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How physiological and physical processes contribute to the phenology of cyanobacterial blooms in large shallow lakes: A new Euler-Lagrangian coupled model

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ABSTRACT

Cyanobacterial blooms have emerged as one of the most severe ecological problems affecting large and shallow freshwater lakes. To improve our understanding of the factors that influence, and could be used to predict, surface blooms, this study developed a novel Euler-Lagrangian coupled approach combining the Eulerian model with agent-based modelling (ABM). The approach was subsequently verified based on monitoring datasets and MODIS data in a large shallow lake (Lake Taihu, China). The Eulerian model solves the Eulerian variables and physiological parameters, whereas ABM generates the complete life cycle and transport processes of cyanobacterial colonies. This model ensemble performed well in fitting historical data and predicting the dynamics of cyanobacterial biomass, bloom distribution, and area. Based on the calculated physical and physiological characteristics of surface blooms, principal component analysis (PCA) captured the major processes influencing surface bloom formation at different stages (two bloom clusters). Early bloom outbreaks were influenced by physical processes (horizontal transport and vertical turbulence-induced mixing), whereas buoyancy-controlling strategies were essential for mature bloom outbreaks. Canonical correlation analysis (CCA) revealed the combined actions of multiple environment variables on different bloom clusters. The effects of buoyancy-controlling strategies (ISP), vertical turbulence-induced mixing velocity of colony (VMT) and horizontal drift velocity of colony (HDT) were quantitatively compared using scenario simulations in the coupled model. VMT accounted for 52.9% of bloom formations and maintained blooms over long periods, thus demonstrating the importance of wind-induced turbulence in shallow lakes. In comparison, HDT and buoyancy controlling strategies influenced blooms at different stages. In conclusion, the approach developed here presents a promising tool for understanding the processes of onshore/offshore algal blooms formation and subsequent predicting.

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1. Introduction

As the third largest freshwater eutrophic lake in China, Lake Taihu has been subject to harmful cyanobacterial blooms (Cyano-HABs), dominated by *Microcystis* spp. (Paerl and Huisman, 2008). Because of excessive nutrient inputs to the lake, these blooms present a serious threat to drinking water supplies, aquatic life, human health, and the ecological sustainability of the freshwater ecosystem of this region. A central question facing water researchers and managers is how to predict the spatial-temporal

* Corresponding author. E-mail address: pfwang2005@hhu.edu.cn (P. Wang). pattern of surface blooms in large shallow lakes. This question is of immense importance for estimating the risk of cyanobacterial occurrence in advance. Understanding the growth and transport process of *Microcystis* is essential for resolving this question (Wynne et al., 2013). Previous studies have identified a host of physiological processes underlying the excessive *in situ* proliferation of *Microcystis* colonies, particularly from the perspective of biological responses (such as nutrient-induced over-enrichment (Reynolds, 2006; Paerl et al., 2011b), photosynthesis (Takamura et al., 1985), colony formation avoiding predation (Reynolds et al., 1981), and buoyancy-controlling strategies (ISP) (Reynolds, 1973; Reynolds et al., 1987; Ndong et al., 2017).

In deep lakes, the response to buoyancy changes (would be on





WATER RESEARCH the order of days) and stationary behavior reduce the chance to accumulation on water surface (Chien et al., 2013; Medrano et al., 2013). Therefore, the occurrence of surface bloom in shallow lake is more sensitive to physical transport process (within minute scale) than that in deep lake (Wallace et al., 2000; Duan et al., 2009; Wang et al., 2017). The physical transport processes of colony comprise of vertical turbulence-induced mixing velocity (VMT) and horizontal drift speed (HDT). Wu et al. (2015) and Cao et al. (2006) emphasized the strong relationship between surface bloom formation and wind-induced turbulence in Lake Taihu (China). The impacts of wind-induced surface drift and wave-induced Stokes drift on offshore/onshore bloom migration have been increasingly acknowledged (Ishikawa et al., 2002; Wu et al., 2010; Deng et al., 2016; Hua et al., 2016). In addition, buoyancy control and vertical transport processes have been also observed to interact (Wallace and Hamilton, 1999; Wallace et al., 2000). Recently, differences in morphology, as a result of different growth environments, which influence colony size, have been shown to contribute to diverse transport patterns (Deng et al., 2016). Therefore, both physiological process (especially ISP) and physical processes (VMT and HDT) should be evaluated to understand the timing and intensity of specific surface blooms (Glibert et al., 2010; Otten et al., 2012). However, few studies and technologies have integrated these nonlinear complex and interactive processes, or compared their respective contributions in shallow lakes.

Using field data to demonstrate the spatial-temporal distribution of surface cyanobacterial blooms presents a considerable challenge. Furthermore, linking this information to bio-physical changes is even more problematic. Recently, satellite imagery (such as MODIS data) has been used to detect the spatiotemporal patterns of surface bloom areas over large domains, relating these patterns to changing environmental conditions (Wynne et al., 2011; Qin et al., 2015). However, the information acquired from satellite imagery might obscure *Microcystis* adaptive migratory movement patterns (buoyancy-controlling strategy), as such patterns are three dimensional, induced by water current and/or wind, especially in shallow lakes. Different responses of growth to variation in light, temperature, and nutrient levels across seasons must also be considered. Thus, numerical techniques might be required to complement satellite data.

Agent-based models (ABM) have been widely applied to capture 2-D and 3-D transport trajectories of cyanobacteria over periods of several days (Dippner et al., 2011; Wynne et al. 2011, 2013; Henrichs et al., 2015). Most ABM models are forced with the physical environment from an Eulerian model, allowing the agents (each representing certain cyanobacteria) to "drift around", thus experiencing different biological processes with water quality variables. In ABM models, the system properties are said to "emerge" from the properties of the individual particles (Grimm and Railsback, 2005). Both individual physiological properties and physical drivers could be easily integrated into agent-based equations to describe complex ecological processes, as described in Hellweger et al. (2008) and Glibert et al. (2010). However, the calibration of phytoplankton parameters in ABM is difficult because of the enormous computation requirements. Therefore, the preliminary calibrated Euler-based physical-biological model (which describes the concentration of the distribution of cumulative individuals) should be integrated into ABM to obtain associated physiological parameters of cyanobacteria and water quality variables. The increasingly complex Euler-based ecological models help us to capture the response of ecological systems to the external environment (Butenschön et al., 2016; Rolighed et al., 2016). The Fortran-based Framework for Aquatic Biogeochemical Models (FABM) was developed by Bruggeman and Bolding (2014), in which the biochemical model was arbitrarily connected to a physical

model. Here, we combined a self-contained complex biological model (called GEM) to a well-known hydrodynamic model (FVCOM) by FABM. This Euler-based model was used to calibrate the physiological parameters for phytoplankton.

In Lake Taihu in China, algae begin to emerge from the sediment and aggregate to form the early blooming stage (April-June) before mass propagation during the mature blooming stage (July-October), when the water temperature is persistently high (Kong and Fao, 2005; Cao and Yang, 2010). Therefore, we assumed that the blooms detected at different stages have specific physiological and physical characteristics. In the present study, we improved the original agent-based model of Wang et al. (2017b), and tested our hypothesis. Furthermore, we evaluated the performance of the coupled Euler-Lagrangian model using field investigated data and MODIS data to demonstrate our ability to reproduce the spatial patterns of algal blooms and characterize the physiological and physical variables of blooms. We also used the coupled model to simulate several scenarios and identify the individual contributions of physiological processes and physical processes of Microcystis to surface bloom in the shallow lake system. Our results are expected to provide new insights on the parameters that drive algal blooms, thus providing a basis on which to predict onshore/offshore blooms in such a large domain.

2. Material and methods

2.1. Study area

Lake Taihu (30°55'40″–31°32'58″ N; 119°52'32″–120°36'10″ E) is located in the lower part of the Yangtze River Delta, China. It is a well-known large, shallow, and eutrophic lake (Fig. 1). Lake Taihu covers an area of about 2338 km² with an average depth of 1.9 m and maximum depth of 2.64 m. Severe cyanobacterial blooms occur between April and October (Hu et al., 2006). The cyanobacteria are primarily *Microcystis* spp., which is a colony-forming cyanobacterial species consisting of mucilage, gas vesicles, and cells (Qin et al.,



Fig. 1. Maps showing the location of the study area and monitoring stations. The main polluted inflows and outflows have been drawn. The red circle represents the sampling area (MLB) where the biomass of *Microcystis* was monitored. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2015). Therefore, the physiological and physical processes of *Microcystis* were chosen to represent that of all the cyanobacterial species in this study. MLB (31.4929°N; 120.2074°E) represents the validation site for the Eulerian model.

2.2. Model overview

We modified a type of model ensemble referred to as an Eulerian/ABM hybrid in Wang et al. (2017b). In this study, the Eulerian model (call as GEM) was improved with ecological processes by FABM, to consider the feedback between nutrient field and physical structure and proliferation of cyanobacteria. Physiological consideration of three phytoplankton species (Diatom, Chlorophytes and Cyanobacteria) has been included into Eulerian model. Neither zooplankton nor fish was considered in our coupled model. ABM focuses on the physiological and physical characteristic of cyanobacteria, i.e. Microcystis, and models the formation of surface bloom. The ABM model is a particle-based framework that describes the agent-based representation of Microcystis. Each agent has its own upscaling number that specifies the number of colonies that it represents and the colony number in agent keeps constant during simulation. The biological processes of Microcystis in these two models were the same.

Overall, the Eulerian models were run first during each time step, followed by the ABM models, allowing the Eulerian variables (nutrient and detritus) to interact with physiological growth (carbon and intracellular nutrient content) of Microcystis, as shown in the schematic of GEM (Fig. A2). Then the calculated physical field (such as temperature) and chemical field (such as dissolved nutrient) from Eulerian model were directly forced to modify agent physiology (such as biomass and colony size) and transport pattern in ABM. Meanwhile, the preliminary Euler-based physical-biological model supplied associated physiological parameters for ABM. Details of this coupled model, including parameters, equations, concepts of agent, summary of agents, are provided in the Supporting Information. Here, we provide a brief description of the agent-based model. The variables of the Microcystis agent and related parameters are presented in Table 1 and Table A1, respectively.

2.2.1. Biological processes of the agent

.2

The intracellular biomass in individual agent changes as a function of limited growth and death,

$$\frac{dPC}{dt} = \left(\mu_p - \mu_D\right)PC\tag{1}$$

where *PC* (g C agent⁻¹) is the agent biomass, i.e., agent size. The Chlorophyll *a* of agent could be acquired by multiplying *PC* by a fixed ratio $\delta_{chla/C}$, which is easier for monitoring and model calibration. μ_p (d⁻¹) is the specific proliferation rate of agent biomass (i.e. physiological growth of agent), and μ_D (d⁻¹) is the mortality rate. For simplicity, the mortality rate, which affects carbon content and therefore buoyancy, includes respiration, excretion and predation loss. Details about biological processes can be seen in Section S3.3, Supporting Information.

Table 1

State Variables	Units	Value
X Y Z PC PN PP d _c ρ _{colony}	m m g C agent ⁻¹ g N g C ⁻¹ g P g C ⁻¹ m kg m ⁻³	Variable Variable Variable Variable Variable Variable Variable Variable

2.2.2. Transport processes of the agent

In the original ABM transport equations, advection and windinduced mixing terms were included, along with the surface wind drift on surface scum under low wind conditions. When the wind speed exceeded a critical value, approximately 3 m/s (Webster and Hutchinson, 1994), and even though surface cyanobacterial cells tended to be distributed in the deeper layer, they were still transported by Stokes drift generated by wind-induced waves (Hua et al., 2016). Therefore, the optimized pyhsical dynamics of the cyanobacterial communities is:

$$X(i, t + \Delta t) = X(i, t) + Udt + U_{additional}dt + \xi_t \sqrt{2D_H(i, t)\Delta t}$$
(2)

$$Y(i, t + \Delta t) = Y(i, t) + Vdt + V_{additional}dt + \xi_t \sqrt{2D_H(i, t)\Delta t}$$
(3)

$$Z(i,t+\Delta t) = Z(i,t) + W_s dt + D'_V(Z(i,t))dt + \xi_t \sqrt{2D_V(Z')}\Delta t$$
(4)

where *X*, *Y* and *Z* are the agent locations. *U* and *V* are the passive current-induced horizontal velocity terms, and W_s is the buoyancycontrolling velocity (i.e. ISP). D_H represents the horizontal dispersion coefficients ($L^2 T^{-1}$). ξ_t is an independent normally distributed random variable with zero mean and unit variance. The second and third terms on the right-hand side of Eq. (2) and Eq. (3) represent horizontal displacement of agent (i.e. HDT). For the third and fourth terms on the right-hand side of Eq. (4), we chose the Visser (1997) scheme as the random-walk vertical mixing scheme to describe the vertical turbulence-induced displacement of colonies (i.e. VMT). D_V $(L^2 T^{-1})$ is the vertical diffusivity and $D'_V = D_V/dZ$ is the vertical gradient of $D_V.Z' = Z(i,t) + 1/2D'_V(Z(i,t))\Delta t$ is the vertical position that is displaced as a function of the diffusivity gradient. The details about surface wind drift and wave-induced Stokes drift can be seen in Section S3.3.5, Supporting Information. W_s , the buoyancycontrolling velocity (termed ISP), is the adaptive biological trait of Microcystis for higher growth rate. This adaptive behaviour was estimated using a modified Stokes' law, which reproduced the observed vertical behaviour of floating up or down. We calculated an equilibrium speed of the agent, which was related to density and diameter of colonies:

$$W_{s} = \begin{cases} \frac{gd_{c}^{2}(\rho_{w} - \rho_{col})}{18\vartheta} \\ \frac{gd_{c}^{2}(\rho_{w} - \rho_{col})}{18\vartheta} \\ \frac{\sqrt{\left[\left(\frac{24}{Re} + 0.124\right)^{0.5} + 0.352\right]^{2}}}{\sqrt{\left[\left(\frac{24}{Re} + 0.124\right)^{0.5} + 0.352\right]^{2}}} \end{cases}$$

for $d_c < 400 \ \mu m$

for
$$d_c > 400 \ \mu m$$

(5)

where d_c is the equivalent diameter of the colony (assumed to be spherical), called colony size. Changes to the morphology of cyanobacteria (i.e. d_c) are related with agent size (i.e. agent biomass) and details can be seen in Section S3.2.5, Supporting Information. As carbon content of agent increasing, the diameter of colony in each agent increased. g is the acceleration due to gravity, ϑ is the viscosity of water, and ρ_{col} and ρ_w are the density of the *Microcystis* colony and the water, respectively. In this version, the non-linear drag was added on Stokes' drag coefficient to avoid the overpredicted rising/sinking velocity of large colonies (>400 µm) with high Reynolds numbers (Medrano et al., 2013; Portalier et al., 2016). Re is the Reynolds number and was approximately estimated as $\frac{\rho_{col}d_c}{R_{col}}$ $\frac{gd_c^2(\rho_w - \rho_{col})}{R_{col}}$, overlooking the recursive relationship between speed and drag. In previous studies, density changes were incorporated as a function of light regime, without considering the influences of temperature and nutrients at an annual scale. Thus, the density equations used here were those of Rabouille et al. (2005), in which the fluctuations of colony density resulted from the dynamics of carbohydrate reserve metabolism (see Section S3.3.6, Supporting Information).

2.3. Data acquisition and statistical analysis

Every 3-h meteorological data were downloaded from http:// www.meteomanz.com. The discharge and water quality data (such as nitrogen, phosphorus, and detritus) of inflow rivers around lakes were collected from 2008 to 2009. The monthly surface (at depths of 0.5 m) biomass of *Microcystis* were recorded in Meiliang Bay, which is the bloom-influenced domain of the lake (Fig. 1). In Eulerian model, the simulated results of temperature, cyanobacteria biomass and nutrient concentration were compared with these measured data in the Supporting Information. The calibration and validation period of Eulerian module are in 2008 and 2009, respectively.

To detect the appearance of blooms in this large lake, cyanobacterial bloom events were obtained from satellite images from April to October in 2008. A total of 20 treated remote sensing images (MODIS) were obtained from the Lake-Watershed Science Data Center, National Earth System Science Data Sharing Infrastructure, National Science & Technology Infrastructure of China (http://lake.geodata.cn). The treated remote sensing images only demonstrate the spatial bloom distribution (green color) on water surface without information about Chlorophyll a concentration. A bloom case is assumed to be detected in remote sensing images when Chlorophyll a (*Cha*) exceed $20 \,\mu g/L$ (Qin et al., 2015). In ABM, the cumulative effect of all the agents was considered when calculating the mass budget from agent pools (PC) to the concentration for bloom detection. The local mesh will be dyed to green (such as a series of pictures in Fig. 3B) when calculated Cha in surface layer exceeds 20 $\mu\text{g/L}.$ The ABM-based model skill assessments were conducted using a binary categorical variable (bloom or no bloom), by comparing pixel-by-pixel the modelled bloom map with remote sensing observations. The skill assessment statistics of Rowe et al. (2016) was applied in this study. The frequency bias (B) gives the ratio of the number of forecasts of occurrence to the number of observed occurrences:

$$B = \frac{a+b}{a+c} \tag{6}$$

where the number of *a*, correctly predicted events (hits); *b*, false events (false alarms); *c*, false negatives (misses); and *d*, correct nonevents. An unbiased forecast has a frequency bias B = 1.0. The Pierce skill score (*PSS*) gives the hit rate minus the false alarm rate:

$$PSS = \frac{ad - bc}{(a+d)(b+c)}$$
(7)

PSS ranges from -1.0 to 1.0, with positive values indicating that the hit rate was greater than the false positive rate; thus, the model had acceptable skills. The pixel setting and skill assessment were achieved by MATLAB programming (details provided in the Section S4, Supporting Information).

A principal component analysis (PCA) was conducted to cluster the bloom events based on different types of characteristics of blooms. Five characteristics have been used in PCA, i.e. biomass (PC), colony density (ρ_{col}), turbulence-induced mixing velocity of colony (VMT), horizontal drift velocity of colony (HDT) and buoyancy-controlling velocity of colony (ISP). Analysis of similarities (ANOSIM), which is a non-parametric statistical method, was used to test the significant difference between clusters. Canonical correlation analysis (CCA) was performed to determine the relationship between significant environmental variables and bloom composition (Wang et al., 2017a). Wind speed, light, water temperature, nutrients (DIN and DIP) and water level were used for significant environmental variables in CCA. The surface bloom characteristic describes bloom composition. The surface bloom characteristic in CCA represented all of the associated auxiliary processes of Microcystis calculated in ABM model. The associated auxiliary processes contained carbohydrate reserve process, intracellular nutrient uptake rate, growth rate, mortality rate, HDT, VMT and so on. PCA, ANOSIM and CCA analyses were carried out using R 3.4.0 software.

2.4. Model application

2.4.1. Model evaluation

The calibration and validation of the Eulerian model with cyanobacteria biomass are presented in Section S1 and Section S2, Supporting Information, which supply associated physiological parameters and water quality variables for the following ABM. A certain number of particles were released at the beginning of the simulation in each water-covered mesh, excluding the plantcovered meshes. The collection of agents and implementation of ABM are shown in Section S3 and S4, Supporting Information. We then ran the ABM to produce a one-year simulation (output at hourly intervals) to evaluate the model performance (bloom coverage in surface layer of local mesh) against detected 20 bloom mapping pixel-by-pixel. The cell-centred tracer control elements were used as control volumes for converting total agent size to the concentration of Chlorophyll a, *Chla*.

2.4.2. Hindcast simulation

Based on the established model, numerical scenarios were conducted to separate the influence of physiological and physical processes of Microcystis colonies on surface bloom formation. To identify the individual contribution of ISP, VMT, and HDT on the occurrence of CyanoHABs, we carried out four groups of scenarios, which are shown in Table 2. The individual components of ISP, VMT, and HDT were embodied or neglected by ABM for the entire annual simulation. All scenarios were conducted with the same external boundaries and model parameters. C0 was the calculated concentration, which should be validated against the field investigated data. The differences between the calculated results of each scenario and CO indicate individual contributions. For all scenarios, the biological processes, which describe the growth and death of agents, were included. This simple additive method can quantify the relative importance among different factors, although interaction between factors exists.

Table 2	
Calculation schemes to identify the individual impacts of HDT ISP	and VMT

Scenario	Result (bloom area)	Influencing weight calculation	Individual fa	Individual factor	
			ISP	VMT	HDT
Α	СО	_	1	1	1
В	C1	$\gamma_{\text{HDT}} = \frac{C1}{C1 + C0 - C2 + C0 - C3 }$	-	-	1
С	C2	$\gamma_{\rm ISP} = \frac{ c0-c2 }{c1+ c0-c2 + c0-c3 }$	-	1	1
D	C3	$\gamma_{VMT} = \frac{ C0-C3 }{C1+ C0-C2 + C0-C3 }$	1	_	1

3. Results

3.1. Summary of skill statistics of the model ensemble

Our previous paper showed that 1-D random walk simulations reasonably approximate the changing vertical distributions of *Microcystis* colonies in response to varying turbulence. In the current study, we advanced this work to test whether the inclusion of biological process in the coupled model could be utilized to predict the occurrence of spatial blooms in a large shallow lake.

Fig. 2A shows the statistical value of biomass calibration in the Eulerian model, whereas Fig. 2B shows the time series of biomass concentration. The time and intensity of biomass peak was well captured, whereas the deviation of the modelled and measured values during the period of calibration and validation was acceptable (Fig. 2). The calibration and statistical evaluation of other water quality variables are presented in Section S2, Supporting Information.

The Frequency bias (B) and Pierce skill (PSS) of 20 scenarios during April to October are shown in Fig. 3A for the 2008 simulation. The Pierce skill score (PSS) produced positive values in all cases. Positive values of PSS indicate that the model was more effective than a random forecast or constant bloom or no-bloom prediction (Hogan and Mason, 2012). The frequency bias remained within a reasonable range. The frequency bias was larger than 1.0 for 13 out of the 20 scenarios, indicating an overall bias towards over-prediction. For simulations 11, 12, 13 and 15, large frequency bias represented oversized simulated blooms. Both indicators showed that our ABM model performed well in most cases.

To test whether the model was able to match the observed spatially varying bloom coverage by MODIS, pixel-by-pixel comparison of a selected simulation day for one scenario per month was conducted (Fig. 3B). Fig. 3B compared the number of pixels that are flagged as likely having cyanobacterial blooms. The critical wind intensity for bloom formation in Lake Taihu is 3.2 m/s (Cao et al., 2006). Large bloom coverage was detected on 19 May, which was a calm day (wind = 1.2 m/s) with intense events throughout the western region (B = 1.19; PSS = 0.6374). The calm wind coupled with enough biomass (seen in Fig. 3B) contributed to this phenomenon. In the following scenario in June, wind increased to 4 m/s, and both MODIS and model indicated reduced surface bloom intensity $(B = 1.11; PSS = 0.2565, 164.5 \text{ km}^2)$. In simulation 11 (27 July) and simulation 13 (26 Aug), wind speed decreased to 2.4 m/s, and oversized simulated bloom coverages were depicted in the western region (B = 1.8359 and 1.4637, respectively). In simulation 16 (18 September), optimum water temperature contributed to the peak in biomass (Fig. 3B). A subsequent easterly calm wind (2.4 m/s) caused the surface bloom to expand (500 km²) toward the northwesterly part of the lake (B = 1.0807; PSS = 0.596). Unfortunately, the emergence of blooms in Meiliang Bay were missed in our model. On 14 Oct (simulation 19), a persistent easterly wind (1.2 m/ s) induced a severe bloom outbreak in the entire area of Meiliang Bay, which was captured by our coupled model. The performance of coupled model for bloom size was acceptable, as seen in Fig. 3C. Comparison of spatial simulation results and detected bloom mapping for all 20 MODIS images are shown in Fig. A7. Therefore, the changing map and size of bloom over long-time scale (from April to October) were successfully captured in most cases,



Fig. 2. (A) Taylor diagram of biomass of *Microcystis* during the calibration (2008) and validation (2009) periods: correlation coefficient, standard deviation, and root mean square differences (RMSD). (B) Modelled and measured time series of biomass of *Microcystis* in MLB in 2008 and 2009. Error bars represent the standard deviation of triplicate samples.



Fig. 3. (A) Statistics evaluating the performance of the Euler-Lagrangian coupled model in simulating the spatial-temporal coverage of cyanobacterial bloom of 2008 year. The plot symbol indicates the simulation day, when surface blooms were detected by MODIS from April to October. Positive Pierce skill score indicates greater skill than a random forecast. Frequency bias of 1.0 indicates the same number of bloom pixels was predicted as observed. (B) Comparison of spatial simulation results (right) and detected bloom mapping (left). In the detected bloom mapping, green colour represents the area where bloom happened. In the spatial simulation results, the local mesh will be dyed to green when calculated Chlorophyll a (*Cha*) in surface layer exceed $20 \,\mu$ g/L. The picture of modeled results and corresponding remote sensing images are compared based on the same pixels. X indicates selected simulation day for one scenario per month. (C) A time-series evaluation of the size of blooms using the satellite images and coupled model. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

although over prediction exists. Overall, both the skill assessment and pixel comparison showed that our coupled model was able to simulate changing surface blooms in response to changing current/ wind-induced movement and physiological status of Microcystis.

3.2. Statistical analysis of bloom characteristics and relationship with environmental conditions

Our coupled model could record the physiological value of surface blooms, such as biomass, colony density, and ISP, while also capturing temporally varying physical value of blooms as VMT and HDT. Therefore, these five variables were used to distinguish 20 sets of surface Microcystis blooms in PCA. When data from the modelled results within the lake were analysed by PCA ordination, the bloom community formed two clusters (Fig. 4A). The first three principal components, Axis1, Axis2 and Axis3, explained 37.5%, 25.28% and 23.16% of total variance, respectively. Thirteen of the simulated blooms (red circles in Fig. 4A) were clustered in one community, and were strongly associated with VMT and HDT of surface Microcystis. The other seven simulated blooms (blue circles in Fig. 4A) were clustered as a single separate community, which was strongly associated with biomass, density, and ISP. The p-value which calculated by ANOSIM equaled 0.017. The low p-value demonstrated the significant difference between two clusters. The former cluster primarily contained blooms from April to June (except for bloom 19 and bloom 20), whereas the latter cluster contained blooms from July to October. CCA was used to analyse the relationship of environmental conditions with bloom composition (Fig. 4B). The CCA model accounted for 48.1% of variation in the bloom composition data. The first two axes explained up to 37.67% (axis 1) and 10.31% (axis 2) of variation. The variables that were most strongly correlated with these axes were DIN. light, and water temperature (as shown by the arrows length in Fig. 4B). Similarly, the first axis of the CCA separated the communities of early bloom events (left part of the graph) from late bloom events (right part of the graph). Early blooms were associated with abundant DIN, high solar radiation, and high temperature. Mature blooms were positively associated with water level and DIP, and were negatively associated with light and temperature. Additionally, wind during bloom period, with shortest arrow length, explained the least variation.

3.3. Contribution of physiological and physical processes to bloom formation

The results of hindcast simulations carried out within whole lake were analyzed to assess the contribution of HDT, ISP and VMT to surface scum area during different bloom stages (Fig. 5). During early bloom stage, HDT and VMT account for bloom occurrences, 33.3% and 43.3% respectively. Otherwise, ISP has the least influence on bloom area extension, 29.8%. As time goes on, VMT and ISP control 82.4% of bloom formation, 55.1% and 27.3% respectively. However, the importance of HDT decreases to 17.6%. Overall, vertical turbulence-induced mixing had the largest impact on bloom formation during the whole bloom stage in the shallow lake. Results of scenarios analysis for all 20 bloom cases are shown in Fig. A8. Smaller (even no) area of bloom happened for most cases when turbulence-induced mixing velocity of agent (VMT) was excluded. An example of a spatial distribution map (bloom 16) was used to reflect the importance of VMT. Fig. 6 shows the spatial distribution of surface blooms under different scenarios at 11:17 on 18 September 2008. Scenario A shows the baseline of the simulation, considering all HDT, VMT, and ISP. A large section of the bloom (approximately 500 km²) was simulated in the northern part of the lake. Scenario B shows the modelled results when considering only HDT. Colonies always remained at the depth at which they were released. A bloom was only detected in the southwestern nearshore region of the lake. Scenario C shows a larger bloom area in



Fig. 4. (A) PCA analysis based on the occurrence of 20 blooms in 2008, according to the physiological and physical characteristics of surface bloom. Numbers within parentheses are the percentage variance explained by each principal component. The low *p*-value, calculated by ANOSIM method, represents the significant difference between these two clusters. All blooms were categorized into two clusters, which are represented by circles. Red and blue circles indicate different bloom clusters. (B) CCA of surface bloom characteristics and the most significant environmental variables. Symbols indicate blooms and Arrows indicate environmental variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



Fig. 5. Individual contribution of buoyancy-controlling movement (ISP), vertical turbulence-induced mixing velocity (VMT) and horizontal drift velocity (HDT) of 20 bloom cases that occurred in 2008.

the northern region, when only excluding ISP. Interestingly, Scenario D shows no blooms occurring in any part of the lake when only VMT was excluded from the ABM model.

4. Discussion

Cyanobacterial blooms occur as a result of the proliferation and migration of cyanobacteria. Because of the complex interaction between active physiological induced growth and passive physical induced transport, a hybrid of Eulerian and agent-based methods represents a useful tool for resolving this non-linear problem. The Eulerian model incorporated FVOM, FABM, and GEM. The previously calibrated FVOM part of the model provided hydrodynamic forcing, such as water current, temperature profile, and turbulence diffusivity, for each super individual in a local mesh. In addition, the validated physiological parameters, which are conveyed as



Fig. 6. Spatial distribution of surface blooms under different scenarios on 18 September 2008. Scenario A shows the baseline of the simulation, considering all HDT, VMT, and ISP. Scenario B shows the modelled results when considering only HDT. Scenario C shows results when only excluding ISP. Scenario D shows results when only VMT was excluded from the ABM model.

biological processes in ABM, are also supplied by FABM-GEM to avoid high computation costs. To capture the spatial-temporal position of *Microcystis* accurately, we added growth responses, wave-generated Stokes drift, and carbohydrate reserve metabolism based on our original agent-based model (Wang et al., 2017b). We then confirmed that the spatial comparison between the hybrid model results with MODIS and sampling data followed the actual pattern in the distribution of cyanobacteria from a small colony to surface scum, along with horizontal or vertical transport. The rigorous verification process used in this study confirmed that our approach, which incorporated the physiological characteristics of surface cyanobacteria, was able to reflect bloom events under different environmental conditions.

Most published papers have analysed the occurrence or characteristics of blooms using simple linear analysis between bloom area and/or biomass with potential explanatory variables (such as wind and temperature) (Zhu et al., 2014: Wu et al., 2015). However, the relationship between environmental variables and bloom events is indirect and non-linear. The specific characteristics of surface blooms, such as growth rate, vertical velocity, and density, have been consistently overlooked in the analyses of previous studies. This issue might lead to the understanding of physical and physiological processes that regulate blooms at different times being incomplete. Therefore, multivariate statistical analysis was used to disentangle the relationship between bloom events and the specific characteristics of surface blooms based on auxiliary information provided by the coupled model. Horizontal transport speed (HDT, mainly wind-induced) and passive vertical speed (VMT, turbulence-induced mixing) of surface Microcystis blooms were used as the physical features of formed surface scum. Biomass (PC), colony density, and buoyant velocity (ISP) were used as the physiological features of blooms. Interestingly, almost all blooms could be divided into two clusters by these features, i.e. early blooms (from April to June) and mature blooms (from July to October) based on PCA. According to the simulation results, enough biomass had satisfied the requirements for surface bloom formation (20 *Chla* μ g L⁻¹) in bloom-affected area. For early blooms, physical processes of colony acted as the main features that differentiated bloom occurrence (red circles in Fig. 4). The colony size of Microcystis during early summer was comparatively small, with an average of 120 µm being calculated by our model. Small size leads to a low capacity to overcome wind-induced entrainment for staying on the water surface (Reynolds et al., 2001; Otten et al., 2012; Wu et al., 2015). According to model simulation, turbulence-induced mixing velocity was much higher than buoyant velocity during early summer (Fig. A6(A)). Therefore, early blooms were more sensitive to physical forcing, with turbulence-induced mixing and advection-induced accumulation being important influences on surface accumulation and extension (i.e. bloom area). For mature blooms, physiological processes (i.e. biomass, ISP, and density) acted as the main features (blue circles in Fig. 4). For mature bloom stages, colony size increased with increasing biomass induced by cell division and cell adhesion by extracellular polymeric substances (Xiao et al., 2017). Average colony size of surface blooms was calculated as 300 µm in our model. Turbulenceinduced mixing velocity and buoyant velocity were comparable, due to the stable water profile. Consequently, enough large colonies could remain at the water surface, as long as they had buoyant status. The colony density from April to October was lower than the water density in our simulations (facilitating persistent buoyancy). However, protracted exposure to high solar intensity at the water surface when water conditions were stable and colony size was large might lead to the formation of heavier colonies in late summer than in early summer (Fig. A6(B)). This suggestion is consistent with the results obtained by Wallace et al. (2000). Heavier colony density might lead to lower flotation velocity according to Stokes law. Therefore, buoyancy-controlling strategies are required for mature bloom diversity. Hindcast simulations using our coupled model helped us to identify the contributions of these processes. For instance, as shown in Fig. 5, the importance of horizontal drift and buoyant velocity alternates with one another during whole bloom stage.

It is difficult to identify a single environmental variable that explains the timing, intensity and area of all surface blooms that occurred in the shallow lake. CCA allowed us to classify the key environmental variables regulating the occurrence of early and late blooms. Sufficient biomass is the basis of surface scum (Paerl et al., 2011a). Therefore, light and temperature are important for biosynthesis in the early stages of bloom formation. Warmer water temperature and increasing global radiation, which are related with climate change, are the main factors controlling the growth of colonies and the initiation of blooms (Kanoshina et al., 2003; Zhang et al., 2012). Lake warming results in extra buoyancy that sustains blooms for longer, and might be associated with vertical stratification. According to model results, nitrogen limitation emphasised the importance of DIN, supporting the results of Paerl et al. (2011b). Paerl et al. (2011b) showed that nitrogen is an essential nutrient regulating the biomass of cyanobacteria in Lake Taihu. For the mature bloom stage, sustained suitable temperature and irradiation guaranteed the maintenance of sufficient biomass. Phosphorous limitation has been emphasized in mature stages, supporting Paerl et al. (2011b). The optimum temperature for Microcystis in our calibrated model was set as 28.2 °C. Temperatures that were too high in August were accompanied with smaller bloom area (Fig. A6(C) and Fig. A6(D)). In addition, relatively lower radiation prevented colonies from forming high densities, favouring their protracted retention on the water surface. Therefore, there was a negative relationship between light and temperature with bloom occurrence during the mature bloom stage in CCA. Wind is a very important forcing parameter for bloom formation and extension (Verhagen, 1994; Wu et al., 2015). Because of the general low wind speed during bloom events, the importance of wind was weak in the CCA. However, wind has a strong influence on both the physical and physiological processes of blooms, which is discussed in following section. Therefore, multiple environmental variables influence the formation of the different stages of bloom occurrence in the study shallow lake, demonstrating its sensitivity to environmental change.

Wind-induced turbulence, which produces the VMT of cyanobacteria, has been emphasized by hindcast simulation in Lake Taihu. Turbulence has direct and indirect effects on bloom formation. Direct effects represent the entrainment of colonies within the vertical water column. For early bloom stages (as shown by the PCA), turbulent-induced mixing velocity of colony has an important influence on the surface accumulation of colonies and, then, area extension. Indirect effects involve vertical mix causing agents to experience different light intensities within the mixed layer, avoiding self-contained buoyancy control. When colonies are entrained into the mixed layer, the loss of light decreases carbon fixation and, hence, ballast accumulation. Therefore, colonies always maintain a buoyant status (as shown in Fig. A6(B)), enhancing their ability to override vertical turbulence, and allowing them to accumulate on the water surface when the wind ceased. Persistent buoyancy followed by bloom formation has been documented by previous studies (Wallace et al., 2000; Ma et al., 2016; Rowe et al., 2016). In addition, the transient response time (τ_r) also helps to avoid the accumulation of too much ballast on the water surface (Wang et al., 2017b). Without vertical mixing, the vertical movement of colonies is only controlled by buoyancy-controlling strategies to avoid becoming mixed in the deep layers. However, this phenomenon cannot be used to interpret the occurrence of monitored blooms at noon versus night time in deep lakes or reservoirs (Serizawa et al., 2010; Chien et al., 2013). Bloom 16 in Fig. 6 shows a general trend of smaller bloom area when VMT was excluded. Therefore, we inferred that VMT is essential for maintaining the buoyancy of colonies and blooms over long periods in shallow lakes. VMT can account for 52.9% of bloom formations as seen in Fig. 5. Interestingly, we can conduct a more in-depth comparison of onshore/offshore blooms through scenarios simulation, along with the actual MODIS data. The obvious downwind accumulation (onshore bloom) was caused by HDT (mainly wind-induced advection, as seen in Scenario B of bloom cases). When only excluding ISP, colonies have poor capability to stay on water surface. The offshore bloom could appear with the existence of VMT (as seen in Scenario C of bloom cases). The wind entrainment can prevent the downwind movement according to our former study (Wang et al., 2017b). The net effect of increasing wind was shown to reduce horizontal transport. Therefore, the turbulence-induced mixing is critical for offshore bloom. This finding is useful for understanding the distribution pattern of surface bloom in large domain. In general, our study provided in-depth finding about the respective importance of physical and physiological feature of cyanobacteria for onshore/offshore bloom formation at different stages.

The model was developed under the Euler-Lagrangian coupled framework, and used Lake Taihu as a case study; this coupled model could be applied to other shallow lakes by adjusting input conditions and initial values of the super-agent. The shallow region of Lake Erie is approximately 5 m, requiring a stronger wind to completely mix the water column. Therefore, the fitness of our finding to this lake could be carefully tested by using our coupled model. However, possible limitation for transferability of the findings to other lake should also be discussed. Firstly, our conclusion about the relative importance of physical and physiological features is only suitable for the shallow area without rooted aquatic vegetation, such as Missisquoi Bay (mean 2.8 m) (Ndong et al., 2017) and Thomsons Lake, a shallow (max. depth 1.4 m), flat bottomed lake (Wallace et al., 2000). Secondly, our coupled model is fit for the Microcystis-dominated bloom. The transferability to Anabaenadominated (Hellweger et al., 2008) or Diatom-dominated bloom is unfeasible.

5. Conclusions

In this study, we used satellite images as a data source and a coupled model as a form of technology to extract information on cyanobacterial blooms in Lake Taihu, China. In particular, we analysed bloom characteristics and their complex correlations with climatic variables. The idea about the generation of onshore and offshore bloom was also evaluated by using scenarios analysis in hindcast simulation. Our study demonstrates that retrieving ecological information from agent-based modelling is valuable for the large-scale research of fresh water ecosystems, despite parameter uncertainties and the complexity of aquatic systems. Our future work will focus on the identification of on-set bloom for advanced bloom prevention, which needs more long-time remote sensing images coupled with elaborately integrated model (such as WRF-FVCOM-ABM modeling system). Meanwhile, shallow lakes are a complex system, and the interaction between sediment and water was not presented in our model, but will be considered in subsequent studies.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.watres.2018.04.018.

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