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Aquatic Sciences

Simulation of vertical position of buoyancy regulating *Microcystis aeruginosa* in a shallow eutrophic lake

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ABSTRACT

Vertical distributions of the cyanobacterium *Microcystis aeruginosa* are examined in a shallow lake in relation to mixing and thermal stratification over three days. A model of buoyancy regulation by *Microcystis aeruginosa,* applicable for turbulent environments, is coupled with a one-dimensional hydrodynamic model. The coupled model is applied to Thomsons Lake in Western Australia to examine the relationship between buoyancy regulation and the daily stratification/destratification cycle. The vertical distribution of *Microcystis aeruginosa* in Thomsons Lake depends on the carbohydrate ballast dynamics and the colony size. When thermal stratification occurs, all the simulations show a similar general pattern of diurnal vertical migration of the *Microcystis aeruginosa* colonies. The colonies accumulate at the surface during the night and in the morning the colonies lose buoyancy, which leads to a reduction by ~ 50 % in colony concentration in the top 0.2–0.3 m of the water column. Afternoon winds redistribute the population over the entire water column. When the lake is fully mixed, the vertical migration pattern of the *Microcystis aeruginosa* colonies may be affected, depending on the colony size and the intensity of the mixing.

Introduction

Phytoplankton communities of shallow eutrophic lakes are often dominated by cyanobacteria (e.g. Reynolds, 1973a, b; Ganf, 1974; Takamura and Yasuno, 1984a). The dominance of cyanobacteria may be attributed to one or more potentially important physiological adaptations to the conditions in shallow eutrophic lakes (Reynolds, 1973b; Reynolds et al., 1987). A potentially advantageous adaptation of some cyanobacteria is the ability to regulate depth within the water column. Depth is regulated through physiological changes, in response to changing environmental conditions that alter cell buoyancy, behaviour that is commonly referred to as buoyancy regulation (Reynolds, 1984). Buoyancy regulation may provide a

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means of overcoming the vertical separation between light and nutrients that often occurs in stratified lakes (Ganf and Oliver, 1982). Buoyancy regulation may also allow access to high irradiance near the water surface while providing a means of migrating downwards to lower irradiances to avoid photoinhibition.

Buoyancy regulation can occur through three mechanisms that may operate together or independently. The first is by collapse of gas vesicles under rising turgor pressure (Walsby, 1971; Dinsdale and Walsby, 1972; Reynolds and Walsby, 1975). It is doubtful, however, that gas vesicle collapse is responsible for buoyancy regulation in most natural populations (Walsby, 1994). Many species (e.g. *Microcystis aeruginosa*) have gas vesicles that are too strong to be collapsed by turgor or hydrostatic pressures (Utkilen et al., 1985; Kromkamp et al., 1986; Thomas and Walsby, 1986). The two mechanisms most likely to occur in natural populations of cyanobacteria are regulation of gas vesicle synthesis (Walsby, 1970, 1971; Utkilen et al., 1985; Kromkamp et al., 1986) and cell ballast (Oliver and Walsby, 1984; Thomas and Walsby, 1986; Kromkamp et al., 1988). Regulation of cell ballast is the mechanism responsible for the frequently observed pattern of cyanobacterial populations accumulating near the surface during the night and early morning and then sinking away from the surface during late morning and the afternoon (Van Rijn and Shilo, 1985).

The position of cyanobacteria cells or colonies in the water column depends on both the buoyancy of the cyanobacteria and the water motions. In shallow lakes that are regularly exposed to moderate to strong winds, the mixing regime may alternate between periods of thermal stratification and complete lake mixing in a single day (Bailey and Hamilton, 1997). The effect of turbulence on the vertical migration of cyanobacterial populations will depend on the size and shape of the organism and the control that a species has over buoyancy (Reynolds, 1984). The objective of this study is to examine, over time scales of hours and days, vertical position of the cyanobacterium *Microcystis aeruginosa* in relation to the mixing and thermal stratification in a shallow lake. A model of buoyancy regulation in *Microcystis aeruginosa* that is applicable for turbulent environments (Wallace and Hamilton, 1999) is coupled with a one-dimensional hydrodynamic model, DYRESM (Imberger, 1985). The coupled model is applied to Thomsons Lake in Western Australia to examine the relationship between buoyancy regulation and the daily stratification/destratification cycle.

Method

Field Data

Field data was collected at Thomsons Lake, a shallow (max. depth ≈ 1.4 m), flat bottomed and roughly circular lake (Fig. 1). The lake is 20 km south of Perth, Western Australia and is primarily a surface expression of the groundwater table, although it is also fed by inflows that enter the lake through the surrounding rush beds. Thomsons Lake is considered to be meso-eutrophic (Cheal and Davis, 1994). Blooms of *Microcystis aeruginosa* and *Anabaena circinalis* have been recorded over the spring-summer period (Bailey and Hamilton, 1997).

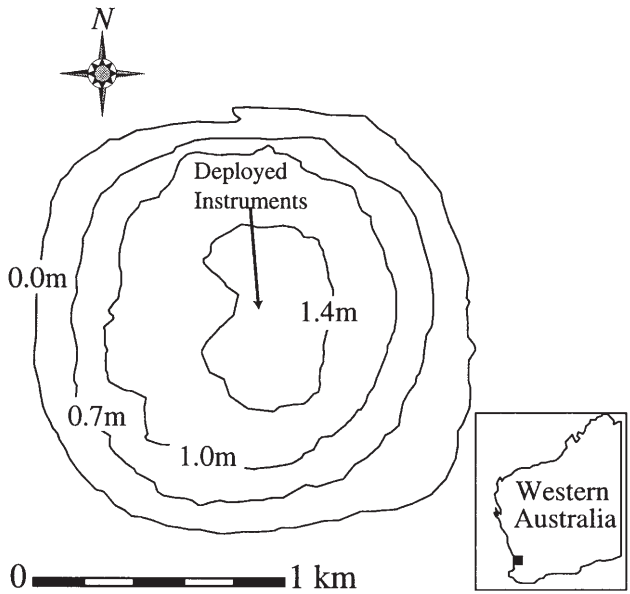

Figure 1. Location and bathymetry of Thomsons Lake, and the location of the instrument support platform

An anemometer, a thermistor chain, two light meters and a fluorometer were deployed from a small platform (location shown in Fig. 1) in 1.4 m of water on 16, 17 and 18 November 1994. The thermistor chain consisted of four Fastip Thermoprobe (series FP10) thermistors secured at distances of 0.15 m, 0.5 m, 0.9 m and 1.35 m from the lake bed. Wind speed was measured with a Pacific Data Systems wind speed (WS100) sensor at a height of 2.5 m. The wind speed measurements were later converted to 10 m values according to the equations of CERC (1994). Fluorescence was measured with a Sea Tech Inc. fluorometer. The fluorometer was positioned at a depth of 0.2 m and was calibrated using acetone extraction of chlorophyll *a* pigment (Strickland and Parsons, 1972). Photosynthetic irradiance (wavelength 400–700 nm) was measured with two Dataflow Systems Terrestrial Cosine Sensor light loggers mounted underwater at depths of 0.3 m and 1.0 m. The recorded light intensities were used to calculate a bulk light attenuation coefficient between the two depths using Beer's Law. Short wave radiation, percentage cloud cover and atmospheric vapour pressure data recorded at Perth Airport (20 km north-east of Thomsons Lake) were acquired from the Perth Meteorological Bureau. All the data consisted of 15 minute readings.

Buoyancy Regulation Model

In *Microcystis*, diurnal changes in buoyancy occur primarily through changes in carbohydrate ballast (Thomas and Walsby, 1986). A simple empirical buoyancy regulation model for *Microcystis aeruginosa* that is applicable for predicting the vertical

position of colonies in turbulent environments is described in Wallace and Hamilton (1999) as:

$$\frac{dD}{dt} = K_r (D - D_{eq}) \tag{1}$$

where D is the rate of cell buoyancy change through the accumulation of stored cellular carbohydrate, D_{eq} is the equilibrium value of D and K_r is given by:

$$K_r = \begin{cases} -\dfrac{1}{\tau_r} & \text{for increasing light} \\ 0 & \text{for decreasing light} \end{cases} \tag{2}$$

where τ_r is the response time of adjustment of the rate of carbohydrate ballast accumulation (see Table 1 for a complete list of symbols). The advantage of modelling carbohydrate ballast accumulation in the form of equation (1) is that if the response time τ_r is longer than the time scales of the light fluctuations experienced in turbulent mixing, the rate of buoyancy change will be less than the optimal rate D_{eq}. Models that do not include the response time are unlikely to correctly predict the buoyancy of cyanobacteria and their water column position after an episode of mixing (see Wallace and Hamilton, 1999).

The response time was set to $\tau_r = 20$ minutes from the calibration of equation (1) with the measurements of Wallace and Hamilton (1999). However, it is not guaranteed that the 20 minute response time would remain constant during consecutive days of intense mixing. It is likely that the physiological processes involved in the storage of carbohydrate would acclimatise to the changing light conditions. A description of the physiological and biochemical processes necessary to model the acclimation of the response time is not possible with present experimental knowledge. The possibility of acclimation of the response time has been addressed by including simulation results with no response time. The importance of the response time in a model of buoyancy regulation in *Microcystis* can be assessed by comparing the predicted vertical distribution of the colonies with and without the inclusion of the response time.

The form of D_{eq} for *Microcystis aeruginosa* was found by Wallace and Hamilton (1999) to be best described by the equation suggested by Kromkamp and Walsby (1990):

$$D_{eq} = c_1 \frac{I(t)}{K_I + I(t)} - c_3 \tag{3}$$

where c_1 is the rate constant determining the increase in density with time, K_I is the irradiance at which the rate of density increase with time is half the maximal rate and c_3 is the minimum rate of density decrease in the dark. The parameter values for *Microcystis aeruginosa* are $c_1 = 0.0427$ kg m^{-3} min^{-1}, $K_I = 536$ µmol photons m^{-2} s^{-1} and $c_3 = 4.6 \times 10^{-6}$ kg m^{-3} min^{-1} (Wallace and Hamilton, 1999).

The rate of cell buoyancy change in the dark due to a decrease of stored cellular carbohydrate is given by Visser et al. (1997) as

$$D = -c_2 \rho - c_3 \tag{4}$$

Table 1. List of symbols

Symbol	Description	Units
D	Rate of cell buoyancy change	kg m^{-3} min^{-1}
D_{eq}	Equilibrium value of D	kg m^{-3} min^{-1}
K_r	Response time coefficient	dimensionless
τ_r	Response time of adjustment of the rate of carbohydrate ballast accumulation	min
c_1	Rate constant determining the increase in density with time	kg m^{-3} min^{-1}
c_2	Rate constant determining the decrease in density with time	min^{-1}
c_3	Minimum rate of density decrease in the dark	kg m^{-3} min^{-1}
K_I	Irradiance at which the rate of density increase with time is half the maximal rate	μmol photons m^{-2} s^{-1}
q_*	Turbulent velocity scale	ms^{-1}
u_*	Friction velocity scale associated with the surface wind	ms^{-1}
w_*	Turbulent velocity scale associated with convective cooling	ms^{-1}
η_e	Efficiency factor of the mixing efficiency of wind stirring and surface cooling	dimensionless
H	Mixed layer depth	m
t	time	min
z	depth	m
V	Volume of the lake	m^3
r	Colony radius	μm
ξ	Calibration parameter	dimensionless
C	Chlorophyll a concentration	μg chla L^{-1}
V_{cell}	Cell volume	μm^3
V_{colony}	Colony volume	μm^3

where c_2 is set to 1.58×10^{-2} min^{-1} (as per Visser et al., 1997) and ρ is colony density (in kg m^{-3}). Nutrient limitation effects on the rates of carbohydrate ballast accumulation and consumption have not been included in the buoyancy regulation model. Measurements of dissolved inorganic nitrogen and inorganic phosphorus were 910 μgL^{-1} and 15 μgL^{-1} respectively during November 1994 (Bailey and Hamilton, 1997). Thus, the effect of nutrient limitation is assumed to be negligible.

Hydrodynamic Model

The vertical hydrodynamics in Thomsons Lake was simulated with a modified version of the one-dimensional numerical model DYRESM (Imberger et al., 1978; Spigel and Imberger, 1980; Imberger and Patterson, 1981; 1989). DYRESM parameterises all of the major processes associated with the cycle of vertical mixing and

thermal stratification. It is essentially an extension of the Kraus-Turner deepening law (Kraus and Turner, 1967) and describes mixed layer deepening as a function of convective overturn, wind stirring, seiche-induced shear and billowing.

In this study, DYRESM was modified to run using a fixed time step of 15 minutes and meteorological inputs at 15 minute intervals. It was also modified to include a simple random walk model of turbulence for the mixed layer. The turbulent velocity scale q_*, resulting from the mixing induced by wind and surface cooling, is given by:

$$q_* = \left(w_*^3 + \eta_e^3\, u_*^3\right)^{\frac{1}{3}} \tag{5}$$

where u_* is the friction velocity scale associated with the surface wind speed, w_* is the turbulent velocity scale associated with convective cooling and η_e is an efficiency factor that reflects the relative mixing efficiency of wind stirring and surface cooling, (= 1.23 from Imberger and Patterson, 1989). The mixed layer depth H is calculated in DYRESM as a function of the balance between the turbulent kinetic energy, which acts to entrain the heavier underlying fluid into the surface mixed layer, and gravitational potential energy which resists lifting the heavy water (see Imberger et al. (1978) or Spigel and Imberger (1980) for details).

The turbulent velocity field in a shallow lake is composed of a spectrum of velocity scales. These motions have been shown to exhibit large variability and patchiness (Imberger and Ivey, 1991; MacIntyre, 1993) that are not yet easily modelled. However, most of the energy is concentrated at the largest eddy scale (scale of the mixed layer depth H) and at a velocity scale of order q_* (Kitaigorodskii et al., 1983). This feature has been used to construct a simple random walk model of turbulence in the mixed layer of the same form as Patterson (1991) and Patterson et al. (1994). The model is an idealised representation of the turbulent motions, but the approach is still useful in evaluating buoyancy regulation by cyanobacteria.

Results

Fig. 2 shows the measured wind speed, surface insolation, predicted value of q_*, predicted mixed layer depth H and light attenuation coefficient calculated from two measurements of PAR at depths of 0.3 m and 1.0 m. Days 320 and 321 are characterised by calm mornings and windy afternoons. On day 322, strong wind persists for the entire day. The wind profile shown in Fig. 2a is closely matched by the predicted turbulent velocity scale (q_*) shown in Fig. 2c, indicating that surface wind shear is the dominant source of turbulent kinetic energy in Thomsons Lake. Convective overturning from night time cooling of the surface layer was also a significant source of turbulent kinetic energy during the night on days 320 and 321.

A comparison of the predicted and measured thermal structure is shown in Fig. 3. The thermistor data is plotted in Fig. 3a and shows that on Julian days 320 and 321 a diurnal mixed layer is formed as a result of strong morning heating and weak winds (see Fig. 2d). The mixed layers are quickly broken down over approximately 2 hours by the afternoon winds (>2 ms^{-1}) on both days. On day 322 there is no stratification due to the strong wind that persists for the entire day. These data are typical of the thermal stratification dynamics in Thomsons Lake during summer

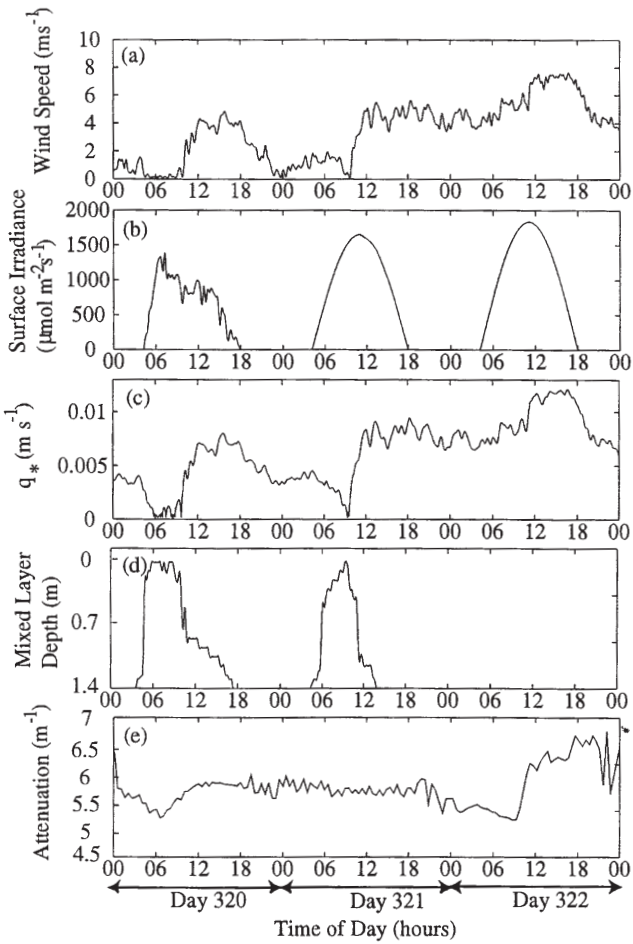

Figure 2. (a) Surface wind speed, (b) surface short wave radiation, (c) q_* calculated by DYRESM, (d) mixed layer depth H calculated by DYRESM and (e) light attenuation coefficient calculated from two measurements of PAR at depths of 0.3 m and 1.0 m

months (Bailey and Hamilton, 1997) and the range of conditions that may typically be experienced by cyanobacteria in Thomsons Lake during summer. The thermal structure calculated by DYRESM (shown in Fig. 3b) accurately captures the pattern of diurnal stratification and complete mixing over the three days. The agreement between the calculated and measured temperature profiles is taken as a strong argument for the validity of q_* and H calculated by DYRESM.

Before the vertical location of colonies in a diurnally stratified system was characterised, the effect of varying the number of colonies tracked in a simulation on the mean colony depth was investigated, using colony sizes of 50 µm, 100 µm, 400 µm and 800 µm. Colonies were initially uniformly distributed over the water column and their densities set to 998 kg m^{-3}. Simulation results were most sensi-

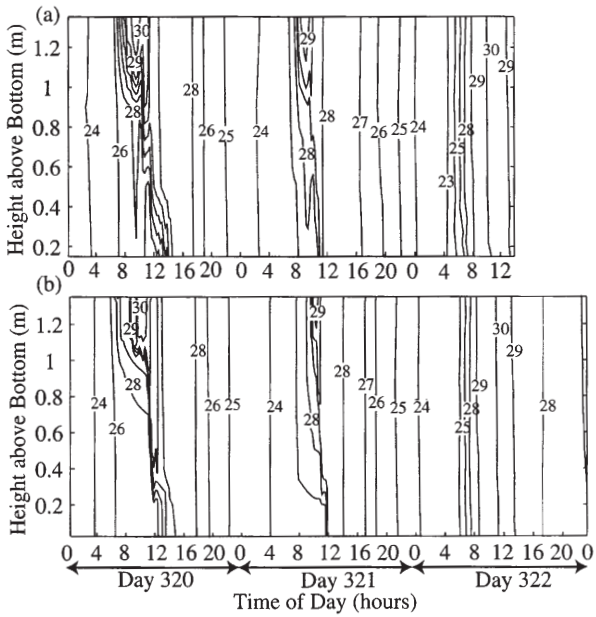

Figure 3. Comparison of (a) thermistor data with (b) predicted thermal structure from the DYRESM simulation for Julian days 320, 321 and 322 in Thomsons Lake, 1994. Note that the thermistor data does not extend over the full three days

tive to the number of colonies simulated when the colony size was set to 50 μm. Fig. 4 shows the sensitivity of the results to the number of colonies simulated for this colony size. When the number of colonies tracked in the simulation exceeds 10^3, there is only a very small difference in the mean colony depth. As a result of the analysis, the number of colonies was set to 1000 for all subsequent simulations.

Comparison between model results and observed chlorophyll *a* concentrations at a depth of 0.2 m (corresponding to the fluorometer depth) is given in Fig. 5. For all simulations, the density was initially set to 998 kg m^{-3} and the colonies were initially uniformly distributed over the depth of the water column. The chlorophyll *a* content corresponding to the number of colonies was determined by assuming that for *Microcystis aeruginosa,* the cellular chlorophyll *a* content is 4.9 μg chla mm^{-3} of cell volume (Reynolds, 1984) and the ratio of cell volume to colony volume (V_{cell}/V_{colony}) is 0.05 (Reynolds, 1984). Thus, the chlorophyll *a* concentration ($C(z)$ in μg chla L^{-1}) at a particular depth (z) within the lake is given by:

$$C(z) = \xi \times \frac{4.9 \times 0.05 \times \frac{4}{3}\pi r^3}{V(z)} \tag{6}$$

where $V(z)$ is the volume of the lake at depth z, the colonies are assumed to be spherical with radius r and ξ is a calibration parameter used to scale the chlorophyll *a* content of the 1000 colonies simulated to the chlorophyll *a* concentration measured in Thomsons Lake.

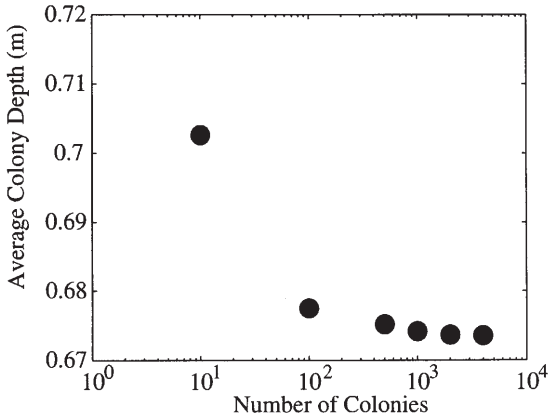

Figure 4. The dependence of the average colony depth on the number of colonies simulated

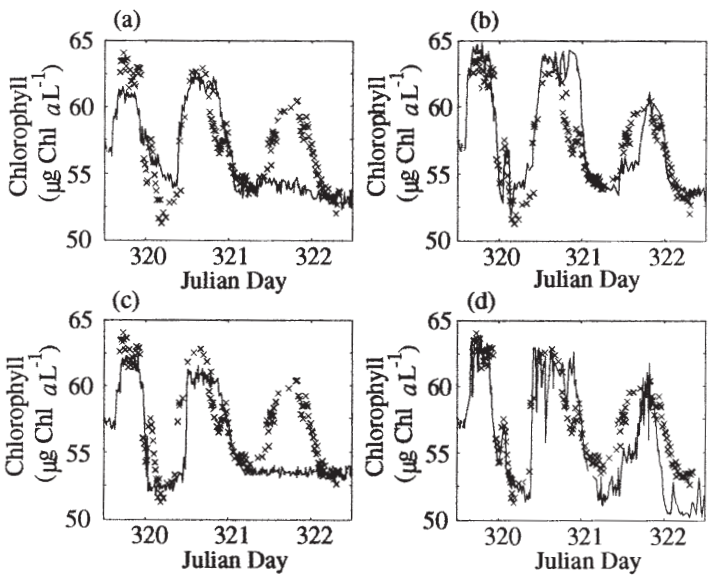

Figure 5. (Measured fluorometric signal at a depth of 0.2 m in Thomson Lake (converted to concentration of chlorophyll *a*) (crosses) plotted with the simulated chlorophyll a concentration at 0.2 m (solid line) with; (a) colony size $r = 100$ μm, response time $\tau_r = 20$ minutes; (b) colony size $r = 400$ μm, response time $\tau_r = 20$ minutes; (c) colony size $r = 100$ μm, no response time; (d) colony size $r = 400$ μm, no response time

Fig. 5 shows that our model is able to reproduce characteristics of the vertical migration of *Microcystis aeruginosa* similar to those observed in Thomsons Lake. In agreement with the fluorometric signal, our model predicts an upward migration during the night and early morning and then a migration away from the water surface during the late morning and afternoon. Figs. 5a and 5c show the results for

the simulations with the colony size set to 100 μm and with a response time of τ_r = 20 minutes and no response time respectively. The 100 μm colonies are able to migrate vertically on days 320 and 321 but on day 322 the intensity of mixing prevents vertical migration. The response time results in a higher average simulated chlorophyll *a* concentration at 0.2 m depth than the simulation with no response time. This is because during mixing, the response time results in a lower net rate of carbohydrate ballast accumulation (see Wallace and Hamilton, 2000). As a result, the colonies with the response time are, on average, more buoyant than the colonies with no response time.

Figs. 5b and 5d show the results for the simulations with the colony size set to 400 μm and with a response time of τ_r = 20 minutes and no response time respectively. For the simulations of the 400 μm colonies there is vertical migration on days 320 and 321 and also on day 322, unlike the 100 μm colonies. The 400 μm colonies were able to migrate vertically on day 322 because the inertial force of the colonies increases with colony size so that large colonies are capable of overcoming the entraining forces of the turbulence. Again, the response time results in a higher average simulated chlorophyll *a* concentration at 0.2 m depth than the simulation with no response time.

The average colony depths have been plotted in Fig. 6 with the mixed region of the water column shaded. Figs. 6a and 6c show that the 100 μm colonies accumulate at the surface during the periods of thermal stratification while Figs. 6b and 6d show that the 400 μm colonies accumulate at the surface before the diurnal

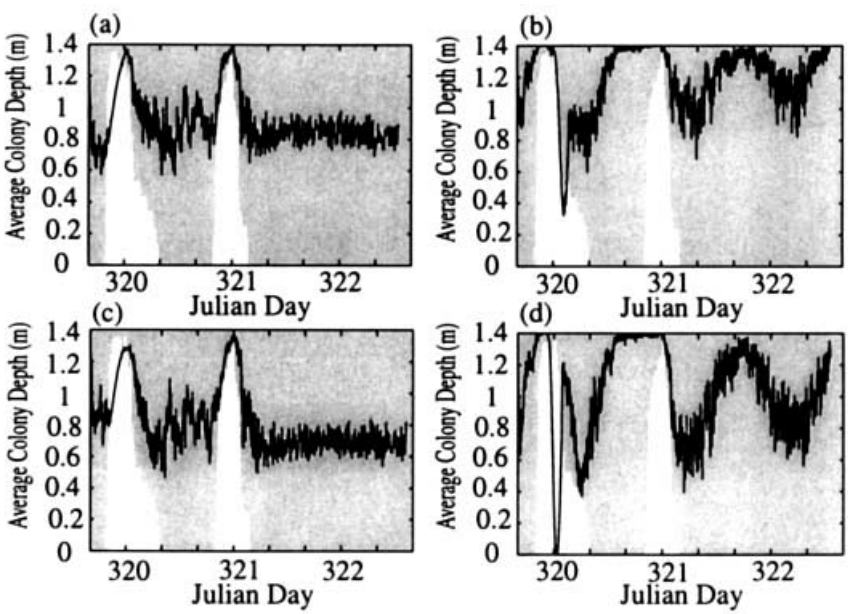

Figure 6. Average colony depth (the mixed layer region is shaded). (a) colony size r = 100 μm, response time τ_r = 20 minutes; (b) colony size r = 400 μm, response time τ_r = 20 minutes; (c) colony size r = 100 μm, no response time; (d) colony size r = 400 μm, no response time

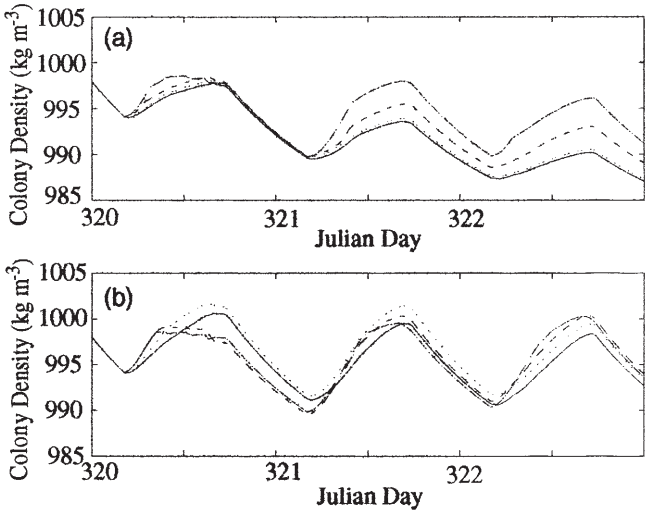

Figure 7. Averaged density variation for colony sizes: 50 μm (solid line), 100 μm (dotted line), 400 μm (dot-dash line), 800 μm (dashed line). (a) Response time τ_r = 20 minutes; (b) no response time

mixed layer forms. The 400 μm colonies lose buoyancy on day 320 and sink away from the mixed layer before the mixed layer deepens as a result of afternoon winds. The average colony depth in simulations with the response time set to 20 minutes was shallower than the average colony depth predicted when there was no response time.

Fig. 7 shows the corresponding density variations for the colonies. The assumption of a response time in the buoyancy regulation model results in a lower average density than that predicted by the model assuming no response time. The effect of the response time is greatest for the smaller colony sizes. The difference between the density predicted by the model assuming a response time and the model assuming no response time decreases as the colony size increases. It is interesting to note that for the simulation with the response time, the 100 μm colonies were always positively buoyant on day 321. Thus, the fluorometric signal is not necessarily due to buoyancy regulation alone but may also be a result of re-entrainment of the colonies away from the surface by the winds.

Discussion

The relationship between the factors controlling the vertical distribution of a population of *Microcystis aeruginosa* in Thomsons Lake show that the distribution depends on the carbohydrate dynamics and the difference in size of the colonies. When thermal stratification occurs, all the simulations show a similar general pattern of diurnal vertical migration of the *Microcystis aeruginosa* colonies. The colonies accumulate at the surface during the night and in the morning the colonies lose buoyancy which leads to a reduction by ~50% in colony concentration in the

top 0.2–0.3 m of the water column. Afternoon winds redistribute the population over the entire water column. When the lake is fully mixed, the vertical migration pattern of the *Microcystis aeruginosa* colonies may be affected, depending on the colony size and the intensity of the mixing.

Few studies have investigated the daily vertical migration patterns of individual cyanobacteria species under different lake stratification conditions. The use of our model enables the complex processes that govern the daily vertical migration patterns of *Microcystis aeruginosa* to be investigated in a manner that would not be possible through the use of field data alone. The results from the simulations reveal that relatively subtle changes in colony buoyancy can result in large vertical migrations by the colonies. Simulation of 400 μm colonies with no response time reveals that the colonies are able to become sufficiently heavy to make contact with the sediment-water interface. This may provide an advantage in allowing access to high nutrients, which are generally concentrated in sediment pore-water.

Sherman and Webster (1994) showed that a light-limited phytoplankton that can locate itself in the upper layer during a period of stratification in a shallow turbid lake will have a significantly greater potential for growth. As a result, it may be expected that the dominant phytoplankton species during the time of the year when the stratification events occur would have adapted to ensure its position in the upper layer. However, the potentially damaging irradiances at the surface must also be avoided. Under these constraints, a phytoplankton that has adapted to control its buoyancy such that it can float during the night and early morning to ensure position in the surface layer, but sink by late morning to escape the high midday irradiances that may cause photoinhibition or cell damage would have a significant competitive advantage. Not surprisingly, Thomsons Lake tends to be dominated by *Microcystis aeruginosa* during spring (Bailey and Hamilton, 1997).

The advantages afforded by the ability to regulate buoyancy and exert control over vertical position in the water column are diminished by competing physiological processes. It appears that *Microcystis aeruginosa* has increased its carbohydrate dynamics to create greater buoyant density changes at the cost of a high growth rate (typically 0.48 day^{-1} from Reynolds, 1973a; Kromkamp and Mur, 1984). As a result, species with a higher growth rate might have an advantage when the water column is fully mixed for a majority of the time. In Thomsons Lake, blooms of *Microcystis aeruginosa* are often preceded by blooms of *Anabaena circinalis* (Bailey and Hamilton, 1997) which have significantly higher growth rates (typically 1.1 day^{-1} from Reynolds, 1973a). The *Anabaena circinalis* of Thomsons Lake are unable to exert control over vertical position (Bailey and Hamilton, 1997) as their inertial forces are unable to overcome the turbulent energy due largely to their relatively small size (spiral colony ~ 60 μm from Reynolds, 1984). The formation of diurnal mixed layers in Thomsons Lake may provide a growth opportunity that the *Microcystis aeruginosa* can exploit and the *Anabaena circinalis* cannot. In order to compete during periods of thermal stratification, *Anabaena circinalis* would need to remain buoyant at all times and retain a superior growth rate to *Microcystis aeruginosa* (Takamura and Yasuno, 1984b) or increase its carbohydrate dynamics and increase flotation velocity through filament aggregation (Brookes et al., 1999). However, persistent buoyancy presents a problem in avoiding prolonged surface exposure, which may only be achievable through gas vesicle collapse, resulting in a buoyancy loss that

may be irrecoverable. Increasing carbohydrate dynamics may result in a reduced growth rate advantage. This may explain the shift in biomass dominance between *Anabaena circinalis* in October when Thomsons Lake was stratified less than 10% of the time to *Microcystis aeruginosa* in November when Thomsons Lake was stratified for more than 40% of the time in 1994 (Bailey and Hamilton, 1997).

Our results also show that larger *Microcystis aeruginosa* colonies are more readily able to overcome the entraining forces of turbulence and gain access to the near-surface region even when the formation of a stratified layer is prevented. However, large colonies sizes result in a decrease in the effective photosynthetic antennae (Reynolds, 1984). Also, in frequently mixed waters, the formation of large colonies may be prevented due to the shear stresses experienced in the turbulence. Thus, it is expected that there is an optimum where the benefits are maximised and the disadvantages minimised between colony size, growth and buoyancy regulation through carbohydrate dynamics that allows *Microcystis aeruginosa* to dominate during summer in Thomsons Lake.

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