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APPLIED ISSUES

Artificial mixing prevents nuisance blooms of the cyanobacterium *Microcystis* in Lake Nieuwe Meer, the Netherlands

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SUMMARY

1. Artificial mixing in the hypertrophic Lake Nieuwe Meer was successful in preventing blooms of the cyanobacterium *Microcystis*. During the 2 years of artificial, deep mixing the number of colonies of *Microcystis* per litre and also per m^2 was lower than in the two preceding control years. Hardly any nuisance scums of *Microcystis* occurred in the lake.

2. The phytoplankton shifted from a cyanobacteria-dominated community in summer to a mixed community of flagellates, green algae and diatoms. Reduced sedimentation losses in the mixed lake, probably in combination with a lower pH, favoured non-buoyant algae, while the entrainment of cyanobacteria in the turbulent flow nullified their advantage of buoyancy.

3. The chlorophyll concentrations were much lower in the mixed lake, but the euphotic depth did not show clear differences between the years. The chlorophyll content integrated through depth (m^{-2}) increased in the artificially mixed lake.

4. The deep lake normally stratified in summer, but artificial mixing of the lake in 1993 resulted in a homogeneous temperature and oxygen distribution with depth. In spring 1994, the mixing was applied intermittently with a reduction of 75% of the energy costs, while the mixing was still sufficient to prevent stratification.

5. Determination of the buoyancy state of the colonies on a sunny and calm day showed that the buoyancy loss was low close to the bubble plumes, and high at some distance from these plumes. This suggests that *Microcystis* could escape the mixing at some distance from the plumes, and could synthesize more carbohydrates during its stay in the upper illuminated layer of the lake than the deep mixed colonies close to the bubble plumes. Determination of the buoyancy state appeared to be a good and simple method to investigate the extent of entrainment of colonies in the turbulent flow.

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Introduction

In Lake Nieuwe Meer, a highly eutrophic lake in Amsterdam, The Netherlands, the summer phytoplankton has been dominated by *Microcystis* for many years. Nuisance scums accumulate in the harbours of the lake, which causes particular problems for the inhabitants of the houseboats. The lake forms part of the nutrient-rich Rhine basin and is connected with the canals of Amsterdam. In the past additional nutrients were added to the sediment of the lake by the dumping of sludge from the canals. Because of these excess nutrients in the water and sediment, any attempt to reduce phytoplankton biomass by the reduction of the nutrient loading, especially phosphate, would be effective only in the long term. Nevertheless, the Rhine Action Programme should eventually result in a lower nutrient loading to the lake.

In the short term, artificial mixing could prevent the growth of *Microcystis* since this organism benefits from a stable, stratified water column (Köhler, 1992). Gas vesicles provide the *Microcystis* colonies with buoyancy, which enables them to concentrate their biomass in the upper mixed layer. In this way, *Microcystis* increases its total daily light dose during periods of low wind speed (Ibelings, Mur & Walsby, 1991a; Köhler, 1992), while non-buoyant phytoplankton suffers from increased sedimentation losses in a (partially) stable lake. In an artificially deep-mixed lake, *Microcystis* loses its advantage of buoyancy and will receive a much lower light dose. Reduction of growth of *Microcystis* by deep mixing has been shown in experimental enclosures in Blelhalm Tarn by Reynolds, Wiseman & Clarke (1984). A whole lake study in Ham's Lake, Oklahoma, where artificial mixing prevented blooming of *Microcystis*, is described by Toetz (1981).

Lake Nieuwe Meer was mixed artificially with compressed air bubble plumes in order to prevent growth of *Microcystis* and other bloom-forming cyanobacteria. Because of the relatively high floating velocity of the *Microcystis* colonies, the equipment for aeration was designed in such a way that the vertical mixing velocity would be sufficient to keep *Microcystis* entrained in the turbulent flow. In this paper, the effects of artificial mixing on physical, chemical and biological variables in the lake, with emphasis on the phytoplankton composition, are studied. Two years without artificial mixing (1990 and 1991) are compared with one year with continuous mixing (April till October 1993) and one year (1994) with intermittent mixing during spring and continuous mixing in summer. The efficiency of the artificial mixing with *Microcystis* entrained in the turbulent flow (hence preventing a rise to near-surface layers) was quantified by the determination of the buoyancy state of the colonies at different spots in the lake. The buoyancy state is linearly related with the light dose received by the cyanobacteria as found by Ibelings *et al.* (1991b) and Visser *et al*. (1996a). Entrainment of *Microcystis* in the deep, turbulent flow will be indicated by little loss of buoyancy during the day.

Materials and methods

Artificial mixing

Lake Nieuwe Meer has a surface area of 1.32 km^2, a volume of 18×10^6 m^3, a mean depth of 18 m and a maximum depth of 30 m. The calculations for the design of the mixing equipment were done by Jungo Engineering, Zurich, Switzerland. These were based on a desired mixing velocity of about 1 m h^{-1} at the surface, in order to exceed the mean vertical flotation velocity of *Microcystis* (0.11 m h^{-1}) and to approach the maximum flotation velocity (2.6 m h^{-1}) as far as possible. Determination of the vertical floating velocity of *Microcystis*, using the method of Booker & Walsby (1979), was performed on six occasions in summer 1990 on samples of Lake Nieuwe Meer.

The mixing was provided by two air compressors connected with a network of seven tubes, (Fig. 1) situated at 20–25 m depth. Care was taken to keep the tubes more than 1 m above the sediment to avoid disturbing the polluted sediment. Air was pumped through polyethylene pipes which were perforated every metre with holes of 1 mm diameter. Compressor 1 delivered 500 N m^3 h^{-1}, had a capacity of 55 kW and was connected to four tubes in the lake; compressor 2 delivered 275 N m^3 h^{-1}, had a capacity of 30 kW and was connected to three tubes in the lake. Five tubes had a length of 200 m and two of 120 m. The amount of air blown into the lake was 13 m^3 min^{-1}.

The mixing was started in early spring to prevent the onset of thermal stratification and an oxygen-depleted hypolimnion. On 23 March 1993 compressor 1 was switched on, and on 7 April compressor 2 was

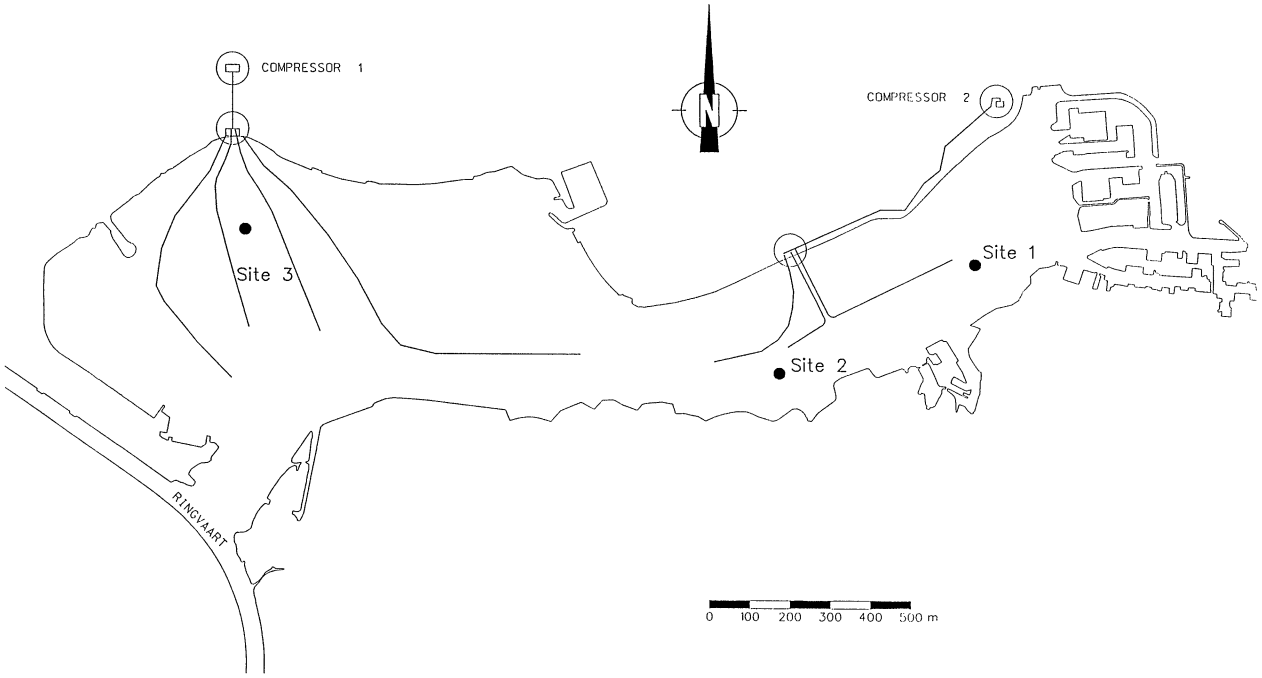

Fig. 1 Map of Lake Nieuwe Meer, showing the location of the two compressors and the seven aeration tubes (—) in the lake as well as the three sampling stations.

switched on. On 27 September both were switched off. Compressor 1 did not work during 10 days in spring due to technical problems. In spring 1994, the mixing was applied intermittently (in order to reduce energy costs) as shown in Fig. 2. The mixing regime was based on the temperature and oxygen profiles: the mixing equipment was switched on when the difference in temperature or oxygen concentration between surface and bottom equalled or exceeded 2 °C or 2 mg l^{-1}, respectively; it was switched off again when the difference had been reduced to less than 1 °C or 1 mg l^{-1}. In the summer months of 1994, when *Microcystis* was present in low numbers in the lake, the mixing was almost continuously in operation because partial stability of the water column, as can occur during intermittent mixing, would offer *Microcystis* the possibility to float into the illuminated surface layer. On 28 April 1994 both compressors were switched on for the first time and on 6 October they were finally switched off. One of the tubes (the most eastern tube connected to compressor 1) was faulty from 24 July to 24 August.

Physical and chemical measurements

Temperature profiles of the water column were measured from 16 March 1990 to 7 July 1991 with a YSI model 2100 thermometer (fitted with a series 400 thermistor probe). Oxygen was measured from 17 April to 7 July 1991 on samples from different depths using Winkler titration. In July, August and September 1991 and in 1993 and 1994, temperature and oxygen profiles were measured with a Surveyor 3 multiparameter water quality logging system. The pH of the water samples was measured potentiometrically with a Microprocessor pH meter pH 539.

The concentration of macronutrients was measured monthly in samples from 0.5 m depth. For determination of total P in the (unfiltered) samples, organic P and poly-P were transformed into orthophosphate (ortho-P) by 30 min boiling with sulphuric acid and potassium peroxide sulphate. Ortho-P in these samples and in filtered samples was measured spectrophotometrically after reduction by ascorbic acid and colouring with molybdate (Murphy & Riley, 1962). The organic nitrogen content was converted into ammonium sulphate by heating the unfiltered samples with concentrated sulphuric acid (Kjeldahl method). Subsequently nitrate-N was distilled and preserved in a solution of sulphuric acid. The ammonium formed in these samples and in filtered samples, and nitrite-N and nitrate-N (which was reduced to nitrite by a cadmium reductor) were measured spectrophoto-

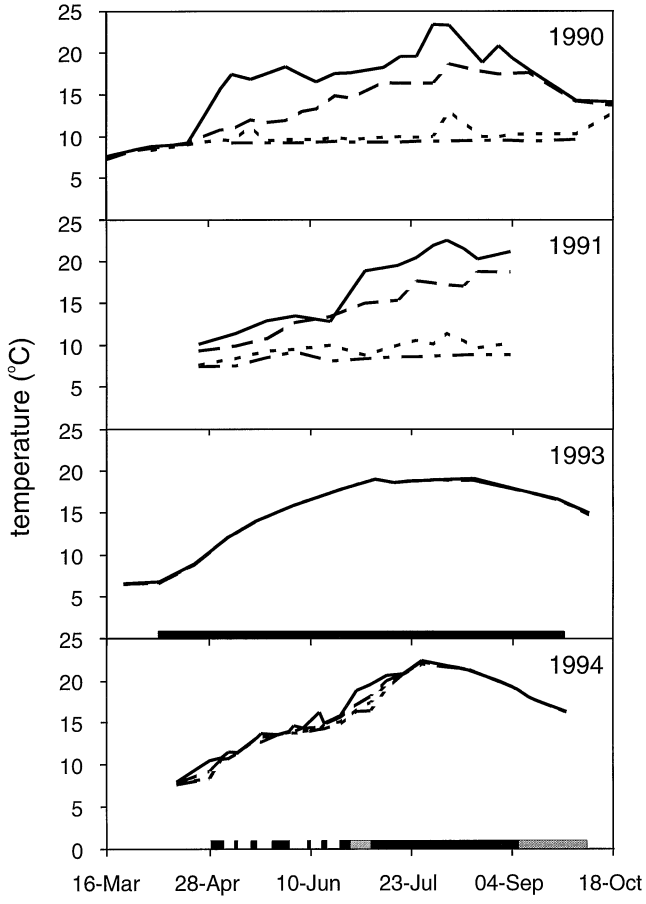

Fig. 2 Seasonal variations in temperature (°C) at different depths in the water column (—, 0 m; — —, 10 m; – – –, 20 m; — – —, 25 m) in two years without artificial mixing (1990, 1991) and two years with artificial mixing (1993, 1994), measured at station 3. The mixing regimes in 1993 and 1994 are shown on the *X*-axis of the figures: solid bands represent periods of continuous mixing, the first grey band represents a period with 7 h mixing day^{-1} and the second grey band represents 18 h mixing day^{-1}.

metrically (APHA, 1985) with an autoanalyser system (Bran and Luebbe). The total nitrogen content in the sample is the sum of the concentration of Kjeldahl-N, nitrite-N and nitrate-N. Silicate was measured spectrophotometrically at 815 nm after complex forming with molybdate at pH 3–4 followed by reduction in order to colour the complex (Golterman, 1971).

Measurements of photosynthetically active photon radiance (PAR) were made with a Li-Cor 185B quantum meter using a cosine-corrected underwater sensor. The depth of the euphotic zone was taken as the depth where the light intensity reached 1% of the surface intensity. The transparency of the water was measured with a Secchi disk.

Data on wind velocity and radiant energy, measured at Schiphol Airport 10 km away from the lake, were provided by the Royal Netherlands Meteorological Institute. The depth of the surface mixed layer (Z_m) was determined from data on wind speed and depth profiles of temperature, and was calculated as the depth where the Wedderburn number reached unity, as described by Imberger & Hamblin (1982).

Chlorophyll and phytoplankton

From April to October, samples were taken at least every 2 weeks for the estimation of chlorophyll and phytoplankton numbers at three stations in the lake (Fig. 1). In 1990 surface samples only were taken; in 1991, 1993 and 1994 mixed samples from 0, 1 and 2 m depths were taken. The depths of the sampling sites were 15 m at site 1, 20 m at site 2 and 27 m at site 3. For the determination of chlorophyll distribution in the water column, samples were taken from the following depths and pooled: 0, 1 and 2 m; 2.5, 3.5 and 4.5 m; 5, 6 and 7 m; 8, 9 and 10 m. In 1993 and 1994 samples were also taken at 11, 12 and 13 m; 16, 18 and 20 m; 21, 23 and 25 m; and at 27 m at station 3. Samples were filtered over glass fibre filters for the determination of chlorophyll *a* and these filters were stored in a freezer. In 1990, 1993 and 1994, chlorophyll *a* concentration was estimated by extraction in 80% ethanol at 75 °C. Calculation was performed according to Nusch & Palme (1975) with correction of the phaeophytin content (measured after addition of HCl). In 1994, no phaeophytin measurements were performed. To be able to compare these values with the other years when the values were corrected, a correction for phaeophytin was made based on the average phaeophytin concentration in the samples in 1990. In 1991, extraction of the samples was done in 90% methanol. The extinction coefficient used for the calculation was taken from Iwamura, Nagai & Ichimura (1970).

The water samples for counting phytoplankton were exposed to a pressure of about 1.1 MPa in order to collapse the gas vesicles of the cyanobacteria. The samples were fixed with formaldehyde in 1990 and with Lugol's iodine in the other years, and concentrated by sedimentation. The number of phytoplankton cells (colonial forms like *Microcystis*, *Aphanizomenon* and *Anabaena* were enumerated as colonies) in these concentrates were counted

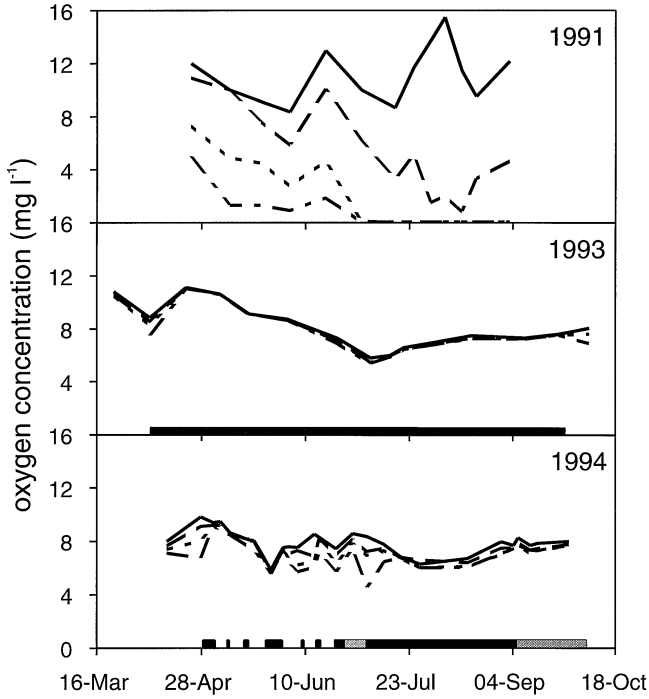

Fig. 3 Seasonal variations in oxygen concentration (mg l^{-1}) at different depths in the water column in one year without artificial mixing (1991) and two years with artificial mixing (1993, 1994), measured at station 3. Symbols and construction as in Fig. 2.

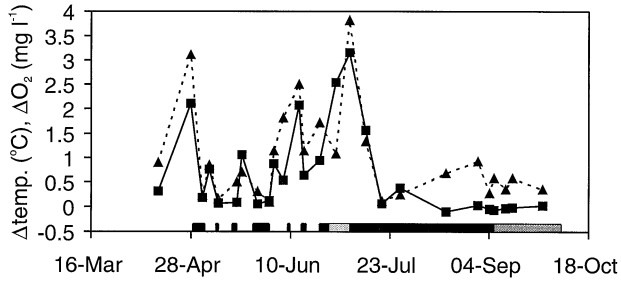

Fig. 4 Seasonal variations in the difference of temperature in °C (■) and oxygen concentration in mg l^{-1} (▲) between the surface and 25 m depth, measured at station 3, during intermittent artificial mixing in 1994. Representation of the mixing regime as in Fig. 2.

microscopically in a Sedgewick–Rafter counting chamber and identified to genus level only.

The number of colonies or cells and chlorophyll per m^2 were calculated in 1990 and 1991 by multiplying the number (m^{-3}) or chlorophyll *a* (g m^{-3}) by the calculated mixing depth in metres, assuming a homogeneous phytoplankton distribution throughout the mixed layer. In 1993 and 1994, the concentration was multiplied by 20 m at station 2 and 25 m at station 3 (as will be discussed later).

Table 1 The mean and maximum temperature and oxygen concentration at the surface, and the mean temperature and oxygen concentration of four depths in May, June, July and August 1993 and 1994 (with artificial mixing) and in the 'control years' 1990 and 1991 measured at station 3. nd, not determined

	1990	1991	1993	1994
Temperature (°C)				
Surface, mean	18.6	17.3	17.1	17.5
Surface, maximum	23.4	22.5	19.1	22.4
0, 10, 20, 25 m, mean	13.4	12.6	17.1	17.0
Oxygen concentration (mg l^{-1})				
Surface, mean	nd	10.6	7.6	7.9
Surface, maximum	nd	13.7	10.7	9.4
0, 10, 20, 25 m, mean	nd	4.6	7.5	7.4

Vertical distribution and buoyancy state of Microcystis

In the morning of 20 July 1994 samples were taken at 5-m intervals at seven sites for the determination of the vertical distribution of *Microcystis*. The samples were concentrated about 400 times with a 20-µm plankton net and fixed with Lugol's iodine (5%). The numbers of colonies were counted in a Sedgewick–Rafter chamber. Temperature and light profiles were measured as described before. In the afternoon of 20 July, surface samples were taken at twenty-two sites in the lake for the determination of the buoyancy state of the colonies. The first sample was taken at 14.00 h and the last at 16.30 h; the sequence of sampling was from west to east. The samples were concentrated about 1000 times with a 20-µm plankton net and then fixed with formaldehyde (2%). The next day, the percentage of colonies sinking was determined by counting the number of colonies floating under the coverslip and the colonies sinking on the bottom of a small counting chamber (depth 3 mm) after standing for 5 min. The effect of formaldehyde on buoyancy was tested beforehand on a laboratory culture of colonies. This showed that the percentage of colonies sinking was a little lower in fixed samples after 24 h (fresh sample: 49.4 ± 7.3%, $n = 35$; sample fixed with formaldehyde (2%) 24 h later: 43.0 ± 6.5%, $n = 36$), but since this difference was only small and all samples were treated in the same way, this effect was ignored.

Table 2 The total insolation and the average wind velocity in the four years of field study

	Total insolation (MJ m^{-2} $month^{-1}$)				Average wind velocity (m s^{-1})			
Month	1990	1991	1993	1994	1990	1991	1993	1994
May	684	469	570	487	4.1	4.6	5.5	4.6
June	480	450	572	529	4.1	5.5	4.2	4.9
July	639	613	519	710	4.1	4.5	4.9	3.6
August	519	521	433	456	4.6	3.6	4.3	4.5
Total period	2322	2053	2094	2182	4.3	4.6	4.7	4.4

Results

Temperature, oxygen and pH

Water temperature and oxygen concentration at different depths in the water column are shown in Figs 2 and 3, respectively, in spring and summer of the two years before (1990 and 1991) and during continuous mixing (1993 and summer 1994) and intermittent mixing (spring 1994). In the untreated lake, stratification during the summer months resulted in a relatively stable temperature of about 9 °C in the hypolimnion, and up to 23 °C at the surface. During the summer months, the hypolimnion became anaerobic while oxygen saturation at the surface was about 100%. When mixing was applied, only small differences in temperature and oxygen concentration with depth were found. The average temperatures at the surface in the period May–August (Table 1) were lower in 1993 and 1994 compared with 1990, but comparable with 1991. This of course depends very much on the weather conditions. Figures for total irradiance in these months (Table 2) confirm that the summers of 1990 and 1994 were somewhat sunnier than the summers of 1991 and 1993. Furthermore, average wind speed was slightly higher in 1991 and 1993 than in 1992 and 1994. The average temperature at four depths in the water column increased by about 4 °C during mixing of the lake. The oxygen concentration at the surface was lower when mixing was applied, with a minimum of 5.8 mg l^{-1} (63% saturation) in 1993.

In 1993, the maximum difference in temperature and oxygen concentration between the surface and 27 m depth was 0.26 °C and 0.39 mg l^{-1}, respectively. In spring 1994, due to intermittent mixing, these differences were greater than the maximum in 1993 and changed with time, as is shown in Fig. 4. A temperature difference of about 2 °C developed during unmixed periods in spring, but was reduced to almost zero after one or two days of continuous mixing. From 26 June to 6 July, a mixing regime of only 7 h day^{-1} was tested. This mixing regime resulted in a relatively high temperature and oxygen difference, which was only reduced to zero after about 2 weeks of continuous mixing. The very warm and sunny weather in July contributed to the rather long period that was needed to reach a homogeneous temperature distribution in the lake. In September the mixing equipment was switched off during two periods of 3 h at night. This apparently did not effect the temperature and oxygen profiles.

The pH (measured at 0.5 m) was lower in the years with mixing, the difference being most pronounced in July and August (Table 3).

Table 3 The pH at 0.5 m depth measured at station 3 from May to August in two years without artificial mixing (1990 and 1991) and two years with artificial mixing (1993 and 1994)

	1990	1991	1993	1994
May	8.55	7.90	7.75	7.55
June	8.10	7.90	7.75	7.55
July	9.05	8.05	7.50	7.95
August	8.95	8.80	7.95	8.05

Table 4 The average euphotic depth Z_{eu}, transparency (Secchi depth) Z_S, ratio of the euphotic layer and mixing depth Z_{eu}/Z_m, chlorophyll *a* l^{-1} and m^{-2} over the period May, June, July and August in two years without artificial mixing (1990 and 1991) and two years with artificial mixing (1993 and 1994). The values are averages of station 2 and 3

	1990	1991	1993	1994
Z_{eu} (m)	3.1	4.6	3.5	4.0
Z_s (m)	1.6	1.9	1.5	1.8
Z_{eu}/Z_m	0.59	0.67	0.16	0.40
Chl *a* (μg l^{-1})	28.1	18.5	11.5	6.3
Chl *a* (mg m^{-2})	118	102	259	158

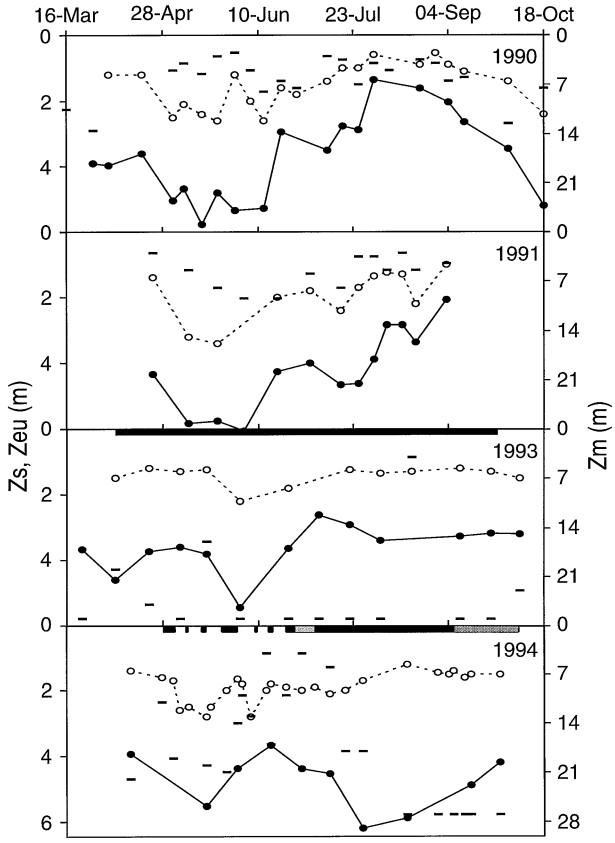

Fig. 5 Seasonal variation in the Secchi depth Z_S (m) (○), the euphotic depth Z_{eu} (m) (●), and the calculated mixing depth (m) (see Materials and methods) (—) in two years without artificial mixing (1990, 1991) and two years with artificial mixing (1993, 1994), measured at station 3. Representation of the mixing regimes as in Fig. 2.

Transparency, mixing depth and chlorophyll a

In Fig. 5, seasonal changes in transparency (Z_s), euphotic depth (Z_{eu}) and mixing depth (Z_m) are shown. The mixing depths in 1990 and 1991 were less than 7 m in the months May–August, whereas in 1993 it was nearly constant at 27 m. In 1994, intermittent mixing resulted in more variable mixing depths than in 1993, as is also indicated by the temperature differences between surface and bottom shown in Fig. 4. Only during continuous mixing in August and September was the mixing depth 27 m. The patterns of Z_s and Z_{eu} showed less fluctuation in the years with mixing compared with those without. The 'clear-water phase' occurred in May in 1990, 1991 and 1994. In 1993, however, highest transparency was measured in June. Very low chlorophyll concentrations in the water column were characteristic of these periods (Fig. 6).

The average values of transparency, depth of the euphotic layer and chlorophyll during the period May–September are shown in Table 4. No clear difference in the average euphotic depth or transparency between the years with and without mixing could be found. The average chlorophyll *a* concentration, however, showed differences between the years: in 1993 and 1994 values were low compared with 1990 and 1991. The depth of the euphotic layer, however, was greatest in 1991. A significant correlation between the depth of the euphotic zone and the chlorophyll concentration was found only in 1990 ($r^2 = 0.65$, $n = 18$, $P < 0.002$) and 1991 ($r^2 = 0.49$, $n = 12$, $P < 0.02$).

Because dilution of chlorophyll in the mixed lake plays an important part in determining the relative chlorophyll *a* concentration between years with and without mixing, the amount of chlorophyll is also expressed per m^2 (Table 4, Fig. 6), enabling a comparison of the total biomass in the water column. In 1990 and 1991, the concentration was multiplied by the calculated mixing depth. Although the calculated mixing depth fluctuated during 1994 (Fig. 5), the distribution of chlorophyll was more or less homogeneous over the entire depth of the water column in 1993 and 1994 (as shown for July, August and September in Fig. 7; only on 28 July 1994 was a higher concentration of chlorophyll in the near-surface layer found). For estimating chlorophyll *a* per m^2 in 1993 and 1994, the concentration was therefore multiplied by 20 m at station 2 and 25 m at station 3. The total amount of chlorophyll increased in the years with mixing. The chlorophyll content in 1990 and 1991 may even have been overestimated in July and August, because of frequent concentration of the chlorophyll in the upper 2 m (Fig. 7). The mixing depth, however, exceeded 2 m (Fig. 5). For that reason, a very high value due to surface bloom formation in August 1990 was not included in the calculations. In 1994 some concentration in the upper layer occurred on July 28, which will have caused the chlorophyll content per m^2 to be overestimated (since it was calculated assuming a homogeneous distribution over the entire depth). Fig. 7 shows how buoyancy of the dominant cyanobacteria in August–September 1990, and to a lesser extent in 1991, led to concentration of the biomass in the upper 2–5 m.

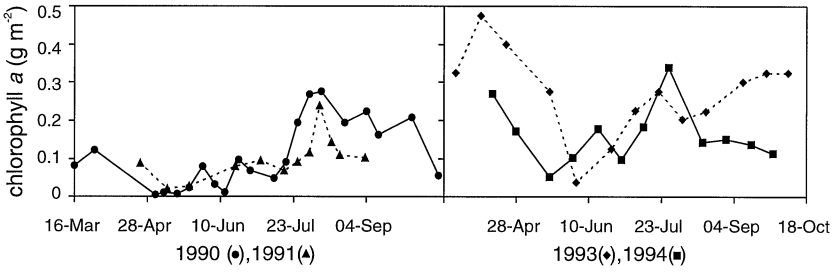

Fig. 6 Seasonal variations in the chlorophyll *a* content in g m^{-2} in two years without artificial mixing (1990, ●; 1991, ▲) and two years with artificial mixing (1993, ◆; 1994, ■) measured at station 3.

Table 5 The average (± SD) total phosphorus, orthophosphate, total nitrogen and dissolved silica in May–August in three years (1988, 1990 and 1991) without artificial mixing and two years with artificial mixing (1993 and 1994). nd, not determined

	1988	1990	1991	1993	1994
Total P (mg l^{-1})	0.47 ± 0.08	0.35 ± 0.12	0.43 ± 0.02	0.45 ± 0.08	0.42 ± 0.06
Ortho-P (mg l^{-1})	0.40 ± 0.07	0.25 ± 0.03	nd	0.38 ± 0.06	0.35 ± 0.07
Total N (mg l^{-1})	4.03 ± 0.37	3.10 ± 0.79	nd	3.91 ± 0.43	4.05 ± 0.36
Si (mg l^{-1})	1.0 ± 0.9	nd	nd	3.0 ± 0.9	nd

Nutrients

The average concentrations of total phosphorus and total nitrogen in May, June, July and August were not significantly different among the 4 years (Table 5). Ortho-P was higher in 1993 and 1994 compared with 1990 but there was no difference compared with 1988 (Table 5). The lower phytoplankton concentrations in 1993 and 1994 presumably contributed to a higher ortho-P concentration. This may also explain the higher nitrite-N + nitrate-N concentration in summer 1993 and 1994. The nitrite-N + nitrate-N concentrations were comparable (± 3 mg N l^{-1}) for all years until June (data not shown). Subsequently the concentration decreased, in 1989 and 1990 to 0.28 mg N l^{-1}, and to 2.1 mg N l^{-1} in August 1993 and 1994. The decrease of the nitrite-N + nitrate-N concentration in the stratified lake may be due, in addition to any uptake by phytoplankton, to diffusion to the anaerobic hypolimnion (where denitrification reduces the nitrogen concentration). Almost the entire water column in the mixed lake was aerobic and, presumably, no denitrification occurred. Ammonium did not differ between years with and without mixing and varied, without showing a clear pattern, between 0.5 mg N l^{-1} and the detection limit of 0.1 mg l^{-1}. The silicate concentrations were higher in May–October 1993 compared with 1988 (Table 5; no data are available from other years). The minimum concentration in August 1988 was 0.2 mg l^{-1}, compared with 1.5 mg l^{-1} in September 1993. It is unlikely that nutrients limited the growth of the phytoplankton at any time, as all values are above the criteria set for nutrient limitation (according to Sas, 1989).

Phytoplankton abundance

The dominance of cyanobacteria in the phytoplankton, which normally occurred in July, August and September (Fig. 8, 1990 and 1991), disappeared in the years with mixing (Fig. 8, 1993 and 1994). The phytoplankton in the mixed lake was dominated (on the basis of cell number) over the entire season by flagellates. Green algae and diatoms were also persistently abundant throughout the summer months, in contrast to years without mixing. In 1994, the abundance of cyanobacteria was somewhat higher compared with 1993. Other groups of phytoplankton were scarce and are ignored in Fig. 8.

In Fig. 9, temporal variation in the number of *Microcystis* colonies, coenobia of the most abundant green alga *Scenedesmus*, centric diatoms (mainly *Stephanodiscus* and *Cyclotella*) and flagellates m^{-2} are shown. The number of *Microcystis* m^{-2} was very high in 1990, but much lower in 1991, as also appears from the average value between May and September (Table 6). This may be due to a sunnier summer in 1990, but direct comparison is complicated by the fact that the samples were taken from station 1 in 1990 and from station 3 in the other years. Station 1 (Fig. 1) is situated in the western part of the lake and scums often accumulated in this area. For comparison, the average numbers of phytoplankton at station 1 are also given

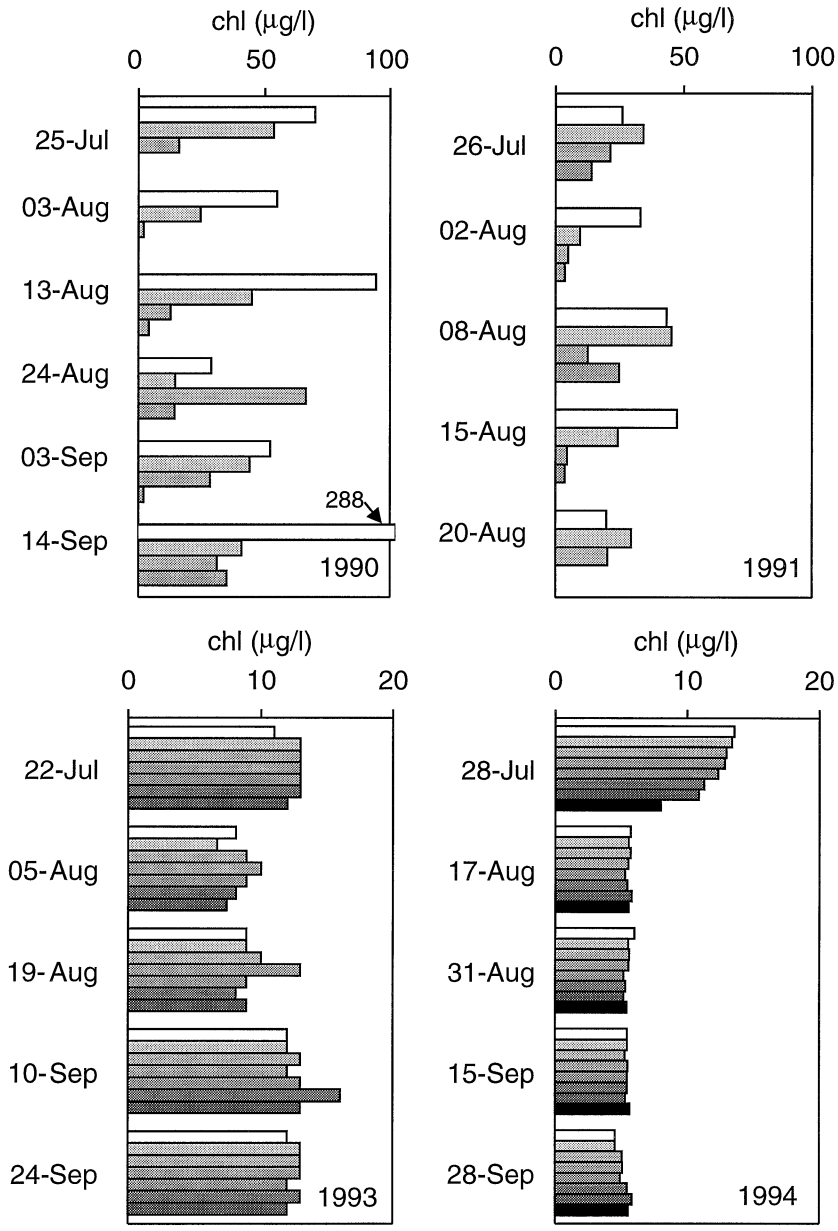

Fig. 7 The chlorophyll concentrations (µg l^{-1}) in two years without artificial mixing (1990, 1991) at different depths (from the top downwards for each sampling day the bars represent pooled samples of: 0, 1 and 2 m; 2.5, 3.5 and 4.5 m; 5, 6 and 7 m; 8, 9 and 10 m depth) and two years with artificial mixing (1993, 1994) at different depths (from the top downwards for each sampling day the bars represent pooled samples of: 0, 1 and 2 m; 2.5, 3.5 and 4.5 m; 5, 6 and 7 m; 8, 9 and 10 m; 11, 13 and 15 m; 16, 18 and 20 m; 21, 23 and 25 m and one sample of 27 m depth). In 1993 the concentration at 27 m depth was not measured. Note the difference in scale of the years with and without mixing.

for 1991 (Table 6). The number of *Microcystis* m^{-2} at station 1 in 1991 was a little higher than at stations 2 and 3, but was still much lower than in 1990. In 1993, the number of *Microcystis* m^{-2} was very low; in 1994 it was higher but still lower compared with 1990 and 1991. During the very warm and sunny month of July 1994, the stability in the water column increased during intermittent mixing (Fig. 4) and was reduced only after 2 weeks of continuous mixing. Because of the increased stability in this period, a higher concentration of *Microcystis* colonies was found in the upper 5 m of the lake on 13 and 18 July. When the temperature difference was reduced, a concentration of phytoplankton in the upper layer still occurred, as is shown by an increased chlorophyll content in the upper layer on 28 July (Fig. 7).

Other cyanobacteria in the lake were *Anabaena*, *Aphanizomenon* and *Aphanocapsa*. The number of *Anabaena* m^{-2} decreased in the years with mixing (Table 6). *Aphanizomenon* was absent in the year with continuous mixing but, during intermittent mixing in 1994, the average number of colonies m^{-2} was ten times higher than in 1991. *Aphanocapsa* was more abundant in 1993 than in 1990 and 1991, but occurred only in low

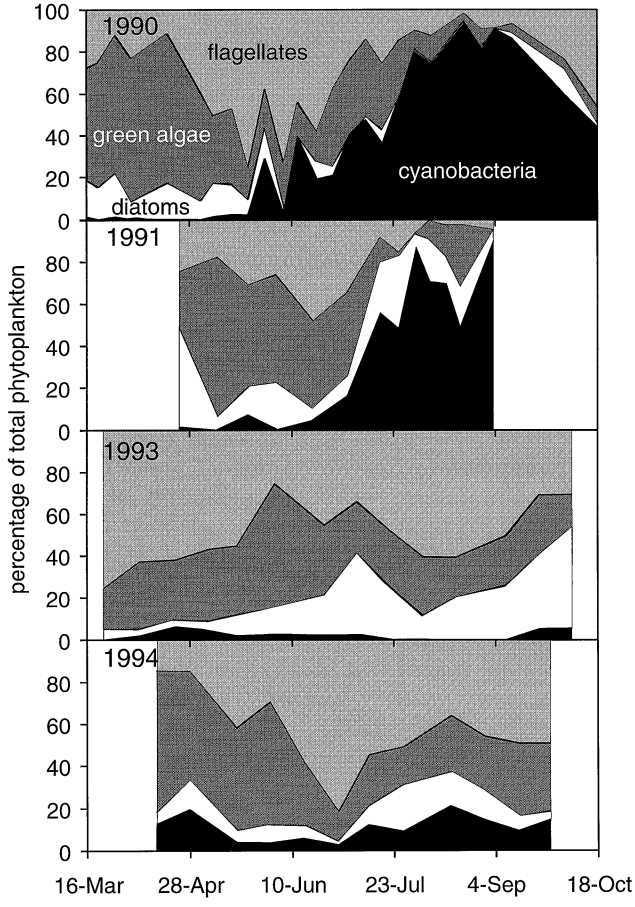

Fig. 8 Seasonal variations in the relative abundance of four phytoplankton groups in two years without artificial mixing (1990 and 1991) and two years with artificial mixing (1993 and 1994) in samples from station 1 in 1990 and from station 3 in the other years.

numbers in 1994. In 1990 and 1991 it peaked in July and June, respectively, while in 1993 and 1994 the highest peaks occurred in the period mid- March to mid-May, with smaller peaks in summer.

The numbers of *Scenedesmus* coenobia were much higher in the years with mixing compared with the years without mixing (Fig. 9, Table 6). In the years without mixing, the highest numbers were found in spring and in June and July, periods characterized by large mixing depths. In the year with continuous mixing, the number of *Scenedesmus* remained high throughout the summer, with two distinct peaks in April and July. In 1994, the number per m^2 was lower than in 1993. Centric diatoms were abundant only in spring in the years without mixing, while they remained abundant almost during the entire summer in years with mixing. The average number of these diatoms was high in 1993 and a little lower in 1994. The number of flagellates showed a large increase in 1993 (especially in spring) and to some extent also in 1994.

Effect of mixing on the entrainment of Microcystis

To investigate the effect of mixing on the entrainment of *Microcystis* colonies in the turbulent flow, determination of the buoyancy state of *Microcystis* was performed. Samples were taken in the afternoon of a sunny (total irradiance was 25.6 MJ m^{-2} day^{-1}), calm (mean wind velocity 3.3 m s^{-1}) day in 1994. Samples at the very shallow spots along the shore were taken as a reference because shallow mixing will result in a high percentage of colonies sinking. The percentage of colonies sinking varied between 30 and 40% at these spots (Fig. 11, open circles). The deeper spots in the middle of the lake showed a variable percentage of colonies sinking. The samples from spots close to the air-bubble plumes showed a very low percentage of sinking colonies, which suggests that the colonies were mixed over the whole water column and received a low light dose. At larger distances from the plumes, the percentage of colonies sinking was much higher. At these locations, *Microcystis* could probably escape the mixing, float upwards, and receive a higher light dose in the upper illuminated layers. This was checked by analysing the distribution of colonies with depth (Fig. 10). At most sites with a high concentration of colonies in the upper layers, the percentage sinking was high. With a homogeneous distribution, on the other hand, the percentage of colonies sinking was low. The calculated mixing depths corresponded with the results: shallower mixing at some distance from the plumes. At the locations from the top of Fig. 10 downwards the mixing depths were 8, 24, 18, 7, 5, 10 and 5 m. In 1993 determination of the buoyancy state at different locations was also performed and similar results were obtained.

Discussion

Phytoplankton abundance

Artificial mixing in Lake Nieuwe Meer was successful in preventing blooms of *Microcystis* in the two years studied. The number of *Microcystis* colonies l^{-1} (and also m^{-2}) was lower during the two years of artificial,

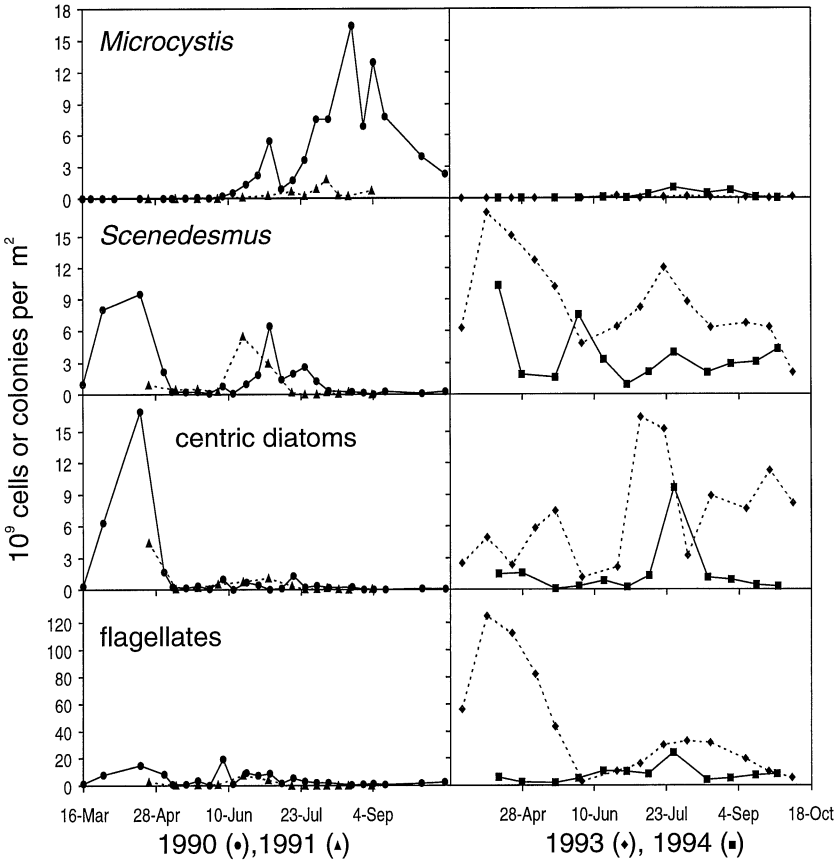

Fig. 9 Seasonal variations in the numbers of cells or colonies (10^9 m^{-2}) of *Microcystis*, *Scenedesmus*, centric diatoms and flagellates in two years without artificial mixing (1990, ●; 1991, ▲) and two years with artificial mixing (1993, ◆; 1994, ■) in samples from station 1 in 1990 and from station 3 in the other years.

Table 6 Average numbers of cells or colonies of phytoplankton in 10^{10} m^{-2} in May, June, July and August in two years without artificial mixing (1990 and 1991) and two years with artificial mixing (1993 and 1994). In 1990, the samples were taken at station 1, in other years the values are averages of stations 2 and 3. For 1991, numbers for station 1 are given in parentheses

	1990	1991	1993	1994
Diatoms	3.8	3.8 (9.8)	89.6	18.8
Centric diatoms	2.8	2.9 (7.6)	74.8	14.5
Green algae	29.6	13.2 (26.9)	214.3	41.9
Scenedesmus	8.5	8.3 (16.8)	93.8	27.2
Cyanobacteria	74.9	7.8 (21.1)	16.7	15.8
Microcystis	47.2	4.7 (16.4)	0.6	2.1
Anabaena	1.8	1.2 (0.5)	0.3	0.5
Aphanizomenon	0.1	0.8 (3.6)	0	9.8
Aphanocapsa	6.0	1.6 (0.4)	12.2	2.6
Flagellates	25.3	13.2 (8.8)	369.2	97.5

deep mixing than during the two control years (Fig. 9). The phytoplankton in summer was no longer dominated by cyanobacteria but shifted to a mixed composition of flagellates, green algae and diatoms (Fig. 8). Although the differences with and without artificial mixing are clear, it should be noted that our conclusions are drawn from a limited dataset of four years in total. From this dataset it is not possible to give an estimation of the variation in the phytoplankton composition between the years. The years with artificial mixing, however, were the first in about 20 years with no or only very few nuisance scums in the lake or its harbours, and cyanobacterial dominance was normally found every summer. Also nearby lakes, that also form part of the Rhine Basin (e.g. Braassemermeer), still developed *Microcystis* scums in 1993 and 1994 as they did in previous years. These two observations make it more convincing that the observed changes were indeed the result of artificial mixing rather than between-years variation.

A shift from cyanobacterial dominance to a phytoplankton community dominated by green algae and diatoms has also been observed in artificially mixed lakes or reservoirs by Symons, Carswell & Robeck (1970), Haynes (1973), Hawkins & Griffith (1993), Cowell *et al.* (1987) and Steinberg & Zimmermann (1988). Several explanations have been offered for this shift: a decreased pH, reduced sedimentation losses

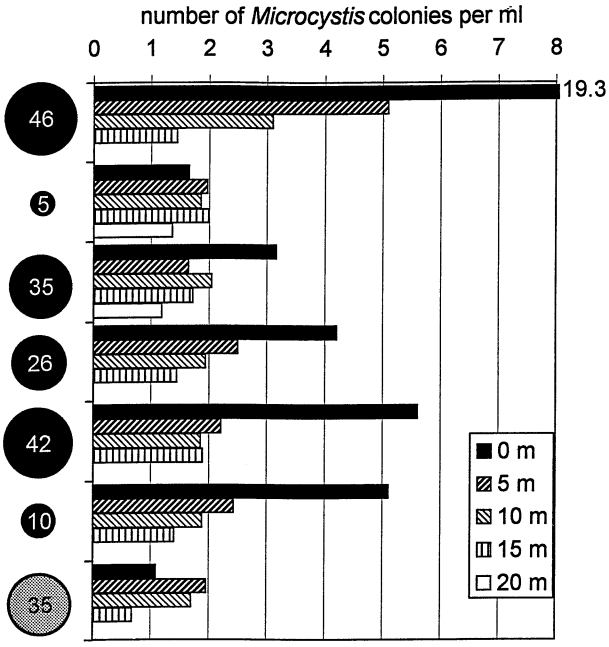

Fig. 10 The number of *Microcystis* colonies ml^{-1} of samples taken at 5-m depth intervals at different locations in the lake, taken on the morning of 20 July 1994. The percentages of colonies sinking (as in Fig. 11) of samples at the same spots taken in the afternoon are shown on the *Y*-axis.

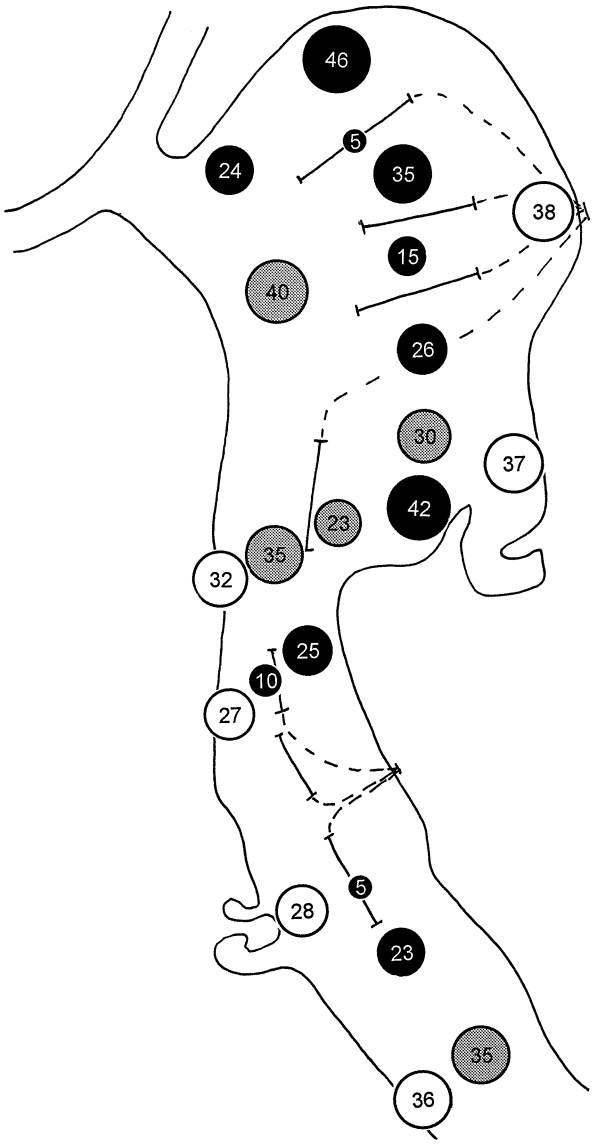

Fig. 11 The percentages of *Microcystis* colonies sinking in surface samples at different sampling points in Lake Nieuwe Meer, indicated by the numbers in the circles. The size of the circle is proportional to the percentages of colonies sinking. The colours of the circles indicate different ranges of the depth at the various sampling locations: black = 19–27 m, grey = 9–15 m and white = 1.5–6 m depth. The samples were taken from the surface. The aeration tubes (—) in the lake are also shown. The sampling was performed on 20 July 1994.

of the algae and the lower received light dose by the cyanobacteria entrained in the turbulent flow. These can also be used to explain the shift in phytoplankton composition in Lake Nieuwe Meer.

The pH fell (Table 3) in the artificially mixed lake as a result of mixing of carbon dioxide-rich water from the hypolimnion with the carbon dioxide-depleted epilimnion, and decreased primary production or a higher rate of heterotrophic growth in the hypolimnion due to a higher average temperature. Pastorok, Ginn & Lorenzen (1980) reviewed shifts in the phytoplankton of artificially mixed lakes and concluded that in lakes where the pH decreased following circulation, in most cases an increase in the ratio of green algae to cyanobacteria occurred, whereas in lakes without a reduction in pH this shift was not found. A lower pH has been shown to favour eukaryotic algae. Shapiro (1973, 1984, 1990) observed a shift from cyanobacteria to green algae at reduced pH (increased CO_2), as was suggested originally by King (1970). This shift has been explained by a higher affinity of cyanobacteria for carbon dioxide or the ability to use bicarbonate, while some eukaryotic algae are limited to carbon dioxide. Shapiro (1984, 1990) also suggested that cyanophages were favoured by low pH and caused cyanobacterial lysis.

Sedimentation losses of non-buoyant algae decreased during deep mixing, as indicated by lower catches in sedimentation traps relative to the standing crop (Visser *et al.*, 1996). In 1990, the average daily increment of *Scenedesmus* cells in sedimentation traps

as a percentage of the standing crop was 36%, while it was only 6% in 1993. A somewhat higher relative sedimentation loss of *Scenedesmus* and centric diatoms was found in May and June 1994 compared with the same period in 1993 (Visser *et al.*, 1996b).

Another factor that may have favoured diatoms during artificial mixing was the silicate concentration, which became less depleted in summer 1993 than in the stratified lake. In the years when no mixing was applied a large spring bloom of diatoms developed which consumed most of the silicate. Subsequent sedimentation losses during stratification removed the silicate from the epilimnion, and the bloom declined. Other nutrients did not affect the phytoplankton composition in the lake since the concentration of phosphate and nitrogen remained more or less the same.

Flagellates were very abundant during artificial mixing, but largely absent in 1990 and 1991. A lower pH might have been favourable for some cryptomonads as they may be less capable of dealing with high pH (Klaveness, 1988). Sedimentation losses are less important in these motile algae. Reynolds *et al.* (1982) found that grazing was an important loss factor for the flagellate *Cryptomonas*, while sedimentation losses were negligible. In the mixed lake, they were possibly favoured by the change in light climate and changes in the zooplankton abundance or species composition. This remains speculative, however, since zooplankton was not included in the study. An increase in the abundance of zooplankton is, however, often found in artificially mixed lakes (Pastorok *et al.*, 1980).

Artificial mixing reduced sedimentation losses of non-buoyant phytoplankton and prevented vertical migration of *Microcystis*. Hence, all phytoplankton species experienced a similar light climate. Species-specific differences in light-dependent growth rates may have contributed to the observed shift in phytoplankton composition. The received light dose was much lower during mixing than in a stratified lake, as the average Z_{eu}/Z_m ratio was almost four times lower in 1993 (Table 4). A Z_{eu}/Z_m ratio of 0.16 in the mixed lake in 1993, with a daylength of 16 h, is roughly equal to a photoperiod of 2.7 h (a calculation also used by Reynolds & Reynolds, 1985), although the phytoplankton in the mixed lake received these 2.6 h of light spread over 16 h. Comparison of the growth v length of the photoperiod curves of *Oscillatoria* and *Scenedesmus* (Loogman, Post & Mur, 1980) showed that *Oscillatoria* grew faster only at photoperiods shorter than 3 h. The growth v length of photoperiod curve of *Microcystis* (Zevenboom & Mur, 1984) is comparable with that of *Oscillatoria*, and thus theoretically *Microcystis* would win the competition for light in the mixed lake. Since this was not the case in the artificially mixed Lake Nieuwe Meer, other factors apparently affect the growth than photoperiod alone. For instance, at low Z_{eu}/Z_m ratios, the light regime will be more dynamic. *Microcystis* showed a poor acclimation to fluctuations in the light climate in comparison with *Scenedesmus* (Ibelings, Kroon & Mur, 1994). Diatoms appeared to be more tolerant than 'summer species' like cyanobacteria to reduced light doses and rapid fluctuations in irradiance (Reynolds & Reynolds, 1985; Reynolds, 1986). Lakes dominated by diatoms are often characterized by a large mixing depth and a low Z_{eu}/Z_m ratio (Schreurs, 1992).

Effect of mixing on the entrainment of Microcystis

The percentage of colonies sinking was higher at locations at some distance from the bubble plumes than at locations close to the bubble plumes. A higher loss of buoyancy means that more carbohydrates had been synthesized, since a linear relation between the loss of buoyancy and the carbohydrate content was found for *Microcystis* both in cultures (Kromkamp & Mur, 1984) and in natural populations (Ibelings *et al.*, 1991a). Ibelings *et al.* (1991b) and Visser *et al.* (1996a) found a linear relationship between the buoyancy state and the light dose received. At the locations at some distance from the bubble plumes *Microcystis* was probably disentrained from the deep mixing and received a higher light dose during its stay in the upper illuminated layers and synthesized more carbohydrates than deep mixed colonies. Differences in buoyancy between locations indicate that horizontal mixing of water masses was restricted to an extent that allowed differences in vertical mixing (and hence buoyancy) to develop.

A linear relation between the carbohydrate content and growth rate was found by Foy (1983), which suggests that in those deep parts of the lake where mixing was ineffective, the growth rate of *Microcystis* was higher than in the fully mixed parts. This explains the higher concentration of *Microcystis* in 1994 compared with 1993, because sunny, calm days were frequent in 1994 but rare in 1993. Furthermore, the water column in July 1994 was more stable than in

1993, as a result of a previous period with only diurnal artificial mixing, resulting in a temperature gradient in the water column. But even in the extremely warm summer of 1994 hardly any nuisance blooms of *Microcystis* occurred. Thus, although the mixing velocity was not sufficient on sunny, calm days to keep *Microcystis* entrained in the turbulent flow in the entire lake, we can conclude that the mixing prevented blooming of *Microcystis*.

We found that the entrainment of cyanobacterial colonies in the turbulent flow can be investigated by determination of the buoyancy state of the colonies. This technique is very simple and less time-consuming than determination of the vertical distribution of colonies. Using this simple technique it is possible to study the efficiency of mixing in various parts of the lake. In those cases where artificial mixing does not prevent blooms of cyanobacteria, it can be used to locate those areas of a lake where mixing is insufficient.

The entrainment of *Microcystis* in the turbulent flow in the entire lake is a very important factor in the success of artificial mixing, and is dependent on the capacity of the mixing equipment. Lorenzen & Fast (1977, in Pastorok *et al.*, 1980) suggested that, as a rule of thumb, a mixing device requires a capacity of at least 9.2 m^3 air min^{-1} $(10^6\ m^2)^{-1}$ lake surface to achieve complete mixing. The capacity of the aeration device in Lake Nieuwe Meer is 9.9 $m^3\ min^{-1}$ $(10^6\ m^2)^{-1}$ lake surface and is thus sufficient according to this rule. The depth of the lake where the aeration tubes are installed, the distribution of the tubes over the lake and the diameter of the holes in the tubes also determine the efficiency of mixing (Cooke *et al.*, 1993). Failure to reduce dominance by colony-forming cyanobacteria can often be ascribed to insufficient mixing velocities and/or a low mean depth of the lake or reservoir (Knoppert *et al.*, 1970; Lackey, 1973; Osgood & Stiegler, 1990).

Chlorophyll a content and transparency

The average total biomass of phytoplankton (chlorophyll *a* m^{-2}) increased during mixing in the lake. Also the peak chlorophyll content of the lake in the years with mixing increased compared with years without mixing. In contrast, a decrease in the maximum biomass of light-limited phytoplankton with increased mixing depth has been described by Lorenzen & Mitchell (1973, 1975) and Oskam (1978). More recently, Huisman & Weissing (1995) showed a decrease of biomass with mixing depth in a model. Loss processes are considered independent of mixing depth in these models. In the stratified lake, however, sedimentation losses were high for non-buoyant algae and much lower in the mixed lake (Visser *et al.*, 1996b). Thus, although the growth rate of the phytoplankton presumably decreased with increasing mixing depth, sedimentation losses decreased as well. This results in a less steep decrease of the peak chlorophyll content with mixing depth than described by Lorenzen & Mitchell (1973, 1975) and Oskam (1978), or even in an increase of the peak chlorophyll content. Only when a cyanobacterial population in a stratified lake is compared with a cyanobacterial or algal population in a mixed lake, may the effect of changes in sedimentation losses be neglected. In that case, as in August in Lake Nieuwe Meer, an increase of the peak or average chlorophyll m^{-2} can be explained by an increased yield on light. A shift in dominance to more shade-adapted species (higher yield at low light) will result in a higher overall biomass. Adaptation to low irradiance will also result in an increased chlorophyll content per cell (e.g. Falkowski, 1980)

The concentration of chlorophyll, however, was much lower during circulation as a result of dilution. But the transparency and the depth of the euphotic layer did not increase. The drop in the abundance of *Microcystis* during mixing will have changed the relation between chlorophyll and transparency (Köhler, 1992). Since a significant correlation between chlorophyll and the depth of the euphotic zone could not be found for 1993 and 1994, other factors might have influenced the attenuation in the water column as well.

Intermittent mixing

Reduction of the energy costs by intermittent mixing appeared to be possible in spring. The energy reduction that was achieved in April, May and June 1994 was 75% of the energy costs in 1993. Calculated for the entire spring/summer period, the energy costs in 1994 were 27% of those in 1993. There were no disadvantageous consequences for the oxygen content in the water. During the months July, August and September 1994, mixing was almost continuously in operation. This seems to be the best way to reduce growth and surface bloom formation of *Microcystis*.

Any stability that occurs during periods without mixing will enable *Microcystis* to spend more time in the upper illuminated layer, due to the high floating velocity of the colonies. Intermittent mixing will give *Microcystis* the opportunity to reach a higher biomass than during continuous mixing.

Intermittent mixing in the Fischkaltersee, Germany, successfully eliminated *Oscillatoria redekei*, explained by the inability of *Oscillatoria* to adapt to rapidly changing conditions (Steinberg & Zimmermann, 1988). A distinction must be made between the effect of mixing on colony-forming cyanobacteria (like *Microcystis*, *Anabaena* and *Aphanizomenon*) and filamentous *Oscillatoria* species. In the classification of Reynolds *et al.* (1984) for the effect of deep mixing on phytoplankton (based on experiments with artificial mixing in enclosures), *Oscillatoria* was classified, together with diatoms, in a group that was favoured by mixing, while *Microcystis* was placed in the group of species whose growth is arrested by episodes of deep column mixing.

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