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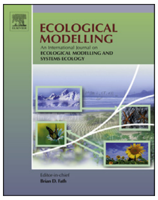

Understanding the transport feature of bloom-forming *Microcystis* in a large shallow lake: A new combined hydrodynamic and spatially explicit agent-based modelling approach

Chao Wang[a,b], Tao Feng[a,b], Peifang Wang[a,b,*], Jun Hou[a,b], Jin Qian[a,b]

[a] *College of Enviroment, Hohai University, Nanjing 210098, People's Republic of China*
[b] *Key Laboratory of Integrated Regulation and Resource Department on Shallow Lakes, Ministry of Education, Hohai University, Nanjing 210098, People's Republic of China*

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ABSTRACT

Understanding the complex transport feature of phytoplankton is important for predicting bloom-forming process. In this study, a coupled hydrodynamic and agent-based approach is developed to characterise the transport behaviour of colony-forming *Microcystis* in a large shallow lake. Two models are combined: a hydrodynamic model to offer a basic flow field, and an agent-based model to incorporate the physiological response (buoyancy-controlling strategies) and migratory behaviour (horizontal advection and random-walk vertical mixing) of *Micorcystis*. The Meiliang Bay in Lake Taihu, which experiences high *Microcystis* blooms every year, was chosen as a case study to test the performance of this coupled approach. By comparing our coupled model with available field measurement, our results can reproduce changes in buoyancy status and three-dimensional distribution exposures to different wind intensities. Meanwhile, our coupled model shows more accurate results than the simulated results from traditional Eulerian approach. In shallow lake systems, strong wind (>6 m/s) can easily mix water column and keep most colonies buoyant. Subsequent gentle wind (<3 m/s) causes more intensive horizontal accumulation of these buoyant *Microcystis* in the downwind area than what happens under strong wind. Small colonies are readily dispersed by wind-induced turbulence and homogenized by local current circumstances. Diurnal temporary stratification and large colony sizes contribute to surface patches formation and downwind migration, leading to the heterogeneity of *Microcystis* bloom under the integrated effect of surface currents and wind drift. Therefore, the transport pattern of *Microcystis* colonies is a dynamic balance between turbulence and wind drift, along with buoyancy which is related to colony size. Overall, our combined model could be used to characterise the detailed movement patterns of *Microcystis* colonies or patches in large shallow lakes.

1. Introduction

Microcystis bloom, which interferes with recreation, water supply and aquatic life, has emerged as one of the most severe ecological problems affecting large and shallow freshwater lakes (Paerl and Huisman, 2008). This has focussed research attention on the physiology and behaviour of *Microcystis*, notably from the perspective of predicting blooms and developing effective engineering countermeasures(Qin et al., 2015). Some researchers have highlighted the link between nutrient levels and *Microcystis* blooms (Xu et al., 2010; Paerl et al., 2011; Ma et al., 2014). Other studies indicate that physiological characteristics of *Microcystis* and hydrodynamics conditions are also critical factors. Buoyancy-controlling strategies have been shown to be effective in controlling the vertical migration that underlies the success of endemic species over green algae and diatoms (Wallace et al., 2000; Chien et al., 2013; Medrano et al., 2013). In addition, wind-induced vertical entrainment and water flow affect the living behaviours of *Microcystis* (Ishikawa et al., 2002; Cao et al., 2006; Moreno-Ostos et al., 2009; Blottière et al., 2014). Shallow lake systems are characterised by horizontal wind-induced currents and evident vertical turbulence. The potential dynamic feedback between hydrodynamic features and the blooming behaviour of *Microcystis* is clear, leading to high degree of spatial-temporal variability of *Microcystis* (Wu et al., 2013, 2015). Therefore, the spatial-temporal motion of *Microcystis* in shallow

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[*] Corresponding author at: Hohai University College of Environment No. 1, Road Xikang Nanjing, Jiangsu 210098, PR China.
E-mail address: pfwang2005@hhu.edu.cn (P. Wang).

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lakes should be investigated in detail to emphasize the role of these covariant influences.

Some field observations have focused on the spatial distribution of *Microcystis*, relating bloom formation in specific areas of lakes to horizontal migration from currents or wind. George and Edwards (1976) demonstrated that horizontal heterogeneity exists in the distribution of lake plankton. The wind history and subsurface illumination are the major factors that control the surface accumulation of blue-green algae in downwelling regions. Ishikawa et al. (2002) examined the gyre-*Microcystis* hypothesis, in which buoyant *Microcystis* colonies readily accumulate in the downwelling center of the gyre through large-scale horizontal hydrodynamic processes. A site investigation of the horizontal motion of *Microcystis* under the influence of wind and currents was conducted by Wu et al. (2010). This study suggested that the horizontal distribution of *Microcystis* is mainly governed by wind drift on shaped surface algal patches. All three of these studies stressed the importance of low wind fetch, high floating speed and locally horizontal circulation on the distribution of *Microcystis*. However, their reliance on traditional and overloaded sampling narrowed the descriptions on some particular areas and overlooked an elaborate description of migration with high temporal resolution. In addition, the point-to-point studies mentioned above failed to isolate the effects of three processes, namely wind-induced turbulence, flow advection, and the self-regulatory motion of cyanobacteria. Numerical modelling technique is another method to study the drift pattern of cyanobacteria, which could easily incorporate the hydrodynamic environment and physiological characteristics of *Microcystis*.

Existing models of phytoplankton motion are typically based on the traditional Eulerian approach to describe concentration distributions of cumulative individuals, assuming that colonies at the same position have same properties. The Eulerian approach is also known as lumped-system model (LSM). To date, only constant vertical migration speeds have been simulated. It failed to track the density changes in cell subjected to diurnal solar intensity, i.e., buoyancy-controlling strategies (Verhagen 1994; Fragoso et al., 2008; Huang et al., 2012). In describing more complex ecological processes, the most popular methods ignored both individual adaptions to local environment and natural internal variability. Aquatic cyanobacteria occur as planktonic cells or colonies or form phototrophic biofilms (algal patches) under certain conditions. Though *Microcystis* exists mainly as isolated cells or small colonies during initial growth, it can form large colonies or surface patches at the mature stage of blooming. Its transport patterns are diverse, depending on the different morphology of *Microcystis* (Deng et al., 2016). So far, our understanding on the effect of different factors, such as light, wind fetch and currents, is inadequate. Therefore, more comprehensive descriptions of the accumulation and transport of *Microcystis* in large shallow lakes are still lacking.

Fortunately, agent-based concepts provide a way to solve this problem in this system by coupling a particle self-identity tracking model with a hydrodynamic model (Eulerian method) (Grimm et al., 2006, 2010; Hellweger et al., 2008; Henrichs et al., 2015). Agent-based (otherwise known as individual-based) models (ABM) have been proved valuable in describing the complex life cycle of cyanobacteria and in considering the random-walk transport and internal variability, as described in Hellweger et al. (2008). A suitably assembled agent-based model should therefore be able to describe the transport trajectories of *Microcystis* with different properties in large shallow lakes and could be utilised to solve two critical problems: (1) whether the coupled Eulerian and agent-based model (EAM) can be applied to reproduce the observed *Microcystis* behaviour in three-dimensional shallow environment? (2) how does the interaction between buoyancy-controlling strategies and migratory behaviour (horizontal advection and random-walk vertical mixing) influences the transport process? We developed a coupled model and chose Meiliang Bay in Lake Taihu as a case study to simulate several short-timescale scenarios to assess these questions. The objectives of this study are: (1) to prepare and validate a coupled hydrodynamic and agent-based model, thereby integrating the physical and physiological parameters that influence the transport of *Microcystis*; (2) to take advantage of our coupled model to unravel the transport features under different physical and physiological conditions in shallow lakes.

2. Methods

2.1. Study area

Lake Taihu (30°55′40″–31°32′58″ N; 119°52′32″–120°36′10″ E), located in the lower part of the Yangtze River Delta, is a well-known large, shallow, and eutrophic lake (Fig. 1). The northwest regions of Lake Taihu(i.e., Meiliang Bay, Zhushan Bay)suffer from frequent algal bloom due to the special location of heavily polluted influent rivers (Hu et al., 2006).

Meiliang Bay covers an area of about 120 km^2 with an average depth of 1.95 m and is an important source of drinking water. The severe cyanobacterial blooms occur between April and October. The algae begin to recover from sediment and aggregate in spring (April and May) before mass propagation during the mature blooming stage in June–October (Kong and Fao, 2005; Cao and Yang, 2010). The cyanobacteria are primarily *Microcystis* spp., a colony-forming cyanobacterial species consisting of mucilage, gas vesicles, and cells (Qin et al., 2015).

Wind is a key driving force for the hydrodynamic and material transport processes in Lake Taihu. Easterly winds (45°–135°) prevail between April and October. Winds with velocities less than 2 m/s, 2–6 m/s, and greater than 6 m/s are qualified as calm, gentle, and strong respectively (Wu et al., 2013).

2.2. Hydrodynamic model of Lake Taihu

The hydrodynamic model is based on the solution of the incompressible Reynolds-averaged Navier-Stokes equations subject to the hydrostatic and Boussinesq approximations. A detailed description of the hydrodynamic model, including the model equations, parameters, bathymetry and computing mesh, can be found in Section S1, Supporting information. To assure convergence and accuracy, the second-order semi-implicit scheme based on a cell-centred finite-volume framework was utilized to solve the time-dependent spatial distribution of the key hydrodynamic variables (Jameson and Mavriplis, 1986; Bassi and Rebay, 1997). A total of 11072 active unstructured triangular elements were employed in the horizontal plane, which ranged from 0.07 km^2 to 0.47 km^2. A fine mesh was used for the smaller localized region of interest in Meiliang Bay. A vertical sigma coordinate (described in Section S1, Supporting information) with an evenly distributed fifteen-layer system was applied. The time step was set to 1 s to obtain a stable and precise solution. Agent-based model is based on the modelling of hydraulic conditions, so verifying the results of hydrodynamic models is critical to ensure the accuracy of transport simulations. The details of the calibration of the 3D hydrodynamic model are illustrated in Section S2, Supporting information.

2.3. Agent-based model of Microcystis

A detailed description of the agent-based model (ABM) following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010), including the model design and equation, can be found in the following.