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WATER MANAGEMENT STRATEGIES AGAINST TOXIC *MICROCYSTIS* BLOOMS IN THE DUTCH DELTA

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Abstract. To prevent flooding of the Dutch delta, former estuaries have been impounded by the building of dams and sluices. Some of these water bodies, however, experience major ecological problems. One of the problem areas is the former Volkerak estuary that was turned into a freshwater lake in 1987. From the early 1990s onward, toxic *Microcystis* blooms dominate the phytoplankton of the lake every summer. Two management strategies have been suggested to suppress these harmful algal blooms: flushing the lake with fresh water or reintroducing saline water into the lake. This study aims at an advance assessment of these strategies through the development of a mechanistic model of the population dynamics of *Microcystis*. To calibrate the model, we monitored the benthic and pelagic *Microcystis* populations in the lake during two years. Field samples of *Microcystis* were incubated in the laboratory to estimate growth and mortality rates as functions of light, temperature, and salinity. Recruitment and sedimentation rates were measured in the lake, using traps, to quantify benthic–pelagic coupling of the *Microcystis* populations. The model predicts that flushing with fresh water will suppress *Microcystis* blooms when the current flushing rate is sufficiently increased. Furthermore, the inlet of saline water will suppress *Microcystis* blooms for salinities exceeding 14 g/L. Both management options are technically feasible. Our study illustrates that quantitative ecological knowledge can be a helpful tool guiding large-scale water management.

Key words: benthic–pelagic coupling; cyanobacteria; harmful algal blooms; population dynamics; recruitment; residence time; salinity; sedimentation; water management.

INTRODUCTION

After a major flooding disaster in the southern part of the Netherlands in 1953, the Dutch Deltaworks were constructed. This undertaking comprised a complex of huge dams and sluices that divided the Dutch delta into smaller compartments (Saeijs 1991). Yet, even before the last part of the Deltaworks was finished, in 1997, it became clear that these changes had a large, and partly undesirable, environmental impact. One of the problem areas is the former Volkerak estuary that was closed off from the Eastern Scheldt in 1987 and turned into a freshwater system. Lake Volkerak became the third largest freshwater system in the Netherlands. From the early 1990s onward, harmful cyanobacteria dominate the phytoplankton in this lake.

Harmful algal blooms may cause problems in coastal and freshwater ecosystems (Codd 1995, Sellner 1997, van Dolah 2000, Huisman et al. 2005). Impounded rivers and eutrophic lakes are especially susceptible to harmful algal blooms because of high nutrient loads and long residence times that often occur in these systems (Wehr and Thorp 1997, Kim et al. 1998). In Lake Volkerak, the nuisance is caused by massive blooms of *Microcystis*. *Microcystis* is a cosmopolitan cyanobacterium that can produce toxins known as microcystins. Microcystins may cause illnesses and sometimes death of fish, birds, cattle, pets, and even humans (Codd 1995, Falconer 1999, Carmichael et al. 2001). Furthermore, *Microcystis* cells contain gas vesicles, which provide buoyancy (Walsby 1994). As a result, *Microcystis* tends to accumulate in dense blooms at the water surface. In the late summer of 2002, during the height of the *Microcystis* bloom, over 5000 birds were killed in Lake Volkerak, including many ducks, geese, swans, and protected species like the spoonbill (Dutch Ministry of Transport, Public Works and Water Management, public communication). Swimming is not allowed in the lake during summer, and water from the lake can no longer be used for agricultural purposes.

The water authorities responsible for Lake Volkerak are urgently looking for water management strategies to reduce the *Microcystis* blooms. Reduction of the

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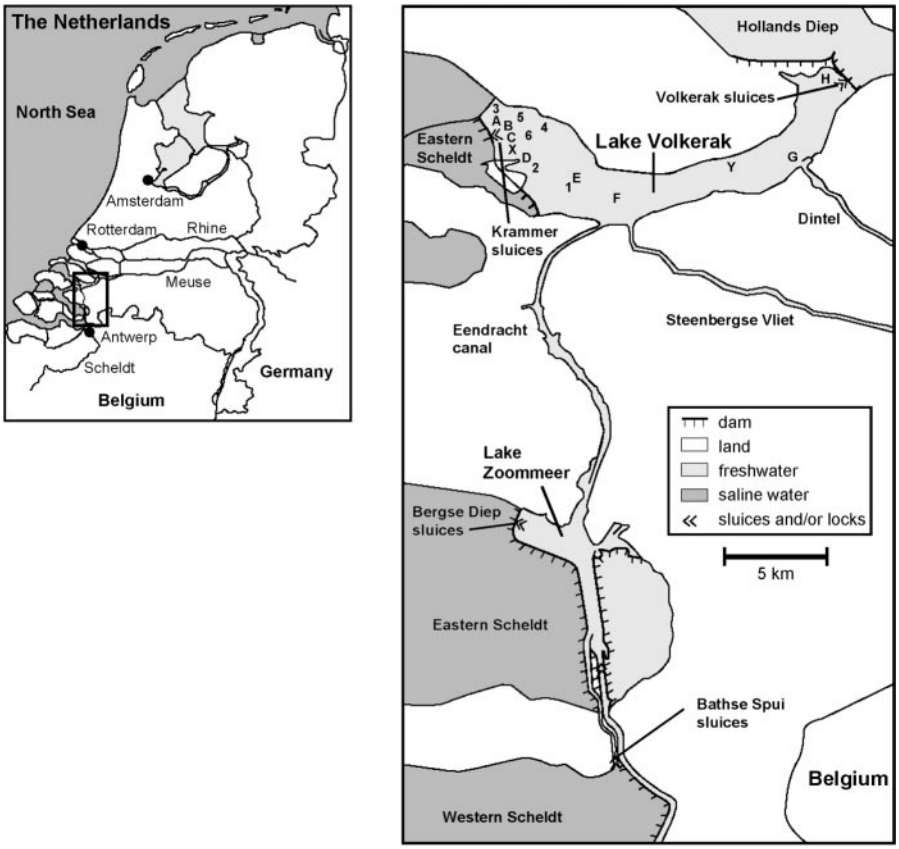

FIG. 1. Location of Lake Volkerak in the Dutch delta. The enlarged map on the right shows the positions of the sampling stations A–H (water and sediment samples) and trap stations 1–6 (sediment traps and recruitment traps). Fluorescence profiles were measured at stations A–H and stations X and Y. Also indicated are the sluices connecting Lake Volkerak with the surrounding water bodies.

nutrient load is a widely applied strategy (Edmondson 1970, Sas 1989) but is not considered feasible in this lake because of the continuous high input of nutrients from surrounding agricultural areas. Artificial mixing of lakes is another method to prevent the growth of *Microcystis* (Visser et al. 1996, Huisman et al. 2004). This method is too costly to apply, due to the large size of Lake Volkerak. Biomanipulation can also be applied to suppress phytoplankton growth. This seems a risky strategy, however, as high grazing pressures may in fact select for *Microcystis* because of their low edibility compared to other phytoplankton species (Rohrlack et al. 1999, Vanderploeg et al. 2001). Large-scale changes in the hydrology of the lake may provide more feasible solutions. One option is to decrease the residence time of water in the lake by flushing the lake with fresh water from the Hollands Diep (Fig. 1). Flushing will increase the losses of the *Microcystis* population, thereby suppressing massive bloom development (Hosper 1984, Bowling and Baker 1996, Hambright and Zohary 2000). An alternative option is to reintroduce saline water from the Eastern Scheldt into Lake Volkerak. An increased salinity will reduce the growth rates of *Microcystis* (Robson and Hamilton 2003, Orr et al. 2004). The Dutch water authorities are currently considering these latter two options. However, before such major hydrological changes can be implemented, it is essential to make advance assessments of the feasibility and likely success of these management strategies.

In this paper, we combine field data and laboratory studies to develop a model that describes the population dynamics of *Microcystis* in Lake Volkerak. Particular attention is paid to benthic–pelagic coupling, since previous work showed that part of the *Microcystis* population is buried in the top layer of the lake sediment (Verspagen et al. 2004, 2005). During two years we sampled the *Microcystis* population in the water and sediments of the lake and deployed sedimentation and recruitment traps. Field samples of *Microcystis* were incubated in the laboratory to estimate growth and mortality rates as functions of light, temperature, and salinity. The model structure is based on recent work on light-limited phytoplankton (Huisman et al. 1999*a*, Thébault and Rabouille 2003). The model is applied to predict the extent to which flushing and the inlet of saline water may suppress the summer bloom of *Microcystis*.

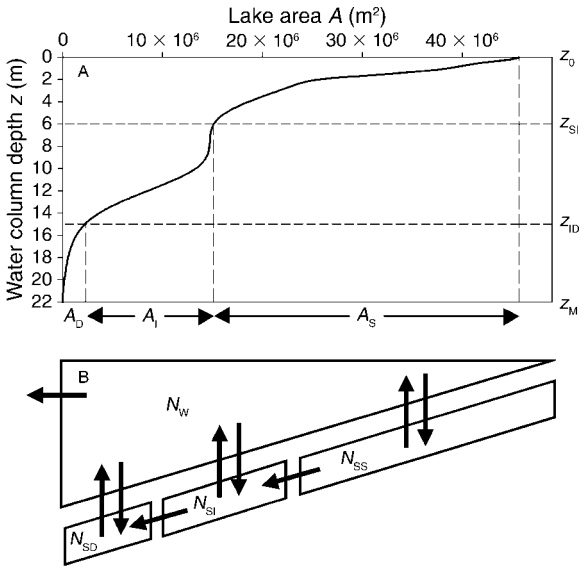

FIG. 2. (A) Hypsographic curve of the lake area, $A(z)$, of Lake Volkerak. The dashed lines indicate the boundaries used in this study between the shallow (A_S), intermediate (A_I), and deep (A_D) sediments of the lake. (B) The model structure is based on one water compartment, comprising the pelagic *Microcystis* population (N_W), and three compartments comprising the benthic populations in the shallow (N_{SS}), intermediate (N_{SI}), and deep (N_{SD}) sediments of the lake. Arrows indicate the fluxes of *Microcystis* among the different compartments. Z_0 is the depth of the surface water (0 m), Z_{SI} is the maximum depth of the shallow compartment (6 m), Z_{ID} is the maximum depth of the intermediate compartment (15 m), and Z_M is the maximum depth of the lake (22 m).

STUDY SITE

Lake Volkerak is situated between the Hollands Diep and the Scheldt estuaries (Fig. 1). It has a surface area of 45.7 km^2, an average depth of 5.5 m, and a maximum depth of 22 m. Before 1987, the lake was a saline estuary with extensive tidal sand flats (67% of the area), a large mainstream canal (28% of the area), and some deep pits (5% of the area). This is reflected in the bathymetry of the lake (Fig. 2A). Currently it is a freshwater lake with an almost constant water table that covers the former sand flats. The current residence time of water in the lake is about 110 days. The lake is relatively shallow and wind exposed, and its length axis is oriented in the direction of the prevailing winds (west-southwest). As a result, the lake does not develop a clear thermocline in the summer.

Lake Volkerak is a highly eutrophic lake, with an ample supply of nitrogen and phosphorus from the surrounding agricultural land. Nitrogen concentrations never reach limiting values, while phosphorus concentrations are depleted only occasionally (Appendix A). The lake is very turbid throughout the year, however. Even during clear skies, light conditions reach limiting values within the upper 5 m of the water column.

During the last decade, the cyanobacterium *Microcystis* has become by far the most dominant phytoplankton species in the lake, comprising more than 95% of the total phytoplankton biomass in summer. The *Microcystis* community of Lake Volkerak consists of different species. Most abundant are *Microcystis aeruginosa* (Kützing) Kützing and *M. flos-aqua* (Wittrock) Kirchner. In smaller amounts, some *M. ichtyoblabe* Kützing and *M. viridis* (A. Braun in Rabenhorst) were observed.

SAMPLING METHODS

To track the population dynamics of *Microcystis* in Lake Volkerak, we set up an intensive monitoring program of meteorological conditions, water quality parameters, and *Microcystis* abundances from January 2000 until October 2001.

Hourly data for incident light intensity and air temperature were obtained from the weather station Wilhelminadorp of the Royal Dutch Meteorological Institute (KNMI), which is located 25 km southwest of the lake. Vertical light profiles were measured at three stations (C, F, and G) in the lake once every two weeks during the summers of 2000 and 2001 with an LI 192 Underwater Quantum Sensor (Li-Cor Biosciences, Lincoln, Nebraska, USA). Daily temperatures of the lake water were calculated from the meteorological data according to Hutter and Jöhnk (2004). Data on wind speed and direction were measured at 10-minute intervals at weather station Stavenisse, 12 km southwest of the lake (*data available online*).[6]

Microcystis abundance in water and sediment was determined once every two weeks at sampling stations covering the depth range of the lake (Fig. 1, Table 1). Water was sampled at sampling stations C, F, and G only. During the bloom period of *Microcystis*, from mid-May to mid-November, 3 L of water were sampled with a siphon from the 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 stations A–H, using a box corer (diameter 30 cm, height 50 cm). From the box corer four subsamples were taken with a perspex corer (diameter 4.7 cm, height 30 cm).

To estimate the vertical population density distribution of *Microcystis* in the lake, we measured vertical

[6] http://www.hmcz.nl

TABLE 1. The sampling stations and trap stations in Lake Volkerak.

Category	Water column depth (m)	Sampling station	Trap station
Shallow part	0–6	D, E, X	1, 2
Intermediate part	6–15	A, F, G, H	3, 4
Deep part	15–22	B, C, Y	5, 6

Notes: The water column was sampled at stations C, F, and G, the sediment at stations A–H, and fluorescence profiles at stations A–H, X, and Y.

profiles of chlorophyll fluorescence on four days during the summer of 2000, when *Microcystis* comprised >95% of the total phytoplankton. On each day, fluorescence was measured at 1 m depth intervals at stations A–H, X, and Y (Fig. 1).

Recruitment and sedimentation of *Microcystis* were measured weekly at six trap stations (Fig. 1, Table 1). To avoid disturbance of the sediments close to the trap stations, the trap stations were positioned at other sites than the sampling stations. The traps were attached to a buoy that was fixed with two anchors. The opening of recruitment traps was directed downward, while the opening of sediment traps was directed upward. The traps are described in detail in Verspagen et al. (2005).

Microcystis abundances in the samples were determined from cyanobacterial chlorophyll *a* (chl *a*) fluorescence measured by flow cytometry, as described by Verspagen et al. (2005). We made no distinction among different *Microcystis* species. For comparison, we counted cell densities of *Microcystis* with an inverted microscope, after disaggregating the colonies according to Box (1981). This showed that 1 μg chl *a* corresponds to 23.6×10^6 *Microcystis* cells (linear regression: $r = 0.77$, $N = 10$, $P < 0.005$).

The Model

To model the population dynamics of *Microcystis*, we divided Lake Volkerak into four compartments (Fig. 2B): (1) the water column, (2) the shallow sediments of the former tidal sand flats (0–6 m), (3) the intermediate sediments of the mainstream canal (6–15 m), and (4) the deep sediments in the pits (15–21 m). Let A_S, A_I, and A_D indicate the lake area with shallow sediments, intermediate sediments, and deep sediments, respectively. Furthermore, let N_W, N_{SS}, N_{SI}, and N_{SD} denote the amount of pelagic *Microcystis* per unit surface area in the water column, in the shallow sediments, the intermediate sediments, and the deep sediments, respectively. The population dynamics of *Microcystis* can then be captured by the following general model structure:

$$\frac{dN_W}{dt} = \mu N_W - mN_W - S + R - qN_W \quad (1)$$

$$\frac{dN_{SS}}{dt} = S_S - R_S - mN_{SS} - T_{SI} \quad (2)$$

$$\frac{dN_{SI}}{dt} = S_I - R_I - mN_{SI} + \frac{A_S}{A_I}T_{SI} - T_{ID} \quad (3)$$

$$\frac{dN_{SD}}{dt} = S_D - R_D - mN_{SD} + \frac{A_I}{A_D}T_{ID}. \quad (4)$$

Here, μ is the specific growth rate of *Microcystis* in the water column [d^{-1}] and m is the specific mortality rate [d^{-1}]. Further, S is the sedimentation rate from the pelagic population to the benthic populations, which is partitioned into S_S, S_I, and S_D to describe the sedimentation rates in the shallow, intermediate, and deep parts of the lake (i.e., $S = A_SS_S + A_IS_I + A_DS_D)/(A_S + A_I + A_D)$. Conversely, R is the recruitment rate from the benthic populations to the pelagic population, which is partitioned in a similar way into R_S, R_I, and R_D. The product qN_W describes the outflow of the *Microcystis* population from Lake Volkerak into the Western and Eastern Scheldt estuaries. We will henceforth refer to q as the specific flushing rate [d^{-1}]. Finally, the terms T_{SI} and T_{ID} describe horizontal transport of benthic *Microcystis* from the shallow to the intermediate sediments, and from the intermediate to the deep sediments, respectively. We note that horizontal transport is weighted by the area of the different compartments.

Specific growth rate

Lake Volkerak is a very turbid lake with high concentrations of nitrogen and phosphorus (Appendix A). We therefore assume that the specific growth rate of *Microcystis* in Lake Volkerak is governed by light conditions (I), temperature (T), and salinity (h), while nutrient limitation is negligible:

$$\mu = \alpha f_1(I)f_2(T)f_3(h) \quad (5)$$

where α is a constant of proportionality, and the functions f_1, f_2, f_3 describe the effects of light intensity, temperature, and salinity on the specific growth rate.

Light conditions.—We first establish a relation between the specific carbon assimilation rate of *Microcystis*, $p(I)$, and light intensity, I. Carbon assimilation of *Microcystis* is strongly inhibited at high light intensities (Visser et al. 1997), which can be adequately described by an equation modified from Platt et al. (1980) (Fig. 3A):

$$p(I) = a(1 - \exp[-bI])\exp[-cI] - dI - e \quad (6)$$

where a is the maximal specific carbon assimilation rate that would be reached without photoinhibition, b indicates the onset of light saturation, c and d describe the impact of photoinhibition on carbon assimilation, and e is the specific carbon respiration rate.

Light intensity (I) in the water column decreases with increasing depth (z) owing to light absorption by water, dissolved organic matter, clay particles, and to a large extent also by *Microcystis* itself. The vertical light gradient is described by Lambert-Beer's Law for nonuniform phytoplankton population density distributions (Huisman et al. 1999*b*):

$$I(z) = I_{in}\exp\left[-k\int_0^z C_W(\sigma)\,d\sigma - K_{bg}z\right] \quad (7)$$

where I_{in} is the incident light intensity at the water surface, k is the specific light extinction coefficient of the phytoplankton (mainly *Microcystis*), K_{bg} is the background turbidity caused by all nonphytoplankton components, $C_W(\sigma)$ is the concentration of *Microcystis*

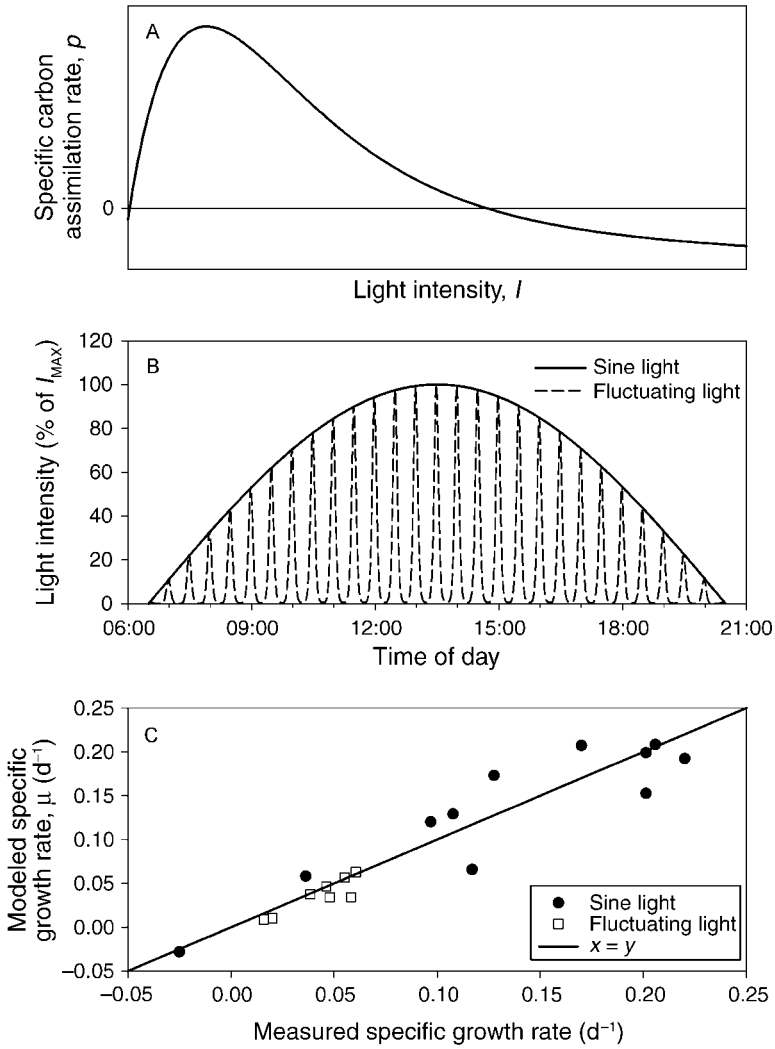

FIG. 3. Light conditions and *Microcystis* growth. (A) Specific carbon assimilation rate, $p(I)$, as a function of light intensity, I. (B) Light regimes given to laboratory incubations of field samples. (C) Comparison between measured specific growth rates (based on ^{13}C incorporation) and modeled specific growth rates, for incubations exposed to sine light and fluctuating light regimes.

at depth σ, and depth σ is used as an integration variable.

To calculate the light-dependent specific growth rate of *Microcystis* we take into account the bathymetry of Lake Volkerak ($A(z)$), the vertical light gradient in the lake ($I(z)$), and the vertical population density distribution of *Microcystis* ($C_W(z)$):

$$f_1(I) = \frac{\int_0^{z_M} p[I(z)]C_W(z)A(z)\,dz}{\int_0^{z_M} C_W(z)A(z)\,dz} \quad (8)$$

Here, $A(z)$ describes the area of the lake, A, as a function of depth (i.e., the hypsographic curve in Fig. 2A), and z_M is the maximum depth of the lake.

Temperature.—The specific growth rate of *Microcystis* increases with temperature (T) according to an Arrhenius relation:

$$f_2(T) = (Q_\mu)^{T-20} \quad (9)$$

where Q_μ describes the change in specific growth rate with a temperature change of 1°C.

Salinity.—The effect of salinity (h) on the specific growth rate of *Microcystis* is described by a polynomial:

$$f_3(h) = \beta_1 + \beta_2 h + \beta_3 h^2 + \cdots. \quad (10)$$

Specific mortality rate

We assume that the specific mortality rate of *Microcystis* increases with temperature, analogous to the specific growth rate:

$$m = m_{20}(Q_m)^{T-20} \quad (11)$$

where Q_m describes the change in specific mortality rate with a temperature change of 1°C and m_{20} is the specific mortality rate at a reference temperature of 20°C.

Sedimentation rate

Sedimentation (S) in Lake Volkerak is mainly caused by the attachment of *Microcystis* colonies to sediment particles (Verspagen et al. 2004). We therefore assume that sedimentation of *Microcystis* depends on the pelagic concentration of *Microcystis* at the sediment–water interface. Taking into account the bathymetry of the lake, the sedimentation rate from the pelagic population to the benthic population of the shallow sediments can then be described as

$$S_S = \frac{v}{A_S}\int_0^{z_{SI}} C_W(z_B)\frac{dA}{dz}(z_B)\, dz_B \quad (12)$$

where v is the sedimentation velocity of *Microcystis*, and z_B is the depth of the sediment–water interface. The descriptions of sedimentation rates from the pelagic population to the intermediate (S_I) and deep (S_D) benthic populations are analogous to the description of S_S.

Recruitment rate

Recruitment of *Microcystis* from the benthic populations to the pelagic population depends mostly on sediment resuspension and light availability (Ståhl-Delbanco and Hansson 2002, Rengefors et al. 2004, Verspagen et al. 2004). Since light availability at the sediments is very low in Lake Volkerak, we assume that its effect is negligible. Based on the data in the recruitment traps, we assume that the recruitment rate of *Microcystis*, R_S, is proportional to the population density of *Microcystis* in the sediment. Hence,

$$R_S = g_S N_{SS} \quad (13)$$

where g_S is the specific recruitment rate from the shallow sediments. Recruitment rates from the intermediate (R_I) and deep (R_D) sediments are analogous to the description of R_S.

Horizontal transport

Monitoring of the benthic *Microcystis* populations indicates horizontal transport of benthic *Microcystis* from shallow to intermediate and deeper parts of Lake Volkerak (Verspagen et al. 2005). This phenomenon is analogous to sediment focusing (Hilton 1985). Sediment focusing is often induced by shear stress at the sediment–water interface. Shear stress at the sediment–water interface of stagnant lakes, like Lake Volkerak, is largely caused by wind-driven water motion (Mian and Yanful 2004). We therefore assume that horizontal transport of the benthic *Microcystis* population from shallow to intermediate and deeper parts of the lake can be described as

$$T_{SI} = (n_S + o_S w^2)N_{SS} \quad (14)$$

where n_S is the baseline horizontal transport rate (e.g., driven by gravitation), o_S describes horizontal transport generated by wind-driven shear stress, and w is the wind speed above the lake's surface. Horizontal transport of benthic *Microcystis* from intermediate to deep sediments (T_{ID}) is analogous to the description of T_{SI}.

Parameter Estimation

Light gradient

To model the light conditions in the lake, we used the hourly values of incident light intensity (I_{in}) measured at weather station Wilhelminadorp. According to Eq. 7, for a uniform population density distribution of *Microcystis*, the background turbidity (K_{bg}) and specific light extinction coefficient of *Microcystis* (k) can be determined as the zero intercept and slope, respectively, of a linear regression of $\ln[I_{in}/I(z)]/z$ against the concentration of *Microcystis* (C_W). We used only the upper 5 m of the water column in the regression analysis, because light was essentially extinguished below 5 m depth.

Impact of light and temperature on growth rate

To estimate the impact of light and temperature on the growth rate of *Microcystis*, we collected field samples of *Microcystis* from Lake Volkerak in the summers of 2001–2003 for laboratory experiments. These field samples were incubated in 2-L flat chemostat vessels made of borosilicate glass with a depth of $z_M = 0.05$ m (Huisman et al. 1999*a*). The vessels were temperature controlled and gently aerated to keep *Microcystis* in suspension. Changes in light intensity were computer controlled by a venetian blind (Kroon et al. 1992). We assume that the growth rate of *Microcystis* is proportional to its carbon assimilation rate. Carbon assimilation rates were measured from the incorporation of ^{13}C-CO_2 into C_{16} and $C_{18:n}$ cellular fatty acids using the ^{13}C-labeling method described by Pel et al. (2003, 2004). The incorporation of ^{13}C into fatty acids was monitored over a period of two days, after one day of acclimation of *Microcystis* in the laboratory experiments. Samples were taken two to three hours after ''sunrise'' in the experimental setup. About 8–12 *Microcystis* colonies, with a diameter of ~50 μm, were hand picked from the samples under a stereomicroscope, using a syringe. The fatty acids were measured using a capillary gas chromatograph coupled to a Finnigan Delta-S isotope ratio monitoring mass spectrometer (Finnigan MAT GmbH, Bremen, Germany; Pel et al. 1997). Time-averaged carbon assimilation rates in the experiments were calculated according to Welschmeyer and Lorenzen (1984) as follows:

$$\overline{p(I)} = -\frac{1}{t}\ln\left(1 - \frac{\Delta\delta^{13}C_{FA}}{\Delta\delta^{13}C_{DIC}}\right) \quad (15)$$

Here, $\Delta\delta^{13}C_{FA}$ is the enrichment in ^{13}C of the fatty acids after an incubation time t, and $\Delta\delta^{13}C_{DIC}$ is the enrichment of dissolved inorganic carbon (DIC) at time zero. For each experiment we obtained two estimates of the carbon assimilation rate, one based on the C_{16} and the other on the $C_{18:n}$ fatty acids. These two estimates were always quite similar, and we therefore used the average of the two as our estimate of the carbon assimilation rate.

To check whether incorporation of ^{13}C into fatty acids can indeed be used to calculate the growth rate of *Microcystis*, we tested the ^{13}C method in a continuous culture under constant light conditions. The specific growth rate in continuous cultures can be experimentally imposed, because at steady state it equals the dilution rate. For this purpose, we used *Microcystis* strain V145 (culture collection Aquatic Microbiology, University of Amsterdam, The Netherlands) isolated from Lake Volkerak. The specific growth rate calculated from the incorporation of ^{13}C into fatty acids (0.159 ± 0.036 d^{-1}; mean ± SD) was in good agreement with the dilution rate of the continuous culture (0.162 ± 0.002 d^{-1}). This validates the use of the ^{13}C incorporation technique to estimate specific growth rates.

Carbon assimilation rates were measured in two ^{13}C-labeling experiments. In the first experiment, light was given as a sine curve with a light:dark cycle of 14:10 h, so that *Microcystis* experienced the light regime it would encounter when floating at a fixed water column depth during a cloudless day (solid line in Fig. 3B). In total, 11 samples were incubated, with maximum light intensities (I_{MAX}) ranging from 0 to 260 μmol photons·m^{-2}·s^{-1}, and a constant temperature of 20°C. In the second experiment, samples were exposed to a fluctuating light regime, so that *Microcystis* experienced the light conditions it would encounter when being mixed up and down through the water column (dashed line in Fig. 3B). For this purpose, a total of eight samples was incubated, with maximum light intensities (I_{MAX}) between 800 and 1400 μmol photons·m^{-2}·s^{-1}, temperatures between 15 and 22°C, and light:dark cycles varying from 12:12 h to 15:9 h.

The specific growth rates of *Microcystis* in these experiments were calculated as

$$\mu(t) = \left\{\frac{1}{z_M}\int_0^{z_M} p[I(z, t)]\, dz\right\}(Q_\mu)^{T-20} \quad (16)$$

where z_M here refers to the depth of the culture vessel, $p(I)$ is the specific carbon assimilation rate as described by Eq. 6 at a reference temperature of 20°C, $I(z, t)$ is the light intensity as a function of depth and time, T is temperature, and Q_μ describes the change in specific growth rate with a temperature change of 1°C using a reference temperature of 20°C. The latter parameter, Q_μ, was estimated from Reynolds (1997). The parameters in the $p(I)$ curve, defined in Eq. 6, were estimated by fitting Eq. 16 to the specific carbon assimilation rates measured in the experiments. For this purpose, Eq. 16 was integrated over time, because the cells were exposed to dynamic light regimes. Model fits were obtained by minimization of the residual sum of squares using the Gauss-Marquardt-Levenberg algorithm carried out by the software package PEST (Watermark Numerical Computing, Brisbane, Australia, fourth version).

Impact of salinity on growth

To study the effect of salinity (h) on the growth of *Microcystis*, field samples were taken just below the surface at the Bergse Diep sluices (Fig. 1) in August and September 2003. The samples were incubated in polycarbonate flasks in the laboratory, using six different salinities obtained by mixing water from Lake Volkerak (h = 1 g/L) with water from the Eastern Scheldt (h = 32 g/L), both previously filtered through Whatman GF/C filters (Whatman International Ltd., Maidstone, UK). The resulting salinities were measured by $AgNO_3$ titration. The incubations were grown at an incident light intensity of 190 μmol photons·m^{-2}·s^{-1} in a light:dark cycle of 14:10 h and a constant temperature of 20°C. The population development of *Microcystis* was measured daily with the EurOPA flow cytometer (developed as part of a European Union project in the Marine Science and Technology [MAST-II] program) (Jonker et al. 1995, Peperzak et al. 2000). The values β_1, β_2, and β_3 were obtained by fitting the polynomial of Eq. 10 to the measured specific growth rates.

Specific mortality rate

Specific mortality rate (m) was determined in field samples of benthic *Microcystis* from which sediment particles had been removed. These samples were dispersed in mineral O2 medium (Van Liere and Mur 1978) and incubated in batches. The batches were incubated in the dark for 84 d at temperatures of 4, 10, and 20°C. At each temperature, the specific mortality rate was calculated by fitting a first order exponential decay curve through the decline in chl *a* concentration. The temperature dependence of the specific mortality rate was estimated by fitting Eq. 11 to the specific mortality rates.

Benthic–pelagic coupling

The specific recruitment rates (g_S, g_I, and g_D) were estimated by fitting Eq. 13 to the recruitment measured in the recruitment traps. The remaining parameters, describing sedimentation velocity (v) and horizontal benthic transport rates (o_S, o_I, n_S, and n_I), were estimated by fitting the model defined by Eqs. 1–4 to the observed benthic and pelagic population dynamics. The fits were obtained by minimization of the residual sum of

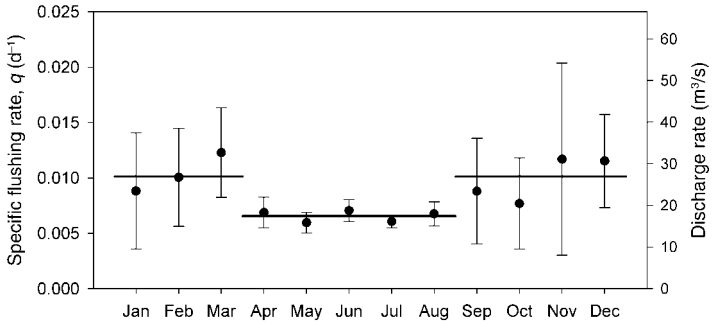

FIG. 4. Seasonal pattern of the specific flushing rates (mean ± SD) of Lake Volkerak into the Western Scheldt Estuary in the period 1996–2000 (N = 5). The corresponding discharge rates are also indicated.

squares using the Gauss-Marquardt-Levenberg algorithm of the software package PEST.

MODEL SCENARIOS

We used the model to simulate the effect of two different water management strategies on the summer bloom of *Microcystis* in Lake Volkerak. The two strategies are based on management options selected by the water authorities of the lake. In one strategy, saline water is reintroduced into Lake Volkerak to reduce the growth rate of *Microcystis*. In the other strategy, fresh water is flushed through the lake to increase the loss rate of the *Microcystis* population.

Inlet of saline water.—This strategy assumes that saline water from the Eastern Scheldt will enter the lake through the Krammer sluices, at the west side of the lake (Fig. 1). The Eastern Scheldt is a tidal estuary, with a reduced tidal movement due to the storm surge barrier at its entrance to the North Sea. It has a rather constant salinity of 32 g/L (Smaal and Nienhuis 1992). The inlet of saline water into Lake Volkerak will not be accompanied by tidal movement, due to the limited capacity of the Krammer sluices.

Flushing with fresh water.—This strategy assumes that fresh water from the Hollands Diep will enter the lake through the Volkerak sluices at the east side of the lake (Fig. 1). The fresh water leaves the lake at the south side through the Eendracht Canal or at the west side through the Krammer sluices (Fig. 1). Since the outflow from Lake Volkerak is ultimately discharged into the saline Scheldt estuary, *Microcystis* cells will die off and cause no problems further downstream. Fig. 4 shows the seasonal pattern of the specific flushing rates of Lake Volkerak during the period 1996–2000. In winter (September–March), the flushing rates are high and fluctuate considerably. In summer (April–August), the flushing rates are low and show little fluctuation. The current capacity of the inlet and outlet sluices allows a maximum discharge of 125 m^3/s, which corresponds to a specific flushing rate of $q = 0.047$ d^{-1}. With modest adaptations the discharge capacity of the sluices can be enhanced to a maximum of ~300 m^3/s ($q = 0.113$ d^{-1}). However, in summer the flushing rates are more likely to be limited by a shortage of fresh water than by the maximum discharge capacity of the sluices.

We ran three different flushing scenarios. In scenario A, specific flushing rates were kept constant during the entire year. In scenario B, specific flushing rates in winter were fixed at the current maximum discharge rate of 125 m^3/s ($q = 0.047$ d^{-1}), while we studied a wide range of different summer values. In scenario C, the specific flushing rate in summer was fixed at the current summer discharge rate of 17 m^3/s ($q = 0.0065$ d^{-1}; Fig. 4), while we studied a wide range of different winter values.

RESULTS

Parameter estimates

Meteorological conditions.—Daily water temperature, maximum light intensity, and wind speed measured in Lake Volkerak in the period February 2000–October 2001 are displayed in Fig. 5. Water temperature ranged between 0 and 24°C, daily maximum light intensity ranged between 70 and 2000 μmol photons·m^{-2}·s^{-1}, and daily averaged wind speed ranged between 0.4 and 15 m/s.

Light conditions.—The light extinction coefficient in Lake Volkerak increased with the *Microcystis* concentration (Fig. 6A; linear regression: $r = 0.79$, $N = 128$, $P < 0.001$). The background turbidity of the water and the specific light extinction coefficient of *Microcystis* were determined as the zero intercept and slope, respectively, of this linear relation. These data illustrate that Lake Volkerak is indeed a rather turbid lake and that *Microcystis* contributes significantly to this turbidity.

Population density distribution.—The vertical population density distribution of *Microcystis*, as measured by the fluorescence profiles, is shown in Fig. 6B. The graph was obtained by normalizing each vertical profile with respect to its depth-averaged population density of *Microcystis*. The concentration of *Microcystis* in the deepest parts of the lake is approximately one-fourth the concentration of *Microcystis* at the water surface.

Growth rate.—The temperature dependence of the specific growth rate was estimated from data of Reynolds (1997) for temperatures <26°C (Fig. 6C; r =

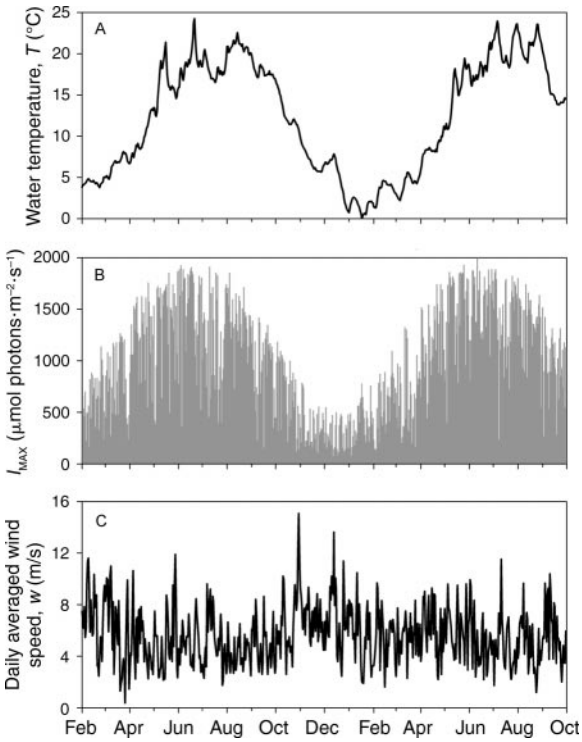

FIG. 5. Meteorological conditions: (A) water temperature, (B) daily maximum light intensity, and (C) daily averaged wind speed during the period February 2000–October 2001.

0.999, $N = 4$, $P < 0.01$). There was a close correspondence between model predictions of the specific growth rate, using Eq. 6 and Eq. 16, and the specific growth rates measured in the two ^{13}C-labeling experiments (Fig. 3C; $r = 0.95$, $N = 19$, $P < 0.001$). This illustrates that the model predictions are consistent over a wide range of different light conditions. Our estimates of the parameters in Eq. 6, obtained from this model fit, are given in Appendix B. These parameter estimates show that *Microcystis* is strongly photoinhibited at light intensities beyond 220 μmol photons·m^{-2}·s^{-1}.

The laboratory incubations at different salinities show that *Microcystis* is quite salt tolerant (Fig. 6D; quadratic polynomial: $r = 0.97$, $N = 12$, $P < 0.01$). The specific growth rate of *Microcystis* is essentially unaffected for salinities <10 g/L. Growth rates become negative for salinities >17 g/L.

Mortality rate.—The specific mortality rate increased with temperature (Fig. 6C; $r = 0.99$, $N = 3$, $P < 0.1$), although it was less temperature sensitive than the growth rate.

Benthic–pelagic coupling.—Specific recruitment rates (g_S, g_I, and g_D) were much higher in shallow parts than in deeper parts of the lake (Appendix B). Sedimentation velocity at the sediment–water interface was ~0.11 m/d.

Estimates of the horizontal transport parameters o_S and n_I converged to zero (Appendix B). This indicates that horizontal transport from the shallow to the intermediate parts of the lake is a continuous process irrespective of wind speed, while transport from the intermediate to the deep parts of the lake is affected by wind.

Population dynamics

The population dynamics of *Microcystis* in the water and sediments of Lake Volkerak were tightly coupled. Seasonal changes in the pelagic *Microcystis* population (Fig. 7A) were closely tracked by changes in the benthic population of the shallow sediments (Fig. 7B). Changes in *Microcystis* abundance in the shallow sediments were followed by changes in the intermediate sediments (Fig. 7C), and a few weeks later by changes in the deep sediments (Fig. 7D). Although there is a lot of scatter in the data, the model predictions were in good agreement with the general seasonal trends of *Microcystis* in the water and sediments of Lake Volkerak.

Evaluation of model scenarios

The current salinity of Lake Volkerak, without inlet of saline water, is 1 g/L. We used the model to simulate the inlet of saline water over the period February 2000–December 2003. An example where the salinity of the lake is raised to 17 g/L from January 2001 onward is shown in Fig. 8A. This example illustrates that an elevated salinity, beyond the tolerance limits of *Microcystis* (Fig. 6D), will lead to a rapid crash of the *Microcystis* population, below the guideline value of 10 μg/L of chl *a* for recreational waters advised by the World Health Organization (Chorus et al. 2000). The results of a large number of simulations at different salinities are summarized in Fig. 8B. The model predicts that dense summer blooms of *Microcystis* will persist for salinities <8–10 g/L. For salinities >14 g/L, the *Microcystis* blooms will disappear. This implies that ~45% of the lake volume has to be replaced by Eastern Scheldt water to prevent *Microcystis* blooms.

Flushing with fresh water may also suppress summer blooms of *Microcystis*. For three different scenarios we calculated which flushing regimes will suppress *Microcystis* concentrations below the guideline value of 10 μg/L of chl *a* for recreational waters advised by the World Health Organization (Chorus et al. 2000).

Scenario A: Model simulations over the period February 2000–December 2003 predict that year-round flushing with an enhanced discharge rate of 75 m^3/s ($q = 0.028$ d^{-1}) will suppress *Microcystis* blooms below the guideline value (Fig. 9A).

Scenario B: Similarly, *Microcystis* blooms can be suppressed below the guideline value by a somewhat lower summer discharge rate of 65 m^3/s ($q = 0.024$ d^{-1}) but a higher discharge rate of 125 m^3/s ($q = 0.047$ d^{-1}) during winter (Fig. 9B).

Scenario C: However, according to the model simulations, it is not possible to effectively suppress *Mi-*

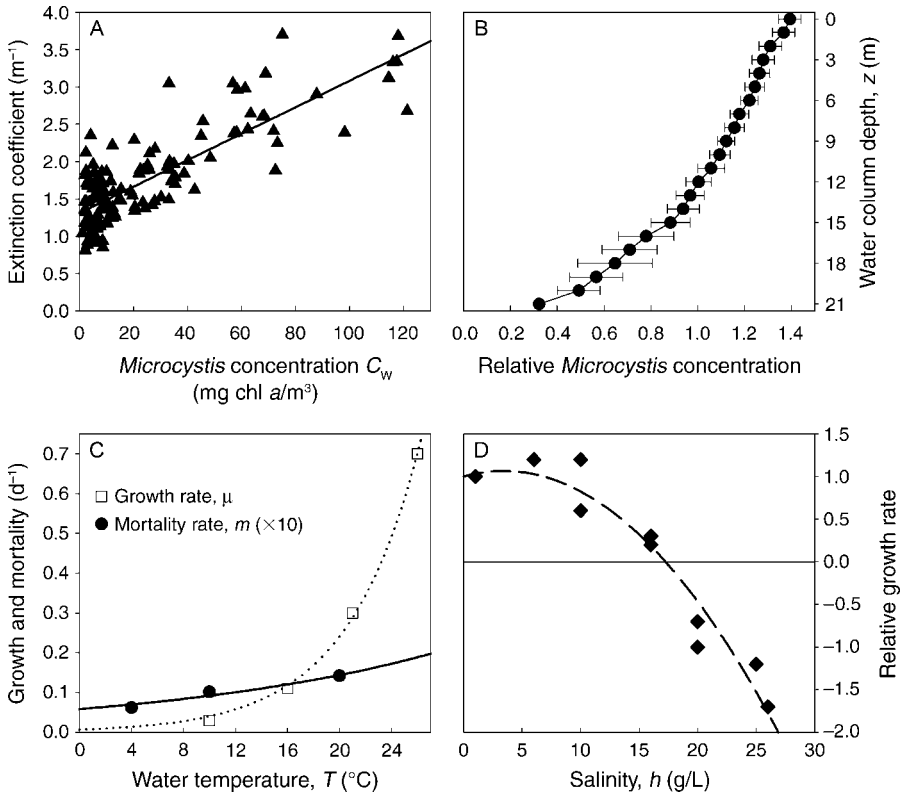

FIG. 6. Relationships observed in this study and incorporated in the model. (A) The light extinction coefficient of Lake Volkerak as a function of the *Microcystis* concentration, C_W, in the surface water. (B) The shape of the vertical population density distribution of *Microcystis* in Lake Volkerak. The ''relative *Microcystis* concentration'' is the measured *Microcystis* concentration normalized to the depth-averaged *Microcystis* concentration. (C) The specific growth rate, μ, and specific mortality rate, *m* (×10), of *Microcystis* plotted as functions of temperature, *T*. (D) The impact of salinity, *h*, on the relative growth rate of *Microcystis*. To obtain the specific growth rate of the whole population, the effects of light, temperature, and salinity on growth rates were multiplied. All data are based on this study, except the temperature dependence of the specific growth rates in (C), which were obtained from Reynolds (1997).

crocystis blooms below the guideline value of 10 μg/L of chl *a* when flushing rates are increased only during winter, but not in summer (Fig. 9C).

DISCUSSION

Population dynamics of Microcystis

Our results show that benthic–pelagic interactions play an important role in the population dynamics of *Microcystis* in Lake Volkerak, similar to observations in several other eutrophic lakes (e.g., Reynolds et al. 1981). The abundance of *Microcystis* in the water column increases after the clear water phase in May and reaches its maximum in August–September, after which the pelagic population declines. Part of the pelagic population sinks to the sediment, creating a large benthic population (Takamura et al. 1984, Tsujimura et al. 2000, Verspagen et al. 2005). During winter, benthic *Microcystis* cells remain viable (Verspagen et al. 2004) and are gradually transported to the deepest parts of the lake. A fraction of this overwintering benthic population eventually recruits to the water column (Preston et al. 1980, Trimbee and Harris 1984, Hansson et al. 1994), most likely due to resuspension (Ståhl-Delbanco and Hansson 2002, Rengefors et al. 2004, Verspagen et al. 2005). Our results show that both recruitment from this benthic population and the overwintering pelagic population contribute to the development of dense *Microcystis* blooms during the next summer.

Management strategies

To suppress *Microcystis* blooms in Lake Volkerak, management strategies focus on either the inlet of saline water or increased flushing with fresh water.

Salinity.—Microcystis is quite salt tolerant for a freshwater species. Our results show that the inlet of saline water will eliminate *Microcystis* blooms if salinities are raised beyond 14 g/L (Figs. 6D and 8). A similar level of salt tolerance of *Microcystis* has recently been reported by Robson and Hamilton (2003) and Orr et al. (2004). According to calculations by the water authorities, it requires ~3 mo of flushing of Lake Volkerak with saline water from the Eastern Scheldt at the maximum capacity of the Krammer sluices (50 m^3/s, $q = 0.019\ d^{-1}$) before a new equilibrium is reached.

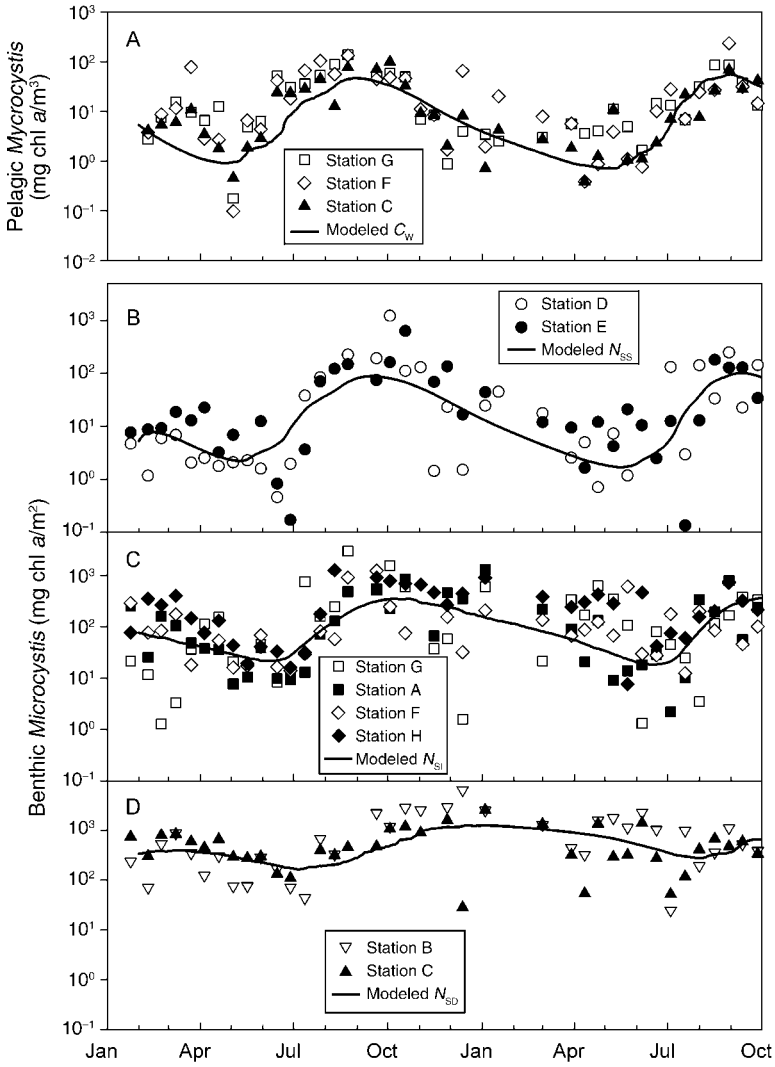

FIG. 7. Population dynamics of *Microcystis* in the period February 2000–October 2001. (A) Concentration of pelagic *Microcystis* in the water column, C_W. (B–D) The amount of benthic *Microcystis* per unit surface area in (B) shallow sediments, N_{SS}; (C) intermediate sediments, N_{SI}; and (D) deep sediments, N_{SD}. Symbols indicate field data, and solid lines indicate the model predictions.

Once the system has settled at this new equilibrium, salinity will be 22–26 g/L during summer. In winter, when flushing of the lake with fresh water is necessary to prevent the rivers Rhine and Meuse from flooding upstream, salinity will be 7–18 g/L. This implies that only during winter, when there is little growth of *Microcystis*, there is a possibility that the salinity will become lower than the threshold value of 14 g/L. Hence the inlet of saline water seems a feasible strategy to eliminate *Microcystis* blooms.

Although a high salinity will suppress *Microcystis*, it may have undesirable side effects. In particular, in stagnant water a stable salinity stratification may develop. Since the sediments of Lake Volkerak contain high amounts of organic matter, including benthic *Microcystis*, this may induce anoxic conditions in the epilimnion with negative effects on biota and water quality. Furthermore, a stagnant brackish reservoir may form an ideal habitat for harmful algal blooms of marine phytoplankton species (Sellner 1997, Van Dolah 2000, Anderson et al. 2002). To minimize the risks for salinity stratification or dense blooms of toxic marine phytoplankton, the reintroduction of tidal movement is probably a better management option than stagnant brackish water.

Flushing.—The model simulations show that flushing will suppress *Microcystis* blooms when the current discharge rate is increased to 75 m^3/s throughout the year or a slightly lower discharge rate during summer (e.g., 65 m^3/s) combined with a higher discharge rate in winter (125 m^3/s). According to calculations by the water authorities, diversion of water from the rivers Rhine and

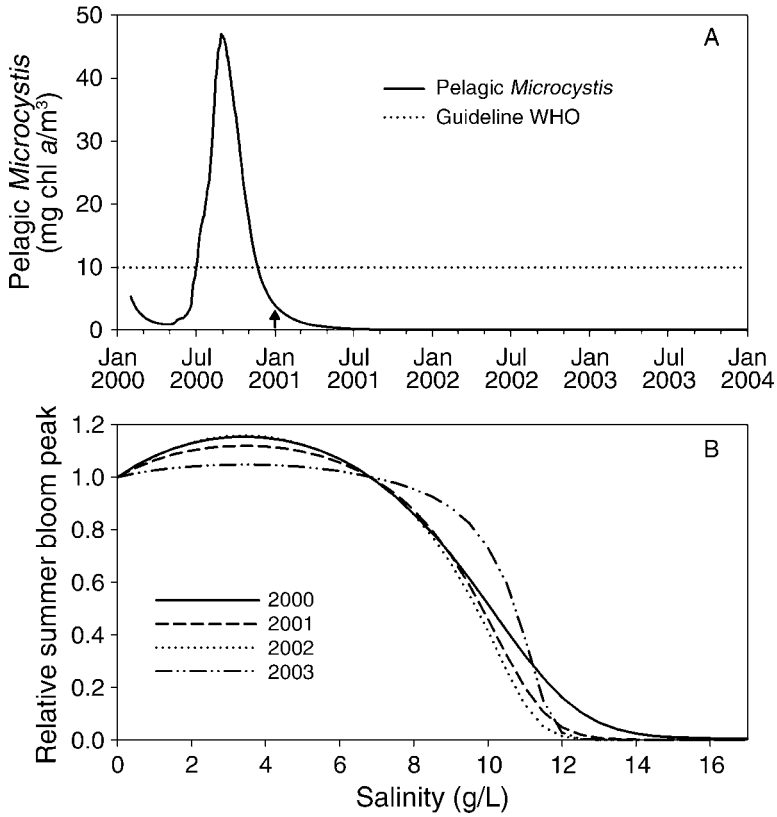

FIG. 8. Model scenarios on the impact of salinity on *Microcystis*. (A) Model prediction of the pelagic *Microcystis* concentration assuming the weather conditions of February 2000–December 2003, when salinity would have been raised to 17 g/L from January 2001 onward (as indicated by the arrow). The horizontal line indicates the guideline value for maximum cyanobacterial abundance in recreational waters provided by the World Health Organization (Chorus et al. 2000). (B) Model predictions of the summer peak of the *Microcystis* bloom as a function of salinity. The summer peak is normalized to the summer peak at zero salinity. The model scenarios were run assuming the meteorological conditions of 2000–2003.

Meuse can make this a feasible management option. Even during dry summers, the freshwater supply by the river Rhine alone is close to 1000 m^3/s. One possible drawback of flushing might be the persistence of *Microcystis* populations in sheltered areas of the lake less affected by flushing. Due to the elongated morphology of Lake Volkerak, however, most of the lake area can be flushed rather effectively. As a consequence of enhanced flushing, *Microcystis* will probably be replaced by phytoplankton species with higher specific growth rates, like green algae and diatoms. Freshwater species of green algae and diatoms native to the lake are not known to be toxic. Accordingly, enhanced flushing will make the lake suitable for recreation, the intake of fresh water for agricultural purposes, and nature conservation.

Strengths and limitations of the model study

Models are, by definition, abstract simplifications of reality. As such, our model study has both strengths and limitations. A major strength of the study is the detailed representation and validation of *Microcystis* growth as a function of environmental conditions. This has enabled accurate estimations of the growth and loss rates of *Microcystis* in Lake Volkerak. Another major strength is the explicit incorporation of benthic–pelagic coupling in the population dynamics of *Microcystis*. Flushing could be a less effective management strategy if benthic *Microcystis* colonies would resuspend into the water column in large amounts. Our study shows, however, that the sediment acts more as a sink than as a source of *Microcystis*. Incorporation of these benthic–pelagic processes has yielded more reliable predictions of the different model scenarios.

A simplification in our model is that the photosynthetic parameters (e.g., in Eq. 6) were fixed. In reality, photosynthetic parameters might vary among *Microcystis* strains and may change under different physiological conditions. This may particularly apply to *Microcystis* colonies recruiting from the sediments. In a previous study we found that the photochemical vitality of benthic colonies from intermediate and deep sediments were lower than the vitality of pelagic colonies and benthic colonies from the shallow sediments (Verspagen et al. 2004). However, since recruitment rates from the deeper sediments are relatively low in Lake Volkerak, we assume that the reduced vitality of these

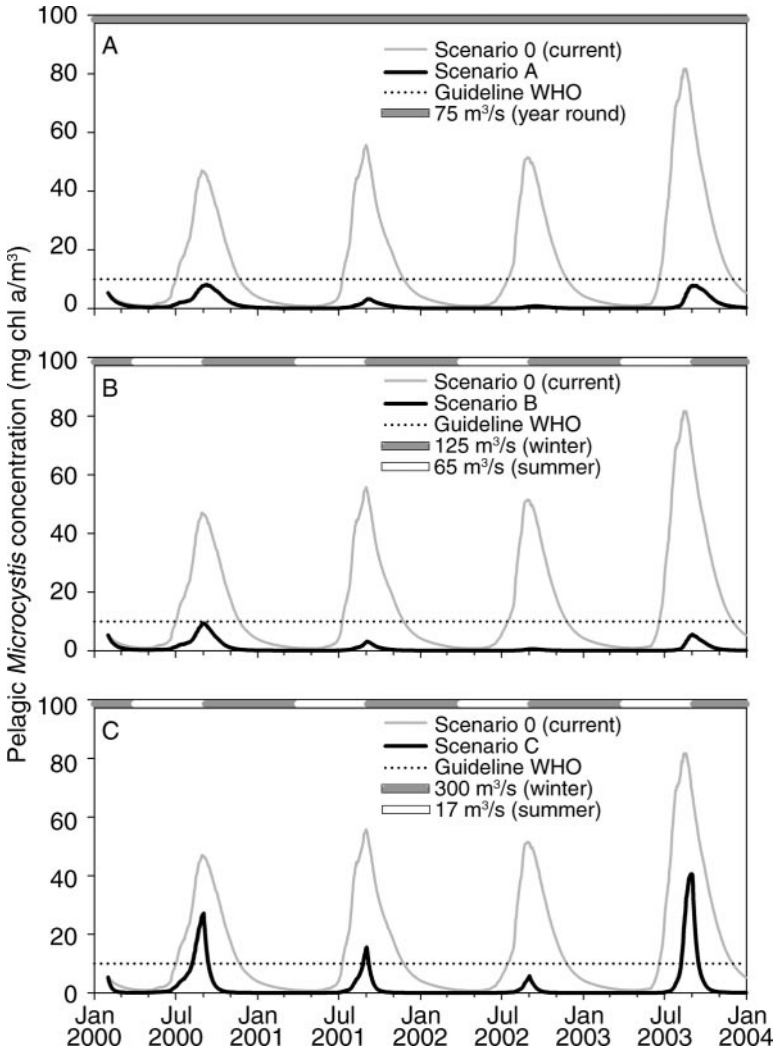

FIG. 9. Model scenarios on the impact of flushing on *Microcystis*. The model predictions assume the weather conditions of February 2000–December 2003. Scenario (A), a constant discharge rate of 75 m^3/s throughout the year. Scenario (B), a discharge rate of 65 m^3/s in summer, and a high discharge rate of 125 m^3/s in winter. Scenario (C), minimum discharge rate of 17 m^3/s in summer, maximum possible discharge rate of 300 m^3/s in winter. Each panel also shows scenario 0, which corresponds to the current situation with a discharge rate of 17 m^3/s in summer and 27 m^3/s in winter. The horizontal line indicates the guideline value for maximum cyanobacterial abundance in recreational waters provided by the World Health Organization (Chorus et al. 2000).

benthic *Microcystis* colonies has little effect on the overall model predictions.

Another simplification is that the model assumes a fixed shape of the vertical distribution of *Microcystis* in the water column (Fig. 6B), though this shape is firmly based on extensive measurements in the lake. Thereby, the model ignores dynamic changes in the *Microcystis* profile due to vertical mixing processes (Huisman et al. 2004) and the vertical migration of *Microcystis* (Visser et al. 1997, Thébault and Rabouille 2003). The model also lacks horizontal mixing processes. In reality, flushing might be less effective in ''dead corners'' of the lake, and the inlet of saline water may lead to horizontal and vertical gradients in salinity. Extensions of the model, with explicit incorporation of three-dimensional hydrodynamic processes, will be required to obtain detailed predictions on the development of surface scums and on the spatial implications of different management options.

In conclusion, this study shows that the inlet of saline water and enhanced flushing with fresh water are both feasible management options that are likely to suppress *Microcystis* blooms in the Dutch delta. In a broader context, these findings illustrate that quantitative ecological knowledge can be incorporated in model scenarios to predict the implications of different water management strategies. This approach will offer a valuable tool in water management.

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APPENDIX A

An assessment of the nutrient status of Lake Volkerak (*Ecological Archives* A016-015-A1).

APPENDIX B

A table providing an overview of all model parameters and their estimated values (*Ecological Archives* A016-015-A2).