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Coupling hydrodynamics and buoyancy regulation in *Microcystis aeruginosa* for its vertical distribution in lakes

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ABSTRACT

In this research we introduce a coupled column model to simulate the vertical migration of *Microcystis aeruginosa* in natural lakes. *M. aeruginosa* is a unicellular cyanobacteria that form colonies. They produce toxins and therefore become a potential threat to water quality and human health. Understanding the distribution of this species in space and time is important for improving water management strategies. The model we propose includes both hydrodynamics and physiological responses including explicitly buoyancy regulation in *Microcystis* cells. Our model applies the Langevin–Fokker–Planck approach to simulate the total colony number concentration along the water column. This approach allows the description of sinking and rising velocities of colonies of different sizes and compositions subjected to turbulent mixing. The model is first applied to the 30 m deep Lake Vlietland in the Netherlands for the summer of 2009. During this summer, the lake showed high blooms of *Microcystis* which eventually led to scum formation along the shore. The simulations show the preferential distribution of *M. aeruginosa* through the water column and their strong dependency on colony size. On a daily cycle, small colonies (50–200 μm) do not remain near the surface but are highly concentrated in the middle of the epilimnion, whereas large colonies (≥800 μm) are able to migrate to greater depths and concentrate only temporarily near the surface. For comparing our computer model with available measurements of *Microcystis* concentration distributions we applied it to Lakes IJsselmeer and Vinkeveen. The results show a good agreement with the observations of diurnal changes in buoyancy status.

1. Introduction

The present research presents a coupled model for the vertical distribution of *Microcystis aeruginosa* in response to light-driven cell density changes and hydrodynamic turbulence mixing. To this purpose we implement a Fokker–Planck equation while simultaneously considering biological assimilation and its effect on density changes in Microcystis cells. At the same time we included a mechanistic model for the density of the colony as a whole by incorporating the gas vesicle to cell volume ratio and the cell volume to colony volume ratio. In the following paragraphs we define the context of our study.

1.1. General introduction

M. aeruginosa is a colony forming cyanobacterial species. A colony is composed by a pack of cells covered by mucilage and each cell contains gas vesicles (Fig. 1). It is a widespread species that can form blooms in freshwaters regardless of the nutrient concentrations (Zohary and Robarts, 1989; Ibelings, 1996; Visser, 1995). Many *Microcystis* strains produce a variety of toxins, of which the so-called microcystins are the best known (Codd, 1999). These microcystins are hepatotoxins that can damage the liver of humans and animals. As a result, *Microcystis* blooms are a world wide serious threat for water quality, ecosystems, fisheries, and human health (Chorus and Bartram, 1999; Codd, 1999).

During summer and at higher latitudes, increasing solar radiation and weak winds create permanent and temporary thermal stratification in sufficiently deep lakes (thermocline formation). The thermocline subdivides the water column in an upper mixing zone (epilimnion) affected by wind-generated turbulence and a lower almost static layer (hypolimnion, Imberger, 1985). After the winter period, in the lake bottom, cysts of several cyanobacteria

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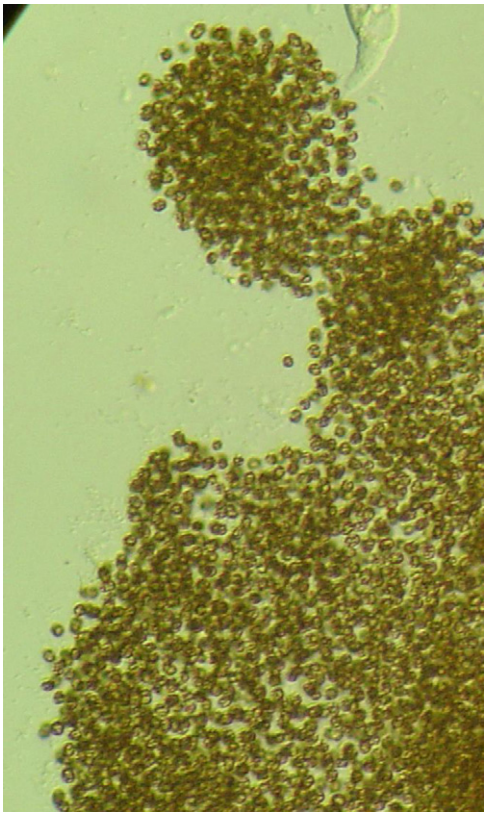

Fig. 1. Microcystis colony. The microscopic picture has been taken by Frank van Oosterhout.

genera develop gas vesicles that allow the cells to enter the water column (Sirenko, 1972; Verspagen et al., 2004). Cyanobacteria grown during spring remain mainly in the epilimnion where they take up nutrients for their further growth.

1.2. Buoyancy regulation mechanism

Cyanobacteria possess a buoyancy regulation mechanism to influence their vertical position along the water column (Ganf and Oliver, 1982). Buoyancy regulation is a property that allows gas vacuolated cyanobacteria to migrate along the water column, moving toward the surface to receive light for photosynthesis and growth and moving downwards to collect nutrients (Reynolds and Walsby, 1975). Cyanobacterial species with gas vacuoles usually belong to the genera *Planktothrix* and *Microcystis* (Walsby, 2005). Observations (e.g. Reynolds et al., 1981) show that in the summer period *Microcystis* colonies mainly remain in the epilimnion (Ibelings et al., 1991), where they take up nutrients, while most phytoplankton species without buoyancy regulation sink in the absence of sufficient turbulent mixing (Huisman et al., 2002).

Initially, vertical migration of *Microcystis* has been explained either by changes in the cell turgor pressure (Reynolds, 1987), by synthesis of gas vesicles (Oliver and Walsby, 1984) or by changes in carbohydrate content (van Rijn and Shilo, 1985; Ibelings et al., 1991; Reynolds, 1984). The turgor pressure hypothesis is less likely to be the mechanism responsible for vertical migration of *Microcystis* due to the high turgor strength of the protein strains around gas vesicles (Walsby, 1994), which makes the cell capable to withstand the pressure existing in a lake. The synthesis of gas vesicles has a low production rate of a few days (Walsby, 1994). According to the carbohydrate hypothesis, the concentration of carbohydrates in the cell tissue depends on the temporal integration of carbon uptake in daytime by photosynthesis and carbon release during the night by respiration. Based on laboratory experiments, Visser et al. (1997) formulated deterministic relations for the rate of cell-tissue density changes to the amount of received light (see Section 2.2). In this study we focus on the carbohydrate mechanism and use the relations of Visser et al. (1997).

1.3. Coupling biology and hydrodynamics

Vertical migration is affected by turbulence mixing directly and also indirectly, by changing their depth level and therefore the light dose received (Humphries and Lyne, 1988). Consequently, for modeling vertical migration under natural conditions, a combination of a density regulation model (Visser et al., 1997) and a model to simulate the hydrodynamics of the lake is necessary. Earlier investigations tried to couple these two factors using various approaches (Howard, 1997; Wallace and Hamilton, 2000; Chen et al., 2009).

Wallace and Hamilton (2000) coupled two models (a buoyancy regulation model and a hydrodynamic model including a random walk for colonies). They successfully applied this methodology to a 1.4 m shallow water body with strong light attenuation. To simulate the actual vertical velocity of the colonies, Wallace and Hamilton (2000) took the sum of the colony vertical velocity due to gravity and the turbulent velocity component along the vertical, a similar procedure was followed by Chen et al. (2009). The latter researchers concluded that colonies are capable of persisting near the surface for several days provided that they are entrained in turbulence long enough for reducing their carbohydrate content and given that carbohydrate uptake is somewhat delayed.

An important aspect of the application of Visser et al.'s (1997) model for the cell-tissue density changes is the determination of the colony mass density (kg mass per m^3 colony volume). Given that the carbohydrate changes were measured in the cell tissue, the volume occupied by cells in a colony and the gas volume present in a cell play a major role in the resulting colony mass density (Rabouille and Salencon, 2005). To our knowledge, this realistic aspect was not considered in the models of Wallace and Hamilton (2000) and Chen et al. (2009). This is the essential improvement and subject of our paper.

Therefore, in this study, an explicit mathematical model description is presented for the rising/sinking velocity of Microcystis colonies that includes gas vesicle to cell volume ratio as well as cell volume to colony volume ratio. This approach allows a generic application of the model of Visser et al. (1997) for cell-tissue density changes. Another aspect is related to the fact that *Microcystis* in the field shows variations in colony size, composition and density which translate into variation in rising/sinking velocities. Rather than tracking individual colonies and afterwards estimating their vertical distribution, we apply a methodology for the ensemble of numerous colonies in which the vertical distribution of colonies is the prime variable. This methodology is based on ensemble-averaging of numerous random-walk tracks yielding the so-called Fokker–Planck equation. The latter we solve in conjunction with a model for turbulent mixing in a thermally stratified lake.

1.4. M. aeruginosa in natural systems

From an observational perspective, the vertical distribution of *Microcystis* reported in the literature (Ibelings et al., 1991) usually shows a top heavy profile during days with low or almost no wind. This profile is characterized by maximum concentrations near the surface reducing along the vertical. During windy days, colonies distributions are nearly uniform along the epilimnion (Moreno-Ostos et al., 2009). Field descriptions of colony size variation along the depth of deep water bodies, however, are scarce. Wu and Kong (2009) have measured *Microsystis* colony size distribution in Lake Taihu (China), a shallow lake of 1.9 m mean