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Diurnal buoyancy changes of *Microcystis* in an artificially mixed storage reservoir

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Abstract

In a storage reservoir, which is artificially mixed in order to reduce algal and especially cyanobacterial growth, the cyanobacterium *Microcystis* is still present. The aim of the research was to investigate why *Microcystis* was able to grow in the artificially mixed reservoir. From the results it could be concluded that the large shallow area in the reservoir allows this growth. The loss of buoyancy during the day was much higher in this shallow part than in the deep part. Assuming that the loss of buoyancy was the result of a higher carbohydrate content, a higher growth rate in the shallow part may be expected. A higher received light dose by the phytoplankton in the shallow mixed part of the reservoir than in the deep mixed part explains the difference in buoyancy loss. A significant correlation between the received light dose (calculated for homogeneously mixed phytoplankton) and the buoyancy loss was found. Apparently, the *Microcystis* colonies were entrained in the turbulent flow in both the shallow and the deep part of the reservoir. With a little higher stability on one sampling day, due to the late start of the artificial mixing, the loss of buoyancy at the deep site was higher than on the other days and almost comparable to the loss at the shallow site. Although the vertical biomass distribution and the temperature profiles showed homogeneous mixing, the colonies in the upper layers apparently received a higher light dose than those deeper in the water column. Determination of the buoyancy state of cyanobacteria appeared to be a valuable method to investigate the light history and hence their entrainment in the turbulent flow in the water column.

Introduction

In storage reservoirs for drinking water supply, cyanobacteria can be a nuisance because of taste and odour problems (Jüttner et al., 1986) and the possible occurrence of toxicity (Lawton & Codd, 1991). A method to reduce algal growth in reservoirs is mixing of the water column (Steel, 1972). Because of deep mixing, the phytoplankton receives less irradiance, which will result in a lowered growth rate. This would be especially effective in reducing the growth of *Microcystis* since deep mixing takes away the specific competitive advantage that large colony-forming cyanobacteria have in partially stable water columns. Ibelings et al. (1991b) described how *Microcystis* used its buoyancy (derived from gas vacuoles) to concentrate

its biomass in the illuminated near-surface mixed layer of a lake, the depth of which varied on a diel time scale. Non-buoyant algae, such as green algae and diatoms, are favoured by deep mixing because of reduced sedimentation losses. Reynolds et al. (1984) found that artificially mixing of large limnetic enclosures arrested growth of *Microcystis*. Reduction of growth of *Microcystis* in an artificially mixed lake has been described by Toetz (1981). Not only will it no longer benefit from its buoyancy controlled vertical positioning, but *Microcystis* also showed a poor acclimation to light regimes simulating those induced by mixing in lakes (Ibelings et al., 1994).

In spite of circulation of the drinking water reservoir De Gijster (Water Storage Corporation Brabantse Biesbosch, The Netherlands), *Microcystis* occasional-

ly still reaches high densities (with a chlorophyll maximum of 60–100 $\mu\text{g l}^{-1}$). Although growth of *Microcystis* is probably not maximal in the reservoir, it is still a nuisance. We tried to explain why growth still occurred in spite of artificial mixing.

One hypothesis that could explain growth of *Microcystis* in the reservoir is that the vertical mixing velocity in the reservoir is lower than the flotation velocity of *Microcystis*. This may enable the *Microcystis* colonies to counter the mixing and so remain in the upper, illuminated layers. In order to keep the buoyant *Microcystis* in suspension, the artificial mixing velocity should exceed the flotation velocity of the cyanobacterium. The mixing velocity needs to be rather high as the maximal vertical velocity of *Microcystis* can be as high as 2.6 m h^{-1} (Visser, 1995); 8.3 m h^{-1} (Humphries & Lyne, 1988) or 10.8 m h^{-1} (Reynolds et al., 1987). This variety of velocities mainly results from differences in the radius of the colonies. Many colonies have a much smaller radii than those with the maximal velocity and the average sinking velocity may be lower (0.11 m h^{-1} ; Visser, 1995).

A second hypothesis is that the shallow area at the edge of the reservoir (35% of the total area) permits growth of *Microcystis*. As the mixing device is situated in the deep part (Figure 1), it is possible that the surrounding shallow part is mixed insufficiently, allowing *Microcystis* to benefit from its buoyancy. But even when the mixing is sufficiently high in both the deep and the shallow part, differences in growth rate between the two parts may still occur as the light dose received by the homogeneously mixed phytoplankton will be higher in the shallow areas.

To investigate these hypotheses, temperature profiles at two sites in the reservoir were measured in order to detect possible density gradients. The vertical distribution of *Microcystis* colonies and other phytoplankton was determined to test whether they were distributed homogeneously through the water column. But even with an apparently homogeneously mixed column, a gradient of biological activity can exist as described by Gibson (1978b), who measured a gradient in carbohydrate content of phytoplankton in a 'well-mixed' lake. Gibson (1978a) found a higher carbohydrate content in the mixed layer only. Carbohydrates as biological indicator of water movement were also tested by Oliver & Kromkamp (1987). They found a vertical and horizontal variation in the carbohydrate-protein ratio which reflected the circulation pattern in the lake. With carbohydrate measurements on field samples no distinction can be made between the carbohydrate con-

tent of different kind of phytoplankton groups. Since in our study only cyanobacteria were of interest, the buoyancy state was determined rather than carbohydrates. A negative correlation between carbohydrate content and buoyancy has been demonstrated before (e.g. Kromkamp & Mur, 1984; Van Rijn & Shilo, 1985; Ibelings et al., 1991b). Ibelings et al. (1991a) found a significant correlation between the degree of buoyancy loss and the total daily light dose received by *Microcystis*. The buoyancy state of *Microcystis* colonies in the reservoir can thus serve as an indicator for the efficiency of the mixing. A high buoyancy loss, the result of a high received light dose, would indicate that the turbulent flow was insufficient to keep *Microcystis* in suspension.

The diurnal changes of the variables described above and the photosynthetic activity were followed during two days in 1991 and one day in 1993 at two sites in the reservoir.

Description of sites studied

De Gijster reservoir is situated in the south-west part of The Netherlands and has a surface area of 305 ha. The reservoir (maximum depth 28 m; mean depth 13 m) consists of a deep central part surrounded by a relatively shallow part (depth 4–6 m) as is shown in Figure 1. The six air injection units, which provide the circulation, are situated in the deep part. The average velocity of the upward water flow is estimated on 0.3 m h^{-1} ; the velocity of the downward flow is dependent on the distance from the injection units. Sampling site 1 was situated in the shallow part (4 metres on day A and B, 5.5 metres on day C) and site 2 in the deep (28 meter) part of the reservoir (Figure 1).

Materials and methods

Sampling scheme and measurements

Temperature at different depths was measured continuously with calibrated thermistors at two locations between 16 August and 15 November 1993. Temperature was measured every second. Every 10 minutes the average of the measurements was calculated and stored in a datalogger (Campbell CS-CR-10).

Samples were taken at different depths during two days in 1991 (August 28th and 29th) and one day in

Figure 1. Map of storage reservoir De Gijster in which the sampling sites 1 and 2 and the six air injection units (providing the circulation in the reservoir) are indicated. A cross-section of the reservoir between A and B is also shown.

1993 (September 7th) from sunrise till sunset. The days will be named day A, B and C respectively.

Temperature profiles were measured with a calibrated WTW-sensor. The turbulent friction velocity u_* was calculated as described by Denman & Gargett (1983):

$$u_*^2 = (\rho_a C U^2) / \rho_w \quad (1)$$

where C is the drag coefficient ($1.3 \cdot 10^{-3}$), ρ_a and ρ_w are the densities of air (1.2 kg m^{-3}) and water (998.2 kg m^{-3}), respectively, and U is the mean windspeed. Data on wind velocity and total daily irradiance at the nearest weather station Cabauw were provided by the Royal Dutch 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 (W) reached unity, as described by Imberger & Hamblin (1982):

$$W = g \Delta \rho z^2 / u_*^2 \rho_w L \quad (2)$$

where g is the gravitational acceleration (9.8 m s^{-2}), $\Delta \rho$ the difference between the density of water at depth z and at the surface, ρ_w the average density of water (998.2 kg m^{-3}) and L the length of the fetch (the distance in metres between the shores of the reservoir measured in the direction of the wind).

Profiles of photosynthetically-active photon irradiance (PAR) were measured with a Li-Cor light meter with a Li 192 B quantum sensor, from which the average light attenuation coefficient (k) was calculated according to Lambert's-Beer's law:

$$I_z = I_0 e^{-kz} \quad (3)$$

in which I_0 is the light intensity at the surface and I_z is the light intensity at depth z . The depth of the euphotic zone was defined as the depth where the light intensity reached 1% of the surface intensity. The total light dose received by homogeneously mixed phytoplankton through the mixed layer of depth z on a given day was calculated as the mean irradiance (I_m) in that layer according to Van Liere & Walsby (1982):

$$I_m = (I_0 - I_z) / \ln(I_0 / I_z) \quad (4)$$

The received light dose till the time of the day that the buoyancy loss reached the highest value of that day was calculated. Therefore the light dose at the surface till this time on a given day was taken as I_0 . With this value and the light attenuation coefficient, the light intensity at depth z was calculated (eqn 3). As depth of

the mixed layer (z), the depth of the water column at site 1 was taken (4 metres on day A and B, 5.5 metres on day C); at site 2 the average calculated mixing depth was used.

Samples for determination of the buoyancy state of the colonies were concentrated with a net with mesh size $55 \mu\text{m}$ (August 28 and 29, 1991) and $20 \mu\text{m}$ (September 7, 1993). The percentages of floating and sinking colonies were determined by counting the colonies in small counting chambers (depth 3 mm) after standing for 5 min. Buoyancy can be affected by nutrient limitation (Klemer, 1991), but in eutrophic reservoirs like De Gijster such limitation can be excluded.

The photosynthesis-irradiance relationship (PI-curve) was determined from rates of oxygen production at various irradiances in a system described by Dubinsky et al. (1987). The photosynthetic efficiency was calculated as the initial slope of the photosynthesis-irradiance curve between 10 and $40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ with linear regression. The maximal oxygen production rate was taken as the maximal photosynthetic capacity (P_{max}). Prior to the measurements, surface samples were concentrated about 20 times with a net with mesh size $20 \mu\text{m}$. For protein and chlorophyll measurements, subsamples were filtered on glass fibre filters (GFF) and stored in a freezer. Protein was analysed with the Lowry method (Herbert et al., 1971) with bovine serum albumin as standard. Chlorophyll a was estimated spectrophotometrically, after extraction in dimethyl formamide at 664 nm. The extinction coefficient described by Volk & Bishop (1968) was used for calculations.

On 23 September 1994, a sample, concentrated in a plankton net of mesh-size $20 \mu\text{m}$, was taken from the surface at each of the sampling sites late in the afternoon. The samples were stored on ice and analysed the next morning. The percentage of colonies sinking (counted as described before) and the total number of *Microcystis* colonies was counted in a Sedgewick-Rafter chamber. The gas vesicle volumes of both samples was determined in a capillary compression tube (Walsby, 1982) using the method of Oliver & Walsby (1988).

Biomass determination

On the sampling days in 1991 (day A and B), samples were about $100 \times$ concentrated by filtration over a $55 \mu\text{m}$ net and preserved in 4% formaldehyde. The biomass of *Microcystis* in these concentrates was measured by use of an Optical Plankton Analyser (Depart-

Table 1. The number of 10 minutes periods (in the period 16 through 23 August 1993), in which a given temperature difference between 0.5 and 2 m was measured. Between brackets the number of days, when these temperature differences occurred.

	Number of 10 minutes periods	
	Site 1	Site 2
$\Delta T > 0.1^\circ\text{C}$	235 (7 days)	213 (6 days)
$\Delta T > 0.3^\circ\text{C}$	122 (5 days)	121 (5 days)
$\Delta T > 0.5^\circ\text{C}$	65 (2 days)	71 (3 days)

ment of Aquatic Ecology, University of Amsterdam). This flowcytometer was specially designed for phytoplankton counting (Dubelaar et al., 1989). On basis of the optical characteristics of the phytoplankton, a distinction can be made between different plankton groups (Balfoort et al., 1992). *Microcystis* could be distinguished from other algae on the basis of its phycocyanin-related fluorescence and its strong perpendicular light scattering. From this selection of the phytoplankton the chlorophyll a related fluorescence (FBR = fluorescence blue to red) was calculated and taken as a measure for biomass.

The samples for biomass determination on the sampling day in 1993 (day C) were pressurised at 1 MPa (to collapse the gas vesicles of cyanobacteria) fixed with formaldehyde (4%) and concentrated by means of sedimentation. From these concentrates, the number of *Microcystis* and the most abundant other phytoplankton, centric diatoms, were counted microscopically using a Sedgewick-Rafter chamber.

Results

Stability

The number of periods of 10 minutes (in the rather sunny period 16 through 23 August 1993), in which a temperature difference exceeding 0.1°C between 0.5 and 2 m was measured, are shown in Table 1. The frequency of periods with a temperature difference of $>0.1^\circ\text{C}$ and $>0.3^\circ\text{C}$ was a little higher at site 1 than at site 2.

Table 2 gives calculations of the Wedderburn number at 4 metres depth. This number is an indication for stability of the water column. The Wedderburn number was smaller than 1 throughout the whole water column at site 1, indicating an unstable water column

Table 2. Data on the wind velocity, the vertical mixing velocity u_* (calculated on basis of wind velocity), temperature difference ΔT between the surface and 4 metres depth and the Wedderburn number W at 4 m at both sites on the three sampling days at different times of the day. The mixing depth Z_m at site 2 is calculated as the depth where the Wedderburn number reached unity.

Time of day (h)	Wind velocity (m s ⁻¹)	<i>u</i> _* (m s ⁻¹)	Site 1	Site 1	Site 2	Site 2	Site 2
			ΔT (°C) (0–4 m)	<i>W</i> (4 m)	ΔT (°C) (0–4 m)	<i>W</i> (4 m)	<i>Z</i> _m (m)
Day A							
13.15	3.5	0.0044	0.4	0.513	0	0	17
16	5.5	0.0069	0.1	0.052	0	0	17
19.15	6.5	0.0081	0	0	0	0	18
Day B							
12	4.5	0.0056	0	0	0	0	14
14.45	3	0.0038	0.1	0.17	0	0	9
17.30	3.5	0.0044	0.1	0.13	0	0	12
20.30	3.5	0.0044	0	0	0	0	14
Day C							
13	4.6	0.0058	0.1	0.062	0.1	0.024	18
15.30	2.6	0.0033	0.2	0.196	0.2	0.154	9
18	3.1	0.0039	0.2	0.137	0.1	0.054	12
20.30	4.1	0.0051	0	0	0	0	18

Table 3. The total light dose at the surface ($\text{MJ m}^{-2} \text{ day}^{-1}$), the calculated depths of the euphotic zone (Z_{eu} in m) and the calculated light dose received by the phytoplankton till the time of the day that the percentage of colonies sinking reached the highest value of that day if the phytoplankton was homogeneously mixed over the entire water column at site 1 (4 m on day A and B, 5.5 m on day C) and over the average calculated mixing depth at site 2 on the three sampling days.

day ⁻¹)	Total light dose at the surface (MJ m^{-2})	Site 1 Z_{eu} (m)	Site 2 Z_{eu} light (MJ m^{-2})	Site 1 received light dose (MJ m^{-2})	Site 2 received dose (MJ m^{-2})
Day A	13.59	9.6	10.1	5.9	1.1
Day B	21.11	7.4	8.1	7.1	2.7
Day C	18.05	5.4	6.4	3.7	1.3

and complete mixing. (Only the values in the afternoon are given, because in the morning the temperatures at the surface were lower than deeper in the water column, which gives a negative Wedderburn number.) At site 2, the Wedderburn number reached unity between 7 and 18 metres. In Table 2, the turbulent friction or shear velocity u_* is also given for the different sampling times. The mean turbulent velocity of the mixed layer,

Figure 2. The distribution of *Microcystis* colonies, expressed as chlorophyll related chlorophyll *a* FBR ml^{-1} (= fluorescence blue to red) or colonies ml^{-1} , through the water column at three sampling days at site 1 and site 2 at different times of the days: at sunrise (●) 7.00 at day A and B; 6.30 at day C and in the afternoon (*) 19.00 at day A; 17.30 at day B; 18.00 at day C. (l) site 1 day A; (b) site 1 day B; (c) site 1 day C; (d) site 2 day A; (e) site 2 day B and (f) site 2 day C.

$u_t \approx 2 u_*$, can be used to compare with the flotation or sinking velocity of the phytoplankton (Reynolds, 1992).

On all days this velocity was higher than the maximal flotation velocity of *Microcystis* ($2.6 \text{ m h}^{-1} = 0.00072 \text{ m s}^{-1}$ determined on samples from Lake Nieuwe Meer, Amsterdam, Visser, 1995), despite the rather calm weather on the sampling days with an average wind velocity of 3.8 m s^{-1} on day A, 3.4 m s^{-1} on day B and 4.0 m s^{-1} on day C. The shear velocities are calculated from the wind velocities only, although in reality artificial mixing will have increased the velocity of the vertical flow.

Biomass distribution

If *Microcystis* flotation velocity exceeds the vertical mixing velocity, it will be able to disentrain and concentrate its biomass in the upper layers. From the calculations on the vertical velocities of mixing and flotation, it is expected that the colonies are distributed homogeneously throughout the mixed layer. In Figure 2, the biomass distributions at sunrise and late afternoon are shown for the three sampling days at both sampling

sites. It can be expected that accumulation of colonies at the surface is more pronounced at sunrise, when a larger proportion of colonies is buoyant (Ibelings et al., 1991b); during the day colonies lose buoyancy which makes interpretation of biomass profiles more difficult. However, no pronounced concentration in the upper layers was found either at sunrise or late in the afternoon.

On day A and B, the distribution of other phytoplankton than *Microcystis* was more or less homogeneous in the water column. On day C, only centric diatoms were counted as most abundant non-buoyant phytoplankton and these also showed a homogeneous depth distribution (data not shown).

The average number of centric diatoms at all depths and sampling times was higher at site 1 (149.4 ± 64.2 cells per ml) than at site 2 (53.2 ± 6.0 cells per ml) on day C. The average number of *Microcystis* was not different: 14.3 ± 3.7 colonies per ml at site 1 and 13.0 ± 3.4 colonies per ml at site 2.

Buoyancy

In the afternoon of day A and B, a large difference between the two sites was found in percentage of colonies sinking (Figure 3); on day C this difference was somewhat smaller. More colonies were sinking at the shallow site 1 than at the deep site 2. In Table 3, the calculated received light dose of the phytoplankton is given till the time of the day that the percentage of colonies sinking reached the highest value of that day. The calculations are made for mixing over the entire depth at site 1 and the average calculated mixing depth at site 2. A significant positive correlation was found between the received light dose and the maximum percentage of colonies sinking ($r^2 = 0.95$, $n = 5$, $p < 0.02$) when the value at site 2 on day C is excluded (Figure 4).

On day C, at the end of the afternoon, the percentage of colonies sinking decreased with depth at both sites as is shown in Figure 5. On day A and B, this pattern with depth was absent at both sites. To investigate if the difference in buoyancy between the two sampling sites was the result of a difference in carbohydrate content or in gas vesicle volume, samples were taken in the afternoon on 23 September 1994. Again a difference in percentage of colonies sinking between the two sites was found: 45% of colonies sinking at site 1 and 27% at site 2. The gas vesicle volumes, however, were not different: $2.13 \pm 0.31 \text{ nl}$ per *Microcystis* colony at site 1 and $2.03 \pm 0.14 \text{ nl}$ per colony at site 2.

Figure 3. Diurnal changes in percentage of colonies sinking at site 1 (■) and site 2 (▲) at day A (a), day B (b) and day C (c). Every value is an average of values of samples from 0, 0.5, 1, 1.5 and 2 metres depth at site 1 and from 0, 0.5, 1, and 2 metres depth at site 2. The error bars represent the standard errors of the mean. The total insolation per hour at the surface is also shown (○).

Figure 4. The relation of the maximum percentage of colonies sinking at the sampling days with the received light dose (till the time of maximum buoyancy loss) that was calculated for homogeneously mixed phytoplankton over 4 metres (day A and B) or 5.5 metres (day C) depth at site 1 and over the average calculated mixing depth at site 2. The value at site 2 on day C (□) is excluded in the regression.

Figure 5. The percentage of colonies sinking plotted against depth at site 1 (a) and at site 2 (b) at 18.00 on day C.

Table 4. The photosynthetic efficiency of α ($\mu\text{g O}_2 \text{ h}^{-1} \text{ mg}^{-1} \text{ chl } \mu\text{mol}^{-1} \text{ photons m}^2 \text{ s}$) and the maximum photosynthetic rate P_{max} ($\text{mg O}_2 \text{ h}^{-1} \text{ mg}^{-1} \text{ chl}$) on basis of chlorophyll *a* on two sampling days at different times of the day at two sampling sites.

	Site 1 α/chl	Site 2 α/chl	Site 1 $P_{\text{max}}/\text{chl}$	Site 2 $P_{\text{max}}/\text{chl}$
Day A at 4 p.m.	46.6	62.4	19.8	12.0
Day B at 9.30 a.m.	59.2	55.2	16.0	12.0
Day B at 2.45 p.m.	66.7	40.1	17.1	10.0

Photosynthesis

In Table 4, the maximal photosynthetic capacity and photosynthetic efficiency per chlorophyll *a* from measurements on day A and B are shown. The photosynthetic capacity in all measurements was higher at site 1 than at site 2, whereas the photosynthetic efficiency was more or less the same at both sites.

On day C, photosynthesis measurements were performed almost every two hours. The photosynthetic capacity was more or less the same at both sites (Figure 6). The photosynthetic efficiency at site 1 was usually lower than at site 2. The photosynthetic parameters decreased during the day.

Figure 6. Changes of the maximum photosynthetic capacity (a) and the photosynthetic efficiency (b) on basis of chlorophyll *a* in samples from site 1 (■) and site 2 (▲) on day C.

Discussion

On the sampling days, the two parts of the reservoir could be considered as two different systems with restricted horizontal mixing, as buoyancy changes during the day and photosynthetic characteristics were different at sites 1 and 2.

During a rather sunny period in August, the number of periods with a temperature difference between 0.5 and 2 m was only a little lower at site 2. On the sampling days, the stability according to the calculated Wedderburn numbers at 4 metres was also a little lower at site 2. A lower stability was expected at site 2 because this site is situated in the deep middle part of the reservoir, where the air injection blocks provide artificial mixing. However, at site 1 the calculated Wedderburn numbers showed mixing over the entire depth of the water column.

The biomass of *Microcystis* was mostly homogeneously distributed at both sites, which was to be expected since the calculated turbulent velocities exceeded the maximum flotation velocity of *Microcystis*. Most articles in which the diurnal changes in the vertical distribution of *Microcystis* is described, show

a concentration of biomass in the upper layers at sunrise during periods of calm weather (Reynolds, 1973; Ganf, 1974; Konopka et al., 1978; Sirenko & Kokyrtsa, 1981; Takamura & Yasuno, 1984; Ibelings et al., 1991b). We did not observe this in our study (Figure 2). Apparently, artificial mixing in the reservoir was sufficient to mix *Microcystis* homogeneously. The homogeneous distribution and the small increase in percentage of colonies sinking at the deep site makes it improbable that growth of *Microcystis* was enabled by an insufficient mixing velocity. The calculated mixed layer did not exceed 18 metres on the sampling days while the depth of the reservoir has a maximum depth of 28 metres. The difference between mixing depth and real depth might have caused sedimentation of centric diatoms, since the concentration of diatoms was three times higher at the shallow site than at the deep site. This can be advantageous for *Microcystis* in the competition for light in the deep part of the reservoir.

The number of colonies sinking increased during the day was higher at the shallow site than at the deep site. This was the result of the shallow depth rather than a higher stability. Colonies mixed over 4–5.5 metres only received a higher light dose than the colonies mixed over the greater depth at site 2 (Table 3). A positive correlation was found between the calculated received light dose for homogeneously mixed colonies and the maximum percentage of colonies sinking (the value of site 2 on day C excluded in the calculation). A correlation between buoyancy loss and the mean irradiance experienced by the colonies within the surface mixed layer was also found by Ibelings et al. (1991a). Our results can be interpreted in the perspective of studies by Gibson (1978a, b) and Oliver & Kromkamp (1987), who used the amount of carbohydrate as an indicator of water movement. The higher carbohydrate accumulation in the shallow part of the reservoir will result in a higher growth rate according to Foy (1983), who found a linear relationship between these two parameters. It can be concluded that the large shallow part of the reservoir allows growth of *Microcystis*. These results, however, do not offer an explanation for the competitive advantage of *Microcystis* upon other phytoplankton in this shallow part. The homogeneous distribution of the non-buoyant phytoplankton shows that they should equally benefit from the higher light dose.

The buoyancy loss at site 2 on day C did not fit in the correlation of maximum buoyancy loss and received light dose as was found for the other data (Figure 4). The buoyancy loss at site 2 on day C was higher than

expected from the received light dose if the phytoplankton were homogeneously mixed over the calculated mixing depth. Probably, this was caused by shallower mixing as a result of a little higher stability on day C, although the mixing depth at site 2 was still rather high (Table 2). An important difference, that might explain a higher stability on day C, was the late start of the artificial mixing. After some days without mixing, it was started on day C at about 10 a.m. The mixing on day A and B had been in operation for a couple of days already. The wind velocities on day B and C were comparable but the average wind velocities prior to the sampling days were different: 3.2 ms^{-1} during 24 hours before sunrise at day B and 1.9 m s^{-1} during 24 hours before sunrise on day C. This may further explain a difference in stability.

Shallower mixing as a result of the higher stability is reflected in the decrease in percentage of colonies sinking with depth at both sites on day C (Figure 5), while this decrease with depth was absent on the other days. A proportion of the colonies were apparently mainly mixed in the upper layer and hence received a higher light dose. But one would expect floating colonies of *Microcystis* to concentrate in the upper-mixed layer under these conditions. No evidence for this was found. Mixing in the upper layer can explain the higher loss of buoyancy at site 2 on day C compared to day A and B. On basis of the decrease with depth of the percentage of colonies sinking at site 1 on day C, a higher stability was apparently also the case at this site although a higher loss of buoyancy than on the other days was not very pronounced. It can be concluded that without artificial mixing part of the *Microcystis* population was able to extend its stay in the upper part of the reservoir and to synthesise more carbohydrates and consequently grow faster. This can still be the case when the artificial mixing is combined with only a very low wind velocity, but this will generally not be very important as these calm weather conditions do not occur often.

The explanation of shallower mixing at site 2 on day C for the higher observed buoyancy loss is also supported by the differences in the photosynthetic characteristics between the sampling days. On day A and B, a higher photosynthetic capacity was found at site 1 than at site 2. A higher photosynthetic capacity results from an acclimation of *Microcystis* to a higher growth irradiance, together with a lower photosynthetic efficiency and a lower chlorophyll *a* content per cell (Raps et al., 1983). This is in agreement with the higher calculated received light dose and the higher loss of buoyancy at

site 1. On day C, however, the photosynthetic capacity was more or less the same for both sites. This can be explained by a higher received light dose by the population at site 2 due to shallower mixing, as was also indicated by a higher buoyancy loss during the day at this site compared to day A and B.

Determination of the buoyancy state of cyanobacteria appeared to be a good method to investigate the light history of cyanobacteria. These determinations are more specific for cyanobacteria than carbohydrates since they exclude non-buoyant phytoplankton. This gives an indication of the growth rate of cyanobacteria at different parts of a reservoir or lake. Stability indication on basis of temperature profiles and biomass distribution is not sufficient to predict the entrainment of *Microcystis* in the turbulent flow. Gibson (1978b) also demonstrated that in an apparently homogeneously mixed lake (according to small differences with depth in chlorophyll, dissolved oxygen and temperature), a gradient of carbohydrate content can exist. Our results also show that determination of the buoyancy state can distinguish between different degrees of stability. This might be an interesting tool for investigating the stability and hence the entrainment of *Microcystis* in the turbulent flow at different spots in a deep lake.

Conclusions

It can be concluded from the results that the large shallow area in the reservoir allows growth of *Microcystis*. The shallow mixed part of the population received a higher daily light dose and could synthesise more carbohydrate during the day (high loss of buoyancy) which will have resulted in a higher growth rate than in the deep part of the reservoir. The higher daily light dose received by the phytoplankton in the shallow part was not caused by a higher stability as mentioned in one of the hypothesis in the introduction. Also the mixing in the deep site seemed under most circumstances to be sufficient to keep *Microcystis* entrained in the turbulent flow. The results on day C, however, showed a higher buoyancy loss than could be expected from the calculated received light dose for homogeneously mixed colonies. Furthermore, the photosynthetic capacity was similar at both sites on day C, while this was lower on the deep site than on the shallow site on the other days. Both results indicate that, due to the late start of the artificial mixing compared to the other days, entrainment was not complete at the deep site

and the colonies received a higher light dose than on the other days.

Determination of the buoyancy state of the *Microcystis* colonies appeared to be a valuable method for investigating the light history of the phytoplankton, which is determined by the mixing through the water column. A significant correlation between the maximum buoyancy loss and the calculated received light dose for homogeneously mixed colonies was found. Determination of the buoyancy state is of more restrictive application than carbohydrate measurements since only cyanobacteria with gas vesicles can be investigated. The results suggest that a distinction between sites with a different extent of stability in a deep lake will be possible on basis of differences in buoyancy state, which cannot be shown by vertical distribution of the colonies or temperature profiles.

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