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An alternative explanation for cyanobacterial scum formation and persistence by oxygenic photosynthesis

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ABSTRACT

The cause of persistent cyanobacteria scum formation in lakes is an unresolved subject. Scum refers to the event in which cyanobacteria are at the water surface of a lake. Factors like low turbulence levels, long day-light, high water temperatures and the buoyant capacity of cyanobacterial cells play a role in the occurrence of scums. However, they do not explain why scums are observed at periods during the day when according to theory they should have disappeared into the deeper water layers. In this study, we present an alternative explanation. The hypothesis we present here is that irreversible buoyancy of cyanobacteria colonies is created by the growth of gas bubbles on or within the mucilage of the colonies. These bubbles grow under oxygen super-saturated conditions. At low wind speed and high chlorophyll levels, the dissolved oxygen (DO) produced during photosynthesis by cyanobacteria, cannot escape sufficiently fast to the atmosphere hence a DO supersaturated condition arises in the water. At this stage, growth of oxygen bubbles may occur inside or attached to the mucilage. We present results of compression experiments to support our hypothesis. In a chamber, the pressure on lake water containing a natural cyanobacteria population is increased. At 3×10^5 and 4×10^5 Pa the cyanobacteria colonies were not able to float anymore and sank. This pressure is lower than the 10^6 Pa needed to collapse all gas vacuoles inside the cyanobacteria cells (Walsby, 1994). The observed change from floating to sinking colonies due to increased water pressure suggests that gas bubbles were present inside the colonies. In lakes, these gas bubbles may lead to permanent buoyancy, *i.e.* a persistent scum.

1. Introduction

Generally, eutrophication has a negative consequence for water quality and the aquatic life. A common symptom of eutrophication is the formation of cyanobacteria blooms (Davis and Gobler, 2016; Harke et al., 2016). Blooms are often composed by species that produce toxins. Such toxins can cause damages to animals and humans (Carmichael and Boyer, 2016; Codd et al., 2005). Blooms can also sometimes be the precursors for scum formation. The most common cyanobacteria species that form nuisance scums are *Microcystis* spp., *Planktothrix* spp., *Anabaena* spp., *Aphanizomenon* spp. (Reynolds and Walsby, 1975). Although these genera differ in form, they all appear as colonies composed of cells with gas vacuoles. The cells of many species are embedded in mucilage with different abundances and consistencies per taxa (Reynolds, 2006). Some species like *Planktothrix* produce mucilage (made of exopolysaccharides) under stress situations (Komárek and Komárková, 2004). An important feature of cyanobacteria is their ability to perform vertical migration (rising/sinking) within the time span of a daily cycle via buoyancy regulation (Reynolds and Walsby, 1975). Their ability to regulate their buoyancy is mainly the result of the cell composition. The cells contain gas vacuoles and mucilage is produced around the cells creating colonies (Walsby, 1994; Reynolds, 2006). The cells produce carbohydrates when exposed to light and these carbohydrates in return are respired under dark conditions (Ibelings et al., 1991; Visser et al., 1997). In deep stratified lakes this capability of buoyancy regulation contributes to the success of cyanobacteria in the competition with green algae for light (Huisman et al., 2005). Oxygen gas bubbles in or on the mucilage (a consequence of oxygen supersaturation) described in this study are *not the same* as the

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gas vacuoles inside the cells of cyanobacteria. Gas vacuoles in the cells are rigid structures *i.e.* hardly compressible, fully permeable for diffusion of surrounding gases and capable to withstand high pressures (Walsby, 1994). Gas bubbles are not rigid structures and can grow and collapse.

In this study the formation and persistence of cyanobacteria scums will be discussed. At present a comprehensive understanding of this phenomenon appears to be lacking. We focus on the transition from a bloom to a scum, *i.e.* the stage of scum formation itself.

Previous research identified three conditions that allow for the formation of a scum (Ibelings et al., 2003): 1) an existing population of cyanobacteria (bloom), 2) the presence of buoyant colonies in the bloom, and 3) a stable water column (stratified) with low turbulence intensities. Different hypotheses for the formation and persistence of a cyanobacterial scum have been suggested in the past: 1) the photoinhibition hypothesis (Reynolds and Walsby, 1975), 2) the self-shading hypothesis (Ibelings and Mur, 1992), 3) the carbon depletion hypothesis (Paerl and Ustach, 1982), 4) the extra gas vacuoles hypothesis (Walsby, 1980), 5) the superbuoyancy hypothesis (Walsby et al., 1997), 6) the dead-stage hypothesis (Reynolds and Walsby, 1975), 7) the sudden bloom at the surface hypothesis (Reynolds and Walsby, 1975), and 8) the apparent scum hypothesis (Kromkamp and Walsby, 1990). The previous hypotheses have been discussed in detail in Aparicio Medrano (2014), showing that they are not generally applicable.

Our hypothesis is the following: Scum formation (colonies overbuoyancy) and persistence is due to oxygen bubble growth within the mucilage of cyanobacteria under oxygen supersaturated conditions. Hints on the possible role of bubbles in mucilage of colonies has already been reported by Walsby et al. (1983) in a study on the buoyancy changes of *Oscillatoria Agardhii* in a lake in Norway. However, a further investigation of this possibility has not been pursued by these investigators. To support our hypothesis we present the results of compression experiments (abbreviated as Riebesell experiments) applied to samples from three different lakes in The Netherlands. The hypothesis includes the sequence of events that result in a scum formation and persistence, the photosynthetic oxygen supersaturation, the conditions for bubble growth, and the stability of oxygen bubbles. The section thereafter describes the experiments to support our hypothesis. We conclude with a brief discussion on the implication of scum formation. There are two Annexes at the end of the paper. Annex A describes the conditions for bubble growth. Annex B elaborates on the stability of gas bubbles.

2. Hypothesis for the formation and persistence of cyanobacterial scums

2.1. Sequence resulting in scum formation

Our hypothesis is that irreversible buoyancy of cyanobacteria colonies occurs due to growth of gas bubbles (not the same as gas vacuoles) in or on the mucilage of the colonies. We consider the pre-existence of a cyanobacteria bloom as a first essential condition for a scum to occur (Ibelings et al., 2003).

A cyanobacteria bloom is usually reflected in high chlorophyll concentrations. The result of the photosynthetic activity is oxygen production and an increase in dissolved oxygen (DO) concentrations (assuming that oxygen consumption is low). Although during respiration DO is consumed (Ibelings and Maberly, 1998; Ploug, 2008), several days of blooms and DO production may increase the DO to supersaturation levels. DO supersaturation could only occur due to the presence of a bloom, which is why we consider a bloom as the essential first condition. When the colony occurs in the upper illuminated layers near the surface it will take up carbon and release oxygen due to photosynthetic processes (Ibelings and Mur, 1992; Visser et al., 1997). As a consequence, the heavier colonies migrate downwards to deeper layers where, due to respiration, carbon is released and oxygen is consumed (Hallegraeff, 1993). Consequently, the processes of photosynthesis and photorespiration create a vertical distribution of high oxygen concentrations near the surface and low concentrations at deeper and darker water layers of the epilimnion (Wetzel, 2001).

When the forcing of wind on the lake is weak, this may have two important consequences for scum formation. The exchange of oxygen with the atmosphere will be reduced (Wanninkhof and Bliven, 1991) and the wind-driven turbulent mixing intensity in the water tends to be low. As a second essential condition for scum formation we consider DO supersaturation in lakes in combination with low wind intensities so that vertical mobility of cyanobacteria colonies dominates over their vertical turbulent transport.

As a third essential condition we assume the existence of gas-nucleation sites for bubble growth (Yount, 1982), probably both in and on the mucilage. There are two possibilities for gas-nucleation (formation of a gas-nucleus[1]): homogeneous and heterogeneous. Homogenous gas-nucleation requires a substantial reduction in pressure (about 10^7 Pa) or, equivalently, saturation levels exceeding 1000% that do not occur in lakes. Heterogeneous nucleation can occur on existing surface impurities, gas-nuclei and due to small supersaturation levels that occur in the top layers of lakes (Ramsey, 1962). Therefore, heterogeneous gas-nucleation is feasible on for example a solid surface with gas filled cracks. If the DO supersaturation is such that the partial pressure in water is higher than the pressure inside the (nano) bubble, then bubble growth may occur (Ramsey, 1962), see Section 2.3 for a brief introduction. The required and feasible level of supersaturation (≈140%) occurs near the surface of a lake (Ramsey, 1962), see Section 2.2. The property of vertical migration observed in cyanobacteria allows the colonies to reach the aforementioned layer in a lake.

Finally, the presence of gas bubbles inside colonies will bring the cyanobacteria colonies to an irreversible highly buoyant state ending at the surface and forming scums that persist. Fig. 1 shows the presence of bubbles in a scum taken on July 27, 2009 in Lake Vlietland, near The Hague in the Netherlands. The image shows the latest stage of a scum. The bubbles responsible for scum formation are initially much smaller than the ones shown here as they kept on growing to millimetric size due to the supersaturation oxygen level (>150%).

2.2. Photosynthetic oxygen supersaturation

In the past, oxygen saturation levels often have not been considered as a highly significant parameter in the formation of cyanobacterial scums (*e.g.* Soranno, 1997; Reynolds and Walsby, 1975; Ibelings et al., 1991). Ploug (2008) measured oxygen levels at millimetric scales in an aggregate (surface scum) and showed that the scums contained high O_2 supersaturation levels (210%). These microenvironments of O_2 supersaturation have also been measured in benthic microbial species (Revsbech et al., 1983).

The basics of photosynthesis can be summarized as conversion of CO_2 (and other elements such as nitrogen and phosphorus) into biomass using hydrogen by splitting water and leaving its molecular oxygen (O_2) in suspension. The produced dissolved oxygen gas is diffused through the cell tissue and increases the dissolved gas level in the surrounding water (Ploug, 2008). Some oxygen is consumed during respiration. However, consecutive

[1] Gas nucleus refers to nucleation sites which are, for example, submicron-sized bubbles for the homogeneous case or, for the heterogeneous case, tiny crevices (micron to submillimetric size) where a free gas-liquid surface is maintained.