leading to liver damage (Chorus, 1993, 1995). Impairment of water quality for many purposes is the result of all these processes.

Since consequences of eutrophication and cyanobacterial dominance as well as their possible correctives are closely linked to the ecotypes mentioned in the introduction, effects will be discussed using examples from various lake types. Colony forming species (*Microcystis* spp.) are exemplified from the large shallow Tai Hu, China. Data from a shallow urban lake, Alte Donau in Austria and some hypertrophic riverine lakes in Germany are used to characterize well mixed species such as *Cylindrospermopsis raciborskii* and *Planktothrix agardhii*. Data on *Planktolyngbya subtilis* originate from a shallow eutrophic lake in Germany. The stratifying species *Planktothrix rubescens* is analyzed from the deep alpine lake Mondsee. Nitrogen fixing species (*Aphanizomenon flos-aquae*) will be typified from a shallow riverine lake in Germany.

Detailed descriptions of the lakes can be found in Cai et al. (1994) for Tai Hu, in Dokulil & Mayer (1996) and Mayer et al. (1997) for Alte Donau, and in Dokulil & Skolaut (1986) and Dokulil (1993) for Mondsee. For the riverine, Northeast-German lakes consult Teubner (1996).

Discussion of steering factors for cyanobacterial dominance focuses primarily on water-temperature and the average under-water light climate, expressed here as the ratio of mixing depth to Secchi-depth (z_m/z_s). If Secchi-depth is used as a proxy for the euphotic zone ($z_{eu} = 3 \times z_s$), the ratio indicates the proportions of light and dark that an algal cell experiences in a mixed water column. The higher the ratio, the greater is the mixed zone relative to the illuminated part of the water column and with it the relative time spent in darkness by the algal cells. At

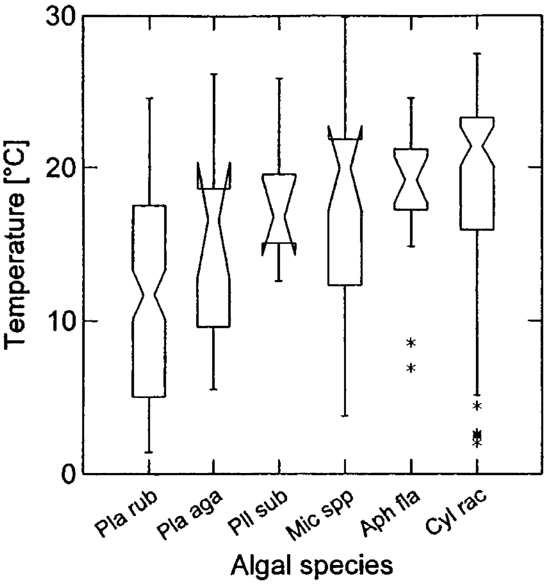

Figure 1. Notched Box-and-Whisker plots of water-temperature for the following algal species: Pla rub – *Planktothrix rubescens*; Pla aga – *Planktothrix agardhii*; Pll sub – *Planktolyngbya subtilis*; Mic spp – *Microcystis* spp.; Aph fla – *Aphanizomenon flos-aquae*; Cyl rac – *Cylindrospermopsis raciborskii.* Boxes are notched at the median and return to full width at the lower and upper confidence interval. The edges of the box include the central 50% of the data. Maximum and minimum values are indicated by whiskers. Outside values are marked by asterix.

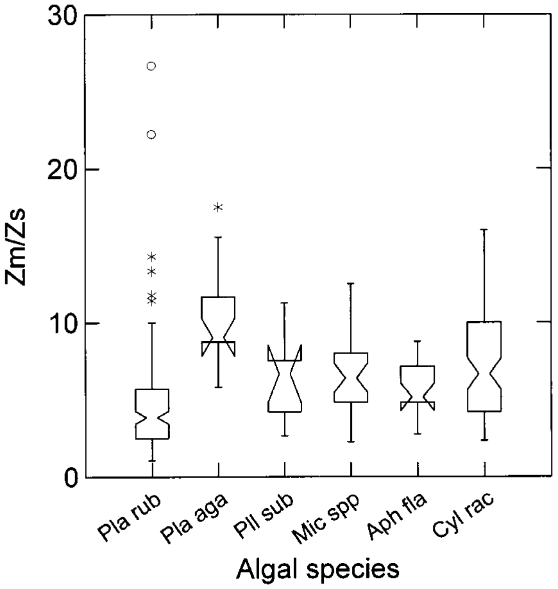

Figure 2. Notched Box-and-Whisker plot for the relation of mixing depth (z_m) to Secchi-depth (z_s) used as light climate correlative. Abbreviations of species and explanations as in Figure 1.

ratios at or below 3, the circulation depth is equal or less than the euphotic depth and hence the algal assemblage remains within the illuminated part of the water column.

Temperature preferences of the algal species are shown in Figure 1. The deep stratifying species, *P. rubescens*, is clearly separated from all other species by its preference for lower temperatures (median 11.7 °C). The highest median temperature of 21.4 °C occurs with *Cylindrospermopsis raciborskii*, a species preferring well mixed environments which differs significantly from both *Planktothrix*-species and from *Planktolyngbya* (Figure 1). The four mixed species arranged between these two forms do not differ significantly from each other. Variability between the forms is greatest in *Planktothrix agardhii* as indicated by the confidence limits in Figure 1.

Based on their light climate preferences both *Planktothrix*-species differ from all other forms (Figure 2). The median of the ratio z_m/z_s is highest in *P. agardhii* indicating that the species can tolerate situations of frequent light fluctuations. This is in agreement with experimental evidence from Foy & Gibson (1982) and Nicklisch & Kohl (1989). In contrast, *P. rubescens* requires more stable conditions. The other four species are intermediate with median ratios of about 6.

Net growth rates calculated from population biomass changes in lakes can now be related to the combined effects of temperature and the average light climate correlative. Positive net rates of population biomass change of *Cylindrospermopsis raciborskii* are shown in Figure 3 in relation to water temperature and the ratio z_m/z_s based on data by Dokulil & Mayer (1996). Growth rates are low at temperatures below 15 °C and z_m/z_s-ratios lower than 10. Rates between 0.10 and 0.15 per day are associated with temperatures >20 °C and, in some cases, light correlatives greater than 10. Comparison between different species or ecotypes is facilitated through two-dimensional projection as shown in Figure 4. In this figure, species are arranged in ascending order of temperature preference (comp. Figure 1). Species, such as *Planktothrix rubescens*, from the metalimnion of a stratified systems grow best at low temperatures and low light climate correlatives. Growth at higher temperatures requires low z_m/z_s-ratios similar to *Planktlyngbya subtilis* which seems to be restricted to temperatures greater than 12 °C. *Planktothrix agardhii* in mixed water columns is related to high z_m/z_s-ratios at a median temperature of 16.6 °C. At a similar range of

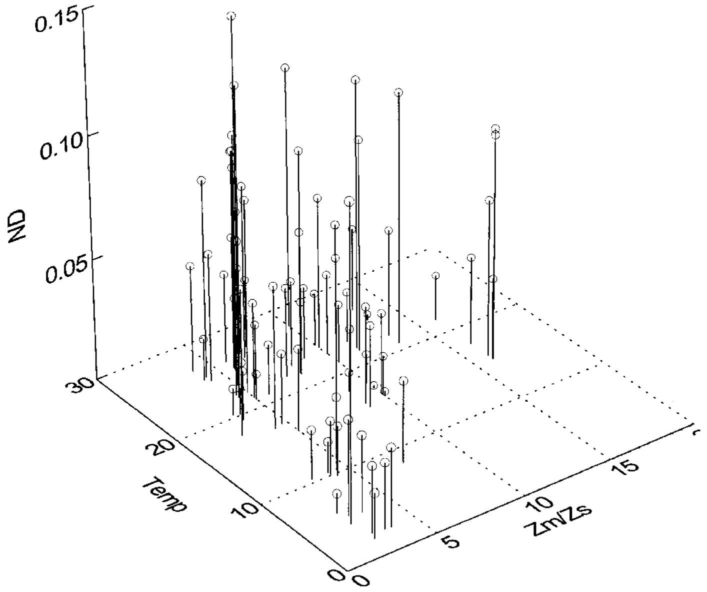

Figure 3. Three-dimensional plot of positive net rates of biomass change (ND) for *Cylindrospermopsis raciborskii versus* water-temperature and the light climate correlative (z_m/z_s).

z_m/z_s-ratios (2–16) and temperatures >20 °C, *Cylindrospermopsis raciborskii* proliferates. Ecotypes of the colony forming group (*Microcystis* spp.) and nitrogen fixing species such *A. flos-aquae* are generally associated with z_m/z_s ratios <10 but have a wide temperature tolerance.

Dependence of annual average cyanobacterial percentage share in relation to annual mean inlake-TP concentrations is shown in Figure 5, upper panel. Results are separated into at least two groups: in the stratified *P. rubescens*-lake, cyanobacteria dominate the phytoplankton biomass at TP-concentrations of around 10 μg l^{-1}. In all the mixed systems, cyanobacteria are abundant at total phosphorus concentrations of >40 μg l^{-1}. Schreurs (1992) estimated ranges of 10–50 μg $l^{-1}$and >50 μg l^{-1} for stratified and mixed systems respectively from the data set he used. For the mixed type of *Planktothrix*-lakes, he reports concentrations of greater than 80 μg l^{-1}. In the present data set, percent abundance of cyanobacteria is high at TP-levels >100 μg l^{-1} when *P. agardhii* or *A. flos-aquae* dominates (Figure 5, upper panel).

Differences in growth rates or uptake kinetics for P-limited growth can not explain the large differences in total phosphorus concentrations required by the two *Planktothrix* species (Andersen, 1997). Growth rates and minimal cell quotas for phosphorus are quite comparable for *P. rubescens* and *P. agardhii*.

Table 1. Mean, minimum and maximum positive net biomass changes calculated from field data (net growth rates, d^{-1}) for the investigated species. Published maximum growth rates in the laboratory are from Istvanovics et al. (2000)* and Andersen (1997, Table A10, p. 265)$^{\$}$

Species/Net growth rate	Mean	Min.	Max.	Max. publ.
Planktolyngbya subtilis	0.032	0.010	0.081	
Cylindrospermopsis raciborskii	0.042	0.002	0.138	1.00*
Planktothrix rubescens	0.048	0.001	0.316	
Planktothrix agardhii	0.063	0.002	0.243	0.57$^{\$}$
Microcystis spp.	0.073	0.001	0.307	0.81$^{\$}$
Aphanizomenon flos-aquae	0.117	0.007	0.423	0.97$^{\$}$

A possible explanation is their different niches in the water-column. Stratifying cyanobacteria are associated with light climate correlatives (z_m/z_s) of about 4 (Figure 5, lower panel), a value where approximately 1% of surface irradiance reaches the metalimnion. The combination of light climate and temperature preferences is responsible for the fine-tuning of the metalimnetic occurrence of *P. rubescens* when nutrient concentrations are moderate. These subsurface maxima are optimized by light absorption through chromatic adaptation and buoyancy regulation (Zimmermann, 1969; Findenegg, 1971; Klemer, 1976;

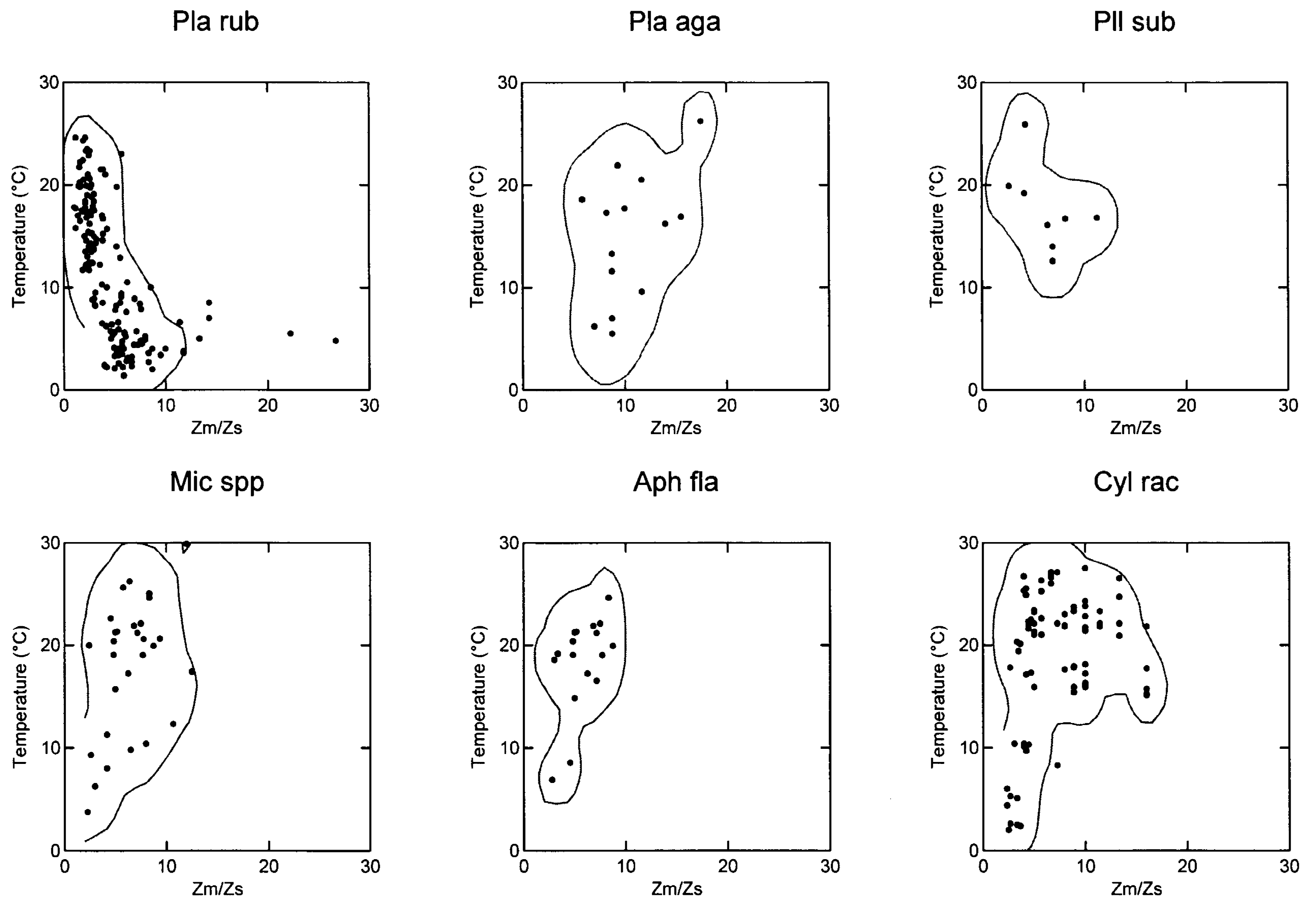

Figure 4. Two-dimensional projections of net biomass changes versus water-temperature and z_m/z_s for the species indicated. Abbreviations of species as in Figure 1.

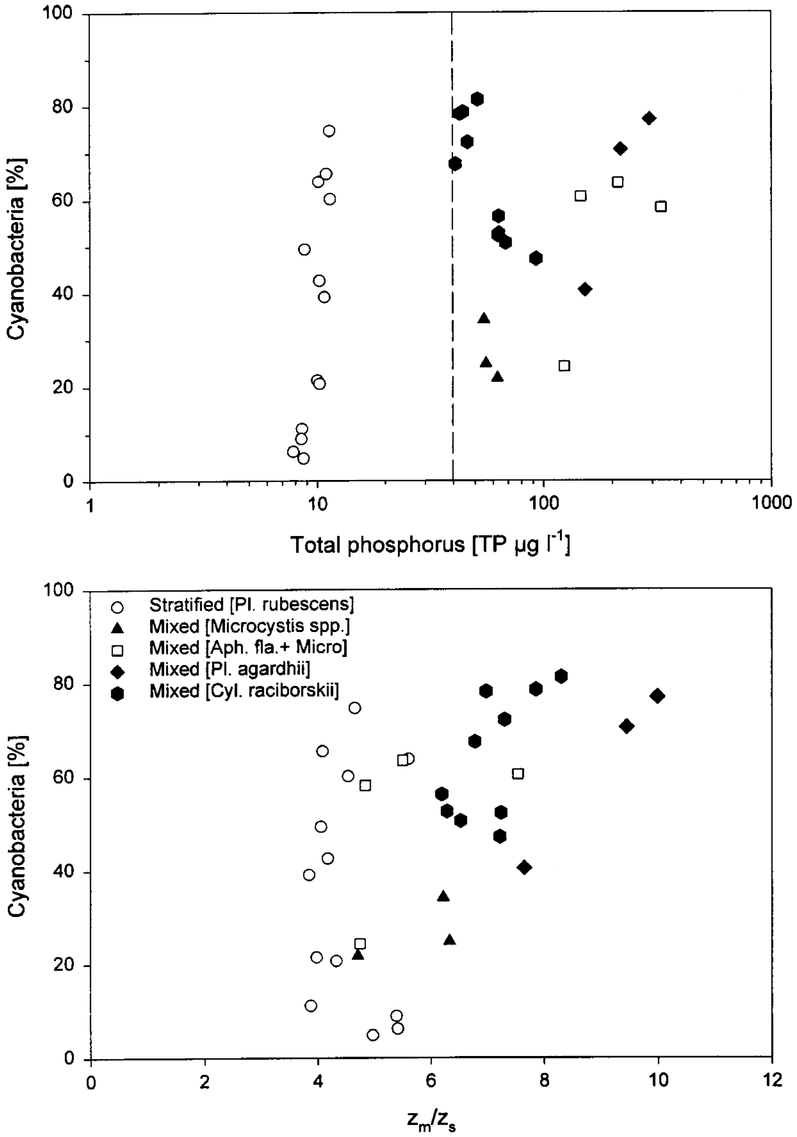

Figure 5. Cyanobacterial share in total algal biomass as a function of epilimnetic total phosphorus concentration (upper panel) and as a function of z_m/z_s (lower panel). Data are annual averages.

Konopka, 1982; Walsby, 1987; see also the discussion in Schreurs, 1992). For well-mixed populations in shallow lakes, ratios of $z_m/z_s > 6$ are required (Figure 5, lower panel). In such turbulent conditions with low light availability in the water column, cyanobacterial dominance is supported when *Microcystis, P. agardhii* or *C. raciborskii* are present.

Average net growth rates estimated from field data (Table 1) generally agree with published data from cultures summarized in Andersen (1997). Highest growth in the field and greatest ranges were observed in *A. flos-aquae* followed by *Microcystis* spp. and *P. agardhii.* Maximum growth rates from laboratory cultures follow the same sequence.

Published phosphorus uptake affinities are lowest in *A. flos-aquae,* highest in *Microcystis aeruginosa,* and intermediate in *P. agardhii,* while *Cylindrospermopsis raciborskii* is opportunistic (Istvanovics et al., 2000) confirming more or less their placement on the phosphorus axis in Figure 5. The storage capacity for phosphorus however is similar in *M. aeruginosa* and *P. agardhii.* Therefore, the two species can compete

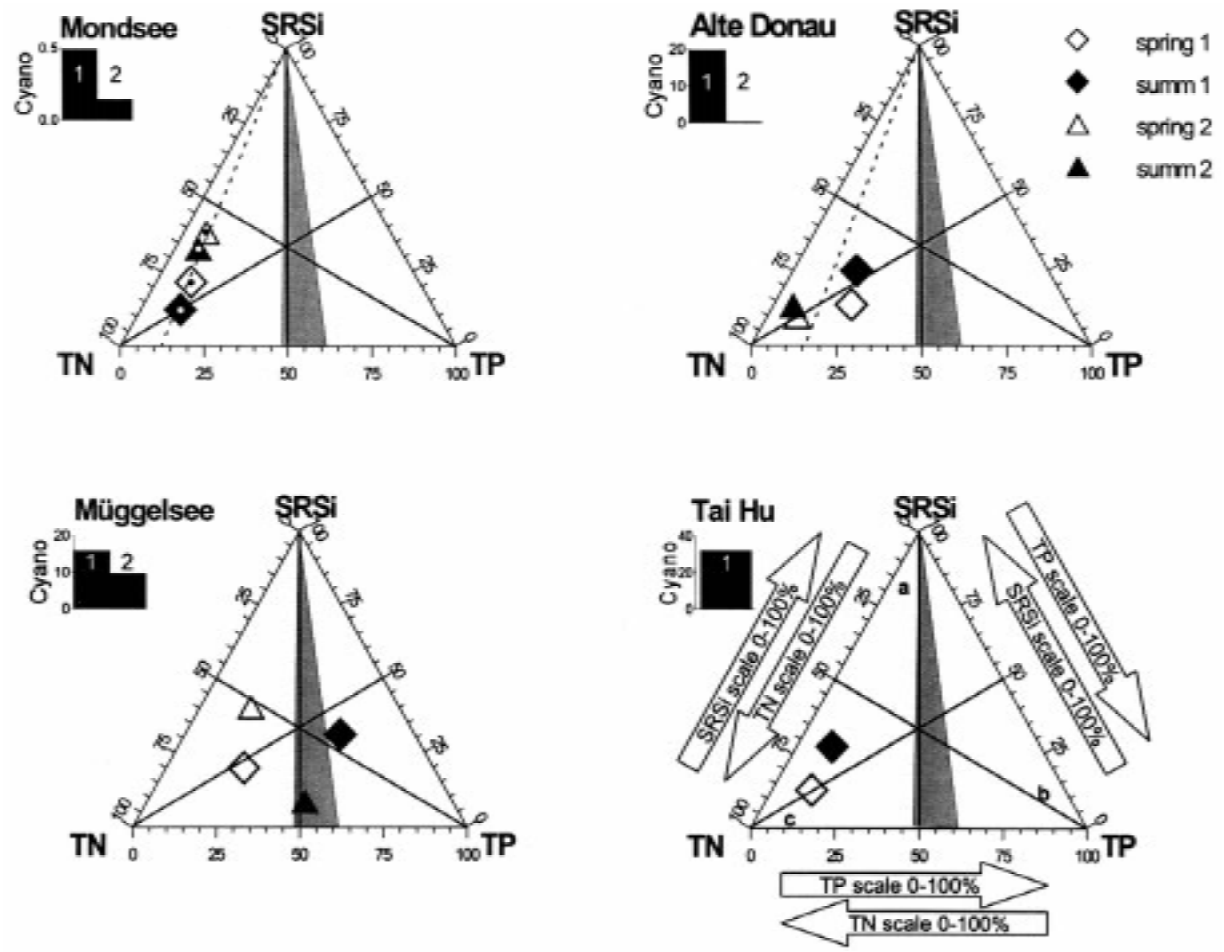

Figure 6. Triangular representation of TN:TP:SRSi ratios for spring and summer in four lakes dominated by *Planktothrix rubescens* (Mondsee), *Cylindrospermopsis raceborskii* (Alte Donau), *Aphanizomenon flos-aquae*/*Microcystis* spp. (Müggelsee) and *Microcystis* spp. (Tai Hu). Each point represents the sum of TN, TP and SRSi equal to 100%. The corners of a triangle represent the concentration of one element only (100%) and the absence of the remaining two nutrients. Reading of the triangles is exemplified in the display 'Tai Hu': The two arrows on the TN-TP-axis indicate that the concentrations for TP runs from left to right and for TN from right to left. Similarly for the two other axis. Because of standardization of the TN:TP:SRSi ratios to the optimum ratio of 17:16:1, the nutrients scaled in physiological proportions (Teubner, 1996, 2000). The intersection of the three solid lines in the centre indicate the triple optimum ratio TN:TP:SRSi=16:1:17. Solid lines indicate optimum molar ratios TN:TP=16:1 (a), SRSi:TN=17:16 (b) and SRSi:TP=17:1 (c); the shadowed area the range of TN:TP from 17:1 to 10:1; the dotted lines separate years with cyanobacterial mass development with low TN:TP from other plankton years with high TN:TP ratios. For example: points have on the left side of line 'a' ratios TN:TP>16:1, on the right side TN:TP<16:1 at variable SRSi. For Müggelsee, the dotted line is overlaid by the line for the optimum ratio of TN:TP=16:1. Bar charts indicate years with high (1) and low (2) cyanobacterial biomass [$\mathrm{mm}^3\ \mathrm{l}^{-1}$].

or even co-exist. Optimum molar N:P ratios do not differ significantly between *Microcystis wesenbergii* (18) and *P. agardhii* (12–21), but are much lower (5.0–8.5) in *M. aeruginosa* (see Andersen, 1997 for references). *Cylindrospermopsis raciborskii* seems to be a successful competitor in a wide variety of environments because of high P-storage adaptation and high P-uptake affinity (Istvanovics et al., 2000).

Cyanobacterial dominance cannot be viewed independently from other members of the phytoplankton. Changes in the structure of phytoplankton dominance caused by TN:TP ratios are, therefore, interrelated to SRSi:TN and SRSi:TP ratios. The molar ratios of the three elements (N, P and Si) for the four lakes mentioned above are shown in Figure 6. In the hypertrophic flushed Müggelsee, years with high cyanobacterial biomass are accompanied by particularly

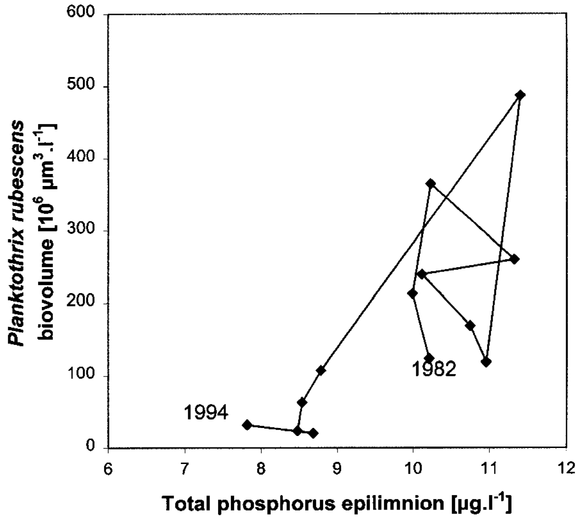

Figure 7. Decrease of *Planktothrix rubescens* biovolume as a function of total epilimnetic phosphorus concentration in the deep stratifying lake Mondsee for the years 1982–1994. Data are annual averages.

low TN:TP ratios at relative high SRSi concentrations (summer 1). The replacement of cyanobacteria in summer by other algae, particularly diatoms, is indicated by relatively high N:P ratios at low Si:N and Si:P proportions (summer 2). The reduction of internal phosphorus-loading from the sediment in the course of in-lake-restoration in Alte Donau effected the replacement of cyanobacteria by other algae. As a result, N:P ratios increased in relation to stronger silica depletion (Figure 6). The N:P ratio in Mondsee increased slightly in years after restoration and was accompanied by the disappearance of *Planktothrix rubescens*.

The lowest N:P ratios, closer to the critical range of 16:1 (range of 10–17:1 see Forsberg & Ryding, 1980), occur in lakes dominated by nitrogen-fixing cyanobacteria in summer (Müggelsee: 70% cyanobacteria, mainly *Aphanizomenon flos-aquae*, Alte Donau: 73% cyanobacteria, mainly *Cylindrospermopsis raciborskii*). In contrast, non N-fixing species of cyanobacteria are usually the dominant contributors to summer plankton in lakes with TN:TP ratios much higher than the optimum ratio of N:P=16:1 (Tai Hu: 57% cyanobacteria, mainly *Microcystis* species, Mondsee: 30% *Planktothrix rubescens*).

Consequences of cyanobacterial dominance do not only depend on the nutrient enrichment, but also on the specific cyanobacterial species involved. Ecological and physiological characteristics, as well as competition between species and interactions to other trophic levels, have to be considered. Dynamics of algal communities can be significantly modified by complex interactions between nutrient supply and food-web structure (Mayer et al., 1997).

Correctives

There are several methods to prevent or reduce long-term cyanobacterial dominance. A necessary prerequisite is almost always a reduction of the nutrient load from the catchment to the lake. In-lake concentrations of C, N and P have to be decreased not only until growth is nutrient limited, but even further until biomass concentrations reach such low concentrations that cyanobacteria are out-competed due to the effects of increased light climate. According to the analysis by Schreurs (1992), the relative probability for prolonged dominance of cyanobacteria is significantly reduced at P-concentrations <100 μg l^{-1}, but still remains high. The absence of abundant cyanobacteria is better guaranteed at levels below 50 μg P l^{-1}, although dominance is still possible.

An example of successful reduction of cyanobacteria of the stratifying ecotype by significant decrease of nutrient load from the catchment is shown in Figure 7 for a deep alpine lake (Dokulil & Jagsch, 1992).

Furthermore, measures to prevent or reduce excessive cyanobacterial biomass must consider the dominant species involved in combination with lake depth and stratification pattern. Metalimnetic populations of the stratifying type of *Planktothrix* can dominate the phytoplankton at summer TP concentrations of 10–15 μg l^{-1} (Steinberg & Hartmann, 1988a, b). Filamentous cyanobacteria of the mixed type such as *P. aghardii*, usually disappear in lakes $<$ 8 m in depth with TP concentrations of around 60 μg l^{-1} (corresponding to chlorophyll-*a* levels of about 40 μg l^{-1}). Mixed type species in deeper lakes ($>$8 m) are low and independent of phosphorus concentrations.

Growth of such homogenous distributed algae is greatly controlled by the average light climate of the water column described here as the ratio z_m/z_s. Cyanobacteria from the *Limnothrix* type can, therefore, be controlled successfully by increasing the light ratio to above 10 (or z_{eu}/z_{mix} = 0.3, Mur et al., 1993).

The behavior of *Microcystis* in the water column is totally different from that of *Limnothrix*. Because *Microcystis*-colonies can regulate their buoyancy, populations can proliferate in somewhat deeper lakes with a higher degree of water column stability. During such periods, they benefit from vertical migration which give them an essential advantage in competing with other phytoplankton species for nutrients and especially light (Humphries & Lyne, 1988; Agusti & Phlips, 1991; Ibelings, 1992). *Microcystis* populations are, therefore, neither regulated by nutrient concentration nor controlled by the amount of biomass. Nutrient reduction will only reduce the maximum biomass formed by *Microcystis*, but not its dominant position in the phytoplankton community. Additional restoration methods are needed to reduce or prevent blooming of *Microcystis*. Artificial mixing of the water column might be particularly useful because deep ($z_{\mathrm{mix}} \gg z_{\mathrm{eu}}$) or intermittent turbulence of the water column reduce the competitive advantage. Mixing should, therefore, be regarded as a quasi-resource (Steinberg & Hartmann, 1988b).

Application of in-lake ecotechnologies will additionally help to reduce both nutrient levels and cyanobacterial biomass. These techniques either aim to remove nutrients from the system or to inactivate them (Ahlgren, 1993; Rönicke et al., 1993). Biomanipulation can be an alternative in shallow lakes but must be considered with care because this method proved to be very lake specific (Perrow et al., 1997). Combinations of these techniques can alter elemental stoichiometry, food-web structure and biological feedback in the desired direction (Teubner et al., 1999). Biomass of cyanobacteria may also be controlled directly by the application of algicides, a technique which is increasingly disregarded because of harmful effects on the ecosystem (Mason, 1996). An alternative approach for the direct elimination of nuisance algae involves the application of microbial organisms as control agents (Sigee et al., 1999). Terrestrial leaf litter, such as barley strew or deciduous leaf litter, releasing algal inhibitors during aerobic decomposition may also be a realistic tool to control excessive algal growth (Ridge et al., 1999). The latter techniques need more elaboration and experimental as well as field testing before they can be generally applied.

Conclusions

Long-term dominance of cyanobacteria is usually caused by a multiplicity of factors. Nutrient concentration, lake morphometry, water-temperature, underwater light availability, mixing conditions and food-web structure are among the most important. Consequences of algal blooms can be severe, depend on the species involved and may include scum-formation and toxicity. Correctives must aim primarily in reducing nutrient loading from the catchment, specifically by controlling P. Additional in-lake ecotechnologies can support more rapid recovery and restoration through manipulating food-web components. Some uncertainty about the success of correctives, however, will remain due to the stochastic nature of the events and pathways leading to cyanobacterial blooms. Truly integrated research programs are required to generate predictive models capable of quantifying key variables at appropriate spatial and temporal scales.

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