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# Colony formation in the cyanobacterium *Microcystis*

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### ABSTRACT

Morphological evolution from a unicellular to multicellular state provides greater opportunities for organisms to attain larger and more complex living forms. As the most common freshwater cyanobacterial genus, *Microcystis* is a unicellular microorganism, with high phenotypic plasticity, which forms colonies and blooms in lakes and reservoirs worldwide. We conducted a systematic review of field studies from the 1990s to 2017 where *Microcystis* was dominant. *Microcystis* was detected as the dominant genus in waterbodies from temperate to subtropical and tropical zones. Unicellular *Microcystis* spp. can be induced to form colonies by adjusting biotic and abiotic factors in laboratory. Colony formation by cell division has been induced by zooplankton filtrate, high Pb<sup>2+</sup> concentration, the presence of another cyanobacterium (*Cylindrospermopsis raciborskii*), heterotrophic bacteria, and by low temperature and light intensity. Colony formation by cell adhesion can be induced by zooplankton grazing, high Ca<sup>2+</sup> concentration, and microcystins.

We hypothesise that single cells of all *Microcystis* morphospecies initially form colonies with a similar morphology to those found in the early spring. These colonies gradually change their morphology to that of *M. ichthyoblabe*, *M. wesenbergii* and *M. aeruginosa* with changing environmental conditions. Colony formation provides *Microcystis* with many ecological advantages, including adaption to varying light, sustained growth under poor nutrient supply, protection from chemical stressors and protection from grazing. These benefits represent passive tactics responding to environmental stress. *Microcystis* colonies form at the cost of decreased specific growth rates compared with a unicellular habit. Large colony size allows *Microcystis* to attain rapid floating velocities (maximum recorded for a single colony,  $\sim 10.08 \text{ m h}^{-1}$ ) that enable them to develop and maintain a large biomass near the surface of eutrophic lakes, where they may shade and inhibit the growth of less-buoyant species in deeper layers. Over time, accompanying species may fail to maintain viable populations, allowing *Microcystis* to dominate. *Microcystis* blooms can be controlled by artificial mixing. *Microcystis* colonies and non-buoyant phytoplankton will be exposed to identical light conditions if they are evenly distributed over the water column. In that case, green algae and diatoms, which generally have a higher growth rate than *Microcystis*, will be more successful. Under such mixing conditions, other phytoplankton taxa could recover and the dominance of *Microcystis* would be reduced.

This review advances our understanding of the factors and mechanisms affecting *Microcystis* colony formation and size in the field and laboratory through synthesis of current knowledge. The main transition pathways of morphological changes in *Microcystis* provide an example of the phenotypic plasticity of organisms during morphological evolution from a unicellular to multicellular state. We emphasise that the mechanisms and factors influencing competition among various close morphospecies are sometimes paradoxical because these morphospecies are potentially a single species. Further work is required to clarify the colony-forming process in different *Microcystis* morphospecies and the seasonal variation in this process. This will allow researchers to grow laboratory cultures that more closely reflect field morphologies and to optimise artificial mixing to manage blooms more effectively.

Key words: colony formation, extracellular polysaccharides (EPs), floating velocity, grazing, Microcystis.

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### I. INTRODUCTION

Evolution from a unicellular to multicellular state provides organisms with a greater ability to protect themselves against enemies, and greater potential to evolve into more complex living forms (Carroll, 2001; Yoshida, Hairston & Ellner, 2004). Cyanobacteria are the oldest unicellular organisms, and gradually evolved into multicellular forms including filaments or colonies in the Early Proterozoic (Carroll, 2001).

*Microcystis* is the most common bloom-forming freshwater cyanobacterium and exhibits high phenotypic plasticity. *Microcystis* spp. exist as single cells or (more rarely) as paired cells in axenic laboratory cultures but form colonies under natural conditions (Xiao *et al.*, 2017). *Microcystis* species as presently defined exhibit a variety of colonial morphologies, including irregular, sponge-like, spherical and elongated, and some show a visible margin (Komárek & Komárková, 2002). Thus, they may be suitable model organisms for research into the evolutionary development of multicellularity.

*Microcystis* spp. have a wide distribution at low and middle latitudes (Paerl & Otten, 2013; Harke *et al.*, 2016). Their distribution range is continuing to extend and both the frequency and intensity of *Microcystis* blooms have increased in response to the higher ambient temperatures, CO<sub>2</sub> levels and eutrophication associated with global climate change (Paerl & Huisman, 2009; O'Neil et al., 2012; Visser et al., 2016).

*Microcystis* blooms can initiate a chain of serious environmental and ecological events, causing blockage of drinking-water supply systems, the production of unpleasant odours, reduction of water clarity and removal of dissolved oxygen during decomposition, etc. (Qin *et al.*, 2010). Some species of *Microcystis* are potentially toxic and can produce microcystins; these may pose severe health risks to humans and mammals (Rastogi, Sinha & Incharoensakdi, 2014). These blooms and toxins involve substantial economic costs due to the requirement for intensive water treatment, to decreased tourism and recreation revenue, and to lowered property values (Dodds *et al.*, 2008; Hamilton *et al.*, 2013).

Previous studies have highlighted the physiological characteristics of *Microcystis* spp. that have contributed to their global spread (Visser *et al.*, 2005; Šejnohová & Maršálek, 2012). In particular, studies have shown their ability to take up nutrients and inorganic carbon efficiently (Shen & Song, 2007; Wang *et al.*, 2014). *Microcystis* spp. can adapt to a wide range of light intensities from darkness (Zhang *et al.*, 2011) to 1100 µmol photons  $m^{-2} s^{-1}$  (Ibelings, Kroon & Mur, 1994) and even ultraviolet (Sommaruga, Chen & Liu, 2009). Additionally, *Microcystis* species have a global distribution from cold-temperate regions to the tropics, and

water temperatures ranging from 12 to 30°C (Li, Peng & Xiao, 2015); in laboratory cultures, the growth of *Microcystis* has been shown to have a wide temperature tolerance, ranging from 16.5 to 35°C (Thomas & Litchman, 2015; Li *et al.*, 2015). Moreover, *Microcystis* colonies are often buoyant, due to specialised gas vesicles, and thus are able to remain in the illuminated layers (Walsby, 1994; Walsby, 1998).

Colony formation of *Microcystis* is thought to contribute to bloom formation and the success of this genus in freshwater ecosystems (Visser et al., 2005; Yamamoto, Shiah & Chen, 2011). A colonial morphology is considered vital in Microcystis ecology, e.g. large Microcystis colonies can resist severe water turbulence as a consequence of their positive buoyancy (Walsby, Hayes & Boje, 1995), reduce zooplankton grazing pressure, and provide protection from heavy metals (Wu et al., 2007) and toxic substances such as linear alkylbenzene sulphonate (LAS) (Li et al., 2013). To date, no review has focused on the ecological implications of colony formation on the dominance and bloom occurrence of Microcystis. Neither is it clear why *Microcystis* exists typically as single cells in long-term laboratory culture conditions, rather than as the colonies found in natural conditions (Reynolds et al., 1981; Yang et al., 2008).

The triggering factors and mechanisms of colony formation in *Microcystis* spp. have been the subject of past studies (Reynolds, 2007), but our knowledge remains limited. This review focuses on the most recent studies on their biogeography, on physiological differences between unicellular and colonial *Microcystis*, on the triggering mechanisms involved in colony formation, and on understanding the role of colony formation in mortality, flotation, protection from predation and other hazards. This new knowledge may shed light on the phenotypic plasticity and successful strategies used by *Microcystis* species.

### II. GLOBAL SUCCESS AND MORPHOLOGY OF MICROCYSTIS

### (1) Global success of Microcystis

*Microcystis* spp. predominate in the plankton of some of the world's largest lakes, such as Lake Erie in North America and Lake Taihu in China (Lehman *et al.*, 2017; Levy, 2017; Zhu *et al.*, 2016). Other cyanobacterial species are also known to dominate freshwater ecosystems, such as *Dolichospermum* (also known as *Anabaena*) spp. (Li, Dreher & Li, 2016b; Wood *et al.*, 2017), *Cylindrospermopsis raciborskii* (Burford *et al.*, 2016), *Aphanizomenon* spp. (Cirés & Ballot, 2016), etc. To provide an updated understanding of the global geographic distribution of *Microcystis* blooms and dominance of *Microcystis* spp., we undertook a systematic literature review of field investigations in freshwater cyanobacterial blooms since the 1990s based on publications from *ISI Web of Science* (see online Supporting Information, Table S1).

At least 1130 freshwater ecosystems, including lakes, rivers, reservoirs and ponds, across all continents except Antarctica,

were researched for blooms (Fig. 1, Table S1). Over 870 systems were found to contain significant populations of *Microcystis* spp. on at least one occasion, while the remainder supported other cyanobacteria to a greater extent (Fig. 1). Dominance by Microcystis occurred throughout water systems in tropical, subtropical and temperate zones, although in variable proportions (Fig. 1, Table S1). Lakes were dominated by Microcystis spp. may have been deliberately selected for study due to the presence of Microcystis, while lakes that were dominated by other cyanobacterial species might have been omitted from reports. However, this literature review does provide a picture of the geographical distribution of Microcystis blooms. A worldwide distribution from low to middle latitudes reflects a wide temperature tolerance and suggests an increasing likelihood of more frequent blooms of this genus under the warming climate (Paerl & Huisman, 2009).

The global success of *Microcystis* spp. is partly attributable to the physiological characteristics of their colony morphology. Even though the available information is still sparse, differences in size, photosynthetic pigments and extracellular polysaccharides (EPs) between unicellular cells and colonies could underlie this global success.

### (2) Microcystis morphospecies

More than 50 Microcystis morphospecies have been recognised according to variations in colony form, mucilage structure, cell diameter, cell arrangement within a colony, ratio of the pigments phycocyanin and phycoerythrin, and details of the seasonal life cycle (Komárek & Komárková, 2002). The most commonly observed variants are M. aeruginosa (Kützing) Kützing, M. flos-aquae (Wittrock) Kirchner, M. ichthyoblabe Kützing, M. novacekii (Komárek) Compére, and M. wesenbergii (Komárek) Komárek (Fig. 2A-E). M. aeruginosa is normally irregular in shape, relatively firm, elongated or lobed containing distinct holes and arbitrarily arranged cells inside the colony. M. ichthyoblabe is normally soft, sponge-like, and with a homogeneous distribution of cells inside the colony. M. novacekii is normally small and firm, not lobed, and with tightly aggregated cells. M. wesenbergii is normally spherical, elongated, and lobed with a visible margin that is filled with mucilage, and with irregularly arranged cells inside the colony.

Traditional taxonomy seems to be inconsistent with results of biochemical or genetic studies among strains that show high phenotypic plasticity of colonies (Otsuka *et al.*, 2000; Xu *et al.*, 2016*b*). While differentiation of *Microcystis* species can seem arbitrary, current nomenclature is still mainly based on their morphology as observed in field populations, and this precedent is followed herein where appropriate, otherwise referring to the entire genus. *M. flos-aquae* was suggested by Watanabe (1996) to be a variant of one type of *M. ichthyoblabe*. Several previous field studies of seasonal variation in *Microcystis* morphospecies have adopted this logic; herein, we retain the use (*sensu* Watanabe) of *M. flos-aquae* as *M. ichthyoblabe*.



Fig. 1. Global geographic distribution and dominance of *Microcystis* from the 1990s to 2017. Water bodies where *Microcystis* was found to dominate are shown as yellow stars (clusters of closely located ecosystems) or red circles (individual water bodies). Purple triangles represent unpublished data from six water bodies investigated by Zhu (unpublished data) and more than 10 sites from Seqwater (a water authority based in southeast Queensland, Australia). Water bodies where *Microcystis* was detected but did not dominate are shown as green diamonds. See Table S1 for details of the survey data used to create this figure.

*Microcystis* cells are microscopic, ranging from approximately 1.7 to 7  $\mu$ m in diameter (Hu & Wei, 2006; Reynolds, 2006), and varying between different morphospecies. For example, the diameter of *M. aeruginosa* cells ranges from 3 to 7  $\mu$ m, while *M. ichthyoblabe* usually has smaller cells ranging from 2 to 3  $\mu$ m (Hu & Wei, 2006). Nevertheless, colony formation allows *Microcystis* to be one of the most widespread freshwater phytoplankton genera (Fig. 1).

The common morphospecies also vary significantly in colony size. *M. ichthyoblabe* colonies have a  $D_{50}$  (50% of the population is smaller than this size) of  $100-300 \,\mu\text{m}$ ; and *M. wesenbergii* and *M. aeruginosa* were found to have a  $D_{50}$  of  $300-700 \,\mu\text{m}$  (Li *et al.*, 2013; Zhu *et al.*, 2015). *M. aeruginosa* and *M. wesenbergii* colonies can reach over 1000  $\mu\text{m}$  in diameter (Li *et al.*, 2013, 2016*a*).

In natural lakes, different morphospecies dominate successively, resulting in a varying colony size distribution. From June to November, Lakes Taihu and Chaohu in China, and Lakes Suwa, Biwa and Hirosawa-no-ike Pond in Japan show succession in dominance (Jia *et al.*, 2011; Ozawa *et al.*, 2005; Park *et al.*, 1993; Yamamoto & Nakahara, 2009; Zhu *et al.*, 2016). In the early bloom period, *M. ichthyoblabe* dominates with small colonies (<100 µm); subsequently, *M. wesenbergü* and *M. aeruginosa* predominate with colonies of an average diameter of 400 µm. The two latter morphospecies are present until autumn (Li *et al.*, 2013; Zhu *et al.*, 2015).

When forming colonies, all these morphospecies seem to have high phenotypic plasticity, and the cell arrangement

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inside a colony may alter. This behaviour, which has been recognised for many years [see, for instance, Reynolds et al., 1981 and Šejnohová & Maršálek, 2012], is counter-intuitive: how does one morphospecies change, apparently spontaneously, into another? Variable forms were referred to in an early survey of bloom-forming cyanobacteria, by Kondrat'eva et al. (1968), as 'stati' (presumably the plural of 'status'). Otsuka et al. (2000) studied the species' morphology in culture, and found that M. novacekii displayed several morphotypes including some characteristics of M. aeruginosa and M. ichthyoblabe, while M. wesenbergii also showed great morphological variability representing similar morphotype characteristics to M. aeruginosa. Species with an arbitrary cell arrangement can become more regular when the cells divide, for example M. aeruginosa transitions to M. novacekii in culture (Sun et al., 2015). Therefore, distinction among these morphospecies seems to be obscure or impossible, and the current classification of the genus Microcystis based on morphological characteristics can be challenged.

### **III. COLONY FORMATION IN MICROCYSTIS**

Colonial morphology plays an important role in dominance and bloom formation of *Microcystis*, but the mechanism of colony formation under different environmental conditions remains unclear (Xiao *et al.*, 2017). Studies of colony



**Fig. 2.** Commonly found *Microcystis* morphospecies in the field: (A) *M. ichthyoblabe* Kützing; (B) *M. wesenbergii* (Komárek) Komárek; (C) *M. aeruginosa* (Kützing) Kützing; (D) *M. novacekii* (Komárek) Compére; (E) unidentified colony from field samples taken in early spring in Lake Taihu, China; (F) single cells from Lake Taihu, China. White arrows point to the visible margin that is filled with mucilage. A–C and E are from Xu *et al.* (2016*a*), D was provided by Junyi Zhang, and F was provided by Ming Li.

formation are hindered by the fact that in culture *Microcystis* typically exists as single cells (Li *et al.*, 2013; Yang *et al.*, 2008), unlike the colonial morphology observed in the field (Reynolds *et al.*, 1981; Yang *et al.*, 2008). A number of biotic and abiotic factors that appear to influence colony formation in *Microcystis* have been studied under laboratory conditions, allowing an improved understanding of how biotic and abiotic factors affect colony formation and colony size.

### (1) Colony formation in response to biotic factors

The presence of grazing zooplankton, e.g. the flagellates Ochromonas sp., was first reported to induce colony formation in Microcystis by Burkert et al. (2001). Since then, a series of studies investigating effects of Ochromonas sp. on colony formation have been carried out (Yang & Kong, 2012; Yang et al., 2006, 2008), and the induced colonies can reach up to 180 µm in diameter (Yang & Kong, 2012). However, not all zooplankton induce colony formation in Microcystis: Ochromonas sp. induce defensive colony formation in Microcystis unicellular cells (Yang et al., 2006), while the copepod Eudiaptomus graciloides, cladoceran Daphnia magna, and rotifer Brachionus calyciflorus do not (Becker, Matthijs & van Donk, 2010; Yang et al., 2006). Yang et al. (2009) suggested that infochemicals released from Ochromonas sp. may be the stimulant causing increased production of EPs in *M. aeruginosa*, leading to the algal cells sticking together to form colonies. The defensive release of microcystin occurs in M. aeruginosa in the presence of cladocerans (Lurling, 2003), and flagellates are known to have the ability to degrade microcystin (Ou et al., 2006). Thus, the effects of grazing on colony formation differ depending on the particular zooplankton involved.

Filtrates from cultures of the cladocerans Moina macrocopa and Daphnia magna have been found to induce colony formation (Ha, Jang & Takamura, 2004; Jang et al., 2003), which might be due to the presence of infochemicals released from the zooplankton. Daphnia pulex was also found to induce morphological changes in Scenedesmus gutwinskii var. heterospina Bodrogközy, through the release of aliphatic sulphates (Yasumoto et al., 2006). In addition, unsterilized filtrates of lake water dominated by zooplankton (Yang, Kong & Shi, 2005) and secretions of Ochromonas sp. (Yang et al., 2009) stimulated unicellular M. aeruginosa to form colonies. The size of the colonies induced by filtrates was normally less than  $5 \,\mu m$ , much smaller than those induced by direct grazing. This difference might reflect a reduction in levels of perceived stress arising from filtration or secretion compared with direct grazing.

Other biotic factors, such as the presence of heterotrophic bacteria (Shen *et al.*, 2011; Wang *et al.*, 2015), the toxic cyanobacterium *C. raciborskii* (Mello *et al.*, 2012) and the microcystins MC-RR, MC-LR and MC-YR (Gan *et al.*, 2012; Sedmak & Elersek, 2006), have also been implicated in inducing colony formation in *Microcystis*. The largest colony size that could be induced from small colonies under the treatment of microcystins was 585  $\mu$ m. Some researchers suggested that polysaccharide production plays a role in colony induction (Shen *et al.*, 2011; Wang *et al.*, 2015). Gan *et al.* (2012) found that MCs led to rapid induction of messenger RNA (mRNA) for genes related to polysaccharide biosynthesis, such as *cap*D, *csa*B, *tag*H and *epsL*. Two of these

genes, *cap*D and *tag*H, are related to capsular polysaccharides (CPs) biosynthesis (Lazarevic & Karamata, 1995; Luna *et al.*, 2006), while *csa*B and *eps*L are responsible for the synthesis of the exopolysaccharide methanolan (Cava *et al.*, 2004; Yoshida *et al.*, 2003). Colony formation in response to *C. raciborskii* may be due to the allelochemicals produced by this cyanobacterium (Mello *et al.*, 2012).

### (2) Colony formation in response to abiotic factors

Some abiotic factors have also been reported to induce colony formation in *Microcystis*. Under a low temperature of  $15^{\circ}$ C and a low light intensity (10 µmol photons m<sup>-2</sup> s<sup>-1</sup>), *Microcystis* cells form colonies of up to 100 µm in diameter (Li *et al.*, 2013; Xu *et al.*, 2016*a*). Higher light intensities led to a faster growth rate of cells, accelerating the consumption of intracellular polysaccharides and other substances, decreasing the propensity to form colonies.

High concentrations of metals, such as calcium (Wang *et al.*, 2011) and lead (Bi *et al.*, 2013) also induced colony formation, with colonies reaching up to 130  $\mu$ m in diameter. When exposed to heavy metals, cells increased the secretion of EPs to precipitate the metal ions; the aggregation of EPs on the cell surface increased in response to these active cations.

The effects of nutrients on colony formation have also been evaluated. Yang & Kong (2013) found that adding nitrogen (1.98 mg l<sup>-1</sup>) and phosphorus (0.65 mg l<sup>-1</sup>) induced colony formation, with the largest colonies reaching 275  $\mu$ m in diameter. Wang, Liu & Yang (2010*a*) found that nutrient addition combined with grazing by *Ochromonas* sp. resulted in larger colonies (> 100  $\mu$ m). However, Ma *et al.* (2014) observed disaggregation of colonies in response to the addition of nitrogen (1.59–51.16 mg l<sup>-1</sup>) and phosphorus (0.08–2.68 mg l<sup>-1</sup>), either together or separately. Zhu *et al.* (2016) found a general decrease in colony size with increasing nutrient concentrations in field investigations, potentially resulting from increased growth rate. Thus, colony formation in *Microcystis* appears to benefit from low ambient nutrient levels.

### (3) Colony disaggregation

Encouraging disaggregation of *Microcystis* colonies is a potential approach to reducing the ecological impact of blooms (Zhu et al., 2016). While the colony size of Microcystis is known to decrease with increasing temperature or nutrient concentrations despite faster growth of unicellular cells (Ma et al., 2014; Zhu et al., 2016), it is impractical to add nutrients or to increase water temperature in order to manage or mitigate Microcystis blooms. However, the application of physical mixing above a critical intensity might represent a more practical way of disaggregating colonies. O'Brien et al. (2004) quantified the effect of turbulence on Microcystis colony size in a grid-stirred tank, and found that colony disaggregation increased with increasing mixing strength. A turbulent dissipation rate in the tank of  $10^{-9}$ – $10^{-4}$  m<sup>2</sup> s<sup>-3</sup> (including or exceeding the range of mixing turbulence in the field by up to two orders of magnitude) led to decreases

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in *Microcystis* colony size to  $200-420 \,\mu\text{m}$ . High turbulence intensities sustained over several days are deleterious to the metabolic activity and viability of *M. aeruginosa* cells (Regel *et al.*, 2004), thus increasing the mixing turbulence might have affected the colonies in a similar way. The bound extracellular polysaccharides (bEPs, which firmly adhere to the algal cell membrane) acting as adhesive molecules to bind the cells together might be disrupted by strong mixing, resulting in reduced floating velocities and greater susceptibility to grazers.

To manage and mitigate *Microcystis* blooms, disaggregation of colonies of different morphospecies under a range of mixing scenarios might be a potential focus for future research. Given that various morphospecies differing in amounts and structure of mucilage dominate at different times (Komárek & Komárková, 2002), and have high phenotypic plasticity under different environmental conditions, different specific responses to various mixing scenarios may be of great importance.

### (4) Mechanisms of colony formation

Two mechanisms of colony formation in *Microcystis* have been recognised (Xiao *et al.*, 2017): (i) 'cell division', where cells remain attached after binary fission and the daughter cells become enveloped in a layer of secreted EPs that prevents their separation (Kessel & Eloff, 1975); (ii) 'cell adhesion', where single cells aggregate *via* the secretion of adhesive EPs (Yang *et al.*, 2008). Differentiating between these two mechanisms is typically done by analysing the arrangement of cells within colonies: cell division leads to a regular arrangement of cells, while cell adhesion leads to a more arbitrary pattern. However, this approach can be problematic because of uncertainty about phenotypic plasticity within and between different morphospecies, as discussed in Section II.2.

A recent meta-analysis of *Microcystis* colony formation (Xiao *et al.*, 2017), compared cell-division and cell-adhesion processes in colony formation. Small colonies of *Microcystis* could be induced either by cell division or by cell adhesion, and the mechanisms involved both biotic and abiotic factors (Table 1). Colony formation by cell adhesion was more rapid, suggesting a response appropriate to an imminent threat, while colony formation *via* cell division was slower and occured in response to an environmental stress.

Based on a meta-analysis of field investigations of *M. ichthyoblabe* and *M. wesenbergii* blooms, colony-formation mechanisms may be morphospecies-specific (Xiao *et al.*, 2017). Generally, *M. ichthyoblabe* colonies form by cell division (Xiao *et al.*, 2017), and gradually increase in size throughout spring (Cao & Yang, 2010; Yamamoto & Nakahara, 2009). Scanning electron microscopy images show a featureless slimy layer, with bEPs around individual cells (Kessel & Eloff, 1975). In comparison, *M. wesenbergii* and *M. aeruginosa* colonies exhibit loosely arranged cells, likely arising from cell adhesion (Xiao *et al.*, 2017). Colonies of these two morphospecies arise quickly and are present until autumn (Li *et al.*, 2013; Zhu *et al.*, 2015). Changes in colony morphology occur as cells

Process	Environmental factors	References		
Cell division	Zooplankton filtrate	Jang et al. (2003); Yang et al. (2005, 2009)		
	High $Pb^{2+}$ concentration	Bi et al. (2013)		
	Cyanobacterium Cylindrospermopsis raciborskii	Mello <i>et al.</i> $(2012)$		
	Heterotrophic bacteria	Shen et al. (2011); Wang et al. (2015)		
	Low temperature and low light intensity	Li et al. (2013); Xu et al. (2016a)		
Cell adhesion	Zooplankton grazing	Burkert et al. (2001); Yang et al. (2006)		
	High $Ca^{2+}$ concentration	Sato et al. (2016); Wang et al. (2011); Zhao et al. (2011)		
	Microcystins	Gan <i>et al.</i> (2012)		

Table 1. Studies providing evidence for colony formation by cell division or cell adhesion under different environmental conditions based on a recent meta-analysis (Xiao *et al.*, 2017)

actively rearrange themselves within the colonies (Mulling, Wood & Hamilton, 2014). Differences in colony morphology of these three *Microcystis* morphospecies suggest they could respond differently to environmental stimuli.

Extracellular polysaccharides (EPs) are key components in *Microcystis* colony formation (Li *et al.*, 2013; Yang *et al.*, 2008), with bEPs present surrounding the cells and soluble EPs (sEPs) secreted into the surrounding media (Yang *et al.*, 2008). In field samples, colony size is correlated with bEPs levels, suggesting that extra bEPs may be secreted once colonies have formed (Li *et al.*, 2013; Xu *et al.*, 2016*a*). Increased bEPs levels in laboratory cultures induced colony formation, while adding sEPs did not (Sato *et al.*, 2016), reflecting the variable roles and compositions of these two different forms of EPs (Pereira *et al.*, 2009).

The bEPs content that promotes *Microcystis* colony formation varies among different experimental and analytical procedures. Yang *et al.* (2008) found that a bEPs content of 2.14 pg cell<sup>-1</sup> induced *Microcystis* colony formation, while Li *et al.* (2013) observed the appearance of *Microcystis* colonies at only 0.6–0.8 pg cell<sup>-1</sup>. An even lower value of 0.34 pg cell<sup>-1</sup> was reported by Wu & Song (2008). Xiao *et al.* (2017) observed that colony formation by cell division showed a positive linear regression with increasing bEPs concentration (P < 0.001, N = 25); the number of cells per colony increased by a factor of 100 for a six-fold increase in bEPs concentration.

Forni, Telo' & Caiola (1997) showed that Microcystis EPs had a carbohydrate composition similar to that of adhesive EPs in diatoms (eukaryotic microalgae) (Willis et al., 2013): rhamnose, fucose and xylose were common components. Additionally, changes in EPs composition affect their adhesive ability, for example, increased uronic acid content gives greater adhesion strength (Verspagen, Visser & Huisman, 2006). Thus, changes in EPs composition stimulated by different environmental conditions could enhance cell adhesion. Evidence that Ca<sup>2+</sup> promotes colony formation by cell adhesion (Sato et al., 2016; Wang et al., 2011) implies a similar adhesive mechanism to that found in diatom EPs (Chiovitti et al., 2008). Together, these findings indicate that differences in the morphology of unicells and colonies in laboratory cultures and field samples could be explained by EPs content and composition.

### IV. COLONY FORMATION IN LABORATORY STUDIES AND IMPLICATIONS FOR UNDERSTANDING MORPHOLOGY CHANGES IN THE FIELD

Inducing colony formation from unicells is possible in the laboratory, however, the derived colonies differ in morphology substantially from forms encountered under natural conditions (Reynolds *et al.*, 1981; Yang *et al.*, 2008). This is a key issue regarding colony formation in *Microcystis*: how can colonies with similar morphologies to those in the field be induced under laboratory conditions?

Xu et al. (2016a) induced colony formation from single cells of five Microcystis species at a low temperature of 15°C; their colonies had similar morphologies but differed from most morphologies observed in the field. However, their induced colonies were similar to small unidentified colonies recorded in Lake Taihu (China) during early spring (Fig. 2E). Otsuka et al. (2000) also reported morphological changes in cultured Microcystis, with M. wesenbergii appearing more like M. aeruginosa. Li, Zhu & Sun (2014) observed morphological changes from M. ichthyoblabe to forms more representative of M. wesenbergii and M. aeruginosa, following soaking field-collected Microcystis colonies in deionized water in the dark at 4°C. The authors suggested that this morphological change might have arisen due to disruption of mucilage under these particular conditions. Interestingly, their observations resembled the known seasonal variation of Microcystis morphospecies in many lakes (Jia et al., 2011; Ozawa et al., 2005; Park et al., 1993; Yamamoto & Nakahara, 2009; Zhu et al., 2016). Sun et al. (2015) reported morphological changes from M. aeruginosa to M. novacekii-like colonies under standard culture conditions.

Otten & Paerl (2011) found that *M. wesenbergii* was morphologically and genetically distinct from other *Microcystis* morphospecies, such as *M. aeruginosa*, *M. flos-aquae*, and *M. ichthyoblabe*, and *M. wesenbergii* can be identified using 16S-23S rDNA-ITS (the internal transcribed spacer of nuclear ribosomal DNA) sequences (Otten & Paerl, 2011) or gene *cpc*BA-IGS [the highly variable intergenic spacer (IGS) region which covers the terminal end of the *cpc*B gene and the proximal end of the *cpc*A gene] (Tan *et al.*, 2010). By contrast, Xu *et al.* (2016*b*) found high homozygosity of

16S-23S and *cpc*BA-IGS in all *Microcystis* samples except for one *M. aeruginosa* colony. It is thus currently impossible to identify different *Microcystis* morphospecies using molecular tools, such as 16S rDNA (Otsuka *et al.*, 1998; Xu, Peng & Li, 2014), 16S-23S rDNA (Otsuka *et al.*, 1999; Xu *et al.*, 2016*b*), genomic DNA (Otsuka *et al.*, 2001), or fatty acid analysis (Le Ai Nguyen *et al.*, 2012). The above studies indicate that the morphology of *Microcystis* colonies can change under different environmental conditions. This process might explain the lack of agreement between classical taxonomy and modern molecular techniques. Furthermore, such morphological changes might explain the observed seasonal variations in different morphospecies in some lakes.

Previous studies have identified potential ways to induce unicellular cells to form colonies similar to those found in the field. However, we still do not know whether single cells of any given morphospecies first form colonies with a similar morphology to those found in the early spring, and then develop into colonies with different classical morphologies under changing environmental conditions.

Our hypothesis herein is that *Microcystis* colonies can be induced to change morphology, giving the seasonal variation sequence observed in the field, i.e. that colonial morphology changes from non-classical to that shown by *M. ichthyoblabe*, *M. wesenbergii* and *M. aeruginosa*. We detail below three possible transition pathways (see also Fig. 3).

### (1) Transition route 1: from non-classical colonies to *M. ichthyoblabe*-like colonies

Recent laboratory work induced smaller colonies with rougher surfaces and rather loosely arranged inner-colony cells (Xu *et al.*, 2016*a*) under non-mixing culture conditions, except for gentle daily shaking to prevent cells sticking to the walls of the culture flasks. By contrast, turbulent mixing in the field will be induced continuously by wind, stream inflow and other physical forces, leading to disaggregation of loosely arranged colonies (O'Brien, 2003). Consequently, under continuous mixing, colonies tend to grow larger, with smoother surfaces and more tightly arranged cells, i.e. could change into *M. ichthyoblabe*-like colonies under laboratory conditions.

### (2) Transition route 2: from *M. ichthyoblabe*-like to *M. wesenbergii*-like colonies

Gelation of mucilage is thought to be a key factor inducing formation of *M. wesenbergii*-like colonies (Li *et al.*, 2014). The CPs in mucilage are very similar to pectin (Parker *et al.*, 1996), the gelling of which can involve appropriate levels of dissolved polysaccharides (May & Stainsby, 1986), low pH and high Ca<sup>2+</sup> concentration (Thakur, Singh & Handa, 1997). Addition of Ca<sup>2+</sup> has been reported to induce colony formation from unicellular cells in *M. aeruginosa* (Sato *et al.*, 2016; Wang *et al.*, 2011; Zhao *et al.*, 2011). It is plausible that increased levels of Ca<sup>2+</sup> could lead to gelation of polysaccharides in the mucilage, thereby inducing a morphological change from *M. ichthyoblabe* to *M. wesenbergii*.

A low pH can occur in the surrounding microenvironment of *Microcystis* colonies that induces the gelation of dissolved polysaccharides. Here, the 'surrounding microenvironment' refers to the intercellular space inside the colonies that is filled by a jelly-like mucilage, as well as the intermediate liquid-filled space gap of several micrometres between the colony and the surrounding environment, characterised by concentration gradients in various environmental components, including pH, nutrients and sEPs. The presence of this transition zone was established by Fang et al. (2014) who cultured field-collected Microcystis colonies in BG-11 media (pH adjusted to >7), and detected a pH of close to 6 in the microenvironment surrounding the colonies. M. wesenbergii blooms at the water surface (Zhu et al., 2014) releasing a smelly odour, indicating that anaerobic decomposition is taking place.

Our proposed Transition route 2 involves an initially large amount of *M. ichthyoblabe* floating at the water surface. Higher concentrations of polysaccharides and a lower pH are then induced in the colony microenvironment by two possible processes: an increase in dissolved polysaccharide substances, and the decomposition of these Eps by acid-producing microorganisms [e.g. *Streptomyces* spp. and *Bacteroides* spp. (Li *et al.*, 2013; Shia *et al.*, 2010; Wang *et al.*, 2015)], raising the levels of organic acids such as benzoic acid (Wang *et al.*, 2015). These processes lead to a morphological change from *M. ichthyoblabe*-like colonies to *M. wesenbergü*-like colonies. However, this proposal requires verification by further investigations of the effects of low pH and high Ca<sup>2+</sup> concentration on the gelation of polysaccharides in mucilage.

## (3) Transition route 3: from *M. wesenbergii*-like to *M. aeruginosa*-like colonies

Under moderate turbulent mixing, mucilage of *M. wesenbergii* colonies can become irregular, with distinct holes, followed by gradual solubilisation (Li *et al.*, 2014), and these colonies take on the appearance of *M. aeruginosa* colonies. Under intense turbulent mixing, *M. wesenbergii* colonies or newly formed *M. aeruginosa* colonies could break up further to form unidentified colonies or even single cells. Conceivably, other morphospecies, such as *M. novacekii*, *M. smithii* Komárek & Anagnostidis and *M. botrys* Teiling, might form, although less often. This might explain why *M. ichthyoblabe*, *M. wesenbergii* and *M. aeruginosa* are common in nature. A process of morphological change from *M. wesenbergii*-like colonies to *M. aeruginosa*-like colonies has been identified in recent experiments (M. Xiao, P. Zhang, D.P. Hamilton & M. Li., in preparation).

The three transition routes postulated above provide new insights into colony formation and taxonomy of *Microcystis*. Further studies are needed to verify the proposed mechanisms of morphological change of colonies under various environmental conditions, and to resolve contradictory results regarding the morphological, biochemical and genetic classification of *Microcystis* morphospecies, potentially to explain seasonal variation in *Microcystis* other than as an outcome of species competition.



**Fig. 3.** Hypotheses of main transition pathways inducing morphological changes in *Microcystis* under various treatments. Transition route 1: from non-classical colonies to *M. ichthyoblabe*-like colonies. Transition route 2: from *M. ichthyoblabe*-like colonies to *M. wesenbergü*-like colonies to *M. aeruginosa*-like colonies. T1, T2 and T3 indicate Transition routes 1, 2, and 3. EPs, extracellular polysaccharides.

Inducing colony formation in culture representative of classical field morphologies will enhance understanding of the mechanisms involved, their environmental drivers and their evolution, including the role of EPs gelation and adhesion.

### V. BENEFITS AND COSTS OF COLONY FORMATION IN *MICROCYSTIS*

### (1) Physiological composition and microenvironments of colonies

*Microcystis* colonies have been found to have higher levels of photosynthetic pigments, especially chlorophyll *a*, phycocyanin and carotenoids, than in unicells (Wu & Song, 2008; Zhang *et al.*, 2007, 2011). Zhang *et al.* (2007) demonstrated that colonial *Microcystis* isolated from Lake Taihu produced twice as much chlorophyll *a* and phycocyanin than unicells when incubated at 25°C and 30 µmol photons m<sup>-2</sup> s<sup>-1</sup>. Li & Li (2012) collected samples from Lake Chaohu, another *Microcystis*-dominated lake in China, and similarly found that contents of carotenoids and phycocyanin increased significantly with increasing colony size during *Microcystis* blooms.

Recent studies have established that colony formation in *Microcystis* leads to a much higher EPs-content compared to isolated cells (Plude *et al.*, 1991; Zhang *et al.*, 2011). Wu & Song (2008) measured EPs content ( $\mu$ g mg<sup>-1</sup> dry mass) of four unicellular and five colonial strains: colonial strains had up to 12 times higher mass-specific EPs content than unicellular cells. Li *et al.* (2016*c*) detected much higher CPs levels in *Microcystis* colonies from Lake Taihu compared with single disaggregated cells. Total polysaccharides (TPs) and RNA levels were also higher in colonies (Li, Nkrumah & Xiao, 2014).

Fang *et al.* (2014) noted that the physiological microenvironment of colonies also differed from that of dispersed cells. The authors proposed that photoprotective carotenoids might prevent the inner-colony cells from experiencing high-irradiance damage; oversaturation of oxygen would provide gaseous oxygen in the intercellular space, enhancing colony buoyancy regulation. In addition, redox potential  $(E_h)$  in colonies was much lower than that in the surrounding water, a difference that might well stimulate nutrient uptake (Fang *et al.*, 2014). Taken together, these features could contribute to the observed dominance of *Microcystis* colonies.

### (2) Adaptation to varying light

The higher content of photosynthetic pigments in Microcystis colonies may provide them with higher photosynthetic capacities compared to isolated cells. Wu & Song (2008) exposed nine *M. aeruginosa* strains, of unicellular to large colonial morphologies with variable sizes, to a range of irradiances ranging from 45 to 1200  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>; the colonies attained higher specific photosynthetic rates  $(P_{max})$  and higher maximum electron transfer rates  $(ETR_{max})$ than unicells. Relative maximum electron transfer rate  $(rETR_{max})$  and onset of light saturation  $(I_k)$  were also higher in M. aeruginosa colonies than in unicellular cells (Zhang et al., 2011). Wu, Kong & Zhang (2011) measured chlorophyll fluorescence of colonial and unicellular Microcystis from both incubated and in situ samples from Lake Taihu, and found higher mean maximum quantum yields  $(F_v/F_m)$  and higher effective quantum yields  $(\Delta F/F_m')$  in colonies. They suggested that a colonial morphology protects Microcystis cells by reducing photoinhibition at high light intensities (Wu et al., 2011). Moreover, their higher content of photosynthetic pigments allowed colonies to survive experimental exposure to poor light better than unicells (Zhang et al., 2011).

*Microcystis* colonies are better adapted than unicells to high intensities of solar ultraviolet (UV) radiation at the water surface. Sommaruga *et al.* (2009) suggested that this could be attributed to the enhanced production of mycosporine-like amino acids and carotenoids in colonies. Beardall *et al.* (2009) reviewed differences in the ecophysiological responses of unicells, colonies and multicellular organisms, concluding that the higher EPs levels in colonial structures do not themselves absorb significant amounts of UV-B but rather facilitate the attachment of UV-B screening compounds, implying that colonial cells are better protected than unicellular cells from high UV-B exposure.

Self-shading of colonies and their higher production of EPs also protect the inner-colony cells from high irradiance and UV-B radiation (Reynolds, 2006). The inner cells in *Microcystis* colonies are exposed to weaker light intensities than more peripheral cells. These cells may produce more chlorophyll *a* and other pigments to optimise light capture.

### (3) Growth under poor nutrition

*Microcystis* colonies have been shown to have a lower requirement for nutrients than unicellular cells and to be less affected by nutrient-limitation. Wang *et al.* (2014) compared the growth of colonial and unicellular *M. aeruginosa* under iron-limited (3  $\mu$ M) and iron-replete (36  $\mu$ M) conditions, and provided evidence that colonial *M. aeruginosa* 

were more able to endure iron-limitation than were unicells. They suggested that higher production of EPs in colonial *Microcystis* resulted in a better iron-chelating capability, facilitating metabolic processes such as higher pigment content, greater photosynthetic activity, and higher siderophore secretion. Li *et al.* (2016*c*) showed that, compared with unicells, a colonial morphology in *Microcystis* enhanced photoprotection and acclimation to iron-deficiency. Iron accumulated in CPs under iron-deficient conditions, and the much higher production of CPs in colonies thus facilitated iron accumulation, avoiding the effects of iron deficiency on light-harvesting ability and photosynthetic capacity in colonies.

Shen & Song (2007) observed a higher affinity among colonial strains for phosphate at low phosphate levels  $(< 50 \,\mu\text{M})$  and a lower consumption of phosphate than in unicellular strains over a range of phosphorus levels. These results indicated an advantage to a colonial habit in low-phosphate conditions. Moreover, fluctuating phosphorus conditions were found to favour growth of colonies more than unicellular cells. Shen & Song (2007) attributed these advantages to polysaccharide compounds in the mucilaginous sheath of colonies, which were involved in nutrient sequestration and processing. Similarly, colonial M. aeruginosa was found to have a higher affinity for inorganic carbon at 25 and 30°C, which triggered the expression of carbonic anhydrase (CA) genes and resulted in a higher capacity to utilise inorganic carbon (Wu, Wu & Song, 2011). Li et al. (2014) compared the growth rate of colonies sampled from Lake Taihu at different seasons and recorded faster growth rates of larger colonies than smaller colonies under low levels of nitrogen and phosphorus, and at high light intensity, emphasising the competitive ability of colonies under nutrient-deficient conditions.

*Microcystis* colonies attract microbial consorts such as bacteria, fungi and other algae, which can enhance nutrient and carbon cycling (and recycling) (Paerl & Millie, 1996). Exchange of growth factors such as vitamins and other allelopathic substances (such as cyanotoxins) benefits the growth of both the *Microcystis* 'host' and the microbial epiphytes or endophytes in colonies (Paerl & Millie, 1996).

Together, these examples demonstrate that the higher photosynthetic capacities and lower nutrient demands of *Microcystis* colonies may compensate for their lower nutrient uptake rates, and provide growth advantages in poor nutrient environments. The richer microbial communities present on colonies further increases nutrient availability and enhances *Microcystis* growth compared with unicellular forms.

### (4) Protection from chemical stressors

A colonial habit could also function to protect against exposure to chemical stressors. Wu *et al.* (2007) exposed colonial and unicellular *M. aeruginosa* strains to 0.25 mg ml<sup>-1</sup> of copper sulphate, and found that photosynthetic parameters ( $F_v/F_m$ ,  $ETR_{max}$ , and oxygen evolution rate) decreased more rapidly in unicellular strains than in colonies, perhaps due to higher activities of antioxidative enzymes [such as superoxide dismutase (SOD) and catalase (CAT)] in colonies compared to unicellular cells. Bi *et al.* (2013) added four different concentrations of Pb<sup>2+</sup> to unicellular *Microcystis*, and found the proportion of cells that formed colonies increased with increasing Pb<sup>2+</sup> concentration. *M. aeruginosa* colonies were also demonstrated to be less growth-inhibited by chloromycetin, linear alkylbenzene sulphonate (LAS) and rice (*Oryza sativa*) hull treatments than unicellular cells (Li, Nkrumah & Peng, 2015; Park *et al.*, 2009).

A higher production of EPs in colonies has also been found to play a key role in protecting colonies from chemical stressors. Bai *et al.* (2016) found that EPs in colonies facilitated biosorption of phenanthrene, with the protein-like substances in EPs thought to be essential in the EPs-phenanthrene binding process. A high effective adsorption of heavy metals by EPs (Kaplan, Christiaen & Arad, 1988) might be due to the presence of a large number of COO<sup>-</sup> and amino groups (Pradhan, Singh & Rai, 2007). EPs could also adsorb organic materials (Wingender, Neu & Flemming, 1999). Since colonies have a higher production of EPs than unicellular cells, the abundant EPs may also serve to protect the inner-colony cells from hazardous pollutants.

### (5) Protection from grazing

Colony formation may provide strategic protection against predators, simply because large colonies are not as easily ingested by zooplankton as are unicells or small colonies. Yang et al. (2009) cultivated colonies and unicellular cells of M. aeruginosa with the flagellate Ochromonas sp., and found that clearance rates by the flagellates were much lower for colonial M. aeruginosa than for unicells alone. Burns (1968) found a positive correlation  $(D_{par} = 22D_{pre} + 4.87)$  between the maximum diameter of particles ingested  $(D_{par}; \mu m)$ and body length  $(D_{pre}; mm)$  of the filter-feeding cladoceran zooplankters. Hansen, Bjornsen & Hansen (1994), using 18 studies reporting the ratio between predator body length and the size of their algal prey, found a wide range of optimal ratios of 1:1 for dinoflagellates, 3:1 for other flagellates, 8:1 for ciliates, 18:1 for rotifers and copepods, and 50:1 for cladocerans and meroplanktic larvae.

A *Microcystis* colony of  $200 \,\mu m$  in diameter could, theoretically, therefore only be ingested by a cladoceran greater than 8.9 mm (Burns, 1968) or 10 mm (Hansen et al., 1994) in length; animals of these sizes are rarely encountered in nature. Given the normal size ranges of common planktonic grazers, the maximum colony size ingested is likely to be rather less than 100  $\mu$ m (Table 2), which is smaller than that attained in nature by many Microcystis colonies. Additionally, a recent study using the stable isotopes  $\delta^{15}N$ and <sup>13</sup>C indicated that two major crustacean zooplankton species, Ceriodaphnia cornuta and Thermocyclops decipiens, were unable to feed on large labelled colonies (>  $100 \,\mu m$  in diameter) or filamentous cyanobacteria (Major et al., 2017). Thus, during a bloom, large *Microcystis* colonies are unlikely to be consumed by grazing zooplankton, making colony formation in Microcystis effective defence against grazing. This deduction has received experimental support using induced colonies of *M. aeruginosa* ranging in size from 30 to 180  $\mu$ m, which remained intact in the presence of *Ochromonas* sp. (Burkert *et al.*, 2001; Yang & Kong, 2012; Yang *et al.*, 2006, 2008).

#### (6) Other strategies and costs

*Microcystis* colonies may produce more MCs with increasing size, which could contribute to bloom formation in natural populations (Jungmann *et al.*, 1996; Kurmayer, Christiansen & Chorus, 2003). Wang *et al.* (2013) investigated MC concentration during *Microcystis* blooms in Lake Taihu, and found that, above a certain colony size (> 50  $\mu$ m), production of MCs increases with increases in colony size. The growing colonies may obtain advantages in growth by outcompeting other phytoplankton species.

Colonies have a smaller surface-to-volume ratio compared with unicells, and have slower specific rates of light harvesting, nutrient uptake, photosynthesis and cell growth (Reynolds, 2006). Negative effects of colony size on growth rate have been recorded in the laboratory (Yamamoto & Shiah, 2010). In field investigations, growth rate has been shown to be negatively correlated with increasing colony size, for colonies greater than 150  $\mu$ m (Li *et al.*, 2014; Wilson, Wilson & Hay, 2006), especially in conditions of low total nitrogen, low total dissolved phosphorus concentration, and high light intensity (Li *et al.*, 2014). Yamamoto & Shiah (2010) proposed that when colonies are small (< 200  $\mu$ m), inner-colony cells grow faster than the peripheral cells and as the colonies become larger, the growth of inner-colony cells is inhibited by greater self-shading.

## VI. *MICROCYSTIS* DOMINANCE AND BLOOM FORMATION

#### (1) Competition

Compared with unicellular cells, large Microcystis colonies gain advantages in their ability to exploit a wide range of environmental conditions, including fluctuating light levels, nutrient deficiency, zooplankton grazing, presence of chemical stressors, etc. However, in the complex environments of the natural world, many phytoplankton species compete with cyanobacteria. For instance, under very high and fluctuating irradiance, Microcystis is more sensitive to photoinhibition than the green alga, Scenedesmus spp., in which chlorophyll a content is more independent of the light regime (Ibelings et al., 1994). Some other cyanobacteria and green have lower half-saturation irradiance levels and higher maximum growth rates than Microcystis (Huisman et al., 1999), against which Microcystis would have no growth advantage at low light intensity. In extended periods of dissolved nitrogen limitation, populations of N<sub>2</sub>-fixers such as C. raciborskii and Dolichospermum spp. can flourish and achieve bloom proportions. C. raciborskii is regarded as being highly competitive when phosphorus and nitrogen availability are

Zooplankton	predator		Optimal algal prey size (µm)		
pecies Size range (µm)		Reference	Based on Burns (1968)	Based on Hansen et al. (1994)	
Flagellate Ochromonas sp.	4-6	Burkert et al. (2001)	_	1.43-2	
· · · · · · · · · · · · · · · · · · ·	$7.8 \pm 0.9$	Yang et al. (2008)	_	$2.6 \pm 0.1$	
	$8.3 \pm 0.8$	Yang & Kong (2012)	_	$2.8 \pm 0.1$	
Cladoceran Daphnia magna	$2100 \pm 400$	Jang et al. (2003)	$51 \pm 0.3$	$42 \pm 0.2$	
Cladoceran Daphnia pulex	$1600 \pm 300$		$40 \pm 0.3$	$32 \pm 0.2$	
Cladoceran Moina macrocoba	$1200 \pm 100$		$27 \pm 0.3$	$24 \pm 0.1$	
Copepod Eudiaptomus graciloides	$1800 \pm 250$	Yang et al. (2006)	-	$100 \pm 0.1$	
Rotifer Brachionus calyciflorus	$220 \pm 30$		_	$12 \pm 0.1$	

Table 2. Size of zooplankton predators and optimal sizes of their algal prey calculated from Burns (1968) and Hansen et al. (1994)

low (Willis, Posselt & Burford, 2017). Thus, *Microcystis* is not the only species that can adapt well to complex light environments or nutrient-limited conditions.

Because of their large size, *Microcystis* colonies might be subject to predation by herbivorous fish (Drenner *et al.*, 1987; Drenner *et al.*, 1984). Fish can move faster and further than zooplankton feeders, so may be more effective predators. Under such circumstances, a large colony size would clearly be less beneficial.

Even though the world's freshwater systems have become more polluted, pollutant concentrations are rarely critical to the survival of *Microcystis*. Thus, it is probably not yet necessary to launch a strategy for its preservation in natural habitats.

Interestingly, the strategies discussed above as beneficial to *Microcystis* represent passive responses to harsh environmental conditions. These passive responses may ensure survival of *Microcystis* but are unlikely to assist them to be dominant. With increasing anthropogenic eutrophication, there is little doubt that the number of freshwater systems dominated by *Microcystis* is increasing. Even though blooms of other harmful cyanobacterial species are increasingly reported, the proportion of systems in which *Microcystis* has become dominant may be higher (Harke *et al.*, 2016).

### (2) Control

In addition to nutrient removal, two solutions are currently considered relatively effective in overcoming frequent blooms. One is biological control (Sigee *et al.*, 1999), by enhancing herbivorous fish grazing and zooplankton grazing (Wang *et al.*, 2010*c*), or by encouraging macrophytes to compete with cyanobacteria (Nakai *et al.*, 2000). However, these methods have proved ineffective in some large lakes, such as Lake Taihu (Ke *et al.*, 2007), Hartbeespoort Dam in South Africa (Gumbo, Ross & Cloete, 2008) and Lake Erie (Vanderploeg *et al.*, 2001). The second approach has been

to apply physical controls, particularly through generating artificial mixing with aerators or diffusers (Visser et al., 2015). Artificial mixing alters the physiological responses of phytoplankton under the changing environmental conditions and, more importantly, alters the temporal and spatial distribution of phytoplankton. Intensified mixing has successfully led to replacement of buoyant cyanobacteria by green algae and diatoms in some lakes resulting from greater access to light (Becker, Herschel & Wilhelm, 2006; Heo & Kim, 2004; Lehman, 2014; Visser et al., 1996). Even though artificial mixing can fail to control blooms (Antenucci et al., 2005; Huisman et al., 2008; Lilndenschmidt, 1999; Tsukada, Tsujimura & Nakahara, 2006), depending on the species involved, the type of mixing (continuous or intermittent), and the mixing duration (a short-term pulse or long term), it remains an effective way to control large blooms without inducing unwanted side effects.

In a nutrient-replete system, sufficient irradiance and a warm temperature are key factors favouring algal growth. In time, buoyant species proliferate and block light from penetrating to deeper layers, subsequently limiting light availability to slower-growing species located at depth (Passarge *et al.*, 2006). Thus, the vertical distribution of phytoplankton plays a key role in their competition and dominance.

The vertical distribution of phytoplankton is a product of the interaction of their floating velocities with water mixing (Reynolds & Walsby, 1975). Even though their density is not the lowest among all buoyant cyanobacterial species, the large colony size and low shape coefficient of *Microcystis* enable them to be relatively buoyant (Ganf & Oliver, 1982), and have higher floating velocities than other cyanobacterial species (Table 3). Li *et al.* (2016*a*) measured the floating velocity of *Microcystis* colonies sampled from the surface water of Lake Taihu in August 2010 during a *Microcystis* bloom, and recorded values up to 10.08 m h<sup>-1</sup> with a colonial diameter of 1200 µm. They also found that colonies of various morphospecies differed in floating velocity: *M. ichthyoblabe* tended to have a higher velocity than *M. aeruginosa* and *M. wesenbergii* for the same colony size (Table 3).

In comparison, Dolichospermum sp., also recorded as positively buoyant, shows much lower floating velocities than *Microcystis*, ranging from 0.02-0.03 m h<sup>-1</sup> when D. circinalis was grown under 100  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup> in laboratory cultures (McCausland, Thompson & Blackburn, 2005), to 0.18 m  $h^{-1}$  in a natural population sampled from a stratified pool (Bormans & Condie, 1997), and  $0.01-1.00 \text{ m h}^{-1}$  in another natural population (Brookes et al., 1999). These much lower velocities could be explained by its filamentous morphology (Reynolds, 2006). Two other widely distributed cyanobacteria, *Planktothrix rubescens* and *C*. raciborskii, maintained a neutral buoyancy at relatively low floating velocities of nearly zero (Kehoe, 2009; Walsby, 2005; Walsby & Holland, 2006) (Table 3). Scenedesmus spp. colonies also had a near-zero velocity of 0-0.03 m h<sup>-1</sup> (Lürling, 2003). Therefore, it appears that large colonies make Microcystis the fastest floating freshwater cyanobacterium.

Under oligotrophic conditions, phytoplankton biomass is not high due to nutrient-limitation. With increasing nutrient concentrations, buoyant *Microcystis* colonies, which always float in the top layer, grow continuously. Their increasing biomass shades light and thereby inhibits growth of green algae and diatoms in deeper layers. Eventually, most green algae and diatoms and other cyanobacteria with weaker buoyancy will disappear, because they are unable to maintain their biomass due to light limitation. This may explain the dominance of most eutrophic lakes around the world by *Microcystis*: their large colony size helps *Microcystis* to achieve dominance in eutrophic lakes.

Where intensified mixing is introduced to eutrophic lakes, the plankton are stirred to achieve random distributions. Under such well-mixed conditions, green algae, diatoms and *Microcystis* will be exposed to similar light conditions and sedimentation losses of green algae and diatoms reduced in the mixed lake. Their higher growth rates will then give them a competitive advantage compared to *Microcystis* (Huisman *et al.*, 2004), allowing their populations to recover and overcome dominance of *Microcystis*.

Many problems in the control of *Microcystis* blooms remain to be addressed. Future work should incorporate: (i) quantitative modelling of *Microcystis* colonies under various mixing conditions; (ii) the effects of the vertical distribution of phytoplankton on light intensity in water column; (iii) competition mechanisms between *Microcystis* and other phytoplankton on timescales of years, with an emphasis on the effects of shading by *Microcystis* colonies; (iv) techniques to control *Microcystis* blooms by adjusting the vertical distribution of phytoplankton in eutrophic lakes and reservoirs.

### VII. EPILOGUE

This review included a discussion of phenotypic plasticity in the cyanobacterium *Microcystis* and detailed a conceptual model of transition pathways for morphological changes Microcystis. Classical Linnaean taxonomy describes several well-recognised forms of *Microcystis*, however, most researchers have encountered an unusual problem – a single population of one 'recognisable' species may, and frequently does, change spontaneously into another. These may in fact be different morphotypes of one genetically consistent species that responds somehow to its environment, but this phenomenon requires systematic investigation. If there is a single, but variable, genotype, then we need to understand its modes of morphological variability. Moreover, the observed morphological variations involve potentially flexible features, such as the number of cells per colony, colony shape, density of cells within the mucilage, width of peripheral clear areas etc., all of which are unlikely to require complex evolutionary adaptation but involve as yet unknown control mechanisms.

Biologists often attempt to reveal the inner connections between classical Linnaean taxonomy and modern molecular taxonomy. Many attempts fail because the chosen phenotypic characters are flexible. Whereas much phenotypic plasticity is described but not explained, our model postulating transition pathways of morphological change in *Microcystis* provides an example that may allow insights into phenotypic plasticity. Ecologists should also remember that the mechanisms and factors influencing competition among various close morphospecies may actually represent a philosophical paradox where these morphospecies are potentially one species, as seems to be the case for *Microcystis*.

### VIII. CONCLUSIONS

(1) Great progress has been made in inducing unicellular *Microcystis* to form colonies by adjusting biotic and abiotic factors. These factors include low temperature, low light intensity, high levels of  $Pb^{2+}$  and  $Ca^{2+}$ , low nutrient concentrations, the presence of heterotrophic bacteria, microcystins, zooplankton grazing, zooplankton filtrate and of another cyanobacterium (*C. raciborskii*). Colony formation is believed to occur in response to environmental stress.

(2) Two mechanisms of *Microcystis* colony formation have been proposed: 'cell division' and 'cell adhesion'. Colony formation through cell division is thought to be the dominant process when the number of cells per colony increases more slowly than the increase in total biomass; conversely, colony formation through cell adhesion is dominant when the number of cells per colony increases faster than the increase in total biomass. Colony formation by cell division is induced by zooplankton filtrate, high Pb<sup>2+</sup> concentrations, the presence of the cyanobacterium *C. raciborskii*, heterotrophic bacteria, low temperature, and low light intensities. Alternatively, colony formation by cell adhesion can be induced by zooplankton grazing, high Ca<sup>2+</sup> concentrations, and microcystins.

(3) How to induce laboratory colonies with morphologies similar to those seen in the field remains a bottleneck

Species	Size (µm)	φ	$ ho~({\rm kg~m^{-3}})$	$Ws \ (m \ h^{-1})$	Morphology	Reference
M. ichthyoblabe	200-1100	1.312-1.441	972-995	1.44-9.36	Non-spherical colony	Li et al. (2016a)
M. wesenbergii	400-1300	1.324 - 1.362	990 - 995	0.72 - 6.48	,	
M. aeruginosa	370 - 1200	2.915 - 4.106	990 - 995	1.08 - 10.08		
	D < 240	1	985-1005	-1.30 - 0.43	Spherical colony	Reynolds, Oliver & Walsby (1987)
	D < 2000			10.8		
	D < 6400			11.88		
Dolichospermum (Anabeana) spp.	ND	ND	975; 992	0.18	Filament	Bormans & Condie (1997); Walsby (1994)
D. circinalis	ND	ND	ND	0.01 - 1.00	Filament	Brookes et al. (1999)
				0.02 - 0.03	Filament	McCausland <i>et al.</i> (2005)
D. flos-aquae	D = 56 - 200	1.7	920-1030	-0.22 - 0.04	Filament	Reynolds <i>et al.</i> (1987)
Scenedesmus sp.	D = 3.5 - 9.5	ND	ND	0 - 0.03	Colony	Lürling (2003)
Plankthotrix rubescens	L = 26 - 322; W = 4.37 - 4.67	3.2	1084-1092	-0.020.03	Cylindrical filaments	Walsby & Holland (2006)
P. agardhii	ND	ND	985-1085	ND	Cylindrical filaments	Reynolds <i>et al.</i> (1987)
Aphanozominan flos-aquae	D < 140	1.5	920-1030	-0.14 - 0.02	Filament	Reynolds <i>et al.</i> (1987)
Oscillatoria rubescens	D = 27.6 - 40.6	6	990-1065	-0.002 - 0.02	Filament	Reynolds <i>et al.</i> (1987)
O. agardhii	D = 27.6 - 36.6	10	985-1085	-0.003 - 0.02	Filament	Reynolds <i>et al.</i> (1987)
O. redekei	D = 11.2 - 14.8	> 5	ND	ND	Filament	Reynolds <i>et al.</i> (1987)
Lyngbya limnetica	D = 19.0 - 20.8	10	ND	? -0.003	Filament	(1987) Reynolds <i>et al.</i> (1987)
Cylindrospermopsis raciborskii	D = 6.5 - 98	ND	977-989	3.6e-04-0.002	Cylindrical filament	Kehoe (2009)
Cyanodictyon sp.	D = 0.4 - 1.0	1	?	< 5.76e - 06	Spherical	Reynolds <i>et al.</i> (1987)
Synechococcus sp.	D = 0.8 - 2.9	1.3	?	< 3.6e-05	Non-spherical cell	(1007)

Table 3. Comparison of colony size, shape coefficient ( $\phi$ ), mass density ( $\rho$ ) and floating velocity (Ws) of buoyant freshwater planktonic species

D, diameter of a sphere of identical volume; L, length of a single cell; ND, no data; W width of a single cell.

to understanding colony formation in *Microcystis*. It seems reasonable to hypothesise that single cells of all *Microcystis* morphospecies initially form colonies with a similar morphology to that found in lakes in early spring. These colonies gradually change their colonial morphology to that representative of *M. ichthyoblabe*, *M. wesenbergii* and *M. aeruginosa* with changing environmental conditions. The mechanism of changes in colonial morphology remains a research objective.

(4) Colony formation provides *Microcystis* with many ecological advantages, including the ability to adapt to varying light, poor nutrition, and protection from chemicals and grazing. All these benefits are responses to environmental stresses, with an associated cost of reduction in specific growth rates of colonial *Microcystis* to below those of unicells.

(5) Large colony size affords *Microcystis* the fastest floating velocity of all freshwater cyanobacteria. A high floating velocity helps *Microcystis* to achieve dominance in eutrophic lakes: their large surface biomass shades light and thereby inhibits the growth of green algae and diatoms in deeper layers. Most green algae and diatoms and some cyanobacteria with weaker buoyancy are thereby outcompeted, as they are unable to grow adequately to sustain their populations.

(6) Intensified mixing of eutrophic lakes allows all plankton present to be stirred and randomized. *Microcystis* colonies are thus pushed into deeper layers, and not confined to the water surface. Under well-mixed conditions, green algae and diatoms, which have higher growth rates, will outcompete *Microcystis* and their populations may recover sufficiently to overcome the dominance of *Microcystis*.

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### XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article. **Table S1.** Survey data used in Fig. 1 including data from studies reporting cyanobacterial blooms and dominance of *Microcystis* spp.

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