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Benthic–pelagic coupling in the population dynamics of the harmful cyanobacterium *Microcystis*

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SUMMARY

1. In eutrophic lakes, large amounts of the cyanobacterium *Microcystis* may overwinter in the sediment and re-inoculate the water column in spring.
2. We monitored changes in pelagic and benthic populations of *Microcystis* in Lake Volkerak, The Netherlands. In addition, sedimentation rates and the rate of recruitment from the sediment were measured using traps. These data were used to model the coupling between the benthic and pelagic populations and to calculate the contribution of overwintering benthic and pelagic populations to the magnitude of the pelagic summer bloom.
3. Changes in the benthic *Microcystis* population showed a time lag of 3–14 weeks compared with the pelagic population. This time lag increased with lake depth. The largest amount of benthic *Microcystis* was found in the deepest parts of the lake. These observations suggest horizontal transport of sedimented *Microcystis* from shallow to deep parts of the lake.
4. Recruitment from and sedimentation to the sediment occurred throughout the year, with highest recruitment and sedimentation rates during summer. Model simulations indicate that the absence of benthic recruitment would reduce the summer bloom by 50%.
5. In spring, the total pelagic population was three to six times smaller than the total benthic population. Yet, model simulations predict that the absence of this small overwintering pelagic population would reduce the summer bloom by more than 64%.
6. Reduction of the overwintering pelagic populations, for instance by flushing, may be a useful management strategy to suppress or at least delay summer blooms of *Microcystis*.

Keywords: harmful algae, *Microcystis*, model, population dynamics, recruitment, sedimentation

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Introduction

Species of the *Microcystis* genus are cosmopolitan cyanobacteria that can completely dominate the freshwater phytoplankton of eutrophic lakes (e.g. Reynolds *et al.*, 1981; Zohary & Robarts, 1990; Visser *et al.*, 1996). Moreover, some species of *Microcystis* can produce a group of hepatotoxins, called microcystins, which can be toxic to both humans and animals (Codd, 1995;

Falconer, 1999; Carmichael *et al.*, 2001; Huisman, Matthijs & Visser, 2005). This makes *Microcystis* a major nuisance species in eutrophic lakes.

In temperate regions, *Microcystis* colonies that have sunk to the sediment overwinter on the bottom of the lake (Reynolds *et al.*, 1981; Boström, Petterson & Ahlgren, 1989; Tsujimura *et al.*, 2000). The size of this benthic population can become quite large, sometimes even larger than the pelagic summer population (Takamura, Yasuno & Sugahara, 1984). The benthic population that has survived winter can provide an inoculum in spring for the pelagic *Microcystis* bloom (Preston, Stewart & Reynolds, 1980). In fact, one may hypothesise that a large overwintering benthic population is one of the reasons why a cyanobacterium with a low specific growth rate like *Microcystis* is able to become so dominant in the summer phytoplankton (Reynolds, 1994). Relatively little is known, however, about the coupling between benthic and pelagic *Microcystis* populations, and whether recruitment from the benthic population is indeed a major factor in the dominance of *Microcystis* during summer.

Recruitment of *Microcystis* from the sediment seems to be largely a passive process that is driven by sediment resuspension (Verspagen *et al.*, 2004). Some studies found recruitment rates of *Microcystis* from the sediment to be <0.2% of the pelagic population size per day (Reynolds *et al.*, 1981; Hansson *et al.*, 1994). Other studies, however, reported recruitment rates as high as 4% of the pelagic population size per day (Trimbee & Harris, 1984; Ståhl-Delbanco, Hansson & Gyllström, 2003). A total of 50% of the benthic *Microcystis* population that had survived winter conditions was found to re-inoculate the water column during summer in shallow parts of a Swedish lake (Brunberg & Blomqvist, 2003). Karlsson-Elfgren *et al.* (2003) recently calculated for another cyanobacterium, *Gloeotrichia echinulata*, that a recruitment of <5% of the pelagic population size per day provided an important inoculum for growth in the water column. Substantial amounts of *Microcystis* have also been reported to overwinter in the water column as well (Reynolds & Rogers, 1976; Kurmayer & Kutzenberger, 2003). If *Microcystis* also overwinters in the water column, and remains viable in sufficient numbers, benthic recruitment might not play a significant role in the spring inoculum.

This study was carried out to quantify the coupling between benthic and pelagic *Microcystis* populations.

We studied seasonal changes in *Microcystis* abundance in water and sediment of a large Dutch lake. In addition, we placed sediment traps and recruitment traps in the lake to study vertical fluxes of *Microcystis*. A straightforward phenomenological model was fitted to these data to describe the dynamics of benthic–pelagic coupling. This model enabled us to calculate the extent to which overwintering benthic and pelagic populations of *Microcystis* contributed to the *Microcystis* bloom in summer.

Material and methods

Site description and sampling

Lake Volkerak is situated in the south-west of the Netherlands (Fig. 1). The surface area of Lake Volkerak is 45.7 km², it has an average depth of 5.5 m and a maximum depth of 22 m. The freshwater lake was created by damming of the Volkerak estuary by the Philipsdam in 1987. From 1988 onwards, summer blooms of *Microcystis* have gradually increased in intensity and nowadays *Microcystis* is by far the most dominant phytoplankton species in the lake.

We sampled the lake once every 2 weeks in the period from January 2000 until October 2001. Eight sampling stations (A–H) were selected ranging in water column depth from 2.1 to 20.7 m. Samples were taken within a radius of 20 m from each station. Water column depths and sediment characteristics of each sampling station are listed in Table 1.

Temperature and oxygen concentration were measured at 1 m depth intervals in the water column at stations C, F and G and at 1 m above the sediment at all other stations. Wind speed and direction were measured at 10-min intervals at weather station Stavernisse, 12 km south-west of the lake (available at <http://www.hmcz.nl>, last accessed 22 March 2005).

Water was sampled at sampling stations C, F and G. During the bloom period of *Microcystis*, from mid May to mid November, water was sampled at the lake surface, at 25% and at 75% of the water column depth, and at 1 m above the sediment. From mid November to mid May, only surface water was sampled.

Sediment was sampled at all stations, using a box corer (Ø 30 cm, height 50 cm), from which four subsamples were taken with a Perspex corer (Ø 4.7 cm, height 30 cm). Cores were sampled down to

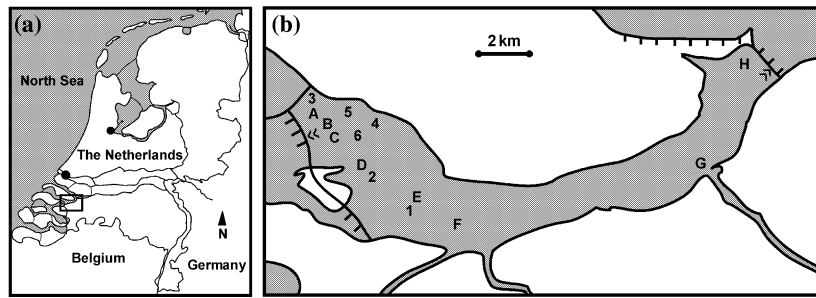


Fig. 1 Location of (a) Lake Volkerak (51°66'N, 4°33'E) and (b) position of sediment sampling stations A-H and trap sites 1-6 in the lake.

Table 1 Some characteristics of the sampling stations. The sediment characteristics include the mean and standard deviation of dry weight (DW) and organic matter (OM) content ($n = 45$).

Sampling station	Water-column depth (m)	DW (g mL ⁻¹)	OM (% of DW)
Shallow sites (0-6 m)			
Station D	3 ± 0.5	0.88 ± 0.14	2.0 ± 0.6
Station E	5 ± 1.0	0.85 ± 0.35	2.4 ± 2.0
Station 1	5		
Station 2	6		
Intermediate sites (6-15 m)			
Station A	10 ± 1.0	0.48 ± 0.29	6.1 ± 3.5
Station F	11 ± 0.6	0.20 ± 0.08	13 ± 2.5
Station G	11 ± 0.9	0.66 ± 0.35	4.2 ± 2.8
Station H	11 ± 0.4	0.28 ± 0.04	9.5 ± 1.3
Station 3	8		
Station 4	12		
Deep sites (15-21 m)			
Station B	19 ± 0.8	0.14 ± 0.02	17 ± 2.4
Station C	19 ± 1.0	0.15 ± 0.02	18 ± 2.5
Station 5	16		
Station 6	21		

the depth were *Microcystis* colonies were no longer visible, which was approximately 1.5-2 cm in shallow parts of the lake, 2-6 cm in intermediate parts and 4-8 cm in deep parts. Subsamples were pooled and stored at 8 °C until further analysis.

Traps were placed in the field at six sites, numbered 1-6 (Fig. 1; Table 1). To avoid interference with sediment resuspension processes, the traps were freely suspended above the sediment (Fig. 2). The opening of recruitment traps was directed downwards and positioned 1.0 m above the sediment. The opening of sediment traps was directed upwards and positioned 1.8 m above the sediment. The position of the traps was stabilised by a weight attached to the traps. We used two types of traps in our study. The first type (Technicap pps4/3, La Turbie, France) was deployed at sampling stations 1 and 6 from January to August

2000, as a recruitment trap only. Within these traps, a preprogrammed carousel changed sampling containers within the traps every 3-4 days. These traps were emptied every 2 weeks. The second type of trap, developed at the University of Amsterdam, consisted of both a sediment trap and a recruitment trap (Fig. 2) and was used from August 2000 to September 2001. These traps were placed at sites 1-6 and were emptied weekly. Some of the traps were lost from the buoys for short periods, resulting in gaps in the data.

Sample analysis

Samples taken from the water column, the traps and the sediments were processed in the laboratory within 24 h. To determine the dry weight (DW) of the sediment and sediment trap samples, 10-30 mL of sample was put in a porcelain cup and dried overnight at 100 °C. Ash free DW was determined by combusting samples at 500 °C for at least 3 h. After both treatments, samples were stored in a desiccator and weighed at room temperature. The amount of organic matter (OM) in the samples was calculated as the difference between DW and ash free DW. To estimate the abundance of *Microcystis* in the water column and the traps, the water and trap samples were preserved with a mixture of 0.01% paraformaldehyde (PFA)/ 0.1% glutaraldehyde (GA) and stored at 4 °C until analysis on the EurOPA flow cytometer (Dubelaar *et al.*, 1989). This flow cytometer is designed to detect and quantify cells and colonies varying in size from 0.5 to 2000 µm. It distinguishes cyanobacteria from other phytoplankton, based on their phycocyanin fluorescence (Jonker *et al.*, 1995). Chlorophyll *a* fluorescence (Chl *a*F) of the cyanobacterial cells and colonies was used as an estimate of cyanobacterial biomass. Surface water samples were also filtered onto glass fibre filters with a pore size of 1.0 µm and stored at -20 °C until chlorophyll *a* (Chl *a*) extraction.

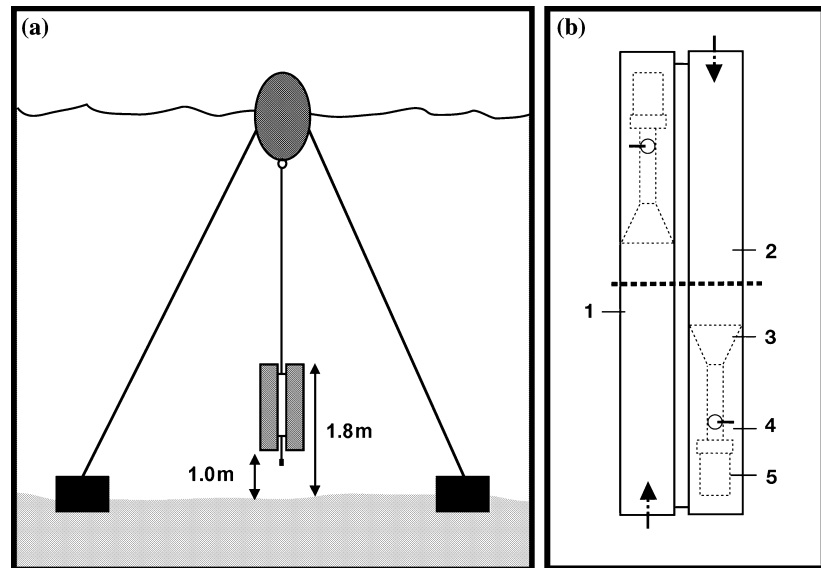


Fig. 2 Deployment of traps in the field. (a) Traps were attached to a buoy that was fixed with two anchors. (b) Cross-section of a recruitment trap (1) and a sediment trap (2). The traps have a height of 80 cm and a diameter of 12 cm. Floating and sinking material was concentrated in a funnel (3) into a sampling bottle (5). The valve (4) was used to close the sampling bottle just before lifting the traps out of the water.

Microcystis colonies were isolated from the sediment. During isolation, samples were stored on ice. The sediment was homogenised by gentle stirring. About 5–25 mL of homogenised sediment was suspended in a Percoll mixture [30% Percoll, 70% mineral medium described by Van Liere & Mur (1978)] and centrifuged (600 *g*, 15 min) to separate *Microcystis* from the sediment. Microscopic inspection indicated that losses of *Microcystis* cells and colonies during centrifugation were negligible. After the first centrifugation, the supernatant with the cells and colonies was transferred to another tube and centrifuged a second time (4600 *g*, 20 min). After the second centrifugation step, the supernatant with the cells and colonies was preserved with 0.01% PFA/0.1% GA and stored at 4 °C until analysis on the EurOPA flow cytometer. The laser set-up of the flow cytometer was optimised to detect only particles containing Chl *a*.

Chlorophyll *a* concentrations of surface water samples collected in summer (when >95% of the phytoplankton consisted of *Microcystis*) were used to convert Chl *a* F values in arbitrary units (a.u. L⁻¹) into actual Chl *a* concentrations (µg L⁻¹). Chl *a* was extracted from lyophilised glass fibre filters using N,N-dimethylformamide for 2 h at room temperature. Chl *a* was measured spectrophotometrically at 647 and 664 nm and concentrations were calculated according to Porra, Thompson & Kriedemann (1989). Based on linear regression, we calculated that 1.8×10^9

a.u. Chl *a* F corresponded to 1 µg Chl *a* ($r^2 = 0.612$, $n = 59$, $P < 0.001$).

Data analysis

Given the morphology of the lake, the sampling sites were divided into three categories: shallow sites (0–6 m), intermediate sites (6–15 m), and deep sites (15–21 m; Table 1). We used the generalised linear models repeated measures procedure (GLM-RM, Vonesh & Chinchilli, 1997) to test if the population dynamics and sedimentation and recruitment fluxes differed significantly between the three categories. The data were log-transformed before analysis to obtain a normal distribution. Each of the databases used for GLM-RM had at least some missing data. To deal with this problem we performed GLM-RM using listwise data deletion. If sphericity could not be assumed (as calculated by using Mauchly's test), we used the Greenhouse–Geisser epsilon to correct the averaged *F*-test. We chose the Greenhouse–Geisser instead of the Huyn–Feldt epsilon, because it is more conservative.

Smoothing of the field data was performed using local quadratic regression on the log-transformed values for each depth category, yielding a smooth curve that preserves the seasonal behaviour of the data. Smoothing was done with the LOCFIT module of Loader (1999), consistently applying the same smoothing procedure to all data sets, i.e. a Gaussian kernel with a bandwidth of 120 days.

Benthic–pelagic model

To assess the contributions of the overwintering benthic and pelagic *Microcystis* populations to the summer bloom, we developed a phenomenological model that is closely tied to the smoothed data. Phenomenological models are different from mechanistic models. Whereas a mechanistic model aims at a realistic description of all relevant processes, a phenomenological model aims at a description that fits the data well. We used this approach because it allows us to quantify the dynamics of the system without full knowledge of all processes involved.

Let N_W denote the amounts of *Microcystis* per unit surface area in the water column, and let N_S denote the amounts of *Microcystis* per unit surface area in the sediment. Furthermore, let $N_T = N_W + N_S$ denote the total amount of *Microcystis* per unit surface area in the entire lake. We assume that growth only takes place in the water column. Growth of benthic *Microcystis* is considered negligible, because very little light reaches the sediment owing to the high turbidity of the lake. Mortality is assumed to occur in both the water column and sediment. Grazing of *Microcystis* is implicitly included in the mortality term. The population dynamics of *Microcystis* can then be described by the following mass balance equation:

$$\frac{dN_T}{dt} = \mu(t)N_W - m(N_W + N_S) \quad (1)$$

where $\mu(t)$ is the specific growth rate in the water column (day^{-1}) and m is the specific mortality rate (day^{-1}). The results of our fieldwork indicated that the dynamics of the *Microcystis* concentration in the water column behaved rather uniformly over the entire lake, whereas the benthic *Microcystis* populations showed different dynamics in shallow, intermediate and deep parts of the lake. Therefore, the model was divided into a total of four compartments: one compartment representing the pelagic *Microcystis* population, and three compartments representing the benthic *Microcystis* populations in the shallow, intermediate, and deep sediments, respectively. In our notation, N_W is the amount of pelagic *Microcystis* per unit surface area, for an average lake depth of $z_M = 5.5$ m. Let N_{SS} , N_{SI} and N_{SD} denote the amounts of *Microcystis* per surface area in the shallow, intermediate and deep sediments, respectively. The dynamics of the four compartments can then be described as:

$$\begin{aligned} \frac{dN_W}{dt} = & \mu(t)N_W - mN_W - V_S s_S(t)N_W - V_I s_I(t)N_W \\ & - V_D s_D(t)N_W + A_S r_S(t)N_{SS} + A_I r_I(t)N_{SI} \\ & + A_D r_D(t)N_{SD} + L_W(t) \end{aligned} \quad (2)$$

$$\frac{dN_{SS}}{dt} = s_S(t) \frac{z_S}{z_M} N_W - r_S(t)N_{SS} - mN_{SS} + L_{SS}(t) \quad (3)$$

$$\frac{dN_{SI}}{dt} = s_I(t) \frac{z_I}{z_M} N_W - r_I(t)N_{SI} - mN_{SI} + L_{SI}(t) \quad (4)$$

$$\frac{dN_{SD}}{dt} = s_D(t) \frac{z_D}{z_M} N_W - r_D(t)N_{SD} - mN_{SD} + L_{SD}(t) \quad (5)$$

Here, $s_S(t)$, $s_I(t)$ and $s_D(t)$ are the specific sedimentation rates from the pelagic population to the benthic populations in the shallow, intermediate and deep parts of the lake (day^{-1}). Conversely, $r_S(t)$, $r_I(t)$ and $r_D(t)$ are the specific recruitment rates from the benthic populations in the shallow, intermediate and deep parts of the lake to the pelagic population (day^{-1}). Furthermore, scaling is required to account for the different dimensions of the shallow, intermediate, and deep parts of the lake. For this purpose, z_S , z_I , and z_D are the average water column depths of the shallow, intermediate and deep parts of the lake (m), A_S , A_I and A_D are the relative surface areas of the shallow, intermediate and deep parts of the lake (dimensionless), and V_S , V_I and V_D are the relative volumes of the shallow, intermediate and deep parts of the lake (dimensionless). Finally, the terms $L_W(t)$, $L_{SS}(t)$, $L_{SI}(t)$ and $L_{SD}(t)$ describe additional population exchanges between the compartments, for instance because of sedimentation not captured by the sediment traps and lateral transport between the different sediment compartments ($\text{mg Chl } a \text{ m}^{-2} \text{ day}^{-1}$). Mass balance of the *Microcystis* population is imposed by the constraint that the sum of all (area-weighted) L -terms adds up to zero. This implies that all exchange terms in the model cancel out against each other, such that addition of eqns 2–5 leads to eqn 1.

The parameters of the benthic–pelagic system defined by eqns 1–5 were estimated as follows. The population sizes in the water column (N_W) and sediments (N_{SS} , N_{SI} and N_{SD}) as well as the rates of population change in the water column (dN_W/dt) and sediments (dN_{SS}/dt , dN_{SI}/dt and dN_{SD}/dt) were obtained directly from the smoothed field data

for each of the depth categories. The specific sedimentation rates (s_S , s_I and s_D) and specific recruitment rates (r_S , r_I and r_D) were obtained directly from the sediment traps and recruitment traps. The average depths of the shallow, intermediate and deep parts of the lake were $z_S = 2.0$, $z_I = 11.9$ and $z_D = 16.9$ m. The relative surface areas of the shallow, intermediate and deep parts of the lake were $A_S = 0.67$, $A_I = 0.28$ and $A_D = 0.05$. The relative volumes of the shallow, intermediate and deep parts of the lake were $V_S = 0.24$, $V_I = 0.61$ and $V_D = 0.15$. For simplicity, we assumed that the specific mortality rate (m) was constant in time; it was calculated by fitting a first-order exponential decay curve to the decline of the total *Microcystis* population (N_T) during winter, from the maximum value of N_T in September to the minimum value of N_T in May ($r^2 = 0.967$, $n = 260$, $P < 0.001$). The specific growth rate (μ) is now the only unknown in eqn 1, and can thus be calculated from the smoothed field data by solving this equation. The remaining terms L_W , L_{SS} , L_{SI} and L_{SD} were calculated by solving eqns 2–5.

Results

Water temperature ranged between 1 °C and 22 °C at the surface and between 2 and 20 °C in the bottom waters overlying the deepest parts of Lake Volkerak (Fig. 3a). There was no temperature stratification in the lake, except for those parts of the lake (only 5% of the whole lake area) where depth exceeds 15 m. Oxygen concentrations were low in summer and high in winter (Fig. 3b). In summer (from June to October) the oxygen concentration gradually decreased from a depth of 10–11 m down to the sediment. Occasionally, water just above the sediment became anoxic. The energy input by wind was generally lower in summer than during the rest of the year (Fig. 3c). Occasional storms in summer led to a partial homogenisation in oxygen concentration (compare Fig. 3b,c).

There was no significant effect of lake depth on the pelagic *Microcystis* concentration (Table 2). This indicates that the pelagic *Microcystis* population behaves uniformly over the entire lake, as assumed by the model. The pelagic *Microcystis* population started to increase in May, reached its maximum in September and declined during autumn (Fig. 4). Small amounts

of *Microcystis* remained present in the water column in winter.

The sizes of the benthic *Microcystis* populations in shallow, intermediate and deep parts of the lake differed significantly from each other (Table 2). The benthic population was almost one order of magnitude smaller in the shallow parts than in the deep parts of the lake. Benthic *Microcystis* populations were lowest in June to July, increased until October at the shallow and intermediate sites and increased until December at the deep sites, after which the benthic populations decreased again (Fig. 5). When expressed per unit surface area, the total pelagic population in early spring was three to six times smaller than the total benthic population.

We correlated the smoothed pelagic population size with the smoothed benthic population sizes using a series of different time delays, to estimate how fast changes in the pelagic population were followed by changes in the different benthic populations. Maximum correlation was found for a time lag of 3 weeks at the shallow sites ($r = 0.944$), a time lag of 6 weeks at the intermediate sites ($r = 0.860$) and a time lag of 14 weeks at the deep sites ($r = 0.906$). Similarly, we correlated the smoothed population sizes of the different sediment compartments, to estimate how fast changes in shallow benthic populations were followed by changes in deeper benthic populations. Maximum correlation was found for a time lag of 2 weeks between the benthic populations in the shallow and intermediate sediments ($r = 0.886$), a time lag of 6 weeks between the benthic populations in the intermediate and deep sediments ($r = 0.962$) and a time lag of 10 weeks between the benthic populations in the shallow and deep sediments ($r = 0.848$). Taken together, these time lags indicate net transport from the pelagic population to the benthic populations, and subsequently from the shallow benthic populations to the benthic populations in deeper parts of the lake.

Accumulation of *Microcystis* in recruitment traps and sediment traps was lowest in March and highest in September (Fig. 6). Changes in recruitment and sedimentation reflected the seasonal changes in the benthic and pelagic populations. Both the recruitment flux and the sedimentation flux did not differ significantly between different parts of the lake (Table 2). Previous work suggested that recruitment from

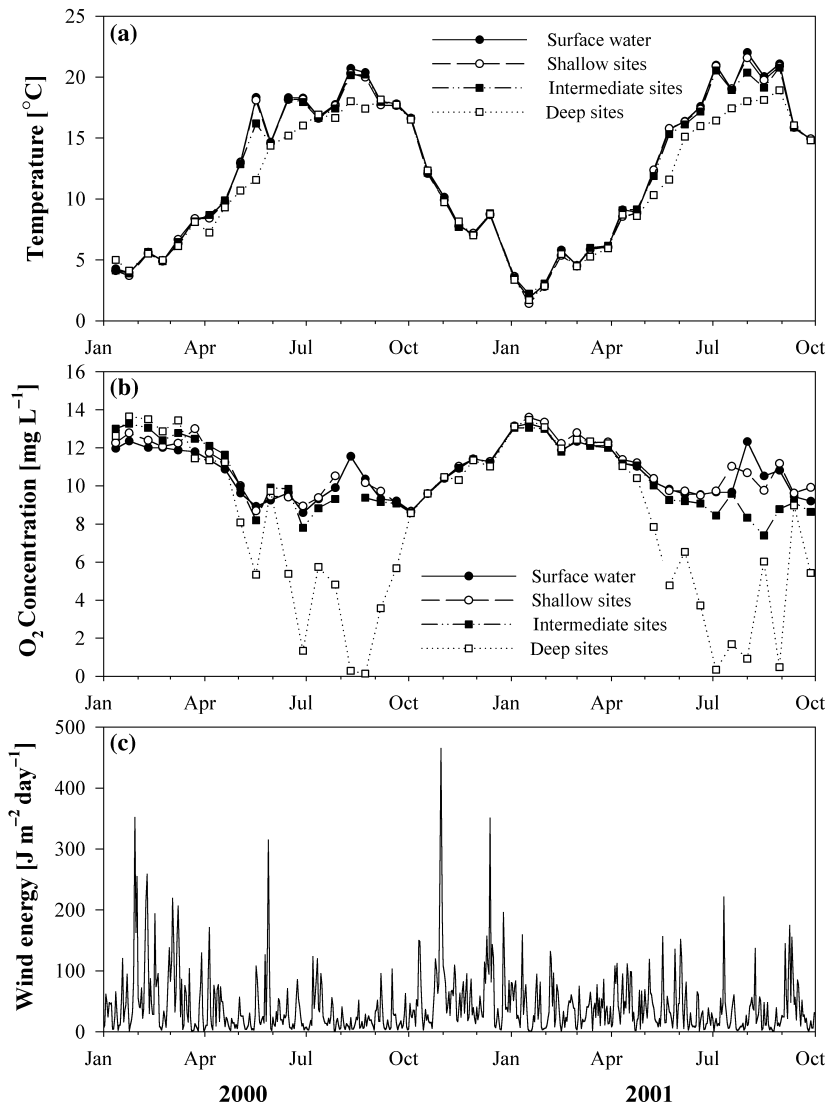


Fig. 3 Seasonal dynamics of (a) temperature and (b) oxygen concentration in surface water and water overlying the sediment in Lake Volkerak. (c) Seasonal dynamics of daily-averaged wind energy flux.

benthic *Microcystis* populations to the water column is largely a passive process driven by resuspension (Verspagen *et al.*, 2004). We therefore calculated the fraction of re-suspended materials caught by the sediment traps, based on the relation between the settling particulate inorganic matter (SPIM) and total settling particulate matter (SPM) in the traps (Weyhenmeyer, Meili & Pierson, 1995). This revealed that 80–95% of the SPM caught by sediment traps could be attributed to resuspension.

Calculated specific growth rates in the water column were rather variable in winter and high in summer, with maximum specific growth rates in July to August (Fig. 7a). The large variation in the specific growth rate of the pelagic *Microcystis* population during winter is most likely a model artefact gener-

ated by the low abundance of pelagic *Microcystis* compared with benthic *Microcystis* in winter.

Specific sedimentation rates did not show distinct seasonal patterns. In contrast, specific recruitment rates were high in summer and autumn, but low in winter and spring (Fig. 7b–d). The specific sedimentation and recruitment rates were much higher at the shallow sites than at the intermediate and deep sites.

The remaining terms L_W , L_{SS} , L_{SI} and L_{SD} describe transport of *Microcystis* that was not directly measured, but deduced from the dynamics in the different model compartments (Fig. 7e,f). The negative values of L_W in the period June to September, together with the positive values of L_{SS} , L_{SI} and L_{SD} in the same period indicate an additional flux from the water column to the sediments, i.e. sedimentation rates are

Table 2 Effects of time and lake depth on the population dynamics of benthic and pelagic *Microcystis*, and on the rate of *Microcystis* accumulation in recruitment traps and sediment traps. Data were analysed using the generalised linear models repeated measures (GLM-RM) procedure.

Measured parameter	G-G ϵ^{\dagger}	d.f.	MS	F-value	P-value
<i>Pelagic Microcystis</i>					
Time	0.053	2.022	42.936	41.586	<0.01*
Time \times depth	0.053	2.022	1.608	1.558	NS
Error (within subjects)	0.053	6.065	1.032		
Depth		1	0.112	0.415	NS
Error (between subjects)		3	0.271		
<i>Benthic Microcystis</i>					
Time	0.122	3.647	12.439	5.861	<0.01*
Time \times depth	0.122	7.293	2.639	1.243	NS
Error (within subjects)	0.122	18.233	2.123		
Depth		2	42.083	38.018	<0.01*
Error (between subjects)		5	1.107		
Recruitment flux					
Time	0.206	2.467	25.099	19.655	<0.01*
Time \times depth	0.206	4.934	3.449	2.701	NS
Error (within subjects)	0.206	7.401	1.277		
Depth		2	2.557	3.316	NS
Error (between subjects)		3	0.771		
Sedimentation flux					
Time	0.19	1.330	24.325	13.053	<0.05*
Time \times depth	0.19	2.659	2.141	1.368	NS
Error (within subjects)	0.190	3.989	1.565		
Depth		2	0.713	6.337	NS
Error (between subjects)		3	0.112		

*Significant relationships.

\dagger G-G ϵ : Greenhouse-Geisser epsilon, a correction factor that is used in GLM-RM to adjust the degrees of freedom (d.f.). As a result, d.f. is not an integer value.

MS, mean squares; NS, not significant.

probably higher than the accumulation of *Microcystis* in sediment traps. The negative values of L_{SS} and L_{SI} in the period September to November together with the peak in L_{SD} in the same period indicate that there is horizontal benthic transport from shallow to deep sites, as discussed above.

We used the model to predict the quantitative contributions of the overwintering benthic and pelagic populations to the size of the pelagic summer bloom. First, we investigated a model scenario in which

recruitment from the benthic population was set to zero from 1 January 2001, onwards. Hence, the overwintering pelagic population was the only source providing the inoculum for the summer bloom of 2001. This model scenario predicts that the summer bloom of 2001 would have been 50% lower (Fig. 8). We also investigated a model scenario in which the pelagic population was set to zero at 1 January 2001. In this case, the overwintering benthic population was the only source providing the inoculum for the next

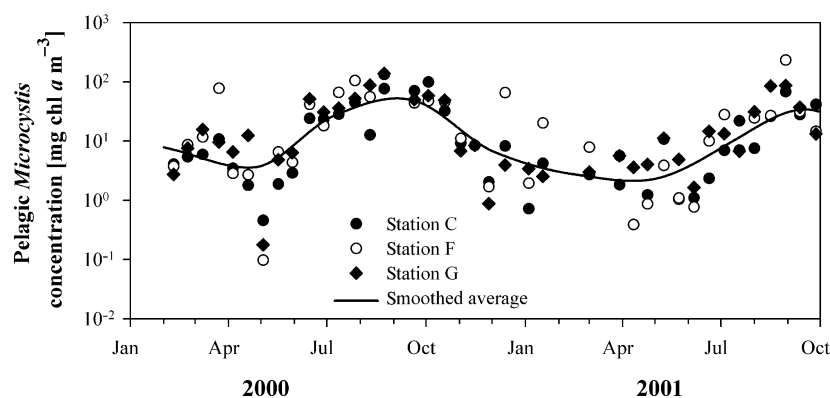


Fig. 4 Seasonal dynamics of the pelagic *Microcystis* population.

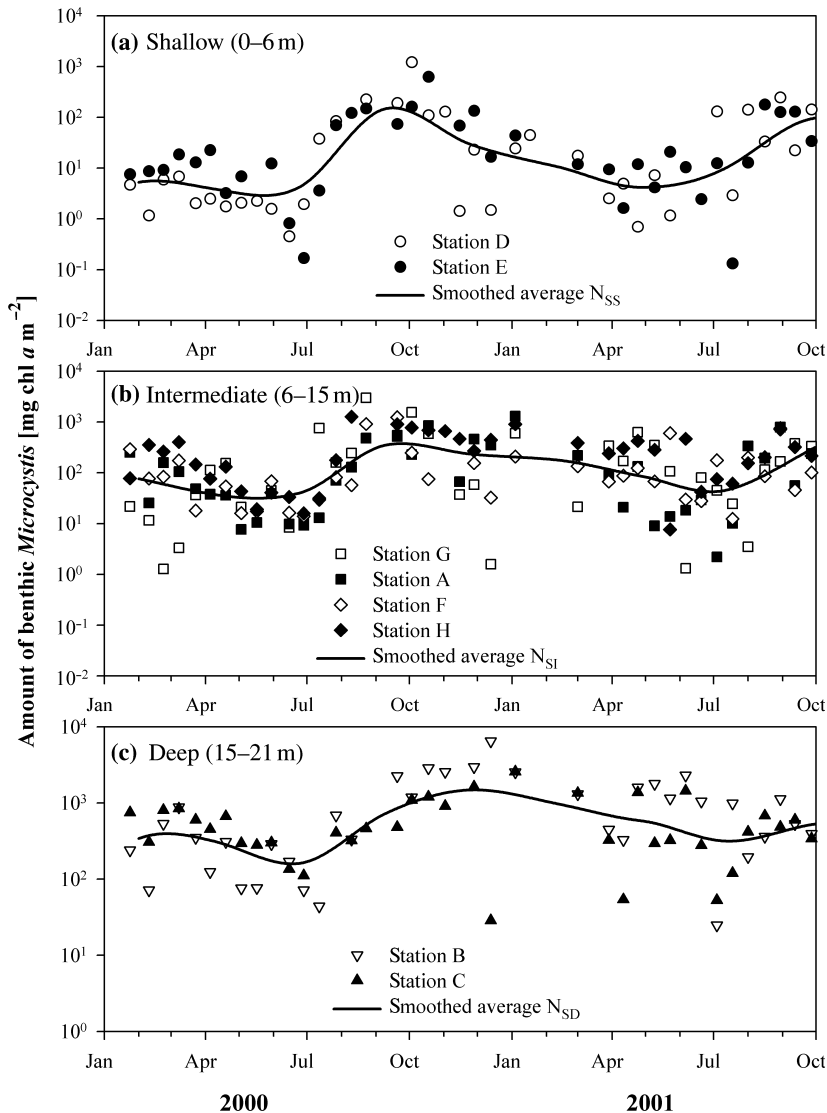


Fig. 5 Seasonal dynamics of the benthic *Microcystis* population, in lake sediments at sampling stations of (a) shallow sites (0–6 m), (b) intermediate sites (6–15 m) and (c) deep sites (15–21 m).

summer bloom. This model scenario predicts that the summer bloom of 2001 would have been reduced by 64% (Fig. 8).

Discussion

Microcystis is a potentially toxic cyanobacterium that has a relatively low specific growth rate compared with many other phytoplankton species (Reynolds, 1997; Huisman *et al.*, 1999). Yet, *Microcystis* dominates in a wide variety of eutrophic lakes (Reynolds *et al.*, 1981; Zohary & Robarts, 1990; Xie, Xie & Tang, 2003), which may in part be attributed to a large spring inoculum from overwintering benthic *Microcystis* populations (Preston *et al.*, 1980). In this study, we

aimed to quantify the extent to which the overwintering benthic and pelagic populations contribute to the development of dense blooms of *Microcystis* during summer.

In Lake Volkerak, the pelagic summer bloom of *Microcystis* typically behaved like *Microcystis* blooms described in other temperate eutrophic lakes (e.g. Reynolds *et al.*, 1981). The bloom started after the clear water phase, reached its maximum in August/September and then declined in autumn. A less common observation, although, is that already during early summer a large part of the pelagic population sank to the sediment, as is illustrated by an increase of *Microcystis* in the sediment traps and on the sediment from June onwards. Sedimentation rates of *Microcystis*

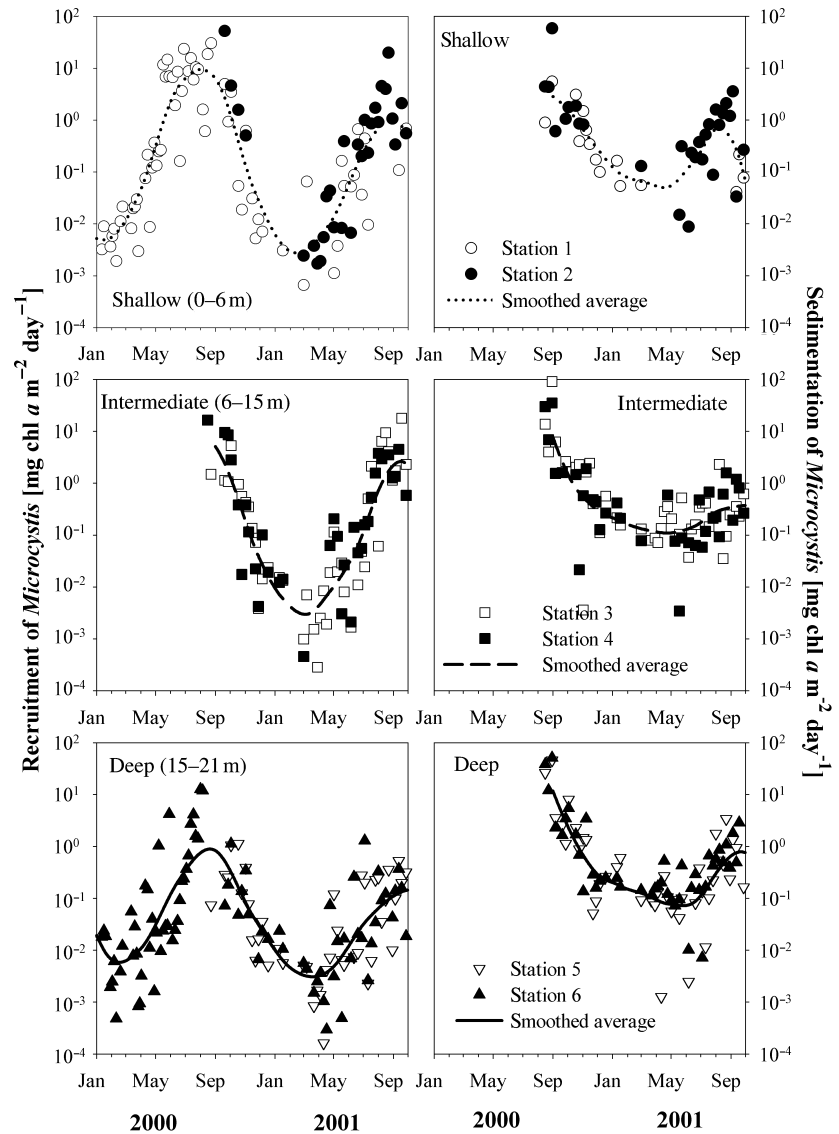


Fig. 6 Recruitment flux (left panels) and sedimentation flux (right panels) of *Microcystis* from sediments at sampling stations with a shallow (0–6 m), intermediate (6–15 m) and deep (15–21 m) water column.

expressed as sinking velocity ($0.0063\text{--}0.25\text{ m day}^{-1}$) in Lake Volkerak are similar to velocities reported earlier for other shallow hypertrophic lakes ($0.0045\text{--}0.24\text{ m day}^{-1}$; Takamura & Yasuno, 1988). Sedimentation of *Microcystis* has been attributed to an increase in cell density as a result of carbohydrate accumulation (Visser, Ibelings & Mur, 1995). In Lake Volkerak, however, freshly sedimented colonies were buoyant after removal of attached sediment particles (Verspagen *et al.*, 2004). Therefore, in this lake, sedimentation in summer most likely results from the attachment of sediment particles to the mucus layer of *Microcystis* colonies (Avnimelech, Troeger & Reed, 1982; Oliver *et al.*, 1985; Stolzenbach, Newman & Wong, 1992).

In addition to sedimentation by means of aggregate formation, interfacial waterflows generated when bottom currents interact with the sediment may also trap suspended *Microcystis* colonies (Huettel & Rusch, 2000). Processes like these, which take place close to the sediment surface, will not be captured by sediment traps, like ours, suspended at some distance above the sediments. In addition, some predation on *Microcystis* by daphnids may have occurred in the traps, although most trapped *Microcystis* colonies were too large to be consumed by daphnids. These processes may explain the observed discrepancy between accumulation on the sediment and accumulation in the sediment traps. In the model, these

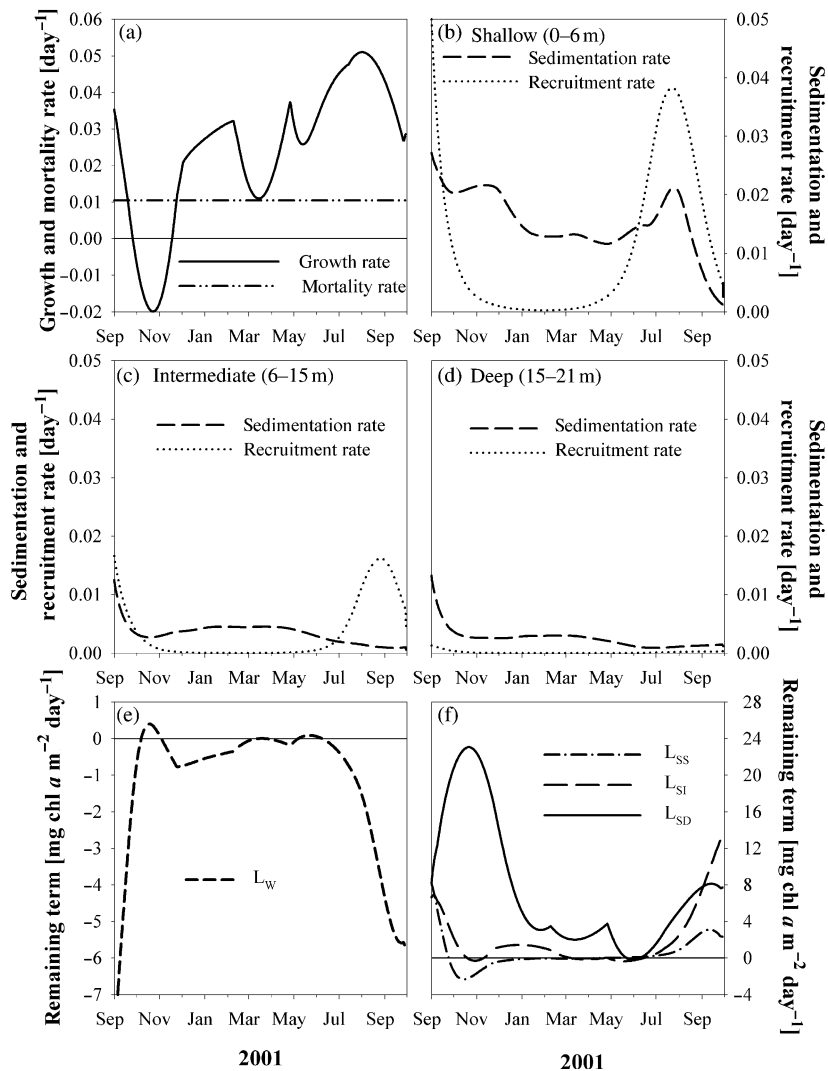


Fig. 7 Parameter estimates. (a) Net specific growth rate (μ) and net specific mortality rate (m), specific sedimentation rates (s) and specific recruitment rates (r) of *Microcystis* in (b) shallow parts (0–6 m), (c) intermediate parts (6–15 m) and (d) deep parts (15–21 m) of Lake Volkerak, and the remaining terms L_W (e) and L_{SS} , L_{SI} and L_{SD} (f).

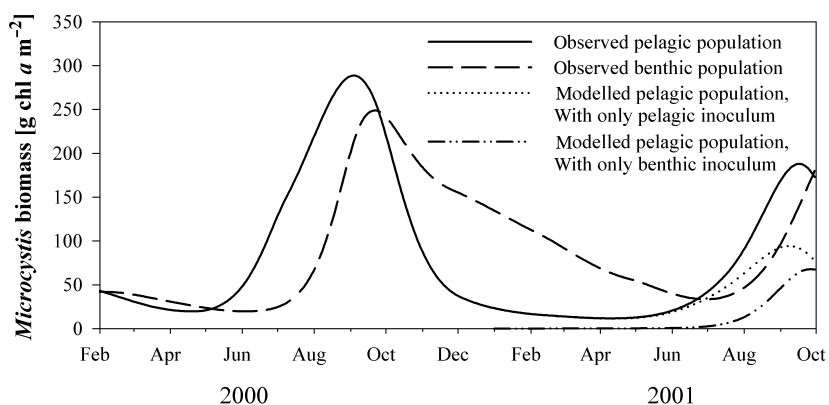
discrepancies were accounted for by implicitly incorporating sedimentation not captured by the traps in the remaining L -terms.

Maximum relative growth rate (0.051 day^{-1}) estimated for Lake Volkerak during summer is relatively low compared with estimates by other authors (Reynolds *et al.*, 1981). This is most likely related to the high turbidity of Lake Volkerak. During the period July to October, 99% of the light is absorbed within the upper 2 m of the water column. Furthermore, the lake was not stratified and, as a result, the pelagic *Microcystis* populations were mixed over the entire water column during most of the summer period. The combination of high turbidity and deep mixing provides unfavourable light conditions, resulting in low growth rates for the pelagic *Microcystis* population. The high turbidity of the water column also

implies that little light reaches the sediments. Only 10% of the total benthic area of the lake is situated in the euphotic zone. We observed that only a few cells of the benthic *Microcystis* populations lie on the sediment surface, and are thus exposed to dim light, whereas the majority are buried deeper down in the sediment. Hence, the light conditions are generally insufficient to allow growth of benthic *Microcystis* in the sediments of Lake Volkerak.

There was a time lag between the dynamics of the pelagic and benthic *Microcystis* populations. Peaks in the pelagic population were followed by peaks in the benthic population. The length of the time lag increased with water column depth, which might be attributed to the time required for settling of the colonies on the sediment; it takes longer for a *Microcystis* colony to sink 20 m than to sink 5 m.

Fig. 8 Seasonal dynamics of the total pelagic and total benthic populations of *Microcystis* in Lake Volkerak, according to the smoothed data. Also shown is the predicted development of the pelagic population in model scenarios where, from January 2001 onwards, either the pelagic population only or the benthic population only provides the inoculum.



There were also time lags between the dynamics of the different benthic *Microcystis* populations. Maximum benthic population size at the deep sites occurred only in December, 10 weeks after the maximum in benthic population size at the shallow sites. This is consistent with estimates of the transport terms L_{SS} , L_{SI} and L_{SD} which show an autumnal loss in the benthic *Microcystis* population at the shallow sites and a simultaneous increase of benthic *Microcystis* at the deep sites. These observations indicate that after autumnal sedimentation, benthic *Microcystis* are gradually transported from shallow to deep sediments, a process also known as sediment focussing (Evans, 1994).

Recruitment of *Microcystis* is largely a passive process, and occurs throughout the year in Lake Volkerak (Verspagen *et al.*, 2004). Many benthic *Microcystis* colonies are buoyant, but they are buried in the sediment and have extra ballast because of attached sediment particles. Release of these buoyant colonies thus requires that the sediment is resuspended, and the attached particles are removed. Resuspension of the sediment occurs year-round, for instance induced by wind action. The size of this recruitment flux largely depends on the number of buoyant colonies in the sediment, which is highest in summer (Verspagen *et al.*, 2004). As a result, recruitment rates are highest during summer. Recruitment rates expressed as percentages of the pelagic standing crop (instead of benthic standing crop) were between 0.05 and 6.0% per day. These data correspond well with recruitment rates previously found in other lakes, which ranged from <0.2% (Hansson *et al.*, 1994) to 4% per day (Trimbee & Harris, 1984; Ståhl-Delbanco *et al.*, 2003). However, a potential problem of the recruitment traps used in this study, which were

freely suspended above the sediment, is that they may have collected pelagic *Microcystis* through lateral transport (Forsell & Pettersson, 1995). As a result, the recruitment traps most likely overestimate the actual recruitment rates. Although other types of recruitment traps may resolve problems of lateral transport (e.g. Brunberg & Blomqvist, 2003; Ståhl-Delbanco *et al.*, 2003), these alternative traps are usually fixed to the sediment and thereby inhibit recruitment of *Microcystis* through wind-induced resuspension processes. Because of these technical limitations, recruitment data should generally be interpreted with caution. They may reflect relative indications rather than absolute estimates of the actual recruitment rates. The measured recruitment rates per unit surface area ($\text{mg Chl } a \text{ m}^{-2} \text{ day}^{-1}$) were similar all over the lake. However, specific recruitment rates (day^{-1}) were highest in shallow areas of the lake and decreased with increasing lake depth (Fig. 7). Shallow sediments may have higher specific recruitment rates because they are more susceptible to resuspension, and because cyanobacteria overwintering in shallow sediments generally have a higher viability than those overwintering in deep sediments (Brunberg & Blomqvist, 2003; Karlsson-Elfgren & Brunberg, 2004; Karlsson-Elfgren, Rengefors & Gustafsson, 2004; Verspagen *et al.*, 2004).

Because *Microcystis* has a relatively low specific growth rate, it has been argued that overwintering of a large benthic *Microcystis* population will facilitate the development of dense *Microcystis* blooms during summer (Preston *et al.*, 1980). Based on our model calculations, and in view of the potential overestimation of the recruitment rates obtained from the traps, we estimate that the absence of benthic recruitment would indeed reduce the summer bloom, but by

<50%. Our study suggests that the sediment acts more as a sink than as a source of *Microcystis*. The overwintering pelagic population is three to six times smaller than the benthic population. Yet, the model calculations indicate that the absence of this small overwintering pelagic population would reduce the summer bloom by more than 64%. This implies that pelagic survival during winter plays a more important role in the life cycle of *Microcystis* than previously thought. From a water management perspective, these findings suggest that removal of the overwintering pelagic population, for instance by flushing of the lake, might suppress or at least delay the development of *Microcystis* blooms during summer.

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