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Cyanobacterial Dominance in Eutrophic Lakes: Causes-Consequences-Solutions*

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Abstract: *Cyanobacterial dominance in lakes has received much attention in the past because of the great success and frequent bloom formation in lakes of higher trophic levels. In this paper underlying mechanism 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 Lake Taihu, 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 discussed as well as consequences for restoration measures. Existing knowledge on cyanobacterial dominance is summarized.

Keywords: *cyanobacteria, eutrophication, restoration, algal-blooms*

1. Introduction

The phytoplankton of many lakes, especially those of higher trophic levels, is dominated by large, colony-forming species of cyanobacteria (blue-greens) like *Microcystis, Planktothrix, Limnothrix, Anabaena,* and *Aphanizomenon*. Permanent cyanobacterial dominance is therefore regarded as the ultimate phase of eutrophication (Berger, 1987). Despite considerable research summarised 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 and Cohen-Bazire, 1977). Several of their prokaryotic properties such as gas-vesicles, low CO_2/high pH optimum, and nitrogen-

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fixation bear special ecological significance. These and further characteristics of cyanobacteria are described in more detail in Schreurs (1992) and Mur *et al.* (1993).

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 behaviour of cyanobacteria.

In practice, the planktonic cyanobacteria can be divided into four ecotypes according to their behaviour 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 and Lyne, 1988, Kromkamp and 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) due to temperature and light preferences (Foy *et al.*, 1976; Niklisch and Kohl, 1989).

The aim of the present review is to summarise the causes and consequences of cyanobacterial dominance based on examples from all four ecotypes. Moreover, solutions will be presented to reduce eutrophication and hence bloom-forming cyanobacterial species.

2. 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. Although it is clear that the increased input of minerals 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 minerals, the morphology of lakes is of decisive importance for cyanobacterial development. According to Schreurs (1992) long-term dominance is related with shallow average lake depth, while colony forming species are more commonly dominating in deeper lakes.

Hypotheses to explain the success of cyanobacteria are many and include:

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; McQueen and Lean, 1987; Robarts and Zohary, 1987, Tilman and Kiesling, 1984).

2) Lower light-energy requirements of cyanobacteria as the steering factor for bloom fomation derived largely from physiological studies of individual species (e.g Zevenboom and Mur, 1980; Niklisch and Kohl, 1989; Schreurs, 1992).

3) Superior uptake kinetics for inorganic carbon (CO_2/pH-hypothesis) were postulated to be responsible for cyanobacterial dominance (King, 1970; Shapiro, 1984, 1990).

4) Low N/P-ratios are beneficial for both nitrogen and non-nitrogen fixing species of cyanobacteria formalised 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 buoyancy hypothesis is related to forms, which bear gas-vesicles, such as *Microcystis* and *Planktothrix,* and are therefore capable to use water column stability as a resource (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 turbulences (Dokulil and Mayer, 1996; Teubner 1996).

6) The minimisation of mortality through an immunity to grazing by zooplankton has been hypothesised by Porter (1973) and substantiated by field and laboratory observations (e.g. Burns, 1987; Haney, 1987; Lampert, 1987).

7) In lakes of low alkalinity carbon dioxide availability did not initiate blue-green maxima but was largely responsible for their maintenance (Shapiro, 1997).

8) Suppression of the growth of other algae through the excretion of organic compounds (Murphy *et al.*, 1976; Keating, 1978).

9) Toxin production by toxigenic strains of cyanobacteria affecting natural grazers and other aquatic biota (Linholm *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 and Harris, 1984), oxygen depletion in the water column and anoxic conditions at the sediment-water interface (Trimbee and 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 (e.g. Spencer and King, 1989; Dokulil and Mayer, 1996). Interaction of factors in catastrophic systems leads to hysteresis in its response to control variables. Dominance of cyanobacteria can thus be an alternative stable state of the algal community in shallow lakes (Scheffer *et al.*, 1997).

3. Consequences of 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. Odour and taste compounds as well as production of toxins. Toxins of cyanobacteria can be of very 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 Lake Taihu, 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 raciborski* and *Planktothrix agardhii*. Data on *Planktolyngbya subtilis* originate from a shallow eutrophic lake in Germany. The stratifying species *Planktothrix rubescens* is analysed from the deep alpine lake Mondsee. Nitrogen fixing species (*Aphanizomenon flos-aquae*) will be typified from a shallow riverine lake in Germany.

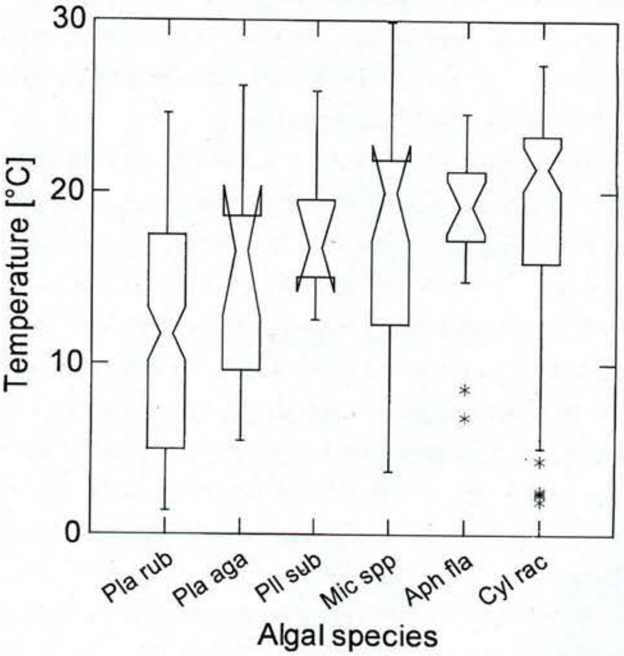
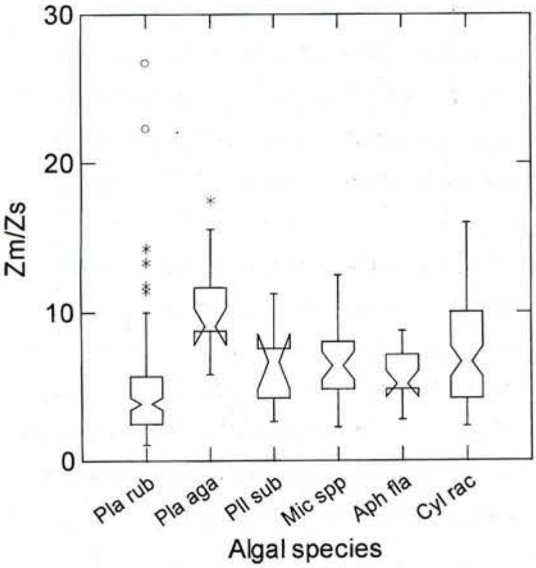


Fig. 1 Notched Box-and-Whisker plots of water-temperature for the following algal species: Pla rub – *Planktothrix rubescens;* Pla aga – *Planktothrix agardhii*; Pll sub – *Planktolyngbya subtilis*; Mic spp – *Microcystis spp.*; Aph fla – *Aphanizomenon flos-aquae*; Cyl rac – *Cylindrospermopsis raciborskii*. 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.

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



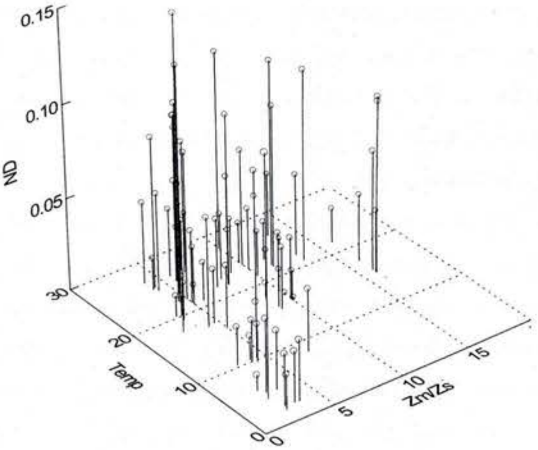


Fig. 2 Notched Box-and-Whisker plot for the relation of mixing depth (z_m) to Secchi-depth (z_s) used as light climate correlative. Abbreviations of species and explanations as in Fig. 1.

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

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).

Temperature preferences of the algal species are shown in Fig. 1. The deep stratifying species, *Pl. 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 in *Cylindrospermopsis raciborskii*, a well mixed species which differs significantly from both *Planktothrix*-species and from *Planktolyngbya* (Fig. 1). The four mixed species arranged between these two forms do not differ significantly from each other. Variability is greatest in *Planktothrix agardhii* as indicated by the confidence limits in Fig. 1.

Both *Planktothrix*-species differ from all other forms by their light climate preferences (Fig. 2). The median of the ratio zm/zs is highest in *Pl. agardhii* indicating that the species can tolerate situations of frequent light fluctuations in agreement with experimental evidence from Foy and Gibson (1982) and Nicklisch and Kohl (1989). In contrast, *Pl. rubescens* needs more stable conditions. The four other 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 Fig. 3 in relation to water temperature and the ratio z_m/z_s based on data by Dokulil and Mayer (1996). Growth rates are small at temperatures below 15°C and z_m/z_s-ratios smaller 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 Fig. 4. In this figure species are arranged in ascending order of temperature preference (comp. Fig.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 *Planktolyngbya subtilis* which seems to be restricted to temperatures grater than 12 ℃. *Planktothrix agardhii* in mixed columns is related to high z_m/z_s-ratios at a median temperature of 16.6 ℃. A similar range of z_m/z_s-ratios (2-16) at temperatures at or above 20 ℃ is found in *Cylindrospermopsis raciborskii*. Ecotypes of the colony forming group (*Microcystis* spp.) and nitrogen fixing species such *Aph. flos-aquae* are associated in general with z_m/z_s ratios < 10 but have a rather wide temperature tolerance.

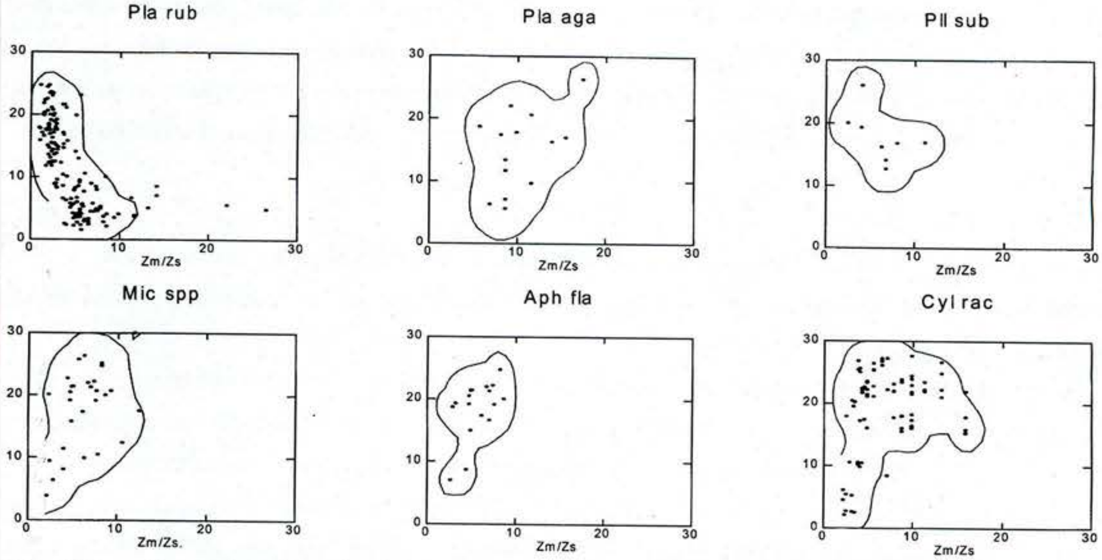


Fig. 4 Two-dimensional projections of net biomass changes versus water-temperature and zm/zs for the species indicated. Abbreviations of species as in Fig. 1.

Dependence of annual average cyanobacterial percentage share in relation to annual mean in-lake-TP concentrations is shown in Fig. 5, upper panel. Results are separated into at least two groups: In the stratified *Pl. rubescens* lake cyanobacteria dominate the phytoplankton biomass at TP-concentrations of around 10. In all the mixed systems cyanobacteria are abundant at total phosphorus concentrations of >40 $\mu g \cdot l^{-1}$. Schreurs (1992) estimated ranges of 10-50 $\mu g \cdot l^{-1}$ 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, percentage abundance of cyanobacteria is high at TP-levels >100 μg·l^{-1} when *Pl. agardhii* or *Aphanizomenon flos-aquae* dominates (Fig. 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. Growth rates and minimal cell quotas for phosphorus are quite comparable for *Pl. rubescens* and *Pl. agardhii.*

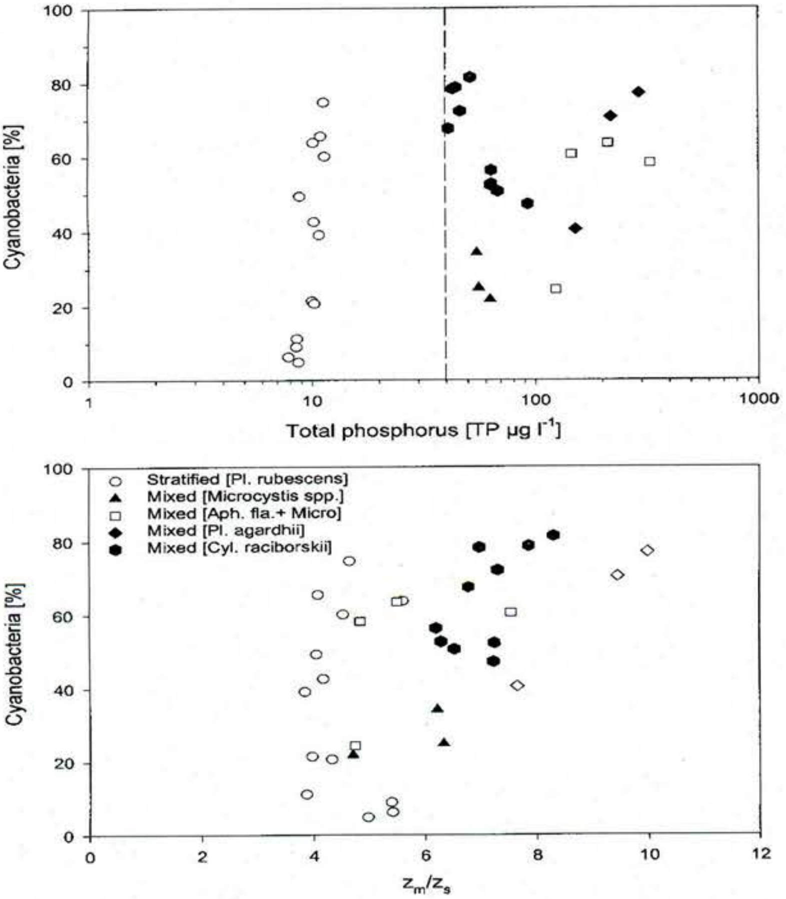


Fig. 5 Cyanobacterial share in total algal biomass as a function of epilimnetic total phosphorus concentration (upper panel) and as a function of z_m/z_s (lower panel). Data are annual averages.

An explanation is offered by their different niches in the water-column. Stratifying cyanobacteria are associated with light climate correlatives (z_m/z_s) of about 4 (Fig. 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 *Pl. rubescens* when nutrient concentrations are moderate. These subsurface maxima are optimised by its light absorption through chromatic adaptation and buoyancy regulation (Zimmermann, 1969; Findenegg, 1971; Klemer, 1976; Konopka, 1982; Walsby, 1987; see also the discussion in Schreurs, 1992). For well-mixed populations in shallow lakes ratios of $z_m/z_s > 7$ are required (Fig. 4, lower panel). In such turbulent conditions with low light availability in the water column cyanobacterial dominance is supported when *Pl. agardhii* or *Cylindrospermopsis raciborskii* are present.

Average net growth rates estimated from field data (Tab. 1) are in general agreement with published data from cultures summarised in Andersen (1997). Highest growth in the field and greatest ranges were observed in *Aph. flos-aquae* followed by *Microcystis* spp. and *Pl. agardhii*. Maximum growth rates from laboratory cultures follow the same sequence.

Tab.1 Mean, Minimum and Maximum positive net biomass changes calculated from field data (net growth rates, day^{-1}) for the investigated species. Published maximum growth rates are extracted from the summarising Table A10, p. 265 in Andersen (1997).

Species / Net growth rate	Mean	Minimum	Maximum	Max. publ.
Planktolyngbya subtilis	0.032	0.010	0.081	
Cylindrospermopsis raciborskii	0.042	0.002	0.138	
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

Published phosphorus uptake affinities are lowest in *Aph. flos-aquae*, highest in *Microcystis aeruginosa*, and intermediate in *Pl. agardhii* confirming more or less their placement on the phosphorus axis in Fig. 5. The storage capacity for phosphorus however is similar in *Mic. aeruginosa* and *Pl. agardhii.* Therefore the two species can compete or even co-exist. Optimum N:P ratios do not differ significantly between *Microcystis wesenbergii* (18) and *Pl. agardhii* (12-21), but are much lower (5.0-8.5) in *Mic. aeruginosa* (see Andersen, 1997 for references).

Consequences of cyanobacterial dominance do therefore not only depend on the nutrient enrichment but also on the specific species involved. Ecological and physiological characteristics as well as competition between species and interactions to other trophic levels have to be considered.

4. Correctives

Several techniques are available to prevent or reduce long-term cyanobacterial dominance. A necessary pre-requisite is almost always a reduction of the nutrient load from the catchment to the lake. In-lake concentrations have to be decreased not only until growth is nutrient limited, but even further until biomass concentrations reach such low concentrations that cyanobacteria are outcompeted due to the effects of increased light climate. According to the analysis by Schreurs (1992) the relative probability for prolonged dominance is significantly reduced at concentrations <100 $\mu g \cdot l^{-1}$, but still remains high. The absence of abundant cyanobacteria is better guaranteed at levels below 50 µg·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 Fig. 6 for a deep alpine lake (Dokulil and Jagsch, 1992).

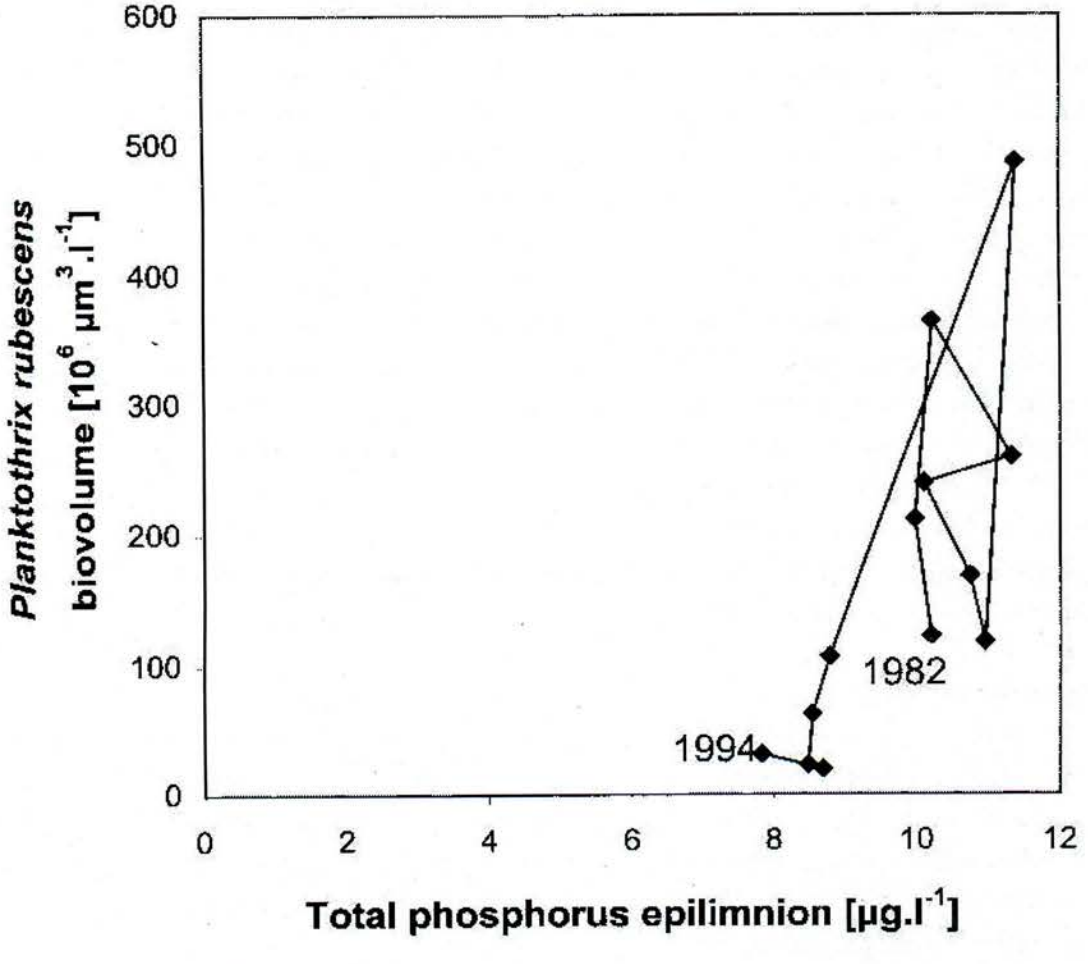


Fig.6 Decrease of *Planktothrix rubescens* biovolume as a function of total epilimnetic phosphorus concentration in the deep stratifying lake, Mondsee for the years 1982 to 1994. Data are annual averages.

Furthermore, measures to prevent or reduce excessive cyanobacterial biomass have to consider the type of species involved in domination in combination with lake depth and the 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 and Hartmann, 1988a). Filamentous cyanobacteria of the mixed type such as *Planktothrix*, usually disappear in lakes not exceeding 8m depth at 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 (>8m) are low and independent of chlorophyll-a 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_{mix}/z_{SD}. Cyanobacteria from the *Limnothrix* type can therefore be controlled successfully by increasing the 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 (Agusti and Phlips, 1991; Humphries and Lyne, 1988; Iblings, 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 ($z_{mix} \gg z_{eu}$) or intermittent turbulence of the water column reduce the competitive advantage. Mixing should therefore be regarded as a quasi-resource (Steinberg and 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 (Perrow *et al.*, 1997).

5. Conclusions

Long-term dominance of cyanobacteria is usually caused by a multiplicity of factors. Nutrient concentration, lake morphometry, water-temperature, under-water light availability, and mixing conditions are the most important. Consequences of algae 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. Additional in-lake ecotechnolgies can support more rapid recovery and restoration.

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References

Agusti, S., and Phlips, E.J. 1991.Light absorption by cyanobacteria: Implications of the colonial growth form. *Limnol. Oceanogr.* 37: 434-441.

Ahlgren, I. 1993. Scientific basis for the application of in-lake ecotechnologies in eutrophication control. p 23-25. In: Giussani G. and C. Callieri (eds.), Strategies for lake ecosystems beyond 2000, Proc. 5th Int, Conf. Conservation and management of Lakes, Stresa 1993.

Andersen, T. 1997. Pelagic nutrient cycles. Herbivores as sources and sinks. 280pp. Springer Verlag, Berlin Heidelberg.

Berg, K., Skulberg, O. M., Skulberg, R., Underdal, B., and Willen, T. 1986. Observations of toxic blue-green algae, Cyanobacteria) in some Scandinavian lakes. *Acta Vet. Scand. 27*: 440-452.

Burns, C. W. 1987. Insight into zooplankton-cyanobacteria interactions derived from enclosure experiments. N.Z. J. *Marine and Freshwater Res*. 21: 477-482.

Cai, Q., Gao, X., Chen, Y., Ma, S., and Dokulil, M. 1994. Dynamic variations of water quality in Lake Tai Hu and multivariate analysis of its influential factors. pp. 217-230. In: Sund, H., H.-H. Stabel, W. Geller, X. Yu, K. Yuan and F. She, (eds.) Environmental protection and lake ecosystem. Proc. Int. Symp. Wuxi March 27 to April 1, 1993, China Science and Technology Press, Nanjing.

Chorus, I. 1993. Algal metabolites and water quality: Toxins, allergens, and taste-and-odor problems. pp. 570-572. In: Giussani G. and C. Callieri, (eds.), Strategies for lake ecosystems beyond 2000, Proc. 5th Int, Conf. Conservation and management of Lakes, Stresa 1993.

Chorus, I. 1995. Cyanobakterientoxine: Kenntnisstand und Forschungsprogramme. Dt. Ges. Limnol., DGL, Tagungsberichte 1995, (Berlin), Krefeld 1996, pp269-280.

Dokulil, M. 1993. Long-term response of phytoplankton population dynamics to oligotrophication in Mondsee, Austria. Verh. Internat. *Verein. Limnol*.25: 657-661.

Dokulil, M.T., and Jagsch, A. 1992. Dynamics of phosphorus and nitrogen loading and its effects on phytoplankton in Mondsee, Austria. - *Hydrobiologia 243/244, (DH79)*: 389-394.

Dokulil, M. T.,and Mayer, J. 1996. Population dynamics and photosynthetic rates of a *Cylindrospermopsis-Limnothrix* association in a highly eutrophic urban lake, Alte Donau, Vienna, Austria. *Algol. Stud.* 83: 179-195.

Dokulil, M., and Skolaut, C. 1986. Succession of phytoplankton in a deep stratifying lake: Mondsee, Austria. *Hydrobiologia.*138: 9-24.

Findenegg, I., 1971. Unterschiedliche Formen der Eutrophierung von Ostalpenseen. Schweiz. Z. *Hydrol*.33: 85-95.

Fott, J., Pechar, L., and Prazakova, M. 1980. Fish as a factor controlling water quality in ponds. p. 255-261. In Barica, J. and Mur, L.R., (eds.) Hypertrophic ecosystems, Developments in Hydrobiology 2, Junk Publ., The Hague.

Foy, R.H., and Gibson, C. E. 1982. Photosynthetic characteristics of planktonic blue-green algae: The response of twenty strains grown under high and low light. *Br. phycol. J.* 17: 169-182.

Foy, R. H., Gibson,C. E., and Smith, R.V. 1976. The influence of daylength, light intensity and temperature on the growth rates of planktonic blue-green algae. *Br. phycol. J.*11: 151-163.

Haney, J. F. 1987. Field studies on zooplankton-cyanobacteria interactions. N.Z. J. *Marine and Freshwater Res*.21: 467-475.

Humphries, S. E., and Lyne, V. D. 1988. Cyanophyte blooms: The role of cell buoyancy. *Limnol.*

*Oceanogr.*33: 79-91.

Ibelings, B. W.1992. Cyanobacterial water blooms: The role of buoyancy in water columns of varying stability. Thesis Univ. Amsterdam, 171 pp.

Jackson, D. F. 1984. Ecological factors governing blue-green algal blooms. Purdue Univ. Extension, Serie 117: 402-420.

Keating, K. I. 1978. Blue-green algal inhibition of diatom growth: transition from mesotrophic to eutrophic community structure. *Science.*199: 971-973.

King, D. L. 1980. The role of carbon in eutrophication. *J. Water Poll. Contr.* Fed.,42: 2035-2051.

Klemer, A.R.1976. The vertical distribution of *Oscillatoria agardhii* var. *isothrix*. *Arch Hydrobiol.* 78: 343-362.

Konopka, A. 1982. Phsiological *Ecology* of a metalimnetic *Oscillatoria rubescens* population. *Limnol. Oceanogr.*27: 1154-1161.

Konopka, A. 1989. Metalimnetic cyanobacteria in hard-water lakes: Buoyancy regulation and physiological state. *Limnol. Oceanogr.*34: 1174-1184.

Kromkamp, J., and Walsby, A. E. 1990. A computer model of buoyancy and vertical migration in cyanobacteria. *J. plankt. Res.*12: 161-183.

Lampert, W. 1987. Laboratory studies on zooplankton-cyanobacteria interactions. N.Z. J. *Marine and Freshwater Res.* 21: 483-490.

Lindholm, T., Eriksson, J. E. and Meriluoto, J. A. O. 1989. Toxic cyanobacteria and water quality problems. Examples from a eutrophic lake on Aland, South West Finland. *Water Res. 23*: 481-486.

Mayer, J., Dokulil, M.T., Salbrechter, M., Berger, M., Posch, T., Pfister, G., Kirschner, A.K.T., Velimirov, B., Steitz, A., and Ulbricht, T., 1997. Seasonal successions and trophic relations between phytoplankton, zooplankton, ciliophora and bacteria in a hypertrophic shallow lake in Vienna, Austria. *Hydrobiologia.342/343*: 165-174.

McQueen, D. J., and Lean, D.R.S. 1987. Influence of water temperature and nitrogen to phosphorus ratios on the dominance of blue-green algae in Lake St. George, Ontario. Can. J. Fish. *Aquat. Sci.* 44: 598-604.

Mur, L.R., Schreurs, H., and Visser, P. 1993. How to control undesirable cyanobacterial dominance. p. 565-569. In: Giussani G. and C. Callieri, (eds.*)*, Strategies for lake ecosystems beyond 2000, Proc. 5th Int, Conf. Conservation and management of Lakes, Stresa 1993.

Murphy, T. P., Lean, D.R.S., and Nalewajko, C. 1976. Blue-green algae: Their excretion of iron-selective chelators enables them to dominate other algae. *Science.*192: 900-902.

Niklisch, A., and Kohl, J.-G. 1989. The influence of light on the primary production of two planktic blue-green algae. Arch. Hydrobiol., Ergebn. *Limnol. 33*: 451-455.

Perrow, M.R., Meijer, M.-L., Dawidowicz, P., and Coops, H. 1997. Biomanipulation in shallow lakes: state of the art. *Hydrobiologia.342/343*: 355-365.

Reynolds, C.S. 1987. Cyanobacterial water-blooms.PP. 67-143. In: Callow P., (ed.) *Advances in Botanical Research* 13,. Academic Press, London.

Reynolds, C. S., Oliver, R. L. and Walsby, A. E.1987. Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. N.Z. J. *Marine and Freshwater Res*. 21: 379-390.

Robarts, R. S., and Zohary, T. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. N.Z. J.*Marine and Freshwater Res*. 21: 391-399.

Rönicke, H., Klapper, H., and Beyer, M. 1993. Control of phosphorus and blue-greens by nutrient preipitation: long-term case study. pp.177-179. In: Giussani G. and C. Callieri, (eds.), Strategies for lake ecosystems beyond 2000, Proc. 5th Int. Conf. Conservation and Management of Lakes, Stresa 1993.

Scheffer, M., Rinaldi, S., Gragnani, A., Mur, L.R., and Van Nes, E.H. 1997. On the dominance of filamentous cyanobacteria in shallow turbid lakes. *Ecology*, 78: 272-282.

Schreurs, H. 1992. Cyanobacterial dominance. Relations to eutrophication and lake morphology. Doctoral thesis, Univ. Amsterdam. 198 pp.

Shapiro, J. 1984. Blue-green dominance in lakes: the role and management significance of pH and CO_2. Int. Rev. ges. *Hydrobiol*. 69: 765-780.

Shapiro, J. 1990. Current beliefs regarding dominance of blue-greens: The case for the importance of CO_2 and pH. Verh. Internat. Verein. *Limnol., 24*: 38-54.

Shapiro, J. 1997. The role of carbon dioxide in the initiation and maintenance of blue-green dominance in lakes. *Freshwat. Biol*. 37: 307-323.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. *Science*, 221: 669-671.

Smith, V. H., Willén, E., and Karlsson, B. 1987. Predicting the summer peak biomass of four species of blue-green algae, Cyanophyta/Cyanobacteria in Swedish lakes. *Water Res. Bull*.23: 397-402.

Spencer, C. N., and King, D. L., 1989. Role of light, carbon dioxide, and nitrogen in regulation of buoyancy, growth and bloom formation of Anabaena flos-aquae. *J. Plankton. Res*. 11: 283-296.

Stanier, R.Y., and Cohen-Bazire, G. 1977. Phototrophic prokaryotes: The Cyanobacteria. Ann. Rev. *Microbiol*.31: 225-274.

Steinberg, C., and Hartmann, H. 1988a. Planktische blütenbildende Cyanobakterien, Blaualgen und die Eutrophierung von Seen und Flüssen. *Vom Wasser*. 70: 1-10.

Steinberg, Ch.E.W., and Hartmann, H.M. 1988b. Planktonic bloom-forming cyanobacteria and the eutrophication of lakes and rivers. *Freshwat. Biol*.20: 279-287.

Teubner, K. 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. Diss. Humboldt-Univ. Berlin. pp.231.

Teubner, K., Feyerabend, R., Henning, M., Nicklisch, A., Woitke, P., and J.-G. Kohl.1997. 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.

Tilman, D., and Kiesling, R.L. 1984. Freshwater algal Ecology: taxonomic tradeoffs in the temperature dependence of nutrient competitive abilities. In: Klug, M.J. and Reddy, V.A., (eds.), *Current problems in Microbial Ecology*. Proc. 3rd Int. Symp. Microbial Ecol. Amer. Soc. Microbiol, Washington, D.C.

Trimbee, A. M., and Harris, G. P. 1984. Phytoplankton dynamics of a small reservoir: use of sedimentation traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green algae. *J. Plankton Res.*5: 897-918.

Trimbee, A. M., and Prepas, E.E. 1988. The effect of oxygen depletion on the timing and magnitude of blue-green algal blooms. Verh. Internat. Verein. *Limnol.* 23: 220-226.

Walsby, A. E. 1987. Cyanobacteria: planktonic gas-vacuolated forms. In: Starr, M., H. Stolp, H. Truper, A. Balows and H. G. Schlegel, (eds.) *The Prokaryotes*. pp. 224-235, Springer Verlag, New York.

Zevenboom, W., and Mur, L. R. 1980. N_2-fixing cyanobacteria: why they do not become dominant in Dutch hypertrophic lakes. pp.123-130. In: Barica, J. and L.R. Mur, (eds.); *Hypertrophic ecosystems*, Developments in Hydrobiology *2,* Junk Publ, The Hague.

Zimmermann, U. 1969. Ökologische und physiologische Untersuchungen an der planktischen Blaualge *Oscillatoria rubescens* D.C. unter besonderer Berücksichtigung von Licht und Temperatur. Schweiz. Z. *Hydrol.* 31: 1-58.