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The Effect of Changing Flushing Rates on Development of Late Summer *Aphanizomenon* and *Microcystis* Populations in a Shallow Lake, Müggelsee, Berlin, Germany

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ABSTRACT

Müggelsee is a shallow lake in the suburban region of Berlin, Germany and included in the lake-river system of the river Spree, having an average annual retention time of 42 days which increases to > 100 days in the summer period. The summer equilibrium phase of phytoplankton results in the development of an *Aphanizomenon flos-aquae* dominated assemblage which, in some years, progresses towards a *Microcystis* dominated assemblage. Continuously high flushing (in range of 1%-2% of lake volume · day^{-1}) does not prevent *Aphanizomenon* development but its biomass remains at low levels as compared to other summers with smaller average flushing. In such years (flushing remains < 1% of lake volume · day^{-1}) a flushing pulse of 1%-2% of lake volume · day^{-1} has been effectual to break development of cyanoprokaryotes and to decrease their biomass to low levels. The major reason of the decrease is not the dilution effect of flushing pulses but the intolerance of cyanoprokaryotes to sudden environmental changes. Considering the case of Müggelsee from the point of view of reservoir ecology it can be concluded that reservoirs with pulsed use are less exposed to development of cyanoprokaryotes if pulses occur in a sufficient frequency (20-30 days) and their intensity falls to the range of 1%-2% of reservoir volume · day^{-1}. Reservoirs with continuous takeoff of water are more exposed to cyanoprokaryota development with all the consequences for water use.

Key words: flushing rate, *Aphanizomenon*, *Microcystis*, disturbance, intensity, frequency.

INTRODUCTION

Reservoirs differ from lakes in many respect that includes origin, age, morphometric properties, etc. summarized in Straškraba (1999). One of the main difference is that they are subjected not only to climatological variations but also to operational management of the dam resulting in great variability in hydrological conditions. As a consequence of these measures, retention time of reservoirs has been usually shorter than that of lakes, moreover, operational events appear as pulse effect. The above features result in a series of limnological differences, among them that community development of phytoplankton has been subjected to interruptions which results in cascading consequences on higher trophic levels and on different kinds of water use.

An increasing number of case studies (Jacobsen & Simonsen, 1993; Sommer, 1993; Romo & Miracle, 1995) have shown the ultimate role of periodic disturbances on the outcome of phytoplankton successions. The lack of disturbances allows equilibrium dynamics to manifest (Reynolds *et al.*, 1993) resulting in communities dominated frequently by one, but in no case more than three species. The above results can be sufficiently explained by Connell's (1978) Intermediate Disturbance Hypothesis (IDH). According to the original IDH concept, diversity maximizes at disturbances intermediate in their frequency and intensity.

While it is relatively easy to document the profound role of disturbance frequency on community development, it is quite problematic to relate it to the intensity of disturbances. This finding is closely connected with the theoretical weaknesses of the IDH concept: disturbance is "measured" as a response to an unquantified event (Juhász Nagy, 1993; Reynolds *et al.*, 1993). Case studies (Ács & Kiss, 1993; Descy, 1993) in riverine algal assemblages showed that it is less the intensity of a physical forcing that is critical for the development of ecological structure than the frequency with which it is applied. In these two cases a readily measurable variable, water discharge appeared to be the major disturbance factor. In case of shallow lakes, the most common disturbance events: summer storms with their consequences in light-climate, nutrient availability, water column stability, etc. are much more difficult to quantify.

Late summer dominance of cyanoprokaryotes has been commonly observed in eutrophic lakes and reservoirs almost regardless of their stratification pattern and geographical location. Cyanoprokaryotes often appear of equlibrial dominants and more recently several associations have also been described. Continuous mixing combined with growth saturating levels of inorganic N predicts the establishment of associations (S in Reynolds, 1997) dominated by shade tolerant species like *Planktothrix agardhii* and/or *Limnothrix redekei* especially in temperate waters (Jacobsen & Simonsen, 1993; Chorus & Schlag, 1993; Romo & Miracle, 1995). The nostocalean *Cylindrospermopsis raciborskii* has been a very successful invader both in tropical reservoirs and temperate lakes (Padisák, 1997) and has to be placed in this group (SN according to Padisák & Reynolds, 1998) as having similar light-photosynthesis regimes and often coexists (Dokulil & Mayer, 1996) with members of association S or even outcompetes them presumably when N-limitation arises (Présing *et al.*, 1996; Padisák & Reynolds, 1998; Borics *et al.*, submitted). More distinct mixing events combined with better light climate and often insufficient N lead to dominance of other nostocalean species, most frequently belonging to genera *Aphanizomenon*, *Anabaena*, described as association H (Reynolds, 1997). Association M is characterized by dominance of *Microcystis*, which needs and tolerates high light intensities and can migrate vertically to the layer of preferred light supply (Zohary & Robarts, 1989). However, as a consequence of alternating competitive arena, mixed blue-green assemblages develop by late summers in many cases.

Müggelsee is not a reservoir but a medium-sized shallow lake in the suburban of Berlin, Germany, which, however, is a part of a river-lake system subjected intensive flushing events and having relatively short retention time. Therefore, data about late summer development of cyanoprokaryote associations can provide a good model for reservoir ecology. Other groups/aspects of phytoplankton succession are described elsewhere (Nixdorf & Hoeg, 1993; Köhler & Nixdorf, 1994; Köhler & Hoeg, 1999).

DESCRIPTION OF STUDY SITE, MATERIALS AND METHODS

Lake Müggelsee (Figure 1) is a shallow, eutrophic lake in Berlin. Morphometric data as well as information about hydrodynamics and water chemistry are given in Table I.

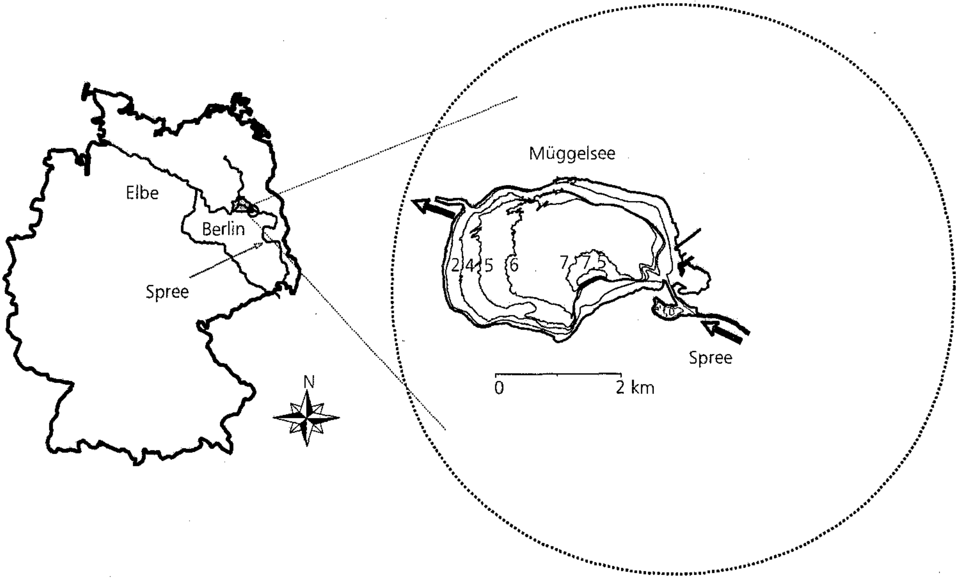

Figure 1 Bathymetric map of Müggelsee, Berlin, Germany.

Müggelsee was loaded by the River Spree with 3.5 + 0.6 g P $\cdot$ m^{-2} $\cdot$ a^{-1} and 70 + 23 g N $\cdot$ m^{-2} $\cdot$ a^{-1}, respectively (average and standard deviation, 1991-97). Concentrations of dissolved reactive phosphorus (DRP) usually fell below 10 μg $\cdot$ l^{-1} in April-May but exceeded 50 µg $\cdot$ l^{-1} in 90% of all samples from August till October. Concentrations of dissolved inorganic nitrogen (DIN) below 100 µg $\cdot$ l^{-1} were measured for 4-6 weeks each summer but never in spring or autumn. Supply of dissolved reactive silicon (DSi) declined during the spring development of diatoms and remained below 0.1 mg $\cdot$ l^{-1} in Müggelsee for more than two weeks in late spring of 1992 and 1995. The ratio zeu/zmix between depth of the euphotic zone and depth of the mixed layer averaged at about 0.5 during the whole season. Water column of Müggelsee is usually completely mixed, weak stratification persists for rarely longer than four weeks. Abiotic conditions of phytoplankton development as well as zooplankton dynamics have been described in more detail by Köhler & Hoeg (1999).

Table I Morphometric and limnological features of Müggelsee. Data are from Driescher *et al.*, 1993.

Altitude	32.37 m a.s.l.
Catchment area	7000 km^2
Surface area	7.7 km^2
Mean depth	4.9 m
Maximum depth	8.0 m
Total length of shoreline	11.5 km
Lake volume	$36 \cdot 10^6\ m^3$
average inflow (river Spree + Fredersdorfer Fließ)	$10.1\ m^3 \cdot s^{-1}$
Lake level fluctuation (1979-1990)	25 cm
Theoretical retention time	42 d
Withdrawal by the waterworks	$1.8 \cdot m^3 \cdot s^{-1}$
Global radiation (1951-1980), annual sum	$356\ kJ \cdot cm^{-2}$
Precipitation (1951-1980), annual sum	580 mm
Water temperature (mean; min-max)	10.3; 0.5-21°C
Ice cover (mean; min-max)	52; 0 – 89
Secchi depth (mean; min-max)	1.22; 0.35-5.10 m
Euphotic zone depth	3.12; 1.73-7 m
pH (mean; min-max)	7.9; 7.2-8.6
conductivity (mean; min-max)	540; 425-657 $\mu S \cdot cm$
Total phosphorus (mean; min-max)	158; 38-751 $\mu g \cdot l^{-1}$
Orthophosphate (mean; min-max)	62; 3-474 $\mu g \cdot l^{-1}$
Nitrate (mean; min-max)	1.0; < 0.02-3.4 $mg \cdot l^{-1}$
Silica (mean; min-max)	4.3; 0.4-7.5 $mg \cdot l^{-1}$

In Müggelsee, spring development started usually in February with growth of diatoms which often attained a maximum biomass above 10 $mg \cdot l^{-1}$ in April or May. Diatoms were joined each April by the filamentous cyanobacterium *Limnothrix redekei*. Spring development was terminated by a distinct clear-water phase in late May. This "gap" was filled at first by some cryptophytes and chlorophytes. Cells and small colonies of *Microcystis* spp. appeared. Towards summer *Aphanizomenon flos-aquae*, in some years accompanied by *Microcystis* spp. became dominant providing a total biomass peak in the range 30-50 mg · l^{-1}. The second important algal group consisted of some centric diatoms. The diverse green algae contributed usually less than 10% of total phytoplankton biomass. Dinophytes, cryptophytes and chrysophytes were even less important. The inflowing Spree imported not only nutrients but also phytoplankton. Biomass of most diatoms and even of *L. redekei* was usually higher in the inflow than in Müggelsee. Biomass of *Aphanizomenon* rose at the same time in inflow and lake but culminated on a higher level in Müggelsee. Taxa like *Microcystis, Ceratium* and *Peridinium* were much more abundant in the lake than in the inflowing river.

Water samples were drawn from 0.5, 4 and 7 m depth with a 5-l-Friedinger sampler at the deepest point of Müggelsee from 1978 to 1987. Since 1987, mixed samples have been used (twenty-one subsamples from 5 stations). Samples were taken weekly from March to October and biweekly from November to February.

Phytoplankton was counted after fixation with Lugol solution in sedimentation chambers (2.5-10 ml) with an inverted microscope according to Utermöhl (1958). Biomass was estimated volumetrically supposing a specific gravity of 1 g · cm^{-3}.

Dilution rate (given as % of lake volume) was calculated from total lake volume and daily sum of inflow, the latter being calculated from daily readings of water level of the inflowing Spree.

RESULTS

Aphanizomenon flos-aquae has been one of the most persistent summer species in the lake. During the period 1979-1994 it occurred regularly in each summer (Figure 2). However, its peak biomass has been quite unexpectable as ranging between 5 and 30 mg · l^{-1}. At annual average, biomass of *Microcystis* spp. has been 1-3 orders of magnitude less than that of *Aphanizomenon* and positive correlation prevailed ($r = + 0.68$, $n = 13$, $P <$) between them at a long term basis (Figure 3).

Although there are differences in the seasonal course of basic inorganic nutrients, the extent of variability has been less than that of appearance of *Aphanizomenon* and *Microcystis*, therefore their (and especially that of the dominant *Aphanizomenon*) seasonal patterns were compared to dilution rates in the period 1991-1994.

In 1991, development of *Aphanizomenon* started in mid-July when flushing rate dropped below 0.5% of the lake volume. After a sudden increase of flushing rate, *Aphanizomenon* biomass suddenly dropped than again peaked (Figure 4). In 1992, dilution rate dropped to very low levels already in early June and *Aphanizomenon* started to increase soon. As a consequence of a temporal and sudden increase in flushing rate, the biomass remained steady for 3 weeks and then a further increase occurred (Figure 4). Small flushing rates in 1993 were observed only in May then, unlike the regular annual pattern, quite high flushing characterized the summer. The *Aphanizomenon* development was considerably delayed, and the species remained at a constant low level all over the summer (Figure 4). In 1994, *Aphanizomenon* started to increase when flushing rate first dropped close to 0.5% of lake volume · day^{-1}, however, subsequent sudden flushing pulses broke its biomass and the population did not recover (Figure 4).

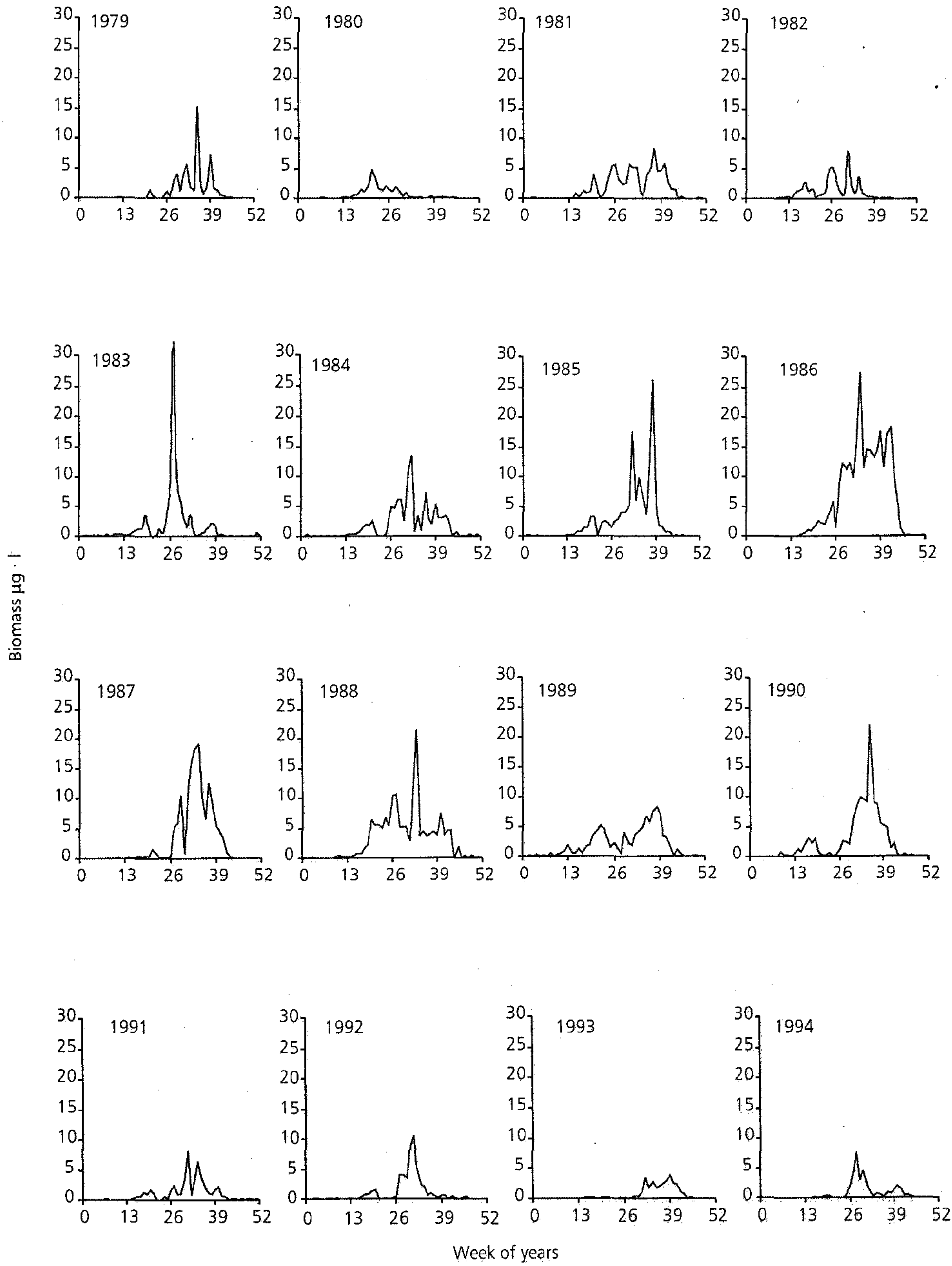

Figure 2 Annual development (biomass, mg · l^{-1}) of *Aphanizomenon* in Müggelsee between 1979 and 1994.

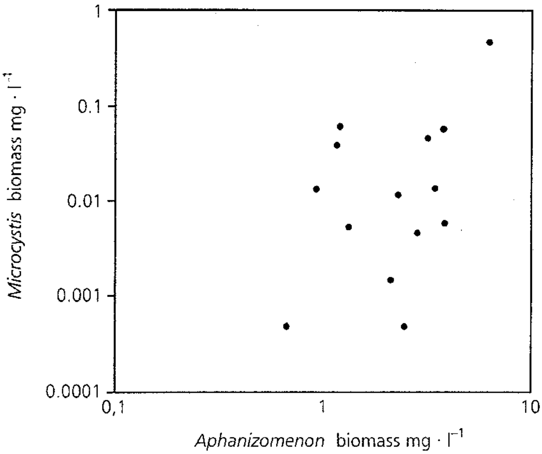

Figure 3 Relationship between annual average biomass (mg · l^{-1}) of *Microcystis* and *Aphanizomenon* in Müggelsee between 1979 and 1994.

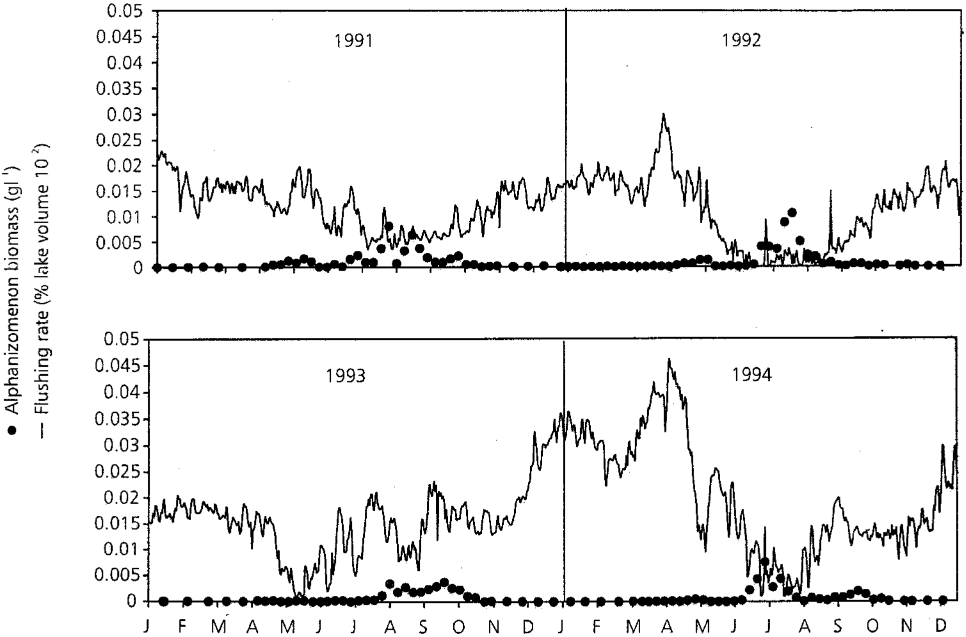

Figure 4 Annual course of flushing rate (% of lake volume · day^{-1} · 10^{-2}, continuous line) and *Aphanizomenon* biomass (mg · l^{-1}, closed circles) in years 1991, 1992, 1993 and 1994.

Summer developments (Figure 5) of *Aphanizomenon* and *Microcystis* paralleled each other in 1991 with the notable difference that *Aphanizomenon* in each periods of growth (late July, mid-August) started to increase one weak earlier than *Microcystis*. Net growth rates of *Microcystis* were higher than that of *Aphanizomenon*. As a consequence of difference in net growth rates and and because there was no considerable flushing pulse in September, *Microcystis* somewhat overgrew *Aphanizomenon* then both species declined after a flushing pulse in early October. While a 1-week delay of *Microcystis* was observed in periods of growth, declines of the two species occurred simultaneously.

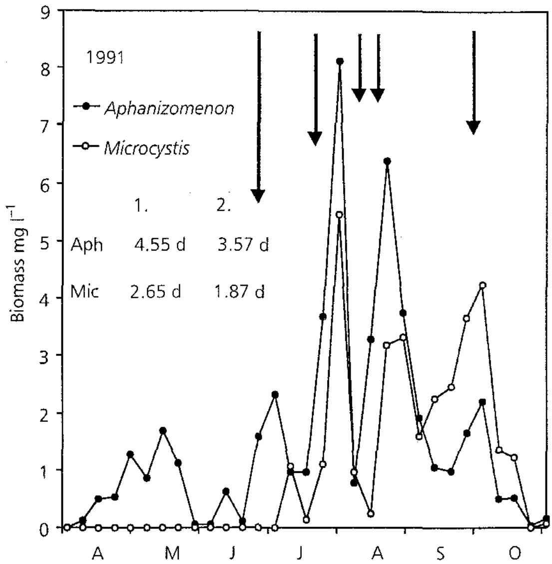

Figure 5 Biomass (mg · l^{-1}) of *Aphanizomenon* (closed circles) and *Microcystis* (open circles) in Müggelsee in 1991. Net increase rates during periods of population increase are given on the figure. Higher flushing pulses are indicates with arrows.

In the very calm summer of 1992 (Figure 6), *Aphanizomenon* started to grow in late June and a sudden flushing pulse delayed its increase by 2 weeks. *Microcystis* was not effected by this pulse effect, however its growth shows a setback when *Aphanizomenon* peaked. As a consequence of its delayed but higher growth rate, *Microcystis* overgrew *Aphanizomenon* and the permanently high flushing rate did not cause a dramatic decrease in its biomass until the end of September.

In 1993, permanently high flushing rates (Figures 4, 7) allowed only a moderate development of cyanoprokaryota, peak biomass of *Aphanizomenon* did not exceed 4 mg · l^{-1}, *Microcystis* reached a peak biomass of approx. 1 mg · l^{-1} then declined rapidly.

Aphanizomenon started to grow in late June in 1994 (Figure 8) and after two flushing pulses it declined very early. During the calm September a second increase occurred but the peak remained about 2 mg · l^{-1}.

Average July/August or July/August/September biomass of cyanoprokaryota (other species than *Aphanizomenon* and *Microcystis* were negligible) showed close negative correlations to average dilution rate (Figure 9): r = 0.80 for July/August/September data and r = 0.91 for July/August data was found (linear relationship).

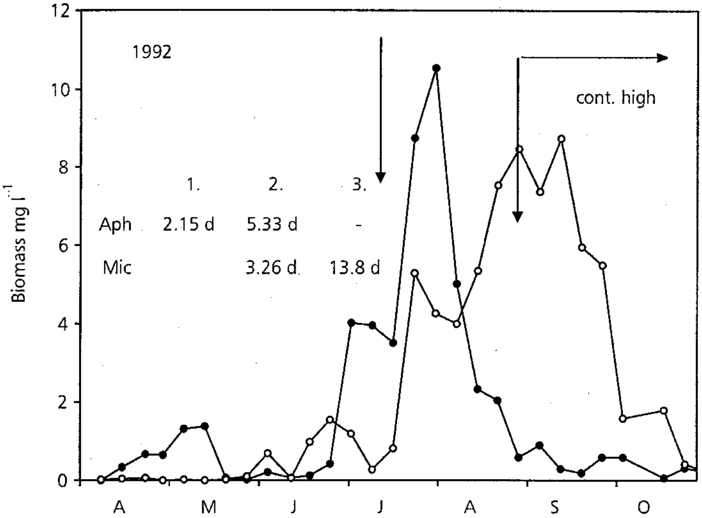

Figure 6 Biomass ($mg \cdot l^{-1}$) of *Aphanizomenon* (closed circles) and *Microcystis* (open circles) in Müggelsee in 1992. Net increase rates during periods of population increase are given on the figure. Higher flushing pulses are indicates with arrows.

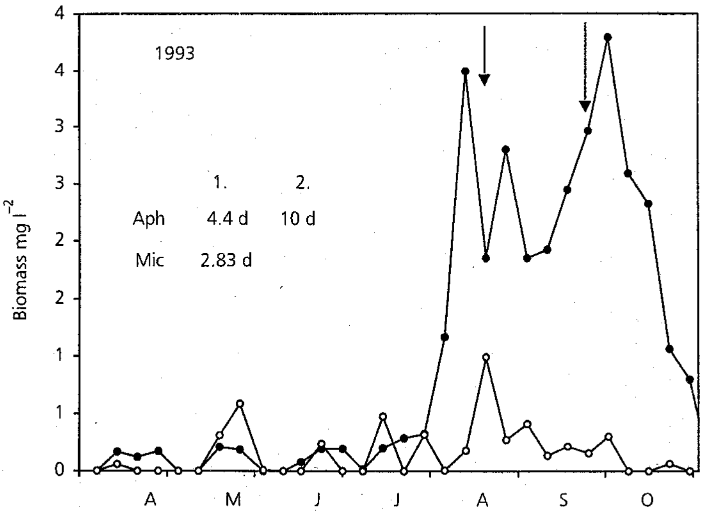

Figure 7 Biomass ($mg \cdot l^{-1}$) of *Aphanizomenon* (closed circles) and *Microcystis* (open circles) in Müggelsee in 1993. Net increase rates during periods of population increase are given on the figure. Higher flushing pulses are indicates with arrows.

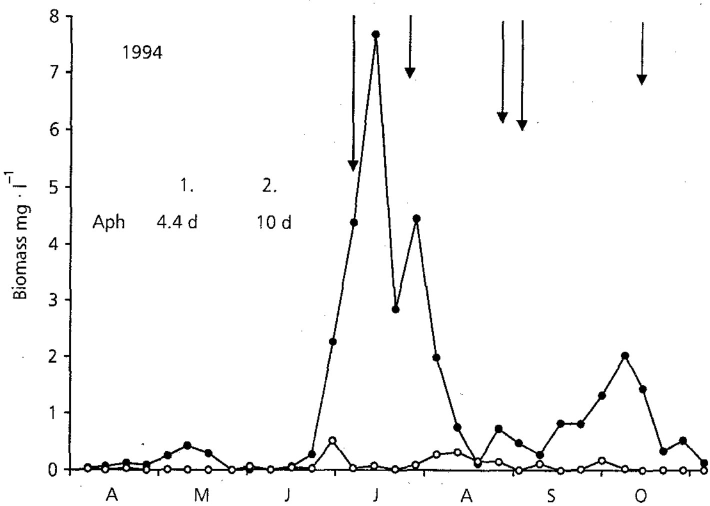

Figure 8 Biomass (mg · l^{-1}) of *Aphanizomenon* (closed circles) and *Microcystis* (open circles) in Müggelsee in 1994. Net increase rates during periods of population increase are given on the figure. Higher flushing pulses are indicates with arrows.

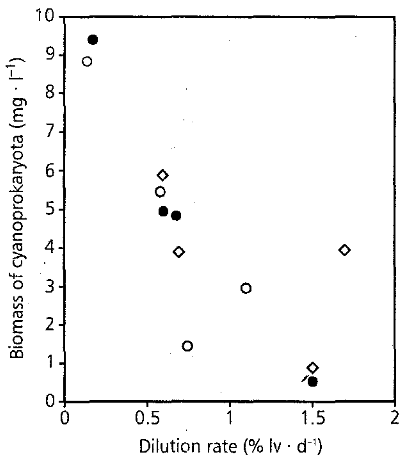

Figure 9 Relationship between flushing rate (% of lake volume d^{-1}) and July (•), August (∘) and September (⋄) average biomass of cyanobacteria in years 1991-1994 in Müggelsee

DISCUSSION

As suggested in Connell's (1978) Intermediate Disturbance Hypothesis (IDH) species diversity reaches its maximum at an intermediate level of disturbance, where "intermediate" refers to both frequency and intensity of disturbance. While frequency has been explored in many studies, mostly on empirical/descriptive ways, intensity of disturbance in maintenance of species diversity has remained largely unexplored. So far, the only existing study by Sommer (1995) on marine phytoplankton combining effects of intensity and frequency has shown that, in line with the IDH, diversity followed a hump-shaped curve along both intensity and frequency. The equations given in the study cited above were further developed by using contribution analysis (Polischuk, 1999).

The reason why intensity of disturbance is difficult to handle under natural conditions lies in the fact that it is a "compose variable" (a storm, e.g., could effect light, turbidity, nutrient concentrations etc.) and in most cases it is impossible to define one dominant effect among many possible ones. The case of Müggelsee differs from others in respect that flushing rate could be selected as ultimate disturbance factor. Despite flushing rate is a clearly defined disturbance factor here it has to be considered that increases of flushing are often proceeded by colder days, storms, overcast, higher turbulence and wave action which themselves also significantly contribute to responses of the phytoplankton assemblage (Padisák *et al.*, 1990).

The *Aphanizomenon* → *Microcystis* assemblages correspond to the consecutive summer equilibrium state of phytoplankton in the lake. The *Microcystis* dominated assemblage develops only in case if preceded by significant amount of *Aphanizomenon*, most probably because phytoplankton growth by that time of the year is limited by N and the *Microcystis* growth is dependent upon the N fixed by the nostocalean *Aphanizomenon*. If this condition is fulfilled, *Microcystis* overgrows *Aphanizomenon* as a consequence of its higher growth rate and apparent (for example, year 1992) better tolerance of high flushing, at least when a considerable population has already developed.

Despite the clear correlation that exists between flushing rate (as disturbance factor in sense of intensity) and biomass of *Aphanizomenon*, the effect of sudden flushing pulses has been inevitable. Development of *Aphanizomenon* in the lake starts when high late spring flushing fall below 2% of lake volume · day^{-1}, corresponding to a retention time of about 50 days. Continuously high flushing, like in 1993, cannot prevent the *Aphanizomenon* but are effectual in keeping its biomass at a constantly low level. Significant development of *Aphanizomenon* occurs only if flushing falls below the level of 1% of lake volume · day^{-1}. In such periods a sudden increase in flushing to no more than 1.5% of lake volume · day^{-1} can stop and set back the population growth. It has to be noted that this decrease is not due to a simple dilution effect, since it is much smaller than the extent of the response of the assemblage.

The case study presented in this paper shows that intensity of disturbance do have a significant role in preventing the development of a cyanoprokaryota dominated assemblage or even a bloom to develop, however, because continuous disturbance also qualifies as environmental constancy (Chorus & Schlag, 1993) is less effectual than if applied as pulses. In agreement with other studies summarized and synthesized in Reynolds *et al.* (1993) it is more the frequency of disturbance than its intensity what sets back the development of summer equilibrium phases of phytoplankton and thus leading to more diverse "plagioclimactic" assemblages.

From the point of view of reservoir ecology and management the example presented in this paper has several consequences. Among many other differences between lakes and reservoirs one has been the lower retention time as a consequence of size and/or operational measures. Average annual retention time of Müggelsee is 45 days (0.12 y), shorter than most of the reservoirs considered in the summary of Thornton & Rast (1993). High flushings occur mostly from autumn to early summer, in the period when low water temperature does not allow the development of *Aphanizomenon flos-aquae* and *Microcystis*. In the warm months (July-September) the highest flushings are about 1%-2% of lake volume · day^{-1} corresponding to a retention time of about 50-100 days. If such flushing occurs continuously (as can be a case in drinking water reservoirs with rather continuous takeoff of water), blue green algae can develop but do not cause huge blooms. It has to be noted that the registered approx. 5 mg · l^{-1} *Aphanizomenon* maximum in 1993, a year with continuously high summer flushings, is enough to appear as surface bloom. If, as is the general case, summer flushing has been < 1% of lake volume · day^{-1} higher cyanoprokaryota can develop, however, sudden flushings in the range of 1%-2% of lake volume · day^{-1} are very effectual to break and reverse population increase. This way, reservoirs with pulsed use are less exposed to development of cyanoprokaryotes if pulses occur in a sufficient frequency (20-30 days, see Reynolds *et al.*, 1993) and their intensity falls to the range of 1%-2% of reservoir volume · day^{-1}.

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