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Recruitment of resting stages may induce blooms of *Microcystis* at low N:P ratios

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Some species of cyanobacteria form resting stages at the sediment surface when environmental conditions become unfavourable. As conditions turn more favourable, these resting stages hatch to the water phase, where the cells grow, reproduce, and sometimes form blooms. Since blooms of cyanobacteria have become an increasing threat to inland and brackish waters, it is important to assess the mechanisms and processes involved in the initiation of such blooms. One such mechanism is recruitment from the sediment surface. Potential factors regulating the recruitment of resting stages include variations in nutrient concentrations and ratios, as well as variations in grazing. To investigate how the recruitment of Microcystis responds to different levels of these factors, we performed an enclosure experiment (zooplankton abundances were regulated by predation from fish). We found that recruitment and growth were most pronounced at the second highest nutrient concentration (average concentrations were 498 μg l^{-1} of dissolved nitrogen and 134 μg l^{-1} of total phosphorus), while no direct response to different grazing levels was detected. We also found that resting stages can be important for initiating and sustaining blooms. The environmental conditions most important in regulating the recruitment rate from resting stages corresponded to the requirements of the plankton cells, namely high nutrient addition and low N:P ratio.

INTRODUCTION

Many phytoplankton species form resting stages when environmental conditions are harsh and these can survive for a long time in the sediment (Livingstone and Jaworski, 1980; Lampert, 1995). When environmental conditions are favourable again, they recruit to the water phase and continue growing (Hansson *et al.*, 1994; Hansson, 1996a). Many species of cyanobacteria, for example *Microcystis*, *Anabaena* and *Aphanizomenon*, form resting stages and are, in addition, the most frequent bloom-forming cyanobacteria (Willén and Mattsson, 1997). Some studies have shown that recruitment of algae from sediment may be important for the pelagic populations (Reynolds and Rogers, 1976; Preston *et al.*, 1980; Forsell and Pettersson, 1995; Hansson, 1996a; Head *et al.*, 1999) and may even be responsible for bloom formation (Reynolds and Walsby, 1975; Hansson *et al.*, 1994; Boero *et al.*, 1996; Perakis *et al.*, 1996). Blooms are sometimes formed rapidly (within days) and can often not be explained by growth of the extant planktonic population alone (Reynolds and Walsby, 1975; Hansson, 1996a), suggesting that the rate of recruitment from sediment to water may be a process of importance in the initiation of algal blooms.

In many urban areas, leaching of nutrients from land to water is a significant and growing problem. Since dense cyanobacterial growths are dependent on high amounts of nutrients, they are favoured by nutrient input from land, and this leads to increasing intensity and frequency of blooms in lakes and estuarine waters (Paerl, 1988). Such algal blooms have become a considerable threat to the quality of surface waters, thereby limiting potential uses, such as drinking water, recreation, fishing, and, more fundamentally, ecological function. To improve the value of water resources, a variety of actions have been undertaken. These include measures on land (e.g. changed agricultural practices and improved sewage treatment) and in aquatic systems [e.g. biomanipulation by fish removal (Shapiro *et al.*, 1975; Hansson *et al.*, 1998) and constructions of wetlands (Mitsch, 1992; Annadotter *et al.*, 1999; Zedler, 2003)] to decrease nitrogen and phosphorus loading. However, the mechanisms and processes involved in algal bloom formation are not well known, and to provide society with useful decision-support tools, further knowledge about what initiates blooms is crucial. Thus, our study aims to address the following questions. Are resting stages important for the development of algal blooms? Do the resting cells need the same environmental

conditions for development as do plankton cells? Are cyanobacterial recruitment ratios affected by the concentrations of nutrients or by their supply ratio? Are cyanobacterial recruitment rates decreased by the presence of grazing zooplankton in the same way as are some other algae with resting stages (Hansson, 1996b, 2000)? To answer these questions we performed a crossed matrix of enclosure experiments, varying nutrient concentrations and zooplankton grazing pressures (as regulated by planktivorous fish).

METHOD

Lake description, experimental design and sampling

The experiment was conducted in a moderately eutrophic (average concentrations of total nitrogen and total phosphorus of 1300 and 38 μg l^{-1}, respectively) and shallow (mean and maximum depths of 1.5 and 3 m, respectively) lake, Lake Krankesjön, in southern Sweden (55°42′N, 13°28′E). Further information about the lake is available elsewhere (Blindow, 1992; Hargeby *et al.*, 1994).

The experiment lasted for 7 weeks during June–August, 1999 including one pre-treatment week. Twenty-four enclosures (diameter 1 m) of transparent polyethylene were attached at 1.0 m depth. To avoid water intrusion from waves, ~0.2 m of each enclosure was above the surface of the lake. The openings of the enclosures were covered with a coarse net to avoid feeding by birds and the entry of bird droppings. Before starting the experiment, all fish were removed from the enclosures by means of netting and electrofishing. The treatments used were zooplankton grazing rates mediated by planktivorous fish additions at three levels (0F, 1F, 2F) and nutrient additions [$Ca(NO_3)_2$ and KH_2PO_4] at four levels (0, 1, 2, 3) with the same N:P ratio (10 by mass), in two replicates (fish abundances and nutrient concentrations are given in Table I). The treatments were spread randomly in two blocks. Planktivorous fish, caught from the lake, were used as regulators of zooplankton grazing pressure. The fish used were mainly 1+ (2 > age > 1 year) roach (*Rutilus rutilus*; <5 cm), but at the end of the experiment there was a lack of this size of the species and we used 0+ (1 > age > 0 years) roach and 1+ bream (*Abramis brama*) instead. Any dead fish were removed and replaced. At the end of the experiment, the fish were removed and the biomasses (fresh weights) were determined; the mean fish biomass (fresh weight) was 8 g m^{-2} (range 3–12 g m^{-2}) in treatment 1F and 18 g m^{-2} (range 10–31 g m^{-2}) in 2F, which corresponded reasonably with the desired levels (Table I).

Once every week, nutrients were added to the enclosures and the water was gently mixed. Once a week, integrated water samples were taken with a tube sampler and pooled (volume 12 l) for analysis of nutrients (total phosphorus and dissolved nitrogen), chlorophyll *a*, phytoplankton and zooplankton. Water for dissolved nutrients (NO_3^- and NH_4^+) were filtered through a GF/F filter, and the nutrient samples were put in a cooling box. A new GF/F filter was used for every sample; they were wrapped in aluminium foil, put in the cooling box, and saved for analysis of chlorophyll *a*. The phytoplankton samples were fixed with Lugol's solution and stored at 4°C until analysis. Samples for large zooplankton were filtered from 7 l of water through a 50 μm mesh and fixed with Lugol's solution. After sampling for background variables, recruitment traps were applied at the sediment surface in the enclosures. The traps consisted of a funnel, facing down, attached to a bottle (Figure 1). To stabilize the trap and to avoid horizontal entrance of algae from the water,

Table I: Fish densities (initial and final[a]) in the fish treatments, together with nutrient concentrations (weekly additions[b] and average concentrations[c]) in the nutrient treatments

Fish level	Fish density		Nutrient level	Weekly nutrient addition		Average nutrient concentration	
	Initial (g m^{-2})	Final (g m^{-2})		Nitrogen (μg l^{-1})	Phosphorus (μg l^{-1})	Nitrogen (μg l^{-1})	Phosphorus (μg l^{-1})
0	0	0	0	0	0	43	34
1	4	8	1	600	60	143	46
2	20	18	2	1500	150	498	134
			3	3000	300	1900	225

[a]Mean values (n = 8).
[b]μg N l^{-1} as $Ca(NO_3)_2$ and μg P l^{-1} as KH_2PO_4.
[c]Mean values from weighted average calculations (n = 36); μg N l^{-1} as nitrate- and ammonium-nitrogen and μg P l^{-1} as total phosphorus.

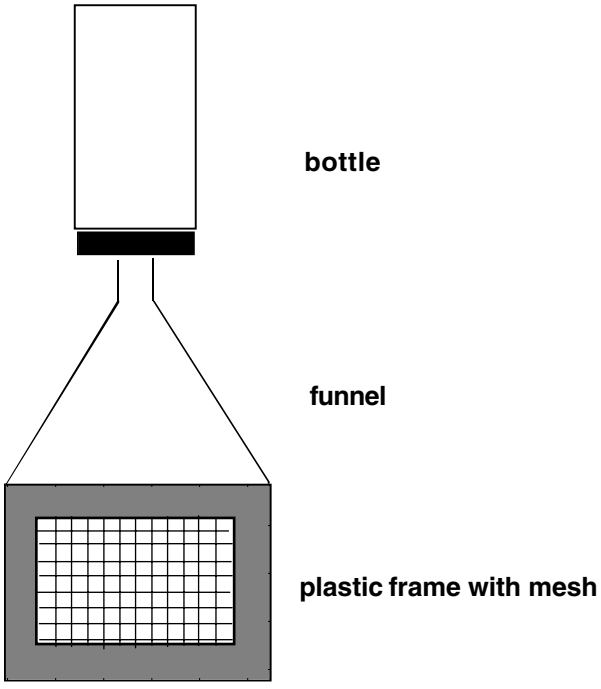

Fig. 1. Illustration of a trap for recruiting algae. The trap consists of a transparent glass bottle, attached to a transparent plastic funnel. Underneath the funnel is attached a circular plastic frame with mesh-covered sides (mesh size 50 μm). The plastic frame excludes any horizontally transported algae and allows the trap to stand by itself at the sediment surface without disturbing the water flow through the trap, and hence, the chemical environment in the trap will be similar to the lake conditions.

a circular plastic frame of the same diameter as the funnel was attached to the mouth of the funnel. The walls of the plastic frame were covered with a mesh of 50 μm to allow a flow of water through when standing upon the sediment. The openings were also covered with mosquito nets (mesh size 3 mm) to prevent large bottom particles (e.g. periphyton) from entering the trap. Before lowering the traps, they were filled with GF/C-filtered lake water to minimize the risk of trapping organisms from the water column when lowering. In addition, security was reinforced by the use of a sieve (mesh size 50 μm) that was held underneath the traps as they were lowered. The traps were left in the enclosures for ~48 h, and when they were emptied, the contents were preserved with Lugol's solution and stored at 4°C until analysis.

Analysis of samples

Nutrients were analysed on a Technicon Autoanalyzer II according to Technicon protocols.

Chlorophyll *a* was analysed following extraction with ethanol (95%) by spectrophotometry according to the Finnish standard SFS 5772, which is a modification of the international standard ISO 10260. Phytoplankton counting was performed according to a modified Utermöhl technique (Utermöhl, 1931) (at ×100 and ×400 magnification) using an inverted microscope. Colonies were treated as one individual. Since *Microcystis* abundance made up a large part (23% in general) of the abundance of the cyanobacteria, and since it dominated in the traps, *Microcystis* was the only organism that was analysed in the traps. Zooplankton counting was performed using the inverted microscope technique at ×40 and ×100 magnification. At least 100 individuals of the most common crustacean were counted per sample and 20 individuals of the major cladoceran and copepod species were measured in each sample; from these we calculated numbers and weights per volume of water.

Statistical analysis

Some analyses were made by the use of weighted averages (WA). In this, we assume that the response would increase over time, and thus a common mean was calculated for the different weeks for different responses. Hence, we calculated:

$$\mathrm{WA} = [(1 \times v1) + (2 \times v2) + (3 \times v3) + (4 \times v4) + (5 \times v5) + (6 \times v6)]/(1 + 2 + 3 + 4 + 5 + 6)$$

Where v followed by a number was any variable on sampling date 1–6 (Stephen *et al.*, 2004). The effects of treatments were analysed by the use of linear or exponential models ($\alpha = 0.05$) after checking for normality. Tests used were analysis of variance (ANOVA) and Pearson's correlation test.

RESULTS

Nutrient concentrations (dissolved nitrogen and total phosphorus) increased over time as a result of nutrient additions and showed significant differences among nutrient treatments (Table II). The increase in nutrient concentrations varied somewhat between different nutrient levels, and as a consequence, the N:P ratios (dissolved nitrogen to total phosphorus concentrations; by mass) were affected. In the lowest nutrient treatments, the N:P ratios were low but they were significantly higher in the highest nutrient treatment, as a result of an excess of nitrate (Table II; Figure 2A).

Both increasing nutrient concentrations and variations in the N:P ratios affected the recruitment and abundance of *Microcystis*. From week three onward, the recruitment and abundance of *Microcystis* increased considerably, and the increase was largest with the second highest nutrient addition where the N:P ratio was low (Figure 2; Table III). In effect, the recruitment and abundance of *Microcystis*, as well as the abundance of cyanobacteria overall, tended to

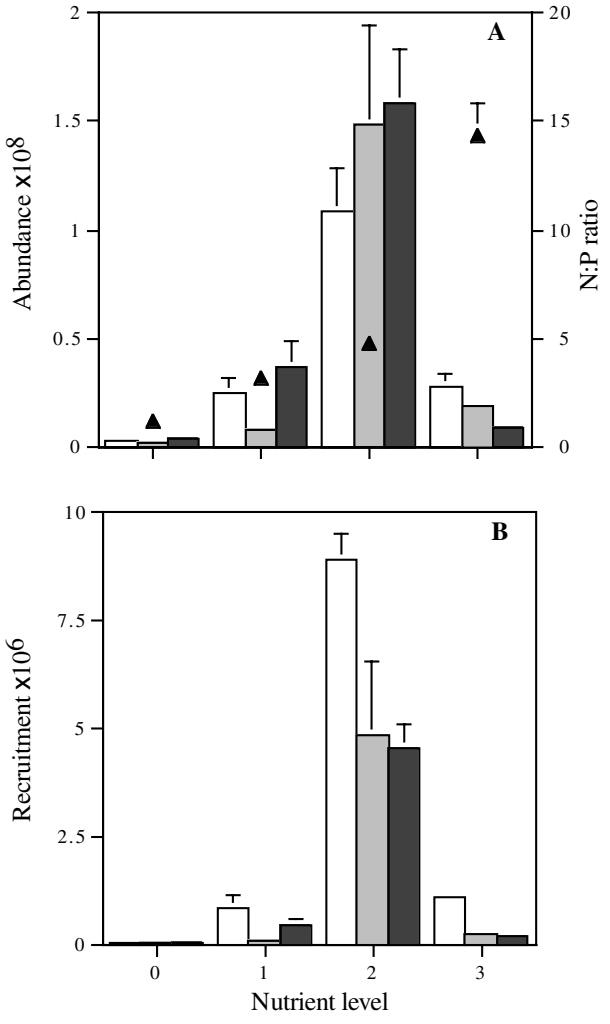

Fig. 2. (**A**) Abundance × 10^8 (mean values from weighted average calculations ± 1 SE, n = 12) of *Microcystis* (no. enclosure^{-1}; bars) at increasing nutrient (0, 1, 2, 3) and fish (0F, white bar; 1F, grey bar; 2F, black bar) levels, together with N:P ratios (dissolved inorganic nitrogen to total phosphorus, by mass; mean values from weighted average calculations + 1 SE, n = 36; triangles) at different nutrient levels. (**B**) Recruitment × 10^6 (mean values from weighted average calculations ± 1 SE, n = 12) of *Microcystis* (no. enclosure^{-1} day^{-1}; bars) at increasing nutrient (0, 1, 2, 3) and fish (0F, white bar; 1F, grey bar; 2F, black bar) levels. Details of nutrient and fish treatments in Table I.

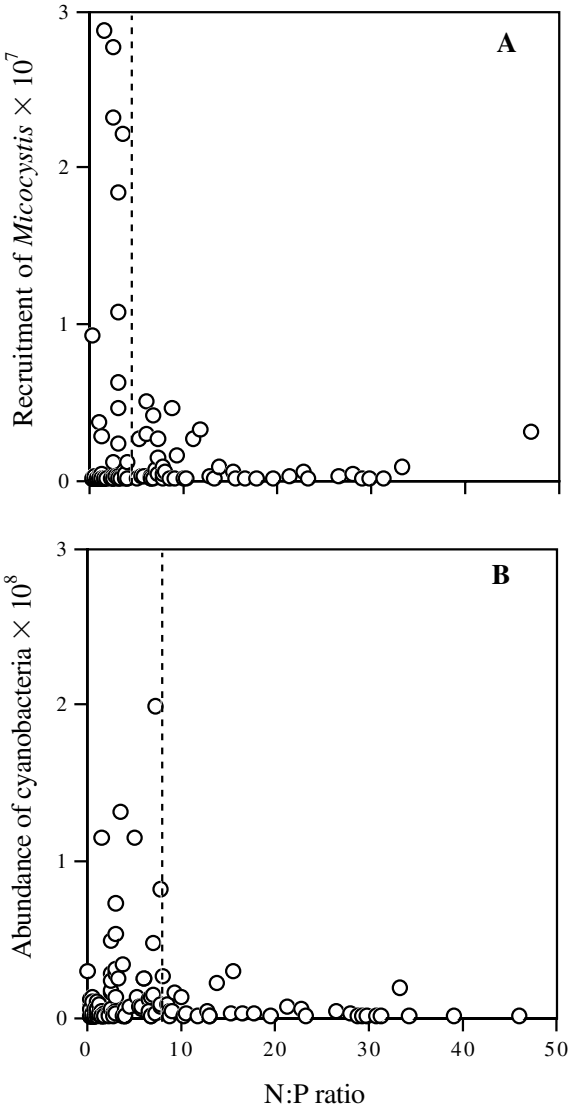

Fig. 3. (**A**) Recruitment of *Microcystis* × 10^7 (no. m^{-2} day^{-1}) at different N:P ratios (dissolved inorganic nitrogen to total phosphorus, by mass; n = 128). Boundary for N:P = 5 is shown by the dashed line. (**B**) Abundance of cyanobacteria × 10^8 (no. l^{-1}) at different N:P ratios (n = 136). Boundary for N:P = 8 is shown by the dashed line. Modified from Smith (Smith, 1983).

decrease with N:P ratios exceeding 8:1 (by mass; Figure 3).

Total phytoplankton biomass, expressed as chlorophyll *a* content, increased over time with increasing nutrient concentrations (Table III; Figure 4). The major phytoplankton groups were cyanobacteria, green algae and cryptomonads, which together accounted for >90% of the total. These groups showed different responses to the different treatments. Cyanobacteria, for example, had the highest abundance and dominated when the nutrient addition was intermediate, while green algae dominated in the highest nutrient treatment (Figure 4).

Different fish levels did not affect the nutrient concentrations or the ratio between them (Table II). However, there was a significant interaction effect of nutrients and fish on the N:P ratio (Table II). This interaction effect was a result of a higher N:P ratio in the highest nutrient treatment when fish were absent, compared with when fish were present. Neither fish nor nutrients affected the total biomass of zooplankton, even though large cladocerans (>500 μm) were eradicated by the fish treatments (Table III). Different zooplankton grazing pressures also

Table II: Summary of the ANOVA for the different abiotic variables (mean values from weighted average calculations; n = 12) affected by different nutrient and fish treatments

Variable	Nutrient	Fish	Interaction term
Dissolved nitrogen concentration[a]	$P < 0.001$; $F = 106.6$	NS[b]	$P = 0.043$; $F = 3.2$
Total phosphorus concentration	$P < 0.001$; $F = 49.6$	NS	NS
N:P ratio[c]	$P < 0.001$; $F = 48.9$	NS	$P = 0.013$; $F = 4.5$

[a]Nutrient data are log-transformed.
[b]NS indicates non-significant effects.
[c]N:P ratio = dissolved inorganic nitrogen to total phosphorus, by mass.

Table III: Summary of the ANOVA for biotic variables (mean values from weighted average calculations; n = 12) affected by different nutrient and fish treatments

Parameter	Nutrient	Fish	Interaction term
Microcystis recruitment	$P < 0.001$; $F = 21.9$	NS[b]	NS
Microcystis abundance	$P < 0.001$; $F = 17.1$	NS	NS
Chl-*a*[a]	$P < 0.001$; $F = 48.5$	NS	NS
Total zooplankton biomass	NS	NS	NS
Cladocerans > 500 μm[a]	NS	$P < 0.001$; $F = 100.0$	NS

[a]Log-transformed.
[b]NS indicates non-significant effects.

had no direct effect on either the recruitment or abundance of *Microcystis* (Figure 2; Table III).

Microcystis growth in the water phase was correlated with the recruitment of *Microcystis* from the sediment the previous week ($r = 0.695$, $t = 9.459$, $P < 0.001$, $n = 98$; Pearson's correlation test; Figure 5). This pattern was especially obvious in some enclosures at the beginning of the experiment when the recruitment rate exceeded the standing stock several fold. In general, the daily recruitment of *Microcystis* was, from week one onward, 17% (median 2%) of the standing stock the following week.

DISCUSSION

Blooms of cyanobacteria have become a worldwide problem in nutrient-enriched lakes and estuarine waters (Codd, 2000). Blooms often smell bad, complicate water purification, are toxic, cause oxygen depletion (which leads to fish mortality en masse), and otherwise cause economic and ecological costs.

Usually, blooms develop when the nutrient load is high, which is often caused by leaching of anthropogenic nutrients from land. Earlier findings suggest that blooms may originate, by recruitment, from resting cells (Reynolds and Walsby, 1975; Hansson *et al.*, 1994; Boero *et al.*, 1996; Perakis *et al.*, 1996). *Microcystis* is known to form resting stages that can over-winter in the sediment; from these, inocula could be provided for the next year's growth season (Preston *et al.*, 1980; Fallon and Brock, 1981; Takamura *et al.*, 1984). In our study, the abundance of *Microcystis* at time (t + 1 week) was correlated with the recruitment rate at time (t) (Figure 5), and the recruitment rate of *Microcystis*, especially in the beginning of the experiment, exceeded the abundance of *Microcystis* in the water many fold. This suggests that recruitment was important for the development of the pelagic population. Overall, the daily recruitment from the sediment surface formed approximately 17% of the standing stock in the enclosure water column 1 week later. Earlier findings suggest that the daily recruitment from the sediment can contribute to the epilimnic population from less than 1% to as much as 53% (Trimbee and Harris, 1984; Barbiero and Welch, 1992; Barbiero and Kann, 1994; Hansson *et al.*, 1994; Hansson, 1996a).

There is an ongoing debate whether the resource ratio is important for cyanobacterial dominance or if other

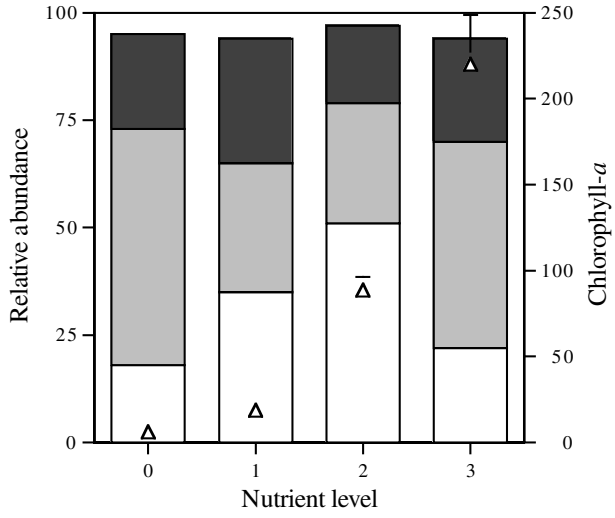

Fig. 4. Relative abundance (% of total abundance; mean values from calculations of weighted averages; $n = 36$), of cryptomonads (black bar), green algae (grey bar) and cyanobacteria (white bar) at increasing nutrient additions, together with the corresponding values of chlorophyll *a* (mg l^{-1}; mean values from calculations of weighted averages ± 1 SE, $n = 36$; triangles). Cryptomonads, green algae and cyanobacteria always made up >90% of the total amount of phytoplankton. The rest of the phytoplankton assemblage consisted of dinoflagellates, chrysophytes, diatoms and euglenoids.

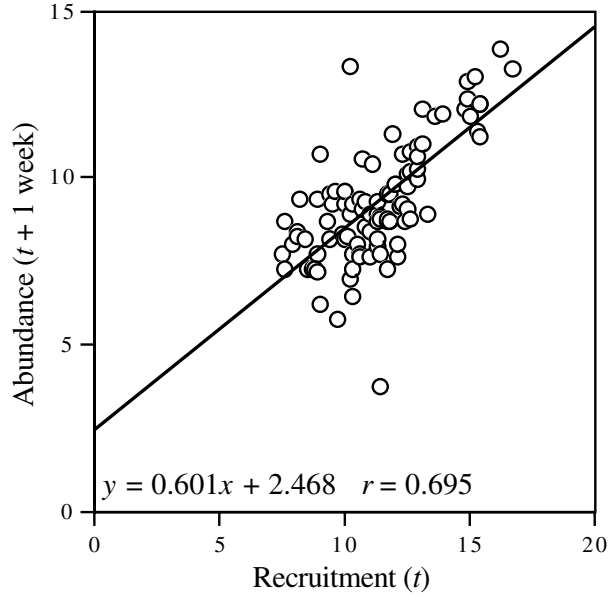

Fig. 5. *Microcystis* abundance (no. enclosure^{-1}) at time ($t + 1$ week) as a function of *Microcystis* recruitment (no. enclosure^{-1} day^{-1}) at time (t), ($n = 97$; log-transformed data). Regression line with linear equation and r value is included.

factors are limiting (Hyenstrand *et al.*, 1998; Reynolds, 1999; Sommer, 1999; Berman, 2001; Downing *et al.*, 2001). Variation in total phosphorus has, for example, also been found to correlate positively with cyanobacterial dominance (Trimbee and Prepas, 1987; Downing *et al.*, 2001). However, this was not the case in our study, since the concentration of total phosphorus increased with increasing nutrient level, and at the highest nutrient level, there was a dominance of green algae instead of cyanobacteria (Figure 4). In support of this conclusion, a major study of shallow lakes found that green algae dominated and tended to outcompete cyanobacteria in hypertrophic conditions with high phosphorus concentrations (Jensen *et al.*, 1994). Other studies have also found that cyanobacteria thrive in nutrient-rich environments with low N:P ratios (Smith, 1983, 1986; McQueen and Lean, 1987; Findlay *et al.*, 1994; Bulgakov and Levich, 1999; Hadas *et al.*, 1999; Smith and Bennett, 1999; Jacoby *et al.*, 2000). Smith found a negative relationship between the proportion of cyanobacteria and total nitrogen to total phosphorus ratios in 17 lakes worldwide (Smith, 1983). Our study confirms this, and in addition, we found that the recruitment rate of the cyanobacteria *Microcystis* was highest with low N:P ratios (Figure 3). One possibility is that not only growth, but also recruitment, are affected by variations in N:P ratios. To our knowledge, this has not been investigated before and further studies are needed.

Previous studies have found that the recruitment rate of phytoplankton can be slowed by the presence of grazers (Hansson, 1996b, 2000). In this study, recruitment of *Microcystis* did not seem to be affected by grazers (Table III). Cyanobacteria are of low nutritional value, they can be toxic, and their shape may mechanically interfere with the filtering processes; for these reasons they are not suitable as food for several zooplankton species (de Bernardi and Giussani, 1990). Since resting stages of *Microcystis* are large, they are also difficult to graze, which can explain why they do not need an avoidance strategy. Still, there might be other ways that zooplankton have exerted an impact on the recruitment rate. Nutrient release resulting from zooplankton grazing may generate high N:P ratios as a result of a high internal phosphorus content (Andersen and Hessen, 1991; Attayde and Hansson, 1999; Elser, 1999). In our study, the highest N:P ratio was recorded in the enclosures with a high abundance of large cladocerans (0F) at the highest nutrient level. This implies that large cladocerans had an influence in generating the higher N:P ratios. However, some other factor must have been involved too, since large cladocerans were more or less absent in the presence of fish.

In conclusion, our results indicate that recruitment of cyanobacterial resting stages from the sediment can be important for the development of blooms, since they act

as inocula and rapidly add new colonies to the growing epilimnic population. We argue that *Microcystis* recruitment is favoured by high concentrations of nutrients in combination with low N:P ratios. We could not find any direct effect of the grazer community, although we found indirect effects of altered N:P ratios in the presence of large cladocerans. To minimize the problem of cyanobacterial blooms, the anthropogenic nutrient leaching from urban and agricultural areas needs to be decreased. However, this may not be a purely technical problem, since ecological and socio-economic aspects of resource use have to be included if future water management plans are to be successful.

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