J. Limnol., 2017; 76(1): 190-198
DOI: 10.4081/jlimnol.2016.1501

ORIGINAL ARTICLE

Numerical simulation of the vertical migration of *Microcystis* (cyanobacteria) colonies based on turbulence drag

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ABSTRACT

The vertical migration and accumulation of Microcystis *is an important process in water blooms, and colony migration is influenced by colony size and wind-wave disturbance. The vertical migration of* Microcystis *colonies in turbulence can be simulated in a numerical model. In this study, we model such migration by coupling the colony size and hydrodynamics, including the gravity, colony buoyancy, and the viscous drag force of turbulence. The turbulence intensity was represented by the turbulent kinetic energy (*K_Z*); the larger the* K_Z*, the stronger the wind-wave disturbance. The simulated vertical distribution of* Microcystis *well agreed with the measured values in a laboratory experiment indicating that our model can simulate the vertical distribution of* Microcystis *under different hydrodynamic conditions. We also found a size-dependent critical turbulent kinetic energy (*TK_Z*), such that if the turbulent kinetic energy of water exceeds the critical value (*i.e., $K_Z > TK_Z$*), the colonies sink under the drag forces of turbulence; conversely, if* $K_Z < TK_Z$*, the colonies can overcome the turbulent mixing and float. The* TK_Z *of each colony was linearly related to colony diameter. The model is crucial for prediction and prevention of water blooms. The simulated threshold turbulent kinetic energy, at which water blooms disappear in Lake Taihu (a large freshwater lake in the Yangtze Delta, Jiangsu Province, China), was* $55.5\ cm^2\ s^{-2}$.

Key words: Viscous drag force of turbulence; colony size; turbulent kinetic energy; vertical migration; TK_Z.

Received: May 2016. Accepted: October 2016.

INTRODUCTION

Cyanobacterial blooms are a major environmental problem in eutrophic lakes and *Microcystis* is the most common genus of bloom forming cyanobacterium. Water blooms can be effectively predicted in numerical models that simulate the occurrence and disappearance of water blooms. The cyclic appearance and disappearance of water blooms is mainly driven by the spatial aggregation and dispersion of *Microcystis* by wind waves (Wu and Kong, 2009; Zhu *et al.*, 2014). Consequently, this process is assumed in numerical simulations of blooms.

Microcystis colonies achieved vertical migration with the help of buoyancy regulating system of gas vesicles and ballast (*e.g.*, carbohydrate) (Oliver and Walsby, 1984; Kromkamp *et al.*, 1984). These mechanisms were well described by Walsby (1994) that *Microcystis* colonies always rise during night due to synthesis of gas vesicles and carbohydrate utilization. In the contrary, they sink in the day because of the accumulation of carbohydrate and collapse of gas vesicles. In a laboratory study, Nakamura *et al.* (1993) found that the measured floating velocity of *Microcystis* is proportional to colony size. Wu and Kong (2009) investigated *Microcystis* blooms in Lake Taihu, a large freshwater lake in the Yangtze Delta of Jiangsu Province, China. They found that large *Microcystis* colonies (>120 μm) can overcome wind-wave disturbance and thus accumulate at the water surface, whereas small colonies (<36 μm) tend to mix with the turbulence. Chien *et al.* (2013) simulated the vertical migration of differently sized colonies in a trajectory model, and reported that large colonies (≥300 μm) can resist turbulent mixing and undertake diurnal vertical migration, whereas smaller colonies are more homogenously scattered in the vertical direction. According to Stokes' law ($V=2gr^2(\rho–)A/(9\Phi n)$, where V and r are the velocity and radius of the colony, respectively, ρ and ρ_w are the densities of the colony and water, respectively, A is the proportion of cell volume relative to colony volume, Φ the form resistance and n the viscosity of the water), without any other interference, the vertical migration velocity of *Microcystis* colonies mainly depends on the cell density and the colony size (Reynolds *et al.*, 1987), and the floating rate is proportional to the square of the colony diameter. All of these studies suggest that colony size directly affects the vertical migration of *Microcystis*.

Besides the internal factors, the vertical distribution of *Microcystis* is mainly driven by wind-wave disturbance. George and Edwards (1976) investigated the relationship between water blooms and wind speed in Lake Nynyod (South Wales), and found that algae gather into blooms at the water surface at wind speeds below 3.0 ms^{-1}, but disperse at wind speeds of 3.0 ms^{-1}. Cao *et al.* (2006) conducted a field investigation of Lake Taihu, and observed that at a wind speed of 2.0 m s^{-1} and wave height of 4.4 cm, approximately 37% of the whole *Microcystis* biomass gathers on the water surface, forming water blooms. Conversely, at a wind speed of 3.1 ms^{-1} and wave height of 6.2 cm, the *Microcystis* tend to distribute homogenously through the water column. Wu *et al*. (2013) found that disturbances mix the *Microcystis* in deeper layers. In a field study, Ding *et al.* (2012) investigated the effect of the tropical storm Morakot on Lake Taihu's water blooms, and observed that chlorophyll a concentration homogenously distributed during the typhoon crossing, and water blooms reappeared on the surface after the typhoon. The above studies show that turbulent mixing determines the vertical distribution of *Microcystis*. However, although these studies relate wind speed to water blooms, they do not clarify the motion mechanism of *Microcystis* under different hydrodynamic conditions, nor the effect of turbulence on the migration of colonies.

Many researchers have established mathematical models to study the vertical migration and distribution of *Microcystis* colonies under different hydrodynamic conditions (Visser *et al.*, 1997; Wallace *et al.*, 2000; Huisman and Sommeijer, 2002; Rabouille *et al*., 2005; Serizawa *et al*., 2008; Chen *et al.*, 2009). Visser *et al.* (1997) combined a model of cell density change with Stokes' law, and simulated the vertical migration of *Microcystis* colonies in static water. Wallace *et al.* (2000) combined a buoyancy regulation model with a hydrodynamic model into a vertical migration model of *Microcystis*, and computed the vertical position of *Microcystis* in a turbulent shallow lake (depth 1.4 m). A similar vertical migration model of *Microcystis* colonies was developed by Chen *et al.* (2009). The fluid mechanics described particle migration in the flow in details and indicated that the viscous drag force was the driven factor making the particles to migrate in the flow (White *et al.*, 1977; Van Rijn, 1984). This principle could also be applied to *Microcystis* colonies. The viscous drag was ignored in the models of the vertical migration of *Microcystis* colony. To more accurately simulate the vertical migration of *Microcystis* colonies, we require numerical models based on the most influential physical processes.

In this study, we investigate the effect of *Microcystis* colony size on resistance to disturbance. To this end, we develop a mathematical model that allows floating and sinking of *Microcystis* colonies under viscous drag as well as gravity and buoyancy. The mathematical model is verified in a laboratory experiment.

METHODS

Forces acting on *Microcystis* colonies

In the present model, the forces acting on *Microcystis* colonies are restricted to the vertical direction. The three main forces acting on *Microcystis* in water (where the *z* axis is positive downward) are listed below.

1) Gravity

$$G = mg = \rho_s g V \tag{eq.1}$$

2) Buoyancy

$$F_f = \rho_w g V_f \tag{eq. 2}$$

3) Viscous drag force of turbulence

$$F_D = \frac{C_D \rho_w \pi D^2 (u_w - v_s)\left|u_w - v_s\right|}{8} \tag{eq. 3}$$

These forces are summed to give the resultant force

$$F_h = \frac{C_D \rho_w \pi D^2 (u_w - v_s)\left|u_w - v_s\right|}{8} - (\rho_w - \rho_s) g V = ma = m\frac{dv_s}{dt} \tag{eq. 4}$$

ρ_w and ρ_s as the densities of water (998 kg m^{-3}) and *Microcystis*, respectively. Reynolds *et al*. (1981) indicated that the lowest density of *Microcystis* colonies in Bleham Tarn, Cumbria was 985 kg m^{-3}. In addition, we recently measured the density of *Microcystis* colonies taken from Lake Taihu and found that the average value was 985 kg m^{-3}. Therefore, we set ρ_s as 985 kg m^{-3} in the current study. We also require the gravitational acceleration *g* (9.8 m s^{-2}), the volumes *V* of a single colony and V_f of the colony in water, the colony diameter *D*, and the drag coefficient C_D. As the colony is assumed to be spherical, its volume is given by $V = \pi D^3/6$; further, we assume $V_f = V$, and set C_D to 0.45 in turbulence (Dong *et al.*, 2007). We also define u_w and v_s as the vertical velocities of flow and vertical migration of *Microcystis* colonies respectively, and *a* as the acceleration of the colonies. The mass *m* of a single colony is calculated as $m = \rho_s V$.

Vertical position of *Microcystis* colonies

As turbulence varies in a transient manner, we divided the motion time *t* into *n* equal segments with a time step *t* of 10^{-4} *s*. After discretizing eq. (4) as eq. (5), we solved the vertical migration velocity of each *Microcystis* colony by a finite difference scheme implemented in MATLAB R2009a software (The MathWorks).

$$F_h = \frac{C_D \rho_w \pi D^2 (u_{wi} - v_{si})\left|u_{wi} - v_{si}\right|}{8} - \rho_s) gV = m\frac{v_{si+1} - v_{si}}{t} \quad \text{(eq. 5)}$$

The initial vertical migration velocity of the colonies (regardless of their diameter) was set to 0 m s^{-1} ($v_{s0} = 0$). v_{si} was determined from the known vertical velocities of flow (u_{wi-1}). Within the very short time step, the motion of the colonies is assumed uniform and their instantaneous displacement is given by $S_i = v_{si} \times t$. The total displacement (S) and position (z) of a *Microcystis* colony in water are described by the following flow equations:

$$S = S_1 + S_2 + \ldots + S_n \quad \text{(eq. 6)}$$

$$z = z_0 + S \quad \text{(eq. 7)}$$

Where z_0 is the initial position of the *Microcystis* colony.

Turbulent kinetic energy

In this study, the disturbance intensity was represented by the turbulent kinetic energy (K_Z), which is calculated by eq. (8):

$$K_Z = \frac{1}{2n}[(u_1 - \bar{u})^2 + (u_2 - \bar{u})^2 + \ldots + (u_n - \bar{u})^2] \quad \text{(eq. 8)}$$

Here, u_i are the instantaneous vertical flow velocities, and $\bar{u}$ is their mean value, n is the number of u_i. The larger the K_Z, the stronger the disturbance.

Laboratory experiment (vertical wave-making simulator) and simulation

The effects of disturbance on the vertical migration and distribution of *Microcystis* colonies were investigated in a vertical wave-making simulator. Survival kinds of amplitude A (4, 6, 8 cm) with variable frequency ($1/T$) were set to obtain different hydrodynamic conditions. *Microcystis* samples taken from Lake Taihu, which were mainly composed of *M. aeruginosa*, were used in this experiment (Xiao *et al.*, 2013).

Measurement of vertical flow velocity

The vertical flow velocity (u) in the simulator was measured by Particle Image Velocimetry (PIV), and the K_Z was calculated by Eq. (8). Fig. 1a shows the working principle of PIV. Before measurement, the tracing particles are placed in the simulator with high flow, and one side of the simulator is illuminated by a pair of lasers. The trajectories of the particles are then tracked perpendicularly to the laser beam by a high-speed CCD camera. The particle trajectories are photographed over 100 μs (the time step of the lasers), and the two-dimensional velocity of the water particle is calculated. Because the laser beam must pass through regions containing liquid, the lowest water level must lie outside the light irradiation area. To ensure this condition, we placed the laser at 50 cm and 80 cm from the bottom of the simulator (Fig. 1b). The verti-

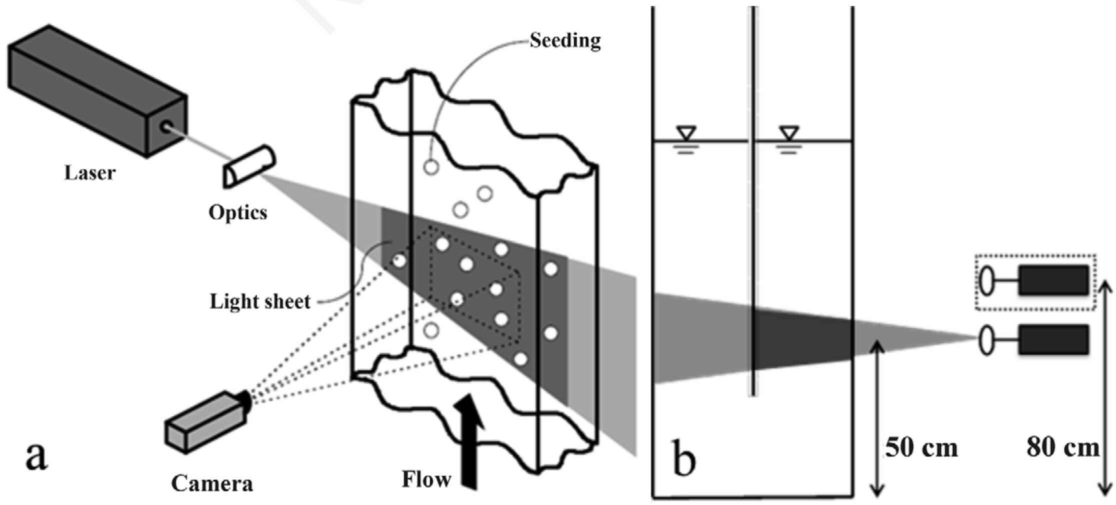


Fig. 1. a) The working principle of PIV. b) Area of flow measurement.

cal flow velocities were calculated from 80 photographs under different hydrodynamic conditions.

Simulation of vertical flow velocity

Considering the wave patterns in the simulator and random turbulence, the vertical flow velocity in the simulator was estimated by Eq. (9), where A, T are amplitude and period set in experiment, respectively, $w=2\pi/T$. A random number R was employed here to indicate random fluctuation component of turbulence which was always described as $u= \bar{u} + u'$ (where u is the instantaneous velocity, $\bar{u}$ is the average velocity, and u' is the random fluctuation component).

$$u_w = Aw\sin(wt) + AR/T \qquad \text{(eq. 9)}$$

The vertical flow of the wave-making simulator under different conditions was simulated by eq. (9). For each hydrodynamic condition, the flow velocities were calculated in one period, and the turbulent kinetic energy (K_Z) was estimated by eq. (8).

Simulation of vertical distribution of *Microcystis*

Four groups of *Microcystis* colonies (un-sieved original mixed-size *Microcystis* samples, colony sizes of 100-300, 300-500 and >500 μm) were operated in the experiment of vertical distribution of *Microcystis* under different hydrodynamic conditions (Xiao *et al.*, 2013).

Simulation was conducted in following steps. All *Microcystis* colonies were initially set at the surface ($zo = 0$). And colonies' displacements at different time (1, 5, 10 min) were calculated by applying eq. (1) - eq. (7). Then, colonies at a particular depth (z) were counted (N_z) according to their displacements. Finally, the Chlorophyll a concentration at different depths was determined through multiplying ratio of Nz and N (the total number of the colonies in the system) by the whole Chlorophyll a concentration C_0 (acquired from laboratory experiment). Thus, the *Microcystis* concentration at depth (z) is given by eq. (10):

$$C_z = C_0 N_Z / N \qquad \text{(eq. 10)}$$

The measured results obtained by Xiao *et al*. (2013) was used to assess the consistency of the predicted results and the measured results.

Critical hydrodynamic conditions

The condition under which the colonies happen to sink is the critical hydrodynamic disturbance, below this hydrodynamic condition, the *Microcystis* colonies can resist the water motions and float up. In this study, the critical turbulent kinetic energy (TK_Z) was used to represent the disturbance intensity. If the turbulent kinetic energy of the water body exceeds the critical kinetic energy of the colonies (*i.e*., $K_Z > TK_Z$), the colonies will sink under the drag forces of turbulence. Conversely, if the turbulent kinetic energy of water is below the critical kinetic energy of the colonies ($K_Z < TK_Z$), the colonies will float.

Individual colony was placed on the water surface separately. The critical turbulent kinetic energy (TK_Z) under varying hydrodynamic conditions was obtained when the colony happened to leave the water surface. The experiments were performed in three times.

In the numerical simulation, the colony displacements were investigated under increasing hydrodynamic disturbances until the displacement is just greater than zero. The critical hydrodynamic conditions of colonies with different diameters (100, 200, 300, 400, 500 μm) were obtained, hence their critical turbulent kinetic energies (TK_Z). Linear regression was used to estimate the dependence of critical kinetic energy on colony size.

RESULTS

Turbulent kinetic energy under different hydrodynamic conditions

The simulated turbulent kinetic energy (K_Z) under different hydrodynamic conditions is showed in Tab. 1 and Fig. 2. The turbulent kinetic energy (K_Z) is a quadratic function of the hydrodynamic conditions (A/T) as equation 11. The measured and simulated values favorably agree, confirming that our model can simulate the flows in a vertical wave-making simulator.

$$K_Z = 10.034(A/T)^2 \qquad \text{(eq. 11)}$$

Vertical distribution of *Microcystis*

After estimating the displacements of all *Microcystis* colonies under various experimental conditions, we calculated the chlorophyll a concentrations at different depths by

Tab. 1. The simulated turbulent kinetic energy in different hydrodynamic conditions.

Amplitude A/period T (cm s^{-1})	8/2	6/2	8/3	6/3	6/4	5/4	4/4
Hydrodynamic condition A/T (cm s^{-1})	4	3	2.67	2	1.5	1.25	1
Turbulent kinetic energy K_Z (cm^2 s^{-2})	160	90	71	40	23	16	10

eq. (10), and compared them with the experimental results. Fig. 3 showed the variation in vertical distribution of *Microcystis* colonies (300-500 µm). At an amplitude of 8 cm and period of 2 s, most of the *Microcystis* gathered at the surface after 1 min. The surface aggregation decreased after 5 min disturbance, and the *Microcystis* were homogeneously distributed after 10 min. The simulated values well agreed with the measured values, and exhibited the same behavior. Under less vigorous hydrodynamic conditions ($A = 6$ cm, $T = 2$ s; $A = 6$cm, $T = 3$ s), the simulated chlorophyll a concentration at the surface was higher than the measured one, and the simulated levels at lower depths agreed with the measured levels.

Critical turbulent kinetic energy

The critical turbulent kinetic energy (TK_Z) was proportional to colony diameter (D) as equation 12. The strong agreement between the measured and simulated values is clarified in Fig. 4.

$$TK_Z = 0.1555\,D - 6.7414\ (R^2 = 0.998\,, P < 0.01)$$

(eq. 12)

DISCUSSION

The 1-D wave simulator designed by Xiao *et al*. (2013) was used to simulate the water movement vertically only. It simplified the water movement of real lakes which varies temporally and spatially, and the simulation was reasonable. The vertical turbulence induced by the motor was strong at the deeper water column, which was consistent with the investigations in Lake Taihu that, deeper layers had more intensive turbulence. Therefore, the effect of vertical water movement on the vertical distribution of *Microcystis* sp. could be well studied with the device and the experimental set up designed by Xiao *et al*. (2013). In the present study, model results have been compared with detailed measurements in three aspects (vertical flow velocity, the vertical distribution of *Microcystis*, and the critical turbulent kinetic energy of different-sized colonies). Simulated values agreed with measured values.

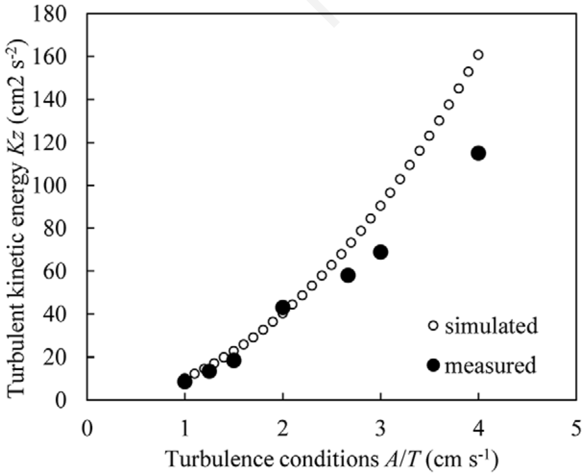


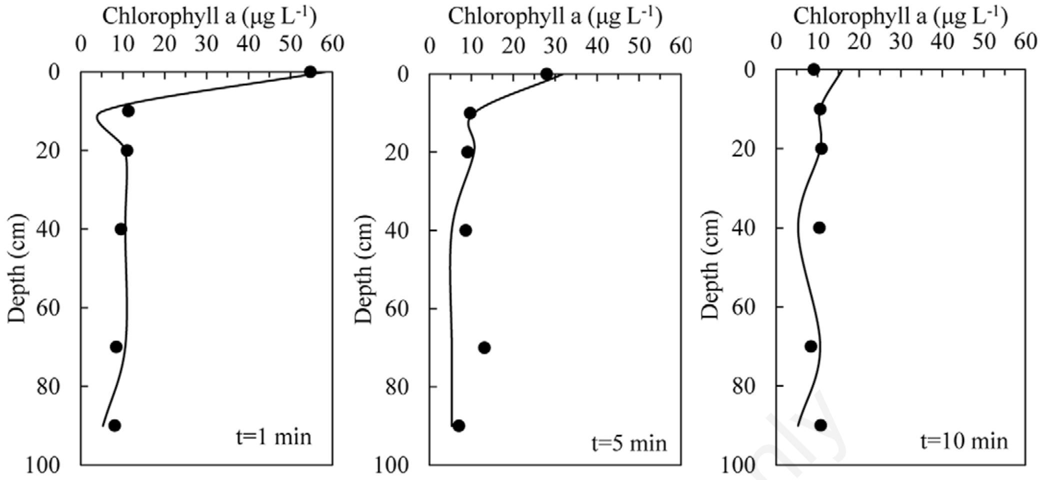
Fig. 2. Turbulent kinetic energy under different hydrodynamic conditions.

Water motion affects the vertical migration and distribution of *Microcystis* in lakes, rivers and reservoirs (Ha *et al.*, 2000; Wallace *et al.*, 2000; Medrano *et al.,* 2013; Cui *et al.*, 2016). *Microcystis* will migrate to the surface forming water blooms under weaker disturbance, and sink to deeper depths as water mixing become stronger. These observations consistent with our experimental data and model results.

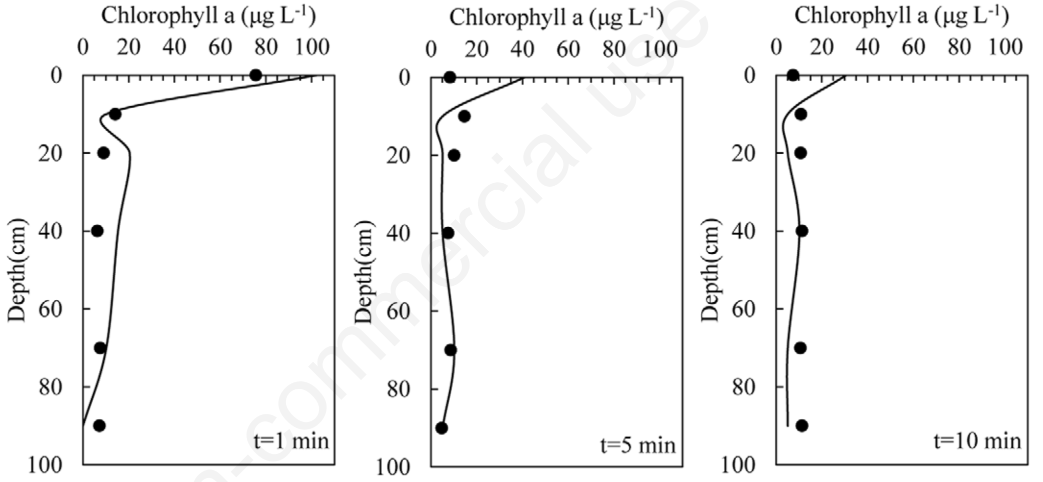
On the other hand, hydrological conditions affect water blooms directly or indirectly by means of affecting the sizes of *Microcystis* colonies, which can alter the floating capacity of colonies. Large colonies may be destroyed to smaller colonies under oscillation mixing (Robarts and Zohary, 1984; O'Brien *et al*., 2004), and these smaller colonies can't overcome the drag force of turbulence and sink. Resulting in decrease of *Microcystis* biomass at the water surface. These may be a reasonable explanation for the discrepancy between measured and simulated *Microcystis* concentration at the surface under moderate mixing ($A = 6$ cm, $T = 2$ s; $A = 6$ cm, $T = 3$ s). Our simulation results showed that larger colonies (>400 µm) can resist the disturbance and remain at the water surface under these two conditions. Some of these large colonies may break up into smaller colonies under sustained oscillation mixing in the experiments. While these smaller colonies would sink for that they can't resist turbulent mixing. Resulting in the decrease of *Microcystis* biomass at the water surface. But colonies break-up was ignored in our simulation, leading to the differences between simulated and measured *Microcystis* concentrations. The relationship between the measured and simulated *Microcystis* concentrations was showed in Fig. 5. The figure indicated that our model can accurately simulate the vertical distribution of *Microcystis* under different hydrodynamic conditions.

However, this kind of dispersion is small even for the highest turbulence intensities experienced by *Microcystis* in the field (O'Brien *et al.*, 2004). Some studies discussed the influence of turbulence on the ecology of *Microcystis* (Reynolds, 1994; Wilkinson *et al.*, 2016). Their results suggested that *M. aeruginosa* are powerful enough to tolerate intensive mixing for a few days (>96 h) (Regel *et al.*, 2004). In summary, it is reasonable to ignore the effect of turbulence on colony viability and size in simulation process, and simulated results are suitable for field.

A: 8cm; T: 2s



A: 6cm; T: 2s



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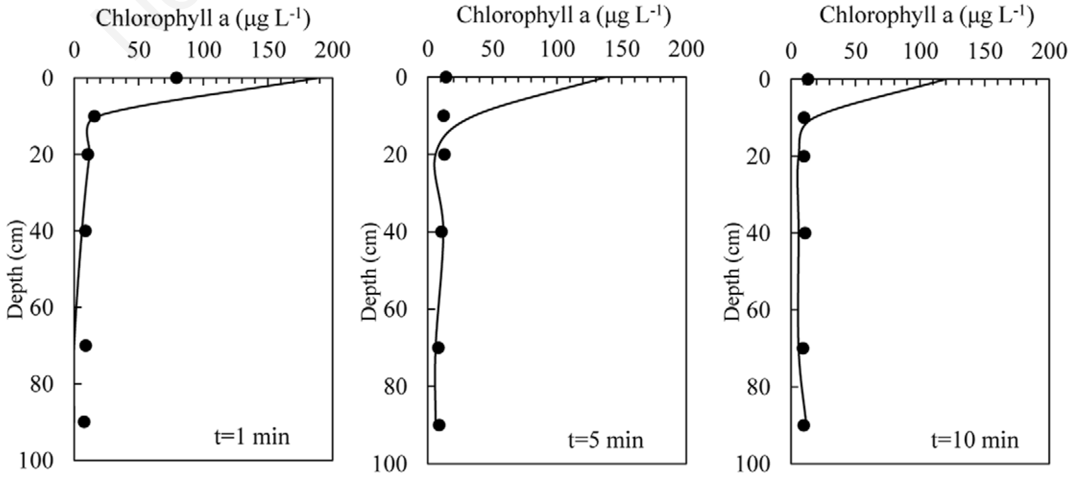

Fig. 3. The vertical distribution of *Microcystis* under different hydrodynamic conditions. The continuous lines are simulated results; the dots are measured results from Xiao *et al.* (2013).

The phenomenon has been found that water blooms occurred under poor weather or nutrient conditions (Ozawa *et al.*, 2005; Ma *et al.*, 2015). The reason may be explained as the effect of water motion. It may not be suitable to predict the outbreaks of water bloom by simply relying on the nutrient, light or temperature. Establishing the relationship between water and *Microcystis* motion is necessary. While existing numerical models and studies reported consistent results. Namely, that *Microcystis* large colonies can resist turbulence and float to the surface whereas small colonies are easily mixed in the water column (Wallace *et al.,* 2000, Medrano *et al.*, 2013). But failed to quantify the relationship between disturbance resistance and colony diameter. In this study, our model computed the critical turbulent kinetic energies as eq. 12, above which the colonies will sink.

According to the long-term monitoring study of Meiliang and Gonghu Bays in Lake Taihu, a large shallow lake (Zhu *et al.*, 2015), reported that during the water blooms season (October to December), *Microcystis* colonies are 300-400 µm wide in Lake Taihu (Zhu *et al.*, 2016). The critical turbulent kinetic energy of 400 µm colony is 55.5 cm^2 s^{-2}, it means that under this condition, most of the colonies will sink and the water blooms will disappear. In addition, the turbulent kinetic energy (K_Z) is the following quadratic function of the wind speed x in Lake Taihu:

$$K_Z = 3.12x^2 - 0.56x + 22.65 \text{ (Xiao, 2014)} \qquad \text{(eq. 13)}$$

Inserting the critical turbulent kinetic energy into this expression, the corresponding wind speed is determined as 3.3 ms^{-1}, similar to the threshold wind speed (3.0 ms^{-1}) at which the water blooms disappears in Lake Taihu (Zhu and Cai, 1997; Cao *et al.*, 2006; Zhang *et al.*, 2008). At a wind speed of 1 m s^{-1}, the turbulent kinetic energy of water is 25.2 cm^2 s^{-2}, indicating that *Microcystis* colonies will sink if their diameters are below 200 µm. When the wind speed increases to 4.02 m s^{-1}, the turbulent kinetic energy of water reaches 71.0 cm^2 s^{-2}, and colonies with diameters smaller than 500 µm will leave the water surface. At a wind speed of 5.61 ms^{-1}, the turbulent kinetic energy is 117.7 cm^2 s^{-2}, ensuring that even large colonies (800 µm) are mixed throughout the water column. The critical turbulent kinetic energy is a useful parameter for predicting the occurrence and disappearance of water blooms and the depth at which *Microcystis* potentially occurs in different type of lakes.

Wind-waves frequently disturb phytoplankton and sediment in shallow lakes. Light, temperature and nutrients are homogeneous in the whole water column mainly affected by water disturbance (Nixdorf and Deneke, 1997). And colonies will be evenly mixed in the whole water column under intensive mixing conditions, assemble at the near surface in calm periods. However, in deep lakes, disturbance degree varies with depth under disturbance, thus different-sized colonies will gather at different depths (at which the turbulent kinetic energy of water no more than their critical energy). *Microcystis* will occur at this lower intensity mixing and deeper locations. Light, temperature, may not be favorable for *Microcystis* growth at deep layers, which will affect algal physiology of *Microcystis*. Thus affecting morphological and size of *Mi-*

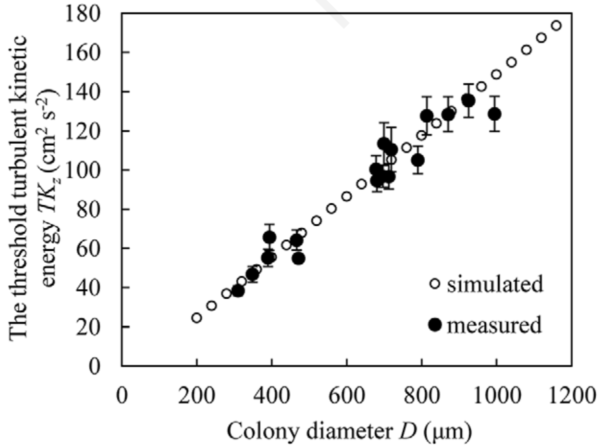

Fig. 4. The critical turbulent kinetic energy of different-sized *Microcystis* colonies. Error bars represent the standard deviation of measured values.

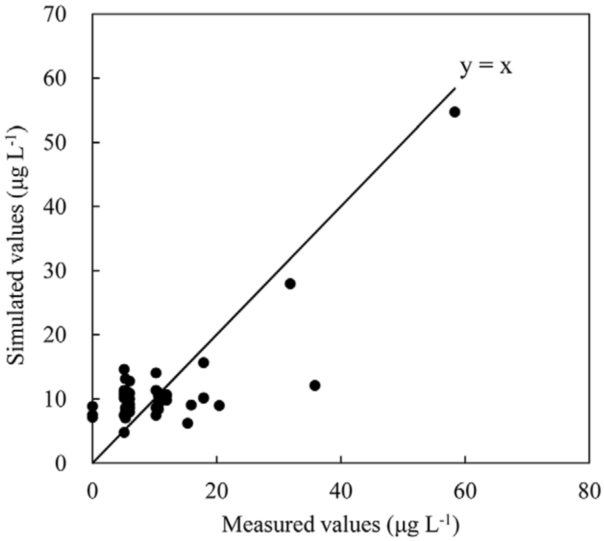

Fig. 5. The relationship between the measured and simulated *Microcystis* concentrations.

crocystis colony. Shallow lakes may hold the potential to bear favorable conditions for the presence of *Microcystis* blooms, because of the homogeneous light, temperature, and turbulence mixing, as well as the frequently disturbance which can cause the release of nutrients from the sediment (Fan *et al.*, 2004).

CONCLUSIONS

This paper introduced a vertical migration model of *Microcystis* colonies based on turbulence drag, revealing the mechanism by which turbulence and colony size affects the vertical migration of *Microcystis*. The critical turbulent kinetic energy (TK_Z), above which the colony cannot resist the turbulence conditions and sinks, depends on the colony diameter. The critical turbulent kinetic energy is a useful parameter for predicting the occurrence and disappearance of water blooms in different type of lakes. The study is crucial for prediction and prevention of water blooms.

ACKNOWLEDGMENTS

The project was funded by the Program on Furtherance of Scientific Research of Japan, Fundament C (15K00630), the Lake Taihu water pollution control special funds (Tenth Phase) Scientific research topic (JSZC-G2016-198), the Fundamental Research Funds for the Central Universities (2015B36214).

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