# Colony formation in the cyanobacterium Microcystis


## Author

Xiao, Man, Li, Ming, Reynolds, Colin S



## Published

2018

## Journal Title

Biological Reviews

## Version

Version of Record (VoR)

## DOI

10.1111/brv.12401

BIOLOGICAL REVIEWS
Cambridge Philosophical Society
*Biol. Rev.* (2018), **93**, pp. 1399–1420.
doi: 10.1111/brv.12401


# Colony formation in the cyanobacterium *Microcystis*

Man Xiao[1,2], Ming Li[1]* and Colin S. Reynolds[3]

[1] *College of Natural Resources and Environment, Northwest A & F University, Yangling, 712100, China*
[2] *Australian Rivers Institute, School of Environment and Science, Griffith University, Nathan, Queensland 4111, Australia*
[3] *Centre of Ecology and Hydrology, Bailrigg, Lancaster LA1 4AP, U.K.*

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 $Pb^{2+}$ 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 $Ca^{2+}$ 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, $\sim 10.08$ 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*.

* Address for correspondence (Tel: +086+029 87080055; E-mail: lileaf@163.com)

The copyright line for this article was changed on 21 September 2018 after original online publication.

 

CONTENTS

I. Introduction ..... 1400
II. Global success and morphology of *Microcystis* ..... 1401
(1) Global success of *Microcystis* ..... 1401
(2) *Microcystis* morphospecies ..... 1401
III. Colony formation in *Microcystis* ..... 1402
(1) Colony formation in response to biotic factors ..... 1403
(2) Colony formation in response to abiotic factors ..... 1404
(3) Colony disaggregation ..... 1404
(4) Mechanisms of colony formation ..... 1404
IV. Colony formation in laboratory studies and implications for understanding morphology changes in the field ..... 1405
(1) Transition route 1: from non-classical colonies to *M. ichthyoblabe*-like colonies ..... 1406
(2) Transition route 2: from *M. ichthyoblabe*-like to *M. wesenbergii*-like colonies ..... 1406
(3) Transition route 3: from *M. wesenbergii*-like to *M. aeruginosa*-like colonies ..... 1406
V. Benefits and costs of colony formation in *Microcystis* ..... 1407
(1) Physiological composition and microenvironments of colonies ..... 1407
(2) Adaptation to varying light ..... 1408
(3) Growth under poor nutrition ..... 1408
(4) Protection from chemical stressors ..... 1408
(5) Protection from grazing ..... 1409
(6) Other strategies and costs ..... 1409
VI. *Microcystis* dominance and bloom formation ..... 1409
(1) Competition ..... 1409
(2) Control ..... 1410
VII. Epilogue ..... 1411
VIII. Conclusions ..... 1411
IX. Acknowledgements ..... 1413
X. References ..... 1413
XI. Supporting Information ..... 1420

## 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, $CO_2$ 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, 2016*b*; 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*.

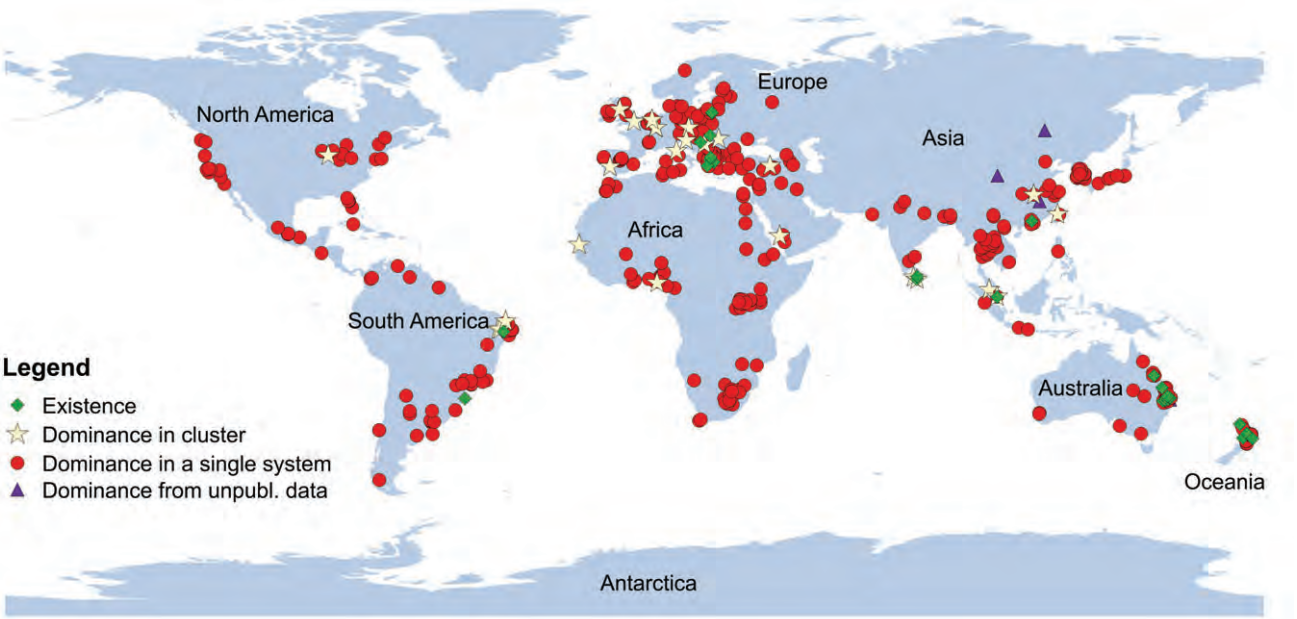


**Fig. 1.** Global geographic distribution and dominance of *Microcystis* from the 1990s to 2017. Water bodies where *Microcystis* was found to dominate are shown as yellow stars (clusters of closely located ecosystems) or red circles (individual water bodies). Purple triangles represent unpublished 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 μm 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 μm, while *M. ichthyoblabe* usually has smaller cells ranging from 2 to 3 μm (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 μm; and *M. wesenbergii* and *M. aeruginosa* were found to have a $D_{50}$ of 300–700 μm (Li *et al.*, 2013; Zhu *et al.*, 2015). *M. aeruginosa* and *M. wesenbergii* colonies can reach over 1000 μm 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. wesenbergii* 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 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

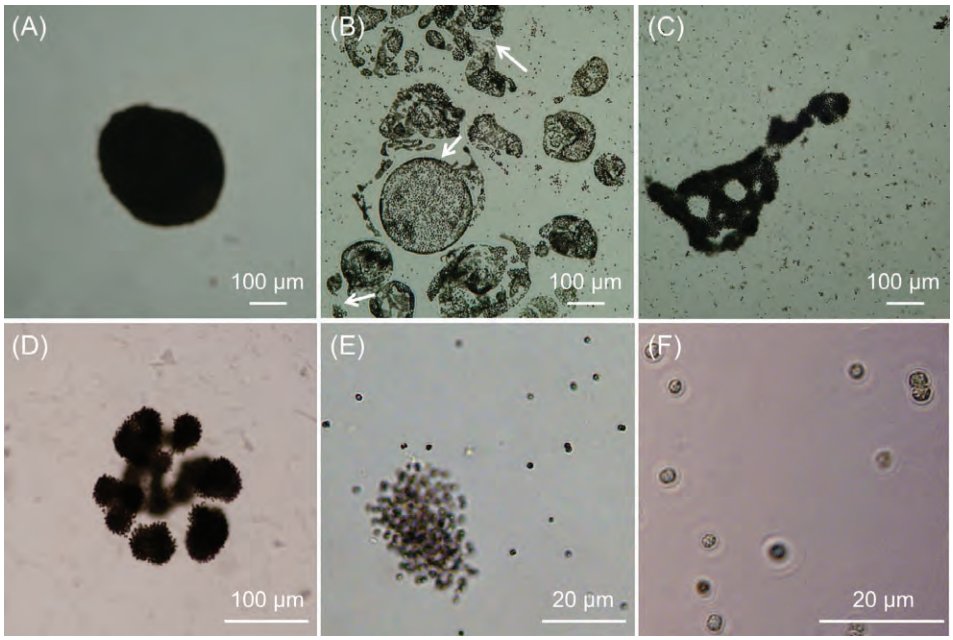


**Fig. 2.** Commonly found *Microcystis* morphospecies in the field: (A) *M. ichthyoblabe* Kützing; (B) *M. wesenbergii* (Komárek) Komárek; (C) *M. aeruginosa* (Kützing) Kützing; (D) *M. novacekii* (Komárek) Compére; (E) unidentified colony from field samples taken in early spring in Lake Taihu, China; (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 μm, 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 μm. 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 *eps*L. 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°C and a low light intensity (10 μmol photons $m^{-2}$ $s^{-1}$), *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 μm 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 $l^{-1}$) and phosphorus (0.65 mg $l^{-1}$) induced colony formation, with the largest colonies reaching 275 μm in diameter. Wang, Liu & Yang (2010*a*) found that nutrient addition combined with grazing by *Ochromonas* sp. resulted in larger colonies (> 100 μm). However, Ma *et al.* (2014) observed disaggregation of colonies in response to the addition of nitrogen (1.59–51.16 mg $l^{-1}$) and phosphorus (0.08–2.68 mg $l^{-1}$), 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 $10^{-9}$–$10^{-4}$ $m^2$ $s^{-3}$ (including or exceeding the range of mixing turbulence in the field by up to two orders of magnitude) led to decreases in *Microcystis* colony size to 200–420 μm. 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

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)

| 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 *et al.* (2012) |
| | Heterotrophic bacteria | Shen *et al.* (2011); Wang *et al.* (2015) |
| | Low temperature and low light intensity | Li *et al.* (2013); Xu *et al.* (2016*a*) |
| 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 *et al.* (2012) |

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 $cell^{-1}$ induced *Microcystis* colony formation, while Li *et al.* (2013) observed the appearance of *Microcystis* colonies at only 0.6–0.8 pg $cell^{-1}$. An even lower value of 0.34 pg $cell^{-1}$ 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 $Ca^{2+}$ 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.* (2016*a*) 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 $Ca^{2+}$ concentration (Thakur, Singh & Handa, 1997). Addition of $Ca^{2+}$ 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 $Ca^{2+}$ 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 $\geq$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. wesenbergii*-like colonies. However, this proposal requires verification by further investigations of the effects of low pH and high $Ca^{2+}$ 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.

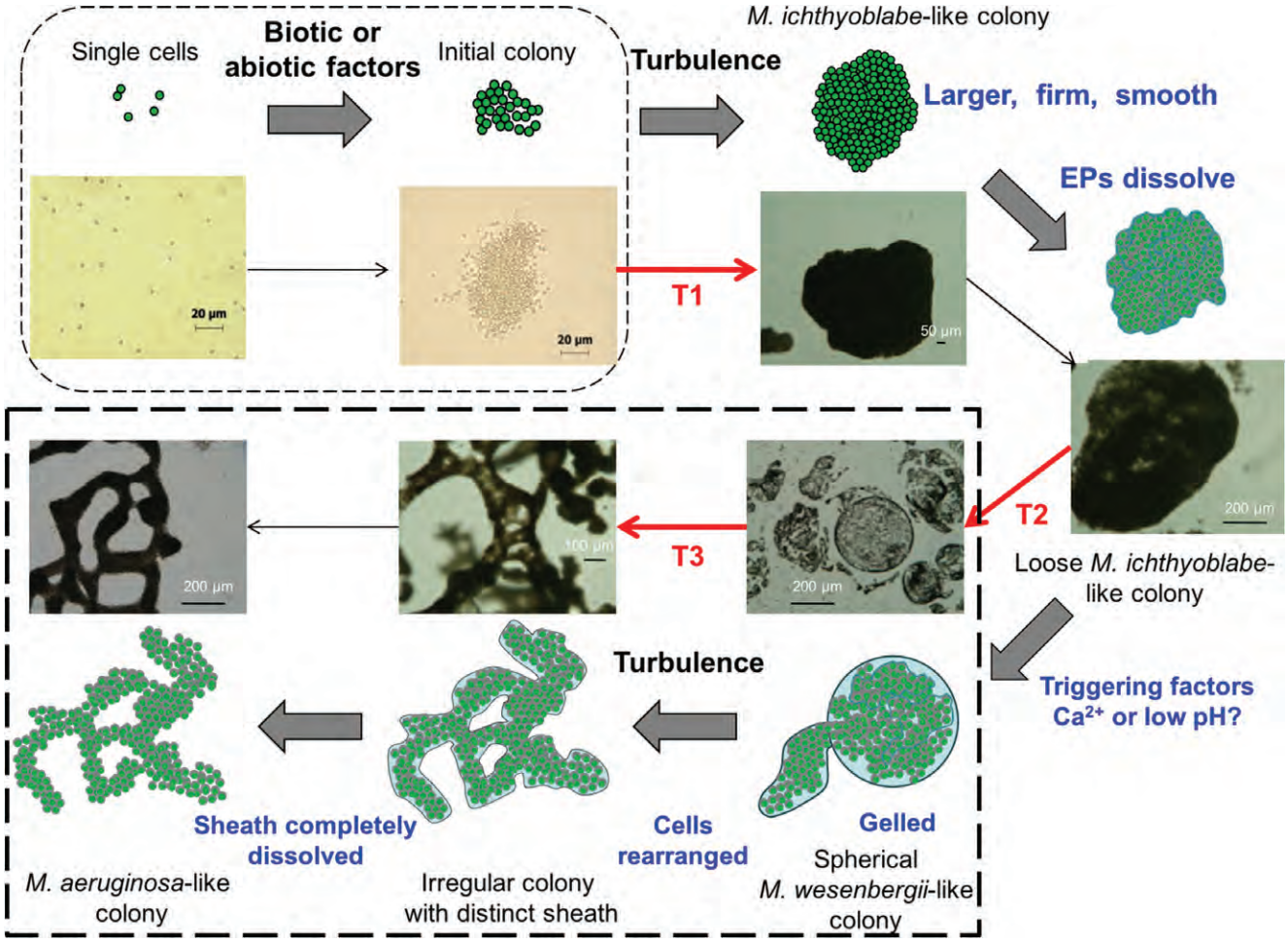


**Fig. 3.** Hypotheses of main transition pathways inducing morphological changes in *Microcystis* under various treatments. Transition route 1: from non-classical colonies to *M. ichthyoblabe*-like colonies. Transition route 2: from *M. ichthyoblabe*-like colonies to *M. wesenbergii*-like colonies. Transition route 3: from *M. wesenbergii*-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 $m^{-2}$ $s^{-1}$. 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 (μg $mg^{-1}$ 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 μmol photons $m^{-2}$ $s^{-1}$; 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 μM) and iron-replete (36 μM) 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 ($< 50$ μM) 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 $ml^{-1}$ 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 $Pb^{2+}$ to unicellular *Microcystis*, and found the proportion of cells that formed colonies increased with increasing $Pb^{2+}$ 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 $COO^-$ 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 ($D_{par}$; μm) 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 μm 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 μm (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 $^{13}C$ indicated that two major crustacean zooplankton species, *Ceriodaphnia cornuta* and *Thermocyclops decipiens*, were unable to feed on large labelled colonies (> 100 μm 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 μm, 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 μm), 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 μm (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 μm), 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 $N_2$-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

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

| Zooplankton predator | | | Optimal algal prey size (μm) | |
|---|---|---|---|---|
| Species | 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 ± 0.9 | Yang *et al.* (2008) | – | 2.6 ± 0.1 |
| | 8.3 ± 0.8 | Yang & Kong (2012) | – | 2.8 ± 0.1 |
| Cladoceran *Daphnia magna* | 2100 ± 400 | Jang *et al.* (2003) | 51 ± 0.3 | 42 ± 0.2 |
| Cladoceran *Daphnia pulex* | 1600 ± 300 | | 40 ± 0.3 | 32 ± 0.2 |
| Cladoceran *Moina macrocopa* | 1200 ± 100 | | 27 ± 0.3 | 24 ± 0.1 |
| Copepod *Eudiaptomus graciloides* | 1800 ± 250 | Yang *et al.* (2006) | – | 100 ± 0.1 |
| Rotifer *Brachionus calyciflorus* | 220 ± 30 | | – | 12 ± 0.1 |

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 $h^{-1}$ 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 $h^{-1}$ when *D. circinalis* was grown under 100 μmol photons $m^{-2}$ $s^{-1}$ 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 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 $h^{-1}$ (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 in *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 $Pb^{2+}$ 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 $Ca^{2+}$ concentrations, and microcystins.

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

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

| Species | Size (μm) | $\varphi$ | $\rho$ (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.* (2016*a*) |
| *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 *et al.* (2005) |
| *D. flos-aquae* | $D = 56$–$200$ | 1.7 | 920–1030 | −0.22–0.04 | Filament | Reynolds *et al.* (1987) |
| *Scenedesmus* sp. | $D = 3.5$–$9.5$ | ND | ND | 0–0.03 | Colony | Lürling (2003) |
| *Planktothrix rubescens* | $L = 26$–$322$; $W = 4.37$–$4.67$ | 3.2 | 1084–1092 | −0.02– −0.03 | Cylindrical filaments | Walsby & Holland (2006) |
| *P. agardhii* | ND | ND | 985–1085 | ND | Cylindrical filaments | Reynolds *et al.* (1987) |
| *Aphanozominan flos-aquae* | $D < 140$ | 1.5 | 920–1030 | −0.14–0.02 | Filament | Reynolds *et al.* (1987) |
| *Oscillatoria rubescens* | $D = 27.6$–$40.6$ | 6 | 990–1065 | −0.002–0.02 | Filament | Reynolds *et al.* (1987) |
| *O. agardhii* | $D = 27.6$–$36.6$ | 10 | 985–1085 | −0.003–0.02 | Filament | Reynolds *et al.* (1987) |
| *O. redekei* | $D = 11.2$–$14.8$ | $> 5$ | ND | ND | Filament | Reynolds *et al.* (1987) |
| *Lyngbya limnetica* | $D = 19.0$–$20.8$ | 10 | ND | ? −0.003 | Filament | Reynolds *et al.* (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 *et al.* (1987) |
| *Synechococcus* sp. | $D = 0.8$–$2.9$ | 1.3 | ? | < 3.6e−05 | Non-spherical cell | |

*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*.

## IX. ACKNOWLEDGEMENTS

This work was supported by the National Natural Science Foundation of China (Grant Nos. 51409216 to M.L.), Tang Scholar of Cyrus Tang Foundation to M.L., a Griffith University International Postgraduate Research Scholarship to M.X., and by the Australian Research Council (ARC: linkage project LP130100311 to M.X.). C.S.R. is an honorary Fellow of the UK Centre for Ecology and Hydrology, supported by the Natural Environment Research Council. We also thank two anonymous reviewers for their comments, and Dr Alison Cooper for the thorough copy-editing of this work.

## X. REFERENCES

References marked with asterisk have been cited within the supporting information

*Abed, I. J. (2015). PCR-based test for the early warning of both cylindrospermopsin and saxitoxin in Iraqi freshwater. *Journal of Al-Nahrain University* **18**, 109–114.

*Aben, H. & Kurnitski, V. (1997). *Proceedings of the Estonian Academy of Sciences, Biology and Ecology*. Estonian Academy Publishers, Estonia.

*Addico, G., Hardege, J., Komarek, J., Babica, P. & de Graft-Johnson, K. (2006). Cyanobacteria species identified in the Weija and Kpong reservoirs, Ghana, and their implications for drinking water quality with respect to microcystin. *African Journal of Marine Science* **28**, 451–456.

*Ahmed, M., Hiller, S. & Luckas, B. (2008). *Microcystis aeruginosa* bloom and the occurrence of microcystins (heptapeptides hepatotoxins) from an aquaculture pond in Gazipur, Bangladesh. *Turkish Journal of Fisheries and Aquatic Sciences* **8**, 37–41.

*Aktan, Y., Luglié, A. & Sechi, N. (2009). Morphological plasticity of dominant species in response to nutrients dynamics in Bidighinzu Reservoir of Sardinia, Italy. *Turkish Journal of Fisheries and Aquatic Sciences* **9**, 137–144.

*Al-Jassabi, S. & Khalil, A. (2006). Microcystin-induced 8-hydroxydeoxyguanosine in DNA and its reduction by melatonin, vitamin C, and vitamin E in mice. *Biochemistry (Moscow)* **71**, 1115–1119.

*Almanza, V., Parra, O., Carlos, E. D. M., Baeza, C., Beltran, J., Figueroa, R. & Urrutia, R. (2016). Occurrence of toxic blooms of *Microcystis aeruginosa* in a central Chilean (36° Lat. S) urban lake. *Revista Chilena de Historia Natural* **89**, 8.

*Al-Shehri, A. (2010). Toxin-producing blooms of the cyanobacterium *Microcystis aeruginosa* in rainwater ponds in Saudi Arabia. *Oceanological and Hydrobiological Studies* **39**, 171–187.

*Amano, Y., Sakai, Y., Sekiya, T., Takeya, K., Taki, K. & Machida, M. (2010). Effect of phosphorus fluctuation caused by river water dilution in eutrophic lake on competition between blue-green alga *Microcystis aeruginosa* and diatom *Cyclotella* sp. *Journal of Environmental Sciences* **22**, 1666–1673.

*Amé, M. V., del Pilar Díaz, M. & Wunderlin, D. A. (2003). Occurrence of toxic cyanobacterial blooms in San Roque Reservoir (Córdoba, Argentina): a field and chemometric study. *Environmental Toxicology* **18**, 192–201.

*Amer, R., Díez, B. & El-Shehawy, R. (2009). Diversity of hepatotoxic cyanobacteria in the Nile Delta, Egypt. *Journal of Environmental Monitoring* **11**, 126–133.

Antenucci, J. P., Ghadouani, A., Burford, M. A. & Romero, J. R. (2005). The long-term effect of artificial destratification on phytoplankton species composition in a subtropical reservoir. *Freshwater Biology* **50**, 1081–1093.

*Arora, J. & Mehra, N. (2009). Seasonal dynamics of zooplankton in a shallow eutrophic, man-made hyposaline lake in Delhi (India): role of environmental factors. *Hydrobiologia* **626**, 27–40.

*Arzate-Cárdenas, M. A., Olvera-Ramírez, R. & Martínez-Jerónimo, F. (2010). *Microcystis* toxigenic strains in urban lakes: a case of study in Mexico City. *Ecotoxicology* **19**, 1157–1165.

*Atoui, A., Hafez, H. & Slim, K. (2013). Occurrence of toxic cyanobacterial blooms for the first time in Lake Karaoun, Lebanon. *Water and Environment Journal* **27**, 42–49.

*Azevedo, S. M., Carmichael, W. W., Jochimsen, E. M., Rinehart, K. L., Lau, S., Shaw, G. R. & Eaglesham, G. K. (2002). Human intoxication by microcystins during renal dialysis treatment in Caruaru-Brazil. *Toxicology* **181**, 441–446.

*Babanazarova, O., Sidelev, S. & Fastner, J. (2015). Northern expansion of *Cylindrospermopsis raciborskii* (Nostocales, Cyanoprokaryota) observed in shallow highly eutrophic Lake Nero (Russia). *International Journal on Algae* **17**, 131–141.

Bai, L., Xu, H., Wang, C., Deng, J. & Jiang, H. (2016). Extracellular polymeric substances facilitate the biosorption of phenanthrene on cyanobacteria *Microcystis aeruginosa*. *Chemosphere* **162**, 172–180.

*Ballot, A., Pflugmacher, S., Wiegand, C., Kotut, K. & Krienitz, L. (2003). Cyanobacterial toxins in lake Baringo, Kenya. *Limnologica-Ecology and Management of Inland Waters* **33**, 2–9.

*Barinova, S., Bragina, T. & Nevo, E. (2009). Algal species diversity of arid region lakes in Kazakhstan and Israel. *Community Ecology* **10**, 7–16.

Beardall, J., Allen, D., Bragg, J., Finkel, Z. V., Flynn, K. J., Quigg, A., Rees, T. A., Richardson, A. & Raven, J. A. (2009). Allometry and stoichiometry of unicellular, colonial and multicellular phytoplankton. *New Phytologist* **181**, 295–309.

Becker, A., Herschel, A. & Wilhelm, C. (2006). Biological effects of incomplete destratification of hypertrophic freshwater reservoir. *Hydrobiologia* **559**, 85–100.

Becker, S., Matthijs, H. C. P. & van Donk, E. (2010). Biotic factors in induced defence revisited: cell aggregate formation in the toxic cyanobacterium *Microcystis aeruginosa* PCC 7806 is triggered by spent *Daphnia* medium and disrupted cells. *Hydrobiologia* **644**, 159–168.

*Belykh, O., Dmitrieva, O., Gladkikh, A. & Sorokovikova, E. (2013). Identification of toxigenic cyanobacteria of the genus *Microcystis* in the Curonian Lagoon (Baltic Sea). *Oceanology* **53**, 71–79.

*Berger, C., Couté, A., Ba, N. G. & Gugger, M. (2005). Cyanobacterial taxa of the Senegal River system (northern Senegal, West Africa). *Algological Studies* **117**, 147–176.

*Berón, L. E. (1990). Features of the limnological behavior of Salto Grande's reservoir (Argentina-Uruguay). *Ecological Modelling* **52**, 87–102.

*Beversdorf, L. J., Miller, T. R. & McMahon, K. D. (2013). The role of nitrogen fixation in cyanobacterial bloom toxicity in a temperate, eutrophic lake. *PLoS One* **8**, e56103.

Bi, X. D., Zhang, S. L., Dai, W., Xing, K. Z. & Yang, F. (2013). Effects of lead(II) on the extracellular polysaccharide (EPS) production and colony formation of cultured *Microcystis aeruginosa*. *Water Science and Technology* **67**, 803–809.

*Bittencourt-Oliveira, M., Carmo, D., Piccin-Santos, V., Moura, A. N., Aragão-Tavares, N. K. & Cordeiro-Araújo, M. K. (2014). Cyanobacteria, microcystins and cylindrospermopsin in public drinking supply reservoirs of Brazil. *Anais da Academia Brasileira de Ciências* **86**, 297–310.

*Borics, G., Grigorszky, I., Szabó, S. & Padisák, J. (2000). Phytoplankton associations in a small hypertrophic fishpond in East Hungary during a change from bottom-up to top-down control. *Hydrobiologia* **424**, 79–90.

Bormans, M. & Condie, S. A. (1997). Modelling the distribution of *Anabaena* and *Melosira* in a stratified river weir pool. *Hydrobiologia* **364**, 3–13.

*Bouvy, M., Falcão, D., Marinho, M., Pagano, M. & Moura, A. (2000). Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. *Aquatic Microbial Ecology* **23**, 13–27.

*Bouvy, M., Molica, R., De Oliveira, S., Marinho, M. & Beker, B. (1999). Dynamics of a toxic cyanobacterial bloom (*Cylindrospermopsis raciborskii*) in a shallow reservoir in the semi-arid region of northeast Brazil. *Aquatic Microbial Ecology* **20**, 285–297.

*Briand, J., Robillot, C., Quiblier-Lloberas, C., Humbert, J., Couté, A. & Bernard, C. (2002). Environmental context of *Cylindrospermopsis raciborskii* (Cyanobacteria) blooms in a shallow pond in France. *Water Research* **36**, 3183–3192.

Brookes, J. D., Ganf, G. G., Green, D. & Whittington, J. (1999). The influence of light and nutrients on buoyancy, filament aggregation and flotation of *Anabaena circinalis*. *Journal of Plankton Research* **21**, 327–341.

Burford, M. A., Beardall, J., Willis, A., Orr, P. T., Magalhaes, V. F., Rangel, L. M., Azevedo, S. M. & Neilan, B. A. (2016). Understanding the winning strategies used by the bloom-forming cyanobacterium *Cylindrospermopsis raciborskii*. *Harmful Algae* **54**, 44–53.

Burkert, U., Hyenstrand, P., Drakare, S. & Blomqvist, P. (2001). Effects of the mixotrophic flagellate *Ochromonas* sp. on colony formation in *Microcystis aeruginosa*. *Aquatic Ecology* **35**, 11–17.

Burns, C. W. (1968). The relationship between body size of filter-feeding *Cladocera* and the maximum size of particle ingested. *Limnology and Oceanography* **13**, 675–678.

*Campos, V., Cantarero, S., Urrutia, H., Heinze, R., Wirsing, B., Neumann, U. & Weckesser, J. (1999). Microcystin in cyanobacterial blooms in a Chilean lake. *Systematic and Applied Microbiology* **22**, 169–173.

Cao, H. & Yang, Z. (2010). Variation in colony size of *Microcystis aeruginosa* in a eutrophic Lake during recruitment and bloom formation. *Journal of Freshwater Ecology* **25**, 331–335.

*Carmichael, W. W., Azevedo, S., An, J. S., Molica, R., Jochimsen, E. M., Lau, S., Rinehart, K. L., Shaw, G. R. & Eaglesham, G. K. (2001). Human fatalities from cyanobacteria: chemical and biological evidence for cyanotoxins. *Environmental Health Perspectives* **109**, 663–668.

*Carrasco, D., Moreno, E., Sanchis, D., Wörmer, L., Paniagua, T., Del Cueto, A. & Quesada, A. (2006). Cyanobacterial abundance and microcystin occurrence in Mediterranean water reservoirs in Central Spain: microcystins in the Madrid area. *European Journal of Phycology* **41**, 281–291.

Carroll, S. B. (2001). Chance and necessity: the evolution of morphological complexity and diversity. *Nature* **409**, 1102–1109.

Cava, F., De Pedro, M. A., Schwarz, H., Henne, A. & Berenguer, J. (2004). Binding to pyruvylated compounds as an ancestral mechanism to anchor the outer envelope in primitive bacteria. *Molecular Microbiology* **52**, 677–690.

*Chan, W. S., Recknagel, F., Cao, H. & Park, H.-D. (2007). Elucidation and short-term forecasting of microcystin concentrations in Lake Suwa (Japan) by means of artificial neural networks and evolutionary algorithms. *Water Research* **41**, 2247–2255.

*Chapman, A. D. & Schelske, C. L. (1997). Recent appearance of *Cylindrospermopsis* (cyanobacteria) in five hypereutrophic Florida lakes. *Journal of Phycology* **33**, 191–195.

*Chellappa, N. T., Chellappa, S. L. & Chellappa, S. (2008). Harmful phytoplankton blooms and fish mortality in a eutrophicated reservoir of Northeast Brazil. *Brazilian Archives of Biology and Technology* **51**, 633–641.

*Chia, A., Oniye, S., Ladan, Z., Lado, Z., Pila, A., Inekwe, V. & Mmerole, J. (2009). A survey for the presence of microcystins in aquaculture ponds in Zaria, Northern-Nigeria: possible public health implication. *African Journal of Biotechnology* **8**, 6282–6289.

Chiovitti, A., Heraud, P., Dugdale, T. M., Hodson, O. M., Curtain, R. C., Dagastine, R. R., Wood, B. R. & Wetherbee, R. (2008). Divalent cations stabilize the aggregation of sulfated glycoproteins in the adhesive nanofibers of the biofouling diatom *Toxarium undulatum*. *Soft Matter* **4**, 811–820.

*Chonudomkul, D., Yongmanitchai, W., Theeragool, G., Kawachi, M., Kasai, F., Kaya, K. & Watanabe, M. M. (2004). Morphology, genetic diversity, temperature tolerance and toxicity of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) strains from Thailand and Japan. *FEMS Microbiology Ecology* **48**, 345–355.

*Chorus, I. & Bartram, J. (1999). *Toxic Cyanobacteria in Water: A guide to their public health consequences, monitoring and management*. London: E & FN Spon, Routledge, London, UK.

*Chung, S., Imberger, J., Hipsey, M. & Lee, H. (2014). The influence of physical and physiological processes on the spatial heterogeneity of a *Microcystis* bloom in a stratified reservoir. *Ecological Modelling* **289**, 133–149.

Cirés, S. & Ballot, A. (2016). A review of the phylogeny, ecology and toxin production of bloom-forming *Aphanizomenon* spp. and related species within the *Nostocales* (Cyanobacteria). *Harmful Algae* **54**, 21–43.

*Codd, G. A., Azevedo, S. M. F. O., Bagchi, S. N., Burch, M. D., Carmichael, W. W., Harding, W. R., Kaya, K. & Utkilen, H. C. (2005). In *CYANONET: A Global Network for Cyanobacterial Bloom and Toxin Risk Management; Initial Situation Assessment and Recommendations* (Volume **76**, ed. UNESCO). UNESCO, Paris.

*Cook, C. M., Vardaka, E. & Lanaras, T. (2004). Toxic cyanobacteria in Greek freshwaters, 1987–2000: occurrence, toxicity, and impacts in the Mediterranean region. *CLEAN–Soil, Air, Water* **32**, 107–124.

*Crossetti, L. O. & Bicudo, C. E. d. M. (2008). Adaptations in phytoplankton life strategies to imposed change in a shallow urban tropical eutrophic reservoir, Garças Reservoir, over 8 years. *Hydrobiologia* **614**, 91–105.

*Cuvin-Aralar, M. L., Fastner, J., Focken, U., Becker, K. & Aralar, E. V. (2002). Microcystins in natural blooms and laboratory cultured *Microcystis aeruginosa* from Laguna de Bay, Philippines. *Systematic and Applied Microbiology* **25**, 179–182.

*Daam, M. A., Van den Brink, P. J. & Nogueira, A. J. (2008). Impact of single and repeated applications of the insecticide chlorpyrifos on tropical freshwater plankton communities. *Ecotoxicology* **17**, 756–771.

*Dao, T. S., Cronberg, G., Nimptsch, J., Do-Hong, L.-C. & Wiegand, C. (2010). Toxic cyanobacteria from Tri An Reservoir, Vietnam. *Nova Hedwigia* **90**, 433–448.

*De Leon, L. & Yunes, J. S. (2001). First report of a microcystin-containing bloom of the cyanobacterium *Microcystis aeruginosa* in the La Plata River, South America. *Environmental Toxicology* **16**, 110–112.

Dodds, W. K., Bouska, W. W., Eitzmann, J. L., Pilger, T. J., Pitts, K. L., Riley, A. J., Schloesser, J. T. & Thornbrugh, D. J. (2008). Eutrophication of US freshwaters: analysis of potential economic damages. *Environmental Science & Technology* **43**, 12–19.

*Dörr, F. A., Pinto, E. & Soares, R. M. (2010). Microcystins in South American aquatic ecosystems: occurrence, toxicity and toxicological assays. *Toxicon* **56**, 1247–1256.

Drenner, R. W., Hambright, K. D., Vinyard, G. L., Gophen, M. & Pollingher, U. (1987). Experimental study of size-selective phytoplankton grazing by a filter-feeding cichlid and the cichlid's effects on plankton community structure. *Limnology and Oceanography* **32**, 1138–1144.

Drenner, R. W., Mummert, J. R., Denoyelles, F. & Kettle, D. (1984). Selective particle ingestion by a filter-feeding fish and its impact on phytoplankton community structure. *Limnology and Oceanography* **29**, 941–948.

*Drugă, B., Welker, M., Sesărman, A., Hegedus, A., Coman, C., Sicora, C. & Dragoş, N. (2013). Molecular characterization of microcystin-producing cyanobacteria from Romanian fresh waters. *European Journal of Phycology* **48**, 287–294.

*Dumont, H. J. (2009). *The Nile: Origin, Environments, Limnology and Human Use*. Springer Netherlands, United States.

*Duong, T. T., Jähnichen, S., Le, T. P. Q., Ho, C. T., Hoang, T. K., Nguyen, T. K., Vu, T. N. & Dang, D. K. (2014). The occurrence of cyanobacteria and microcystins in the Hoan Kiem Lake and the Nui Coc reservoir (North Vietnam). *Environmental Earth Sciences* **71**, 2419–2427.

*Eguzozie, K., Mavumengwana, V., Nkosi, D., Kayitesi, E. & Nnabuo-Eguzozie, E. C. (2016). Bioaccumulation and quantitative variations of microcystins in the swartspruit river, South Africa. *Archives of Environmental Contamination and Toxicology* **71**, 286–296.

*Ekman-Ekebom, M., Kauppi, M., Sivonen, K., Niemi, M. & Lepistö, L. (1992). Toxic cyanobacteria in some Finnish lakes. *Environmental Toxicology* **7**, 201–213.

*Engström-Öst, J., Rasic, I. S., Brutemark, A., Rancken, R., Simić, G. S. & Laugen, A. T. (2015). Can *Cylindrospermopsis raciborskii* invade the Baltic Sea? *Environmental Reviews* **23**, 161–169.

*Eynard, F., Mez, K. & Walther, J.-L. (2000). Risk of cyanobacterial toxins in Riga waters (Latvia). *Water Research* **34**, 2979–2988.

Fang, F., Yang, L., Gan, L., Guo, L., Hu, Z., Yuan, S., Chen, Q. & Jiang, L. (2014). DO, pH, and Eh microprofiles in cyanobacterial granules from Lake Taihu under different environmental conditions. *Journal of Applied Phycology* **26**, 1689–1699.

*Farkas, O., Gyémant, G., Hajdú, G., Gonda, S., Parizsa, P., Horgos, T., Mosolygó, Á. & Vasas, G. (2014). Variability of microcystins and its synthetase gene cluster in *Microcystis* and *Planktothrix* waterblooms in shallow lakes of Hungary. *Acta Biologica Hungarica* **65**, 227–239.

*Fastner, J. (1994). First results on the occurrence of microcystin-LR in Berlin and Brandenburg lakes. In *Detection Methods for Cynobacterial Toxins* (Volume **149**, eds G. A. Codd, T. M. Jefferies, C. W. Keevil and E. Potter), p. 149. Special Publication-Royal Society of Chemistry, Cambridge.

*Fastner, J., Heinze, R., Humpage, A., Mischke, U., Eaglesham, G. & Chorus, I. (2003). Cylindrospermopsin occurrence in two German lakes and preliminary assessment of toxicity and toxin production of *Cylindrospermopsis raciborskii* (Cyanobacteria) isolates. *Toxicon* **42**, 313–321.

*Fernald, S. H., Caraco, N. F. & Cole, J. J. (2007). Changes in cyanobacterial dominance following the invasion of the zebra mussel *Dreissena polymorpha*: long-term results from the Hudson River estuary. *Estuaries and Coasts* **30**, 163–170.

*Fernández, C., Estrada, V. & Parodi, E. R. (2015). Factors triggering cyanobacteria dominance and succession during blooms in a hypereutrophic drinking water supply reservoir. *Water, Air, & Soil Pollution* **226**, 73.

*Fishman, D. B., Adlerstein, S. A., Vanderploeg, H. A., Fahnenstiel, G. L. & Scavia, D. (2010). Phytoplankton community composition of Saginaw Bay, Lake Huron, during the zebra mussel (*Dreissena polymorpha*) invasion: a multivariate analysis. *Journal of Great Lakes Research* **36**, 9–19.

*Fonseca, B. M. & Bicudo, C. E. D. M. (2009). How important can the presence/absence of macrophytes be in determining phytoplankton strategies in two tropical shallow reservoirs with different trophic status? *Journal of Plankton Research* **32**, 31–46.

Forni, C., Telo', F. R. & Caiola, M. G. (1997). Comparative analysis of the polysaccharides produced by different species of *Microcystis* (Chroococcales, Cyanophyta). *Phycologia* **36**, 181–185.

*Fortin, N., Aranda-Rodriguez, R., Jing, H., Pick, F., Bird, D. & Greer, C. W. (2010). Detection of microcystin-producing cyanobacteria in Missisquoi Bay, Quebec, Canada, using quantitative PCR. *Applied and Environmental Microbiology* **76**, 5105–5112.

Gan, N., Xiao, Y., Zhu, L., Wu, Z., Liu, J., Hu, C. & Song, L. (2012). The role of microcystins in maintaining colonies of bloom-forming *Microcystis* spp. *Environmental Microbiology* **14**, 730–742.

Ganf, G. & Oliver, R. (1982). Vertical separation of light and available nutrients as a factor causing replacement of green algae by blue-green algae in the plankton of a stratified lake. *Journal of Ecology* **70**, 829–844.

*Gillett, N. D. & Steinman, A. D. (2011). An analysis of long-term phytoplankton dynamics in Muskegon Lake, a Great Lakes Area of Concern. *Journal of Great Lakes Research* **37**, 335–342.

*Gkelis, S., Harjunpää, V., Lanaras, T. & Sivonen, K. (2005). Diversity of hepatotoxic microcystins and bioactive anabaenopeptins in cyanobacterial blooms from Greek freshwaters. *Environmental Toxicology* **20**, 249–256.

*Gkelis, S., Papadimitriou, T., Zaoutsos, N. & Leonardos, I. (2014). Anthropogenic and climate-induced change favors toxic cyanobacteria blooms: evidence from monitoring a highly eutrophic, urban Mediterranean lake. *Harmful Algae* **39**, 322–333.

*Gobler, C., Davis, T., Coyne, K. & Boyer, G. (2007). Interactive influences of nutrient loading, zooplankton grazing, and microcystin synthetase gene expression on cyanobacterial bloom dynamics in a eutrophic New York lake. *Harmful Algae* **6**, 119–133.

*Gomes, L. N. L., Oliveira, S. M. A. C., Giani, A. & von Sperling, E. (2012). Association between biotic and abiotic parameters and the occurrence of cyanobacteria in a Brazilian reservoir. *Environmental Monitoring and Assessment* **184**, 4635–4645.

*Government of Western Australia. (2005). *Algal Blooms in the Swan-Canning Estuary: Patterns, Causes and History*. Department of Environment, Western Australia.

*Grace, M. R., Scicluna, T. R., Vithana, C. L., Symes, P. & Lansdown, K. P. (2010). Biogeochemistry and cyanobacterial blooms: investigating the relationship in a shallow, polymictic, temperate lake. *Environmental Chemistry* **7**, 443–456.

*Green, J. (2011). Geographical variation in rotifers associated with *Microcystis* blooms. *Hydrobiologia* **662**, 197–204.

Gumbo, R. J., Ross, G. & Cloete, E. T. (2008). Biological control of *Microcystis* dominated harmful algal blooms. *African Journal of Biotechnology* **7**, 4765–4773.

*Gunnarsson, H. & Sanseovic, A.-M. (2001). *Possible linkages between algae toxins in drinking water and related illnesses in Windhoek, Namibia*. Bachelor's degree project: Kristianstad University, Kristianstad.

*Ha, J. H., Hidaka, T. & Tsuno, H. (2008). Quantification of toxic *Microcystis* and evaluation of its dominance ratio in blooms using real-time PCR. *Environmental Science & Technology* **43**, 812–818.

Ha, K., Jang, M.-H. & Takamura, N. (2004). Colony formation in planktonic algae induced by zooplankton culture media filtrate. *Journal of Freshwater Ecology* **19**, 9–16.

Hamilton, D. P., Wood, S. A., Dietrich, D. R. & Puddick, J. (2013). Costs of harmful blooms of freshwater cyanobacteria. In *Cyanobacteria: An Economic Perspective* (eds N. K. Sharma, A. K. Rai and L. J. Stal), pp. 245–256. John Wiley & Sons, Ltd, Chichester.

*Hamilton, P. B., Ley, L. M., Dean, S. & Pick, F. R. (2005). The occurrence of the cyanobacterium *Cylindrospermopsis raciborskii* in Constance Lake: an exotic cyanoprokaryote new to Canada. *Phycologia* **44**, 17–25.

Hansen, B., Bjornsen, P. K. & Hansen, P. J. (1994). The size ratio between planktonic predators and their prey. *Limnology and Oceanography* **39**, 395–403.

*Harding, W. (1992). Zeekoevlei-water chemistry and phytoplankton periodicity. *Water SA* **18**, 237–237.

Harke, M. J., Steffen, M. M., Gobler, C. J., Otten, T. G., Wilhelm, S. W., Wood, S. A. & Paerl, H. W. (2016). A review of the global ecology, genomics, and biogeography of the toxic cyanobacterium, *Microcystis* spp. *Harmful Algae* **54**, 4–20.

*Haynie, R., Morgan, J., Bartelme, B., Willis, B., Rodgers, J. H. Jr., Jones, L. & Wilde, S. (2013). *Harmful Algal Blooms and Toxin Production in Georgia Ponds*. Georgia Institute of Technology, University of Georgia.

*Henriksen, P. & Moestrup, Ø. (1997). Seasonal variations in microcystin contents of Danish cyanobacteria. *Natural Toxins* **5**, 99–106.

Heo, W.-M. & Kim, B. (2004). The effect of artificial destratification on phytoplankton in a reservoir. *Hydrobiologia* **524**, 229–239.

*Herrera, N. A., Echeverri, L. F. & Ferrao-Filho, A. S. (2015). Effects of phytoplankton extracts containing the toxin microcystin-LR on the survival and reproduction of cladocerans. *Toxicon* **95**, 38–45.

*Herry, S. E., Fathalli, A., Rejeb, A. J.-B. & Bouaïcha, N. (2008). Seasonal occurrence and toxicity of *Micyocystis* spp. and 7 Oscillatoria Tenuis in the Lebna dam, Tunisia. *Water Research* **45**, 1263–1273.

*Hirooka, E. Y., Pinotti, M. H. P., Tsutsumi, T., Yoshida, F. & Ueno, Y. (1999). Survey of microcystins in water between 1995 and 1996 in Parana, Brazil using ELISA. *Natural Toxins* **7**, 103–109.

*Hodgkiss, I. (1974). Studies on Plover Cove Reservoir, Hong Kong: composition and distribution of the phytoplankton and its relationship to environmental factors. *Freshwater Biology* **4**, 111–126.

*Hofbauer, B. & Jüttner, F. (1988). Occurrence of isopropylthio compounds in the aquatic ecosystem (Lake Neusiedl, Austria) as a chemical marker for *Microcystis flos-aquae*. *FEMS Microbiology Letters* **53**, 113–121.

Hu, H. & Wei, Y. (2006). *The Freshwater Algae of China: Systematics, Taxonomy and Ecology*. Science Press, Beijing, China.

Huisman, J., Jonker, R. R., Zonneveld, C. & Weissing, F. J. (1999). Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology* **80**, 211–222.

Huisman, J., Sharples, J., Stroom, J. M., Visser, P. M., Kardinaal, W. E. A., Verspagen, J. M. & Sommeijer, B. (2004). Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology* **85**, 2960–2970.

*Humbert, J., Duris-Latour, D., Le Berre, B., Giraudet, H. & Salençon, M. (2005). Genetic diversity in *Microcystis* populations of a French storage reservoir assessed by sequencing of the 16S-23S rRNA intergenic spacer. *Microbial Ecology* **49**, 308–314.

*Hur, M., Lee, I., Tak, B.-M., Lee, H. J., Yu, J. J., Cheon, S. U. & Kim, B.-S. (2013). Temporal shifts in cyanobacterial communities at different sites on the Nakdong River in Korea. *Water Research* **47**, 6973–6982.

*Hwang, S.-J., Kim, H.-S., Park, J.-H. & Kim, B.-H. (2010). Effects of cyanobacterium *Microcystis aeruginosa* on the filtration rate and mortality of the freshwater bivalve *Corbicula leana*. *Journal of Environmental Biology* **31**, 483–488.

Ibelings, B. W., Kroon, B. & Mur, L. R. (1994). Acclimation of photosystem II in a cyanobacterium and a eukaryotic green alga to high and fluctuating photosynthetic photon flux densities, simulating light regimes induced by mixing in lakes. *New Phytologist* **128**, 407–424.

*Imai, H., Chang, K.-H., Kusaba, M. & Nakano, S.-I. (2008). Temperature-dependent dominance of *Microcystis* (Cyanophyceae) species: *M. aeruginosa* and *M. wesenbergii*. *Journal of Plankton Research* **31**, 171–178.

*Infante, A. & Riehl, W. (1984). The effect of cyanophyta upon zooplankton in a eutrophic tropical lake (Lake Valencia, Venezuela). *Hydrobiologia* **113**, 293–298.

*Jahan, R., Khan, S., Haque, M. M. & Choi, J. K. (2010). Study of harmful algal blooms in a eutrophic pond, Bangladesh. *Environmental Monitoring and Assessment* **170**, 7–21.

*Jakubowska, N., Zagajewski, P. & Gołdyn, R. (2013). Water blooms and cyanobacterial toxins in lakes. *Polish Journal of Environmental Studies* **22**, 1077–1082.

Jang, M. H., Ha, K., Joo, G. J. & Takamura, N. (2003). Toxin production of cyanobacteria is increased by exposure to zooplankton. *Freshwater Biology* **48**, 1540–1550.

*Janse van Vuuren, S. & Kriel, G. P. (2008). *Cylindrospermopsis raciborskii*, a toxic invasive cyanobacterium in South African fresh waters. *African Journal of Aquatic Science* **33**, 17–26.

*Jayatissa, L., Silva, E., McElhiney, J. & Lawton, L. (2006). Occurrence of toxigenic cyanobacterial blooms in freshwaters of Sri Lanka. *Systematic and Applied Microbiology* **29**, 156–164.

Jia, X., Shi, D., Shi, M., Li, R., Song, L., Fang, H., Yu, G., Li, X. & Du, G. (2011). Formation of cyanobacterial blooms in Lake Chaohu and the photosynthesis of dominant species hypothesis. *Acta Ecologica Sinica* **31**, 2968–2977.

*John, J. & Kemp, A. (2006). Cyanobacterial blooms in the wetlands of the Perth region, taxonomy and distribution: an overview. *Journal of the Royal Society of Western Australia* **89**, 51–56.

Jöhnk, K. D., Huisman, J. E. F., Sharples, J., Sommeijer, B. E. N., Visser, P. M. & Stroom, J. M. (2008). Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology* **14**, 495–512.

*Jones, W. W. & Sauter, S. (2005). *Distribution and Abundance of Cylindrospermopsis raciborskii in Indiana Lakes and Reservoirs*. Indiana University, Bloomington.

Jungmann, D., Ludwichowski, K. U., Faltin, V. & Benndorf, J. (1996). A field study to investigate environmental factors that could effect microcystin synthesis of a *Microcystis* population in the Bautzen reservoir. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **81**, 493–501.

Kaplan, D., Christiaen, D. & Arad, S. (1988). Binding of heavy metals by algal polysaccharides. In *Algal Biotechnology* (ed. T. Stadler, Y. Karamanas, J. Mollion, H. Morvan, J. Mollion and D. Christiaen), pp. 179–187. Elsevier, London.

*Kaštovský, J., Hauer, T., Mareš, J., Krautová, M., Bešta, T., Komárek, J., Desortová, B., Heteša, J., Hindáková, A. & Houk, V. (2010). A review of the alien and expansive species of freshwater cyanobacteria and algae in the Czech Republic. *Biological Invasions* **12**, 3599–3625.

*Katsiapi, M., Moustaka-Gouni, M., Michaloudi, E. & Kormas, K. A. (2011). Phytoplankton and water quality in a Mediterranean drinking-water reservoir (Marathonas Reservoir, Greece). *Environmental Monitoring and Assessment* **181**, 563–575.

*Katsiapi, M., Moustaka-Gouni, M., Vardaka, E. & Kormas, K. A. (2013). Different phytoplankton descriptors show asynchronous changes in a shallow urban lake (L. Kastoria, Greece) after sewage diversion. *Fundamental and Applied Limnology / Archiv für Hydrobiologie* **182**, 219–230.

Ke, Z., Xie, P., Guo, L., Liu, Y. & Yang, H. (2007). In situ study on the control of toxic *Microcystis* blooms using phytoplanktivorous fish in the subtropical Lake Taihu of China: a large fish pen experiment. *Aquaculture* **265**, 127–138.

Kehoe, M. (2009). *Modelling of physical and physiological processes controlling primary production and growth in toxic filamentous cyanobacteria*. PhD Thesis: University of Queensland, Queensland.

*Kemka, N., Njiné, T., Zébazé Togouet, S., Niyitegeka, D., Monkiedje, A., Foto Menbohan, S., Nola, M. & Compère, P. (2003). Quantitative importance of cyanobacteria populations in a hypertrophic shallow lake in the subequatorial African region (Yaounde Municipal Lake, Cameroon). *Archiv für Hydrobiologie* **156**, 495–510.

Kessel, M. & Eloff, J. N. (1975). The ultrastructure and development of the colonial sheath of *Microcystis marginata*. *Archives of Microbiology* **106**, 209–214.

*Keto, J., Horppila, J. & Kairesalo, T. (1992). Regulation of the development and species dominance of summer phytoplankton in Lake Vesijärvi: predictability of enclosure experiments. *Hydrobiologia* **243/244**, 303–310.

*Kokociński, M., Dziga, D., Spoof, L., Stefaniak, K., Jurczak, T., Mankiewicz-Boczek, J. & Meriluoto, J. (2009). First report of the cyanobacterial toxin cylindrospermopsin in the shallow, eutrophic lakes of western Poland. *Chemosphere* **74**, 669–675.

*Komárek, J. (2005). Studies on the cyanophytes (Cyanobacteria, cyanoprokaryota) of Cuba 11. Freshwater *Anabaena* species. *Preslia* **77**, 211–234.

Komárek, J. & Komárková, J. (2002). Review of the European *Microcystis*-morphospecies (Cyanoprokaryotes) from nature. *Czech Phycology, Olomouc* **2**, 1–24.

Kondrat'eva, N., Topachevskii, A., Braginskii, L., Kul'skii, L. & Sirenko, L. (1968). Problems of morphology and taxonomy of *Microcystis aeruginosa* Kütz. emend. Elenkin and its related species. In *Tsveteniye vody* (eds A. V. Topachevskii, L. P. Braginskii, N. V. Kondrat'eva, L. A. Kul'skii and L. A. Sirenko), pp. 13–42. Kiev, Naukova Dunka. (in Russian).

*Krienitz, L., Ballot, A., Wiegand, C., Kotut, K., Codd, G. A. & Pflugmacher, S. (2002). Cyanotoxin-producing bloom of *Anabaena flos-aquae*, *Anabaena discoidea* and *Microcystis aeruginosa* (Cyanobacteria) in Nyanza Gulf of Lake Victoria, Kenya. *Journal of Applied Botany* **76**, 179–183.

*Krishnan, A. A., Krishnakumar, P. & Rajagopalan, M. (2007). *Trichodesmium erythraeum* (Ehrenberg) bloom along the southwest coast of India (Arabian Sea) and its impact on trace metal concentrations in seawater. *Estuarine, Coastal and Shelf Science* **71**, 641–646.

*Krokowski, J. & Jamieson, J. (2010). A decade of monitoring and management of freshwater algae, in particular cyanobacteria in England and Wales. *Freshwater Forum* **18**, 1–6.

*Krokowski, J., Lang, P., Bell, A., Broad, N., Clayton, J., Milne, I., Nicolson, M., Ross, A. & Ross, N. (2012). A review of the incidence of cyanobacteria (blue-green algae) in surface waters in Scotland including potential effects of climate change, with a list of the common species and new records from the Scottish Environment Protection Agency. *The Glasgow Naturalist* **25**, 99–104.

Kurmayer, R., Christiansen, G. & Chorus, I. (2003). The abundance of microcystin-producing genotypes correlates positively with colony size in *Microcystis* sp. and determines its microcystin net production in Lake Wannsee. *Applied and Environmental Microbiology* **69**, 787–795.

*Lagos, N. (1998). Microalgal blooms: a global issue with negative impact in Chile. *Biological Research* **31**, 375–386.

*Lagos, N., Onodera, H., Zagatto, P. A., Andrinolo, D. O., Azevedo, S. M. & Oshima, Y. (1999). The first evidence of paralytic shellfish toxins in the freshwater cyanobacterium *Cylindrospermopsis raciborskii*, isolated from Brazil. *Toxicon* **37**, 1359–1373.

*Lan, W., Qing-hua, C., Min, Z., Lu, T., Yao-yang, X. & Ling-hui, K. (2009). Spatiotemporal dynamics and related affecting factors of summer algal blooms in Xiangxi Bay of Three Gorges Reservoir. *Yingyong Shengtai Xuebao* **20**, 1940–1946.

*Lashari, K. H., Laghari, Z. A., Palh, Z. A., Sahato, G. A. & Mastoi, G. M. (2015). Studies of fresh water toxic phytoplanktonic (*Microcystis*) of Keenkjhar Lake, Thatta, Sindh, and Pakstan. *International Journal of Emerging Trends in Science and Technology* **2**, 1747–1751.

*Laugaste, R., Panksep, K. & Haldna, M. (2013). Dominant cyanobacterial genera in Lake Peipsi (Estonia/Russia): effect of weather and nutrients in summer months. *Estonian Journal of Ecology* **62**, 229.

Lazarevic, V. & Karamata, D. (1995). The tagGH operon of Bacillus subtilis 168 encodes a two-component ABC transporter involved in the metabolism of two wall teichoic acids. *Molecular Microbiology* **16**, 345–355.

Le Ai Nguyen, V., Tanabe, Y., Matsuura, H., Kaya, K. & Watanabe, M. M. (2012). Morphological, biochemical and phylogenetic assessments of water-bloom-forming tropical morphospecies of *Microcystis* (Chroococcales, Cyanobacteria). *Phycological Research* **60**, 208–222.

*Leão, P. N., Vasconcelos, M. T. S. & Vasconcelos, V. M. (2009). Allelopathic activity of cyanobacteria on green microalgae at low cell densities. *European Journal of Phycology* **44**, 347–355.

*Lee, T. A., Rollwagen-Bollens, G., Bollens, S. M. & Faber-Hammond, J. J. (2015). Environmental influence on cyanobacteria abundance and microcystin toxin production in a shallow temperate lake. *Ecotoxicology and Environmental Safety* **114**, 318–325.

Lehman, J. T. (2014). Understanding the role of induced mixing for management of nuisance algal blooms in an urbanized reservoir. *Lake and Reservoir Management* **30**, 63–71.

Lehman, P. W., Kurobe, T., Lesmeister, S., Baxa, D., Tung, A. & Teh, S. J. (2017). Impacts of the 2014 severe drought on the *Microcystis* bloom in San Francisco Estuary. *Harmful Algae* **63**, 94–108.

*Lei, L., Peng, L., Huang, X. & Han, B.-P. (2014). Occurrence and dominance of *Cylindrospermopsis raciborskii* and dissolved cylindrospermopsin in urban reservoirs used for drinking water supply, South China. *Environmental Monitoring and Assessment* **186**, 3079–3090.

*Lemaire, V., Brusciotti, S., van Gremberghe, I., Vyverman, W., Vanoverbeke, J. & De Meester, L. (2012). Genotype × genotype interactions between the toxic cyanobacterium *Microcystis* and its grazer, the waterflea *Daphnia*. *Evolutionary Applications* **5**, 168–182.

Levy, S. (2017). *Microcystis* rising: why phosphorus reduction isn't enough to stop cyanoHABs. *Environmental Health Perspectives* **125**, A34.

Li, L., Zhu, W., Wang, T., Luo, Y., Chen, F. & Tan, X. (2013). Effect of fluid motion on colony formation in *Microcystis aeruginosa*. *Water Science and Engineering* **6**, 106–116.

Li, M., Zhu, W., Dai, X. & Li, X. (2013). Effects of linear alkylbenzene sulfonate on extracellular polysaccharide content and cells per particle of *Microcystis aeruginosa* and *Scenedesmus obliquus*. *Fresenius Environmental Bulletin* **22**, 1189–1194.

Li, M., Zhu, W., Gao, L., Huang, J. & Li, L. (2013). Seasonal variations of morphospecies composition and colony size of *Microcystis* in a shallow hypertrophic lake (Lake Taihu, China). *Fresenius Environmental Bulletin* **22**, 3474–3483.

Li, M., Zhu, W., Gao, L. & Lu, L. (2013). Changes in extracellular polysaccharide content and morphology of *Microcystis aeruginosa* at different specific growth rates. *Journal of Applied Phycology* **25**, 1023–1030.

Li, M., Nkrumah, P. & Xiao, M. (2014). Biochemical composition of *Microcystis aeruginosa* related to specific growth rate: insight into the effects of abiotic factors. *Inland Waters* **4**, 357–362.

Li, M., Zhu, W., Dai, X., Xiao, M., Appiah-Sefah, G. & Nkrumah, P. N. (2014). Size-dependent growth of *Microcystis* colonies in a shallow, hypertrophic lake: use of the RNA-to-total organic carbon ratio. *Aquatic Ecology* **48**, 207–217.

Li, M., Zhu, W. & Sun, Q. (2014). Solubilisation of mucilage induces changes in *Microcystis* colonial morphology. *New Zealand Journal of Marine and Freshwater Research* **48**, 38–47.

Li, M., Nkrumah, P. N. & Peng, Q. (2015). Different tolerances to chemical contaminants between unicellular and colonial morph of *Microcystis aeruginosa*: excluding the differences among different strains. *Journal of Hazardous Materials* **285**, 245–249.

Li, M., Peng, Q. & Xiao, M. (2015). Using interval maxima regression (IMR) to determine environmental optima controlling *Microcystis* spp. growth in Lake Taihu. *Environmental Science and Pollution Research* **23**, 774–784.

Li, M., Zhu, W., Guo, L., Hu, J., Chen, H. & Xiao, M. (2016*a*). To increase size or decrease density? Different *Microcystis* species has different choice to form blooms. *Scientific Reports* **6**, 37056.

Li, X., Dreher, T. W. & Li, R. (2016*b*). An overview of diversity, occurrence, genetics and toxin production of bloom-forming *Dolichospermum* (*Anabaena*) species. *Harmful Algae* **54**, 54–68.

Li, Z. K., Dai, G. Z., Juneau, P. & Qiu, B. S. (2016*c*). Capsular polysaccharides facilitate enhanced iron acquisition by the colonial cyanobacterium *Microcystis* sp. isolated from a freshwater lake. *Journal of Phycology* **52**, 105–115.

*Li, R., Carmichael, W., Brittain, S., Eaglesham, G., Shaw, G., Mahakhant, A., Noparatnaraporn, N., Yongmanitchai, W., Kaya, K. & Watanabe, M. (2001). Isolation and identification of the cyanotoxin cylindrospermopsin and deoxy-cylindrospermopsin from a Thailand strain of *Cylindrospermopsis raciborskii* (Cyanobacteria). *Toxicon* **39**, 973–980.

Li, Y. & Li, D. (2012). Physiological variations of bloom-forming *Microcystis* (Cyanophyceae) related to colony size changes during blooms. *Phycologia* **51**, 599–603.

*Lifshits, M. & Carmeli, S. (2012). Metabolites of *Microcystis aeruginosa* bloom material from Lake Kinneret, Israel. *Journal of Natural Products* **75**, 209–219.

Lilndenschmidt, K. E. (1999). Controlling the growth of *Microcystis* using surged artificial aeration. *International Review of Hydrobiology* **84**, 243–254.

*Lind, O., Dávalos-Lind, L., López, C., López, M. & Bressie, J. D. (2016). Seasonal morphological variability in an in situ cyanobacteria monoculture: example from a persistent *Cylindrospermopsis* bloom in Lake Catemaco, Veracruz, Mexico. *Journal of Limnology* **75**, 66–80.

*Lou, I., Han, B. & Zhang, W. (2016). *Advances in Monitoring and Modelling Algal Blooms in: Freshwater Reservoirs*. Springer, Netherlands, Dordrecht.

*Low, E., Clews, E., Todd, P., Tai, Y. & Ng, P. K. (2010). Top-down control of phytoplankton by zooplankton in tropical reservoirs in Singapore? *Raffles Bulletin of Zoology* **58**, 311–322.

Luna, V. A., King, D. S., Peak, K. K., Reeves, F., Heberlein-Larson, L., Veguilla, W., Heller, L., Duncan, K. E., Cannons, A. C. & Amuso, P. (2006). *Bacillus anthracis* virulent plasmid pX02 genes found in large plasmids of two other *Bacillus* species. *Journal of Clinical Microbiology* **44**, 2367–2377.

Lurling, M. (2003). Effects of microcystin-free and microcystin-containing strains of the cyanobacterium *Microcystis aeruginosa* on growth of the grazer *Daphnia magna*. *Environmental Toxicology* **18**, 202–210.

*Lürling, M. (2003). Phenotypic plasticity in the green algae Desmodesmus and Scenedesmus with special reference to the induction of defensive morphology. *Annales de Limnologie-International Journal of Limnology* **39**, 85–101.

Lürling, M. & Faassen, E. J. (2012). Controlling toxic cyanobacteria: effects of dredging and phosphorus-binding clay on cyanobacteria and microcystins. *Water Research* **46**, 1447–1459.

*Lv, J., Wu, H. & Chen, M. (2011). Effects of nitrogen and phosphorus on phytoplankton composition and biomass in 15 subtropical, urban shallow lakes in Wuhan, China. *Limnologica-Ecology and Management of Inland Waters* **41**, 48–56.

Ma, J., Brookes, J. D., Qin, B., Paerl, H. W., Gao, G., Wu, P., Zhang, W., Deng, J., Zhu, G. & Zhang, Y. (2014). Environmental factors controlling colony formation in blooms of the cyanobacteria *Microcystis* spp. in Lake Taihu, China. *Harmful Algae* **31**, 136–142.

*Magalhaes, V. F. & Azevedo, S. (1998). Ecological implications of hepatotoxic *Microcystis aeruginosa* in the Jacarepaguá Lagoon, Brazil. In *Proceedings of the Seventh International Conference on Harmful Algae*, pp. 26–28. Vigo, Espanha.

Major, Y., Kifle, D., Niedrist, G. H. & Sommaruga, R. (2017). An isotopic analysis of the phytoplankton-zooplankton link in a highly eutrophic tropical reservoir dominated by cyanobacteria. *Journal of Plankton Research* **39**, 1–12.

*Mankiewicz-Boczek, J., Izydorczyk, K. & Jurczak, T. (2006). Risk assessment of toxic cyanobacteria in Polish water bodies. *Environmental Toxicology* **10**, 49–58.

*Maršálek, B., Bláha, L. & Hindák, F. (2000). Review of toxicity of cyanobacteria in Slovakia. *Biologia* **55**, 645–652.

May, C. & Stainsby, G. (1986). Factors affecting pectin gelation. In *Gums and Stabilisers for the Food Industry*, 3rd Edition (eds G. O. Phillips, D. J. Wedlock and P. A. Williams), pp. 515–523. Elsevier Applied Science Publishers, London and New York.

*Mbukwa, E., Msagati, T. A., Mamba, B. B., Boussiba, S., Wepener, V., Leu, S. & Kaye, Y. (2015). Toxic *Microcystis novacekii* T20-3 from Phakalane Ponds, Botswana: PCR amplifications of microcystin synthetase (mcy) genes, extraction

and LC-ESI-MS identification of microcystins. *Journal of Analytical & Bioanalytical Techniques* **6**, S7. https://doi.org/10.4172/2161- 0525.S4177-4010.

*McCarthy, M. J., James, R. T., Chen, Y., East, T. L. & Gardner, W. S. (2009). Nutrient ratios and phytoplankton community structure in the large, shallow, eutrophic, subtropical Lakes Okeechobee (Florida, USA) and Taihu (China). *Limnology* **10**, 215–227.

McCausland, M. A., Thompson, P. A. & Blackburn, S. I. (2005). Ecophysiological influence of light and mixing on *Anabaena circinalis* (Nostocales, Cyanobacteria). *European Journal of Phycology* **40**, 9–20.

*McDonald, K. E. & Lehman, J. T. (2013). Dynamics of *Aphanizomenon* and *Microcystis* (cyanobacteria) during experimental manipulation of an urban impoundment. *Lake and Reservoir Management* **29**, 103–115.

*McGregor, G. B. (2013). Freshwater cyanobacteria of north-eastern Australia: 2. Chroococcales. *Phytotaxa* **133**, 1–130.

*McGregor, G. B., Fabbro, L. D. & Lobegeiger, J. S. (2007). Freshwater planktic Chroococcales (Cyanoprokaryota) from north-eastern Australia: a morphological evaluation. *Nova Hedwigia* **84**, 299–331.

*McKenzie, J., Dalton, M. & Percy, M. (2006). Fitzroy river water-resource operations plan & cyanobacteria management. In *31st Annual Qld Water Industry Workshop – Operations Skills*, University Central Queensland, Rockhampton.

*Medja, N., Panariti, E., Biba, N. & Duro, S. (2013). Effect of crude extract of cyanobacteria from Shkodra lake for larvae of *Hypophthalalmichthys Molitrix* (Valenciennes 1844). *Annals of West University of Timisoara. Series of Chemistry* **22**, 43–48.

Mello, M. M. E., Soares, M. C. S., Roland, F. & Lürling, M. (2012). Growth inhibition and colony formation in the cyanobacterium *Microcystis aeruginosa* induced by the cyanobacterium *Cylindrospermopsis raciborskii*. *Journal of Plankton Research* **34**, 987–994.

*Messineo, V., Bogialli, S., Melchiorre, S., Sechi, N., Lugliè, A., Casiddu, P., Mariani, M. A., Padedda, B. M., Di Corcia, A. & Mazza, R. (2009). Cyanobacterial toxins in Italian freshwaters. *Limnologica-Ecology and Management of Inland Waters* **39**, 95–106.

*Mhlanga, L. & Mhlanga, W. (2013). Dynamics of a cyanobacterial bloom in a hypereutrophic reservoir, Lake Chivero, Zimbabwe. *African Journal of Aquatic Science* **38**, 313–321.

*Mihaljević, M. & Gucunski, D. (1993). Comparative study of phytoplankton in the nature reserve of Kopački Rit. *Acta Botanica Croatica* **52**, 41–47.

*Mikheyeva, T. M., Belykh, O., Sorokovikova, E. G., Gladkikh, A. S., Luk'yanova, E. V., Potapov, S. A., Tikhonova, I. V., Fedorova, G. A., Korneva, E. S. & Kuzmin, A. V. (2012). Detection of microcystin producing cyanobacteria in the Svisloch River, Belarus. *Baltic Coastal Zone. Journal of Ecology and Protection of the Coastline* **16**, 131–146.

*Miller, T. R., Beversdorf, L., Chaston, S. D. & McMahon, K. D. (2013). Spatiotemporal molecular analysis of cyanobacteria blooms reveals *Microcystis-Aphanizomenon* interactions. *PLoS One* **8**, e74933.

*Minasyan, A. (2016). Taxonomic richness and quantitative characteristics of the phytoplankton community in the epilimnion of Lake Yerevan (Armenia). *Lakes, Reservoirs and Ponds* **10**, 77–95.

*Mohamed, Z. A. (2006). First report of toxic *Cylindrospermopsis raciborskii* and *Raphidiopsis mediterranea* (Cyanoprokaryota) in Egyptian fresh waters. *FEMS Microbiology Ecology* **59**, 749–761.

*Mohamed, Z. A. & Al-Shehri, A. M. (2013). Assessment of cylindrospermopsin toxin in an arid Saudi lake containing dense cyanobacterial bloom. *Environmental Monitoring and Assessment* **185**, 2157–2166.

*Mohebbi, F., Mohsenpour Azari, A., Heidari, M. & Asem, A. (2012). Cyanobacterium *Microcystis aeruginosa* bloom in Aras Dam Reservoir. *International Journal of Environmental Research* **6**, 309–312.

*Mol, J. H. (2012). *The Freshwater Fishes of Suriname*. Brill, The Netherlands.

*Mooney, K. M., Hamilton, J. T., Floyd, S. D., Foy, R. H. & Elliott, C. T. (2011). Initial studies on the occurrence of cyanobacteria and microcystins in Irish lakes. *Environmental Toxicology* **26**, 566–570.

*Moreira-González, A., Seisdedo-Losa, M., Muñoz-Caravaca, A., Comas-González, A. & Alonso-Hernández, C. (2014). Spatial and temporal distribution of phytoplankton as indicator of eutrophication status in the Cienfuegos Bay, Cuba. *Revista de Gestão Costeira Integrada-Journal of Integrated Coastal Zone Management* **14**, 597–609.

*Mukankomeje, R., Laviolette, F. & Descy, J.-P. (1994). Diet of the Nile tilapia, Oreochromis niloticus, in Lake Muhazi (Rwanda). *Annales de Limnologie* **30**, 297–312.

Mulling, B., Wood, S. & Hamilton, D. (2014). Intra-colony motility of *Microcystis wesenbergii* cells. *New Zealand Journal of Botany* **52**, 153–159.

*Mur, L. & Schreurs, H. (1995). Light as a selective factor in the distribution of phytoplankton species. *Water Science and Technology* **32**, 25–34.

Nakai, S., Inoue, Y., Hosomi, M. & Murakami, A. (2000). Myriophyllum spicatum-released allelopathic polyphenols inhibiting growth of blue-green algae *Microcystis aeruginosa*. *Water Research* **34**, 3026–3032.

*Naselli-Flores, L., Barone, R., Chorus, I. & Kurmayer, R. (2007). Toxic cyanobacterial blooms in reservoirs under a semiarid Mediterranean climate: the magnification of a problem. *Environmental Toxicology* **22**, 399–404.

*Nasri, H., El Herry, S. & Bouaïcha, N. (2008). First reported case of turtle deaths during a toxic *Microcystis* spp. bloom in Lake Oubeira, Algeria. *Ecotoxicology and Environmental Safety* **71**, 535–544.

*Ndlela, L., Oberholster, P., Van Wyk, J. & Cheng, P. (2016). An overview of cyanobacterial bloom occurrences and research in Africa over the last decade. *Harmful Algae* **60**, 11–26.

*Nwadiaro, C. & Idabor, P. (1990). Proximate composition and nutrient elements in the "Uusual" algal "Jellies" of Lake Oguta in Southern Nigeria. *International Review of Hydrobiology* **75**, 413–420.

O'Brien, K. R., Meyer, D. L., Waite, A. M., Ivey, G. N. & Hamilton, D. P. (2004). Disaggregation of *Microcystis aeruginosa* colonies under turbulent mixing: laboratory experiments in a grid-stirred tank. *Hydrobiologia* **519**, 143–152.

O'Neil, J. M., Davis, T. W., Burford, M. A. & Gobler, C. J. (2012). The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. *Harmful Algae* **14**, 313–334.

O'Brien, K. R. (2003). *The effects of turbulent mixing on the vertical distribution and biomass of phytoplankton populations*. PhD Thesis: University of Western Australia, Perth.

*Odada, E. O., Olago, D. O., Bugenyi, F., Kulindwa, K., Karimumuryango, J., West, K., Ntiba, M., Wandiga, S., Aloo-Obudho, P. & Achola, P. (2003). Environmental assessment of the east African rift valley lakes. *Aquatic Sciences-Research Across Boundaries* **65**, 254–271.

*Odokuma, L. O. & Isirima, J. C. (2007). Distribution of cyanotoxins in aquatic environments in the Niger Delta. *African Journal of Biotechnology* **6**, 2375–2385.

*Ohkubo, N., Yagi, O. & Okada, M. (1993). Studies on the succession of blue-green algae, *Microcystis*, *Anabaena*, *Oscillatoria* and *Phormidium* in Lake Kasumigaura. *Environmental Technology* **14**, 433–442.

*Okello, W. & Kurmayer, R. (2011). Seasonal development of cyanobacteria and microcystin production in Ugandan freshwater lakes. *Lakes & Reservoirs: Research & Management* **16**, 123–135.

*Okello, W., Portmann, C., Erhard, M., Gademann, K. & Kurmayer, R. (2010). Occurrence of microcystin-producing cyanobacteria in Ugandan freshwater habitats. *Environmental Toxicology* **25**, 367–380.

*Olivares Pavez, A. P. (2013). *Abundancia y distribución de cianobacterias (Microcystis sp, Anabaena sp, Oscillatoria sp) en el Lago de Ilopango, El Salvador*: Bachelor Thesis, Universidad El Salvador, San Salvador.

Otsuka, S., Suda, S., Li, R., Matsumoto, S. & Watanabe, M. M. (2000). Morphological variability of colonies of *Microcystis* morphospecies in culture. *Journal of General and Applied Microbiology* **46**, 39–50.

Otsuka, S., Suda, S., Li, R., Watanabe, M., Oyaizu, H., Matsumoto, S. & Watanabe, M. M. (1998). 16S rDNA sequences and phylogenetic analyses of *Microcystis* strains with and without phycoerythrin. *FEMS Microbiology Letters* **164**, 119–124.

Otsuka, S., Suda, S., Li, R., Watanabe, M., Oyaizu, H., Matsumoto, S. & Watanabe, M. M. (1999). Phylogenetic relationships between toxic and non-toxic strains of the genus *Microcystis* based on 16S to 23S internal transcribed spacer sequence. *FEMS Microbiology Letters* **172**, 15–21.

Otsuka, S., Suda, S., Shibata, S., Oyaizu, H., Matsumoto, S. & Watanabe, M. M. (2001). A proposal for the unification of five species of the cyanobacterial genus *Microcystis* Kutzing ex Lemmermann 1907 under the rules of the Bacteriological Code. *International Journal of Systematic and Evolutionary Microbiology* **51**, 873–879.

Otten, T. G. & Paerl, H. W. (2011). Phylogenetic inference of colony isolates comprising seasonal *Microcystis* blooms in Lake Taihu, China. *Microbial Ecology* **62**, 907–918.

Ou, M. M., Wang, Y., Zhou, B. X. & Cai, W. M. (2006). Effects of iron and phosphorus on *Microcystis* physiological reactions. *Biomedical and Environmental Sciences* **19**, 399–404.

*Oudra, B., Loudiki, M., Sbiyyaa, B., Martins, R., Vasconcelos, V. & Namikoshi, N. (2001). Isolation, characterization and quantification of microcystins (heptapeptides hepatotoxins) in *Microcystis aeruginosa* dominated bloom of Lalla Takerkoust lake–reservoir (Morocco). *Toxicon* **39**, 1375–1381.

*Oudra, B., Loudiki, M., Vasconcelos, V., Sabour, B., Sbiyyaa, B., Oufdou, K. & Mezrioui, N. (2002). Detection and quantification of microcystins from cyanobacteria strains isolated from reservoirs and ponds in Morocco. *Environmental Toxicology* **17**, 32–39.

Ozawa, K., Fujioka, H., Muranaka, M., Yokoyama, A., Katagami, Y., Homma, T., Ishikawa, K., Tsujimura, S., Kumagai, M., Watanabe, M. F. & Park, H. D. (2005). Spatial distribution and temporal variation of *Microcystis* species composition and microcystin concentration in Lake Biwa. *Environmental Toxicology* **20**, 270–276.

Paerl, H. W. & Huisman, J. (2009). Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports* **1**, 27–37.

Paerl, H. W. & Millie, D. F. (1996). Physiological ecology of toxic aquatic cyanobacteria. *Phycologia* **35**, 160–167.

Paerl, H. W. & Otten, T. G. (2013). Harmful cyanobacterial blooms: causes, consequences, and controls. *Microbial Ecology* **65**, 995–1010.

*Palaniswami, R., Manoharan, S. & Mohan, A. (2015). Characterisation of tropical reservoirs in Tamil Nadu, India in terms of plankton assemblage using multivariate analysis. *Indian Journal of Fisheries* **62**, 1–13.

*Palmer, S. C. J., Odermatt, D., Hunter, P. D., Brockmann, C., Présing, M., Balzter, H. & Tóth, V. R. (2015). Satellite remote sensing of phytoplankton phenology in Lake Balaton using 10 years of MERIS observations. *Remote Sensing of Environment* **158**, 441–452.

*Park, H.-D., Kim, B., Kim, E. & Okino, T. (1998). Hepatotoxic microcystins and neurotoxic anatoxin-a in cyanobacterial blooms from Korean lakes. *Environmental Toxicology and Water Quality* **13**, 225–234.

Park, H. D., Watanabe, M. F., Harada, K. I., Suzuki, M., Hayashi, H. & Okino, T. (1993). Seasonal variations of *Microcystis* species and toxic heptapeptide microcystins in Lake Suwa. *Environmental Toxicology and Water Quality* **8**, 425–435.

Park, M.-H., Chung, I.-M., Ahmad, A., Kim, B.-H. & Hwang, S.-J. (2009). Growth inhibition of unicellular and colonial *Microcystis* strains (Cyanophyceae) by compounds isolated from rice (*Oryza sativa*) hulls. *Aquatic Botany* **90**, 309–314.

Parker, D. L., Schram, B. R., Plude, J. L. & Moore, R. E. (1996). Effect of metal cations on the viscosity of a pectin-like capsular polysaccharide from the cyanobacterium *Microcystis flos-aquae* C3-40. *Applied and Environmental Microbiology* **62**, 1208–1213.

Passarge, J., Hol, S., Escher, M. & Huisman, J. (2006). Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? *Ecological Monographs* **76**, 57–72.

*Pawlik-Skowrońska, B. & Toporowska, M. (2011). Blooms of toxin-producing cyanobacteria - a real threat in small dam reservoirs at the beginning of their operation. *Oceanological and Hydrobiological Studies* **40**, 30–37.

*Pedro, O., Lie, E., Correia, D., Neves, L., Skaare, J. U., Sandvik, M. & Berdal, K. G. (2013). Quantification of microcystin-producing *Microcystis* in freshwater bodies in the Southern Mozambique using quantitative real time polymerase chain reaction. *African Journal of Biotechnology* **12**, 4850–4857.

Pereira, S., Zille, A., Micheletti, E., Moradas-Ferreira, P., De Philippis, R. & Tamagnini, P. (2009). Complexity of cyanobacterial exopolysaccharides: composition, structures, inducing factors and putative genes involved in their biosynthesis and assembly. *FEMS Microbiology Reviews* **33**, 917–941.

*Piccini, C., Conde, D., Alonso, C., Sommaruga, R. & Pernthaler, J. (2006). Blooms of single bacterial species in a coastal lagoon of the southwestern Atlantic Ocean. *Applied and Environmental Microbiology* **72**, 6560–6568.

Plude, J. L., Parker, D. L., Schommer, O. J., Timmerman, R. J., Hagstrom, S. A., Joers, J. M. & Hnasko, R. (1991). Chemical characterization of polysaccharide from the slime layer of the cyanobacterium *Microcystis flos-aquae* C3-40. *Applied and Environmental Microbiology* **57**, 1696–1700.

*Pobel, D., Godon, J.-J., Humbert, J.-F. & Robin, J. (2012). High-frequency monitoring of the genetic diversity and the potential toxicity of a *Microcystis aeruginosa* bloom in a French shallow lake. *FEMS Microbiology Ecology* **79**, 132–141.

*Porfirio, Z., Ribeiro, M. P., Estevam, C. S., Houly, R. L. & Sant'Ana, A. E. G. (1999). Hepatosplenomegaly caused by an extract of cyanobacterium *Microcystis aeruginosa* bloom collected in the Manguaba Lagoon, Alagoas-Brazil. *Revista de Microbiologia* **30**, 278–285.

Pradhan, S., Singh, S. & Rai, L. C. (2007). Characterization of various functional groups present in the capsule of *Microcystis* and study of their role in biosorption of Fe, Ni and Cr. *Bioresource Technology* **98**, 595–601.

*Prasath, B., Nandakumar, B., Jayalakshmi, T. & Santhanam, P. (2014). First report on the intense cyanobacteria *Microcystis aeruginosa* Kützing, 1846 bloom at Muttukkadu Backwater, Southeast coast of India. *Indian Journal of Geo-Marine Sciences* **43**, 258–262.

Qin, B., Zhu, G., Gao, G., Zhang, Y., Li, W., Paerl, H. W. & Carmichael, W. W. (2010). A drinking water crisis in Lake Taihu, China: linkage to climatic variability and lake management. *Environmental Management* **45**, 105–112.

*Rahman, S. & Jewel, M. A. S. (2008). Cyanobacterial blooms and water quality in two urban fish ponds. *University Journal of Zoology, Rajshahi University* **27**, 79–84.

*Ranković, B., Simić, S. & Bogdanović, D. (2006). Phytoplankton as indicator of water quality of lakes Bubanj and Šumarice during autumn. *Kragujevac Journal of Science* **28**, 107–114.

*Rao, P., Bhattacharya, R. & Gupta, S. D. (1994). Isolation, culture, and toxicity of the cyanobacterium (blue-green alga) *Microcystis aeruginosa* from a freshwater source in India. *Bulletin of Environmental Contamination and Toxicology* **52**, 878–885.

Rastogi, R. P., Sinha, R. P. & Incharoensakdi, A. (2014). The cyanotoxin-microcystins: current overview. *Reviews in Environmental Science and Bio/Technology* **13**, 215–249.

*Recknagel, F., French, M., Harkonen, P. & Yabunaka, K.-I. (1997). Artificial neural network approach for modelling and prediction of algal blooms. *Ecological Modelling* **96**, 11–28.

Regel, R. H., Brookes, J. D., Ganf, G. G. & Griffiths, R. W. (2004). The influence of experimentally generated turbulence on the Mash01 unicellular *Microcystis aeruginosa* strain. *Hydrobiologia* **517**, 107–120.

*Ren, X., Yang, K., Che, Y., Wang, M., Zhou, L. & Chen, L. (2016). Spatial and temporal assessment of the initial pattern of phytoplankton population in a newly built coastal reservoir. *Frontiers of Earth Science* **10**, 546–559.

*Ren, Y., Pei, H., Hu, W., Tian, C., Hao, D., Wei, J. & Feng, Y. (2014). Spatiotemporal distribution pattern of cyanobacteria community and its relationship with the environmental factors in Hongze Lake, China. *Environmental Monitoring and Assessment* **186**, 6919–6933.

*Retnaningdyah, C., Suharjono, S., Soegianto, A. & Irawan, B. (2010). Blooming stimulation of *Microcystis* in Sutami Reservoir using nutrients nitrate and phosphate in different ratio. *Journal of Tropical Life Science* **1**, 42–46.

*Reynolds, C. & Bellinger, E. (1992). Patterns of abundance and dominance of the phytoplankton of Rostherne Mere, England: evidence from an 18-year data set. *Aquatic Sciences* **54**, 10–36.

*Reynolds, C., Dokulil, M. & Padisák, J. (2000). Understanding the assembly of phytoplankton in relation to the trophic spectrum: where are we now? *Hydrobiologia* **424**, 147–152.

Reynolds, C., Jaworski, G., Cmiech, H. & Leedale, G. (1981). On the annual cycle of the blue-green alga *Microcystis aeruginosa* Kütz. emend. Elenkin. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **293**, 419–477.

Reynolds, C. & Walsby, A. (1975). Water-Blooms. *Biological Reviews* **50**, 437–481.

Reynolds, C. S. (2006). *Ecology of Phytoplankton*. Cambridge University Press, Cambridge.

Reynolds, C. S. (2007). Variability in the provision and function of mucilage in phytoplankton: facultative responses to the environment. *Hydrobiologia* **578**, 37–45.

Reynolds, C. S., Oliver, R. L. & Walsby, A. E. (1987). Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *New Zealand Journal of Marine and Freshwater Research* **21**, 379–390.

*Rolland, D. C., Bourget, S., Warren, A., Laurion, I. & Vincent, W. F. (2013). Extreme variability of cyanobacterial blooms in an urban drinking water supply. *Journal of Plankton Research* **35**, 744–758.

*Romo, S., Fernández, F., Ouahid, Y. & Barón-Sola, Á. (2012). Assessment of microcystins in lake water and fish (Mugilidae, *Liza* sp.) in the largest Spanish coastal lake. *Environmental Monitoring and Assessment* **184**, 939–949.

*Ryan, N., Dabovic, J., Bowling, L., Driver, B. & Barnes, B. (2009). In *The Murray River algal bloom: Evaluation and Recommendations for the Future Management of Major Outbreaks* (ed. NSW Government, Office of Water), p. 37. NSW Office of Water, Sydney, NSW.

*Sabour, B., Loudiki, M., Oudra, B., Vasconcelos, V., Martins, R., Oubraim, S. & Fawzi, B. (2002). Toxicology of a *Microcystis ichthyoblabe* waterbloom from lake oued Mellah (Morocco). *Environmental Toxicology* **17**, 24–31.

*Saker, M., Fastner, J., Dittmann, E., Christiansen, G. & Vasconcelos, V. (2005). Variation between strains of the cyanobacterium *Microcystis aeruginosa* isolated from a Portuguese river. *Journal of Applied Microbiology* **99**, 749–757.

*Saker, M. L. & Griffiths, D. J. (2001). Occurrence of blooms of the cyanobacterium *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya and Subba Raju in a north Queensland domestic water supply. *Marine and Freshwater Research* **52**, 907–915.

*Saker, M. L., Neilan, B. A. & Griffiths, D. J. (1999). Two morphological forms of *Cylindrospermopsis raciborskii* (cyanobacteria) isolated from Solomon Dam, Palm Island, Queensland. *Journal of Phycology* **35**, 599–606.

*Sarmento, H., Isumbisho, M. & Descy, J.-P. (2006). Phytoplankton ecology of Lake Kivu (eastern Africa). *Journal of Plankton Research* **28**, 815–829.

Sato, M., Amano, Y., Machida, M. & Imazeki, F. (2016). Colony formation of highly dispersed *Microcystis aeruginosa* by controlling extracellular polysaccharides and calcium ion concentrations in aquatic solution. *Limnology* **18**, 111–119.

Sedmak, B. & Elersek, T. (2006). Microcystins induce morphological and physiological changes in selected representative phytoplanktons. *Microbial Ecology* **51**, 508–515.

Šejnohová, L. & Maršálek, B. (2012). *Microcystis*. In *Ecology of Cyanobacteria II*. (ed B. A. Whitton), pp. 195–228. Springer Dordrecht, The Netherlands.?>

Shen, H., Niu, Y., Xie, P., Tao, M. & Yang, X. (2011). Morphological and physiological changes in *Microcystis aeruginosa* as a result of interactions with heterotrophic bacteria. *Freshwater Biology* **56**, 1065–1080.

Shen, H. & Song, L. (2007). Comparative studies on physiological responses to phosphorus in two phenotypes of bloom-forming *Microcystis*. *Hydrobiologia* **592**, 475–486.

Shia, L., Cai, Y., Wang, X., Li, P., Yu, Y. & Kong, F. (2010). Community structure of bacteria associated with *Microcystis* colonies from cyanobacterial blooms. *Journal of Freshwater Ecology* **25**, 193–203.

Sigee, D., Glenn, R., Andrews, M., Bellinger, E., Butler, R., Epton, H. & Hendry, R. (1999). Biological control of cyanobacteria: principles and possibilities. *Hydrobiologia* **395/396**, 161–172.

*Sinang, S. C., Poh, K. B., Shamsudin, S. & Sinden, A. (2015). Preliminary assessment of cyanobacteria diversity and toxic potential in ten freshwater lakes in Selangor, Malaysia. *Bulletin of Environmental Contamination and Toxicology* **95**, 542–547.

*Singh, J., Upadhyay, S. K. & Pathak, R. K. (2013). Seasonal variations in physicochemical characteristics and cyanobacterial diversity of a lake in Northern India. *Toxicological & Environmental Chemistry* **95**, 458–471.

*Soares, M. C. S., Huszar, V. L., Miranda, M. N., Mello, M. M., Roland, F. & Lürling, M. (2013). Cyanobacterial dominance in Brazil: distribution and environmental preferences. *Hydrobiologia* **717**, 1–12.

Sommaruga, R., Chen, Y. & Liu, Z. (2009). Multiple strategies of bloom-forming *Microcystis* to minimize damage by solar ultraviolet radiation in surface waters. *Microbial Ecology* **57**, 667–674.

*Steffen, M. M., Zhu, Z., McKay, R. M. L., Wilhelm, S. W. & Bullerjahn, G. S. (2014). Taxonomic assessment of a toxic cyanobacteria shift in hypereutrophic Grand Lake St. Marys (Ohio, USA). *Harmful Algae* **33**, 12–18.

*Stirling, D. J. & Quilliam, M. A. (2001). First report of the cyanobacterial toxin cylindrospermopsin in New Zealand. *Toxicon* **39**, 1219–1222.

Sun, Q., Zhu, W., Li, M. & Tan, X. (2015). Morphological changes of *Microcystis aeruginosa* colonies in culture. *Journal of Limnology* **75**, 14–23.

*Svirčev, Z. B., Tokodi, N., Drobac, D. & Codd, G. A. (2014). Cyanobacteria in aquatic ecosystems in Serbia: effects on water quality, human health and biodiversity. *Systematics and Biodiversity* **12**, 261–270.

*Tabi, E., Oben, P. & Oben, B. (2015). Diversity and dynamics of potentially toxic cyanobacteria and their public health significance in lake Koto Barombi, Cameroon. *Tropical Freshwater Biology* **24**, 89–110.

Tan, W., Liu, Y., Wu, Z., Lin, S., Yu, G., Yu, B. & Li, R. (2010). cpcBA-IGS as an effective marker to characterize *Microcystis wesenbergii* (Komárek) Komárek in Kondrateva (cyanobacteria). *Harmful Algae* **9**, 607–612.

*Te, S. H. & Gin, K. Y.-H. (2011). The dynamics of cyanobacteria and microcystin production in a tropical reservoir of Singapore. *Harmful Algae* **10**, 319–329.

*Temponeras, M., Kristiansen, J. & Moustaka-Gouni, M. (2000). Seasonal variation in phytoplankton composition and physical-chemical features of the shallow Lake Doïrani, Macedonia, Greece. *Hydrobiologia* **424**, 109–122.

*Teneva, I., Mladenov, R., Belkinova, D., Dimitrova-Dyulgerova, I. & Dzhambazov, B. (2010). Phytoplankton community of the drinking water supply reservoir Borovitsa (South Bulgaria) with an emphasis on cyanotoxins and water quality. *Open Life Sciences* **5**, 231–239.

Thakur, B. R., Singh, R. K. & Handa, A. K. (1997). Chemistry and uses of pectin--a review. *Critical Reviews in Food Science and Nutrition* **37**, 47–73.

Thomas, M. K. & Litchman, E. (2015). Effects of temperature and nitrogen availability on the growth of invasive and native cyanobacteria. *Hydrobiologia* **763**, 357–369.

*Tonetta, D., Laudares-Silva, R. & Petrucio, M. (2015). Planktonic production and respiration in a subtropical lake dominated by cyanobacteria. *Brazilian Journal of Biology* **75**, 460–470.

*Tryfon, E., Moustaka-Gouni, M. & Nikolaidis, G. (1997). Planktic cyanophytes and their ecology in the shallow Lake Mikri Prespa, Greece. *Nordic Journal of Botany* **17**, 439–448.

Tsukada, H., Tsujimura, S. & Nakahara, H. (2006). Seasonal succession of phytoplankton in Lake Yogo over 2 years: effect of artificial manipulation. *Limnology* **7**, 3–14.

*Ulcay, S., Taşkin, E., Kurt, O. & Öztürk, M. (2015). Marine benthic cyanobacteria in Northern Cyprus (Eastern Mediterranean Sea). *Turkish Journal of Botany* **39**, 173–188.

*Urrutia-Cordero, P., Ekvall, M. K. & Hansson, L.-A. (2016). Controlling harmful cyanobacteria: taxa-specific responses of cyanobacteria to grazing by large-bodied *Daphnia* in a biomanipulation scenario. *PLoS One* **11**, e0153032.

*Utkilen, H., Skulberg, O., Underdal, B., Gjølme, N., Skulberg, R. & Kotai, J. (1996). The rise and fall of a toxigenic population of *Microcystis aeruginosa* (Cyanophyceae/Cyanobacteria) - a decade of observations in Lake Akersvatnet, Norway. *Phycologia* **35**, 189–197.

*Valério, E., Faria, N., Paulino, S. & Pereira, P. (2008). Seasonal variation of phytoplankton and cyanobacteria composition and associated microcystins in six Portuguese freshwater reservoirs. *Annales de Limnologie-International Journal of Limnology* **44**, 189–196.

*van Vuuren, S. J., van der Walt, N. & Swanepoel, A. (2007). Changes in algal composition and environmental variables in the high-altitude Mohale dam—an important water supply reservoir to South Africa. *African Journal of Aquatic Science* **32**, 265–274.

Vanderploeg, H. A., Liebig, J. R., Carmichael, W. W., Agy, M. A., Johengen, T. H., Fahnenstiel, G. L. & Nalepa, T. F. (2001). Zebra mussel (Dreissena polymorpha) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1208–1221.

Verspagen, J. M., Visser, P. M. & Huisman, J. (2006). Aggregation with clay causes sedimentation of the buoyant cyanobacteria *Microcystis* spp. *Aquatic Microbial Ecology* **44**, 165–174.

*Via-Ordorika, L., Fastner, J., Kurmayer, R., Hisbergues, M., Dittmann, E., Komarek, J., Erhard, M. & Chorus, I. (2004). Distribution of microcystin-producing and non-microcystin-producing *Microcystis* sp. in European freshwater bodies: detection of microcystins and microcystin genes in individual colonies. *Systematic and Applied Microbiology* **27**, 592–602.

*Vidal, L. & Kruk, C. (2008). *Cylindrospermopsis raciborskii* (Cyanobacteria) extends its distribution to Latitude 34 53'S: taxonomical and ecological features in Uruguayan eutrophic lakes. *Pan-American Journal of Aquatic Sciences* **3**, 142–151.

Visser, P., Ibelings, B., van der Veer, B., Koedood, J. & Mur, R. (1996). Artificial mixing prevents nuisance blooms of the cyanobacterium *Microcystis* in Lake Nieuwe Meer, the Netherlands. *Freshwater Biology* **36**, 435–450.

Visser, P. M., Ibelings, B. W., Bormans, M. & Huisman, J. (2015). Artificial mixing to control cyanobacterial blooms: a review. *Aquatic Ecology* **50**, 1–19.

Visser, P. M., Ibelings, B. W., Mur, L. R. & Walsby, A. E. (2005). The ecophysiology of the harmful cyanobacterium *Microcystis*. In *Harmful Cyanobacteria* (eds J. Huisman, H. C. P. Matthijs and P. M. Visser), pp. 109–142. Springer Netherlands, Dordrecht.

Visser, P. M., Verspagen, J. M., Sandrini, G., Stal, L. J., Matthijs, H. C., Davis, T. W., Paerl, H. W. & Huisman, J. (2016). How rising $CO_2$ and global warming may stimulate harmful cyanobacterial blooms. *Harmful Algae* **54**, 145–159.

Walsby, A. (1998). Gas vesicles and buoyancy in cynobacteria: interrelations with light. In *Symposia-Society for General Microbiology* (ed. M. X. Caddick, S. Baumberg, D. A. Hodgson and M. K. Phillips-Jones), pp. 69–94. Cambridge University Press, University of Nottingham.

Walsby, A. E. (1994). Gas vesicles. *Microbiological Reviews* **58**, 94–144.

Walsby, A. E. (2005). Stratification by cyanobacteria in lakes: a dynamic buoyancy model indicates size limitations met by *Planktothrix rubescens* filaments. *New Phytologist* **168**, 365–376.

Walsby, A. E., Hayes, P. K. & Boje, R. (1995). The gas vesicles, buoyancy and vertical distribution of cyanobacteria in the Baltic Sea. *European Journal of Phycology* **30**, 87–94.

Walsby, A. E. & Holland, D. P. (2006). Sinking velocities of phytoplankton measured on a stable density gradient by laser scanning. *Journal of the Royal Society, Interface* **3**, 429–439.

Wang, W., Liu, Y. & Yang, Z. (2010*a*). Combined effects of nitrogen content in media and *Ochromonas* sp. grazing on colony formation of cultured *Microcystis aeruginosa*. *Journal of Limnology* **69**, 193–198.

*Wang, X., Qin, B., Gao, G. & Paerl, H. W. (2010*b*). Nutrient enrichment and selective predation by zooplankton promote *Microcystis* (cyanobacteria) bloom formation. *Journal of Plankton Research* **32**, 457–470.

Wang, Y., Wang, Z., Wu, W., Hu, M., Wang, Z., Xu, A., Li, G. & Liu, Y. (2010*c*). Seasonal regime shift of an alternative-state Lake Xingyun, China. *Fresenius Environmental Bulletin* **19**, 1474–1485.

Wang, W., Shen, H., Shi, P., Chen, J., Ni, L. & Xie, P. (2015). Experimental evidence for the role of heterotrophic bacteria in the formation of *Microcystis* colonies. *Journal of Applied Phycology* **28**, 1111–1123.

Wang, X., Sun, M., Xie, M., Liu, M., Luo, L., Li, P. & Kong, F. (2013). Differences in microcystin production and genotype composition among *Microcystis* colonies of different sizes in Lake Taihu. *Water Research* **47**, 5659–5669.

Wang, Y., Wu, M., Yu, J., Zhang, J., Zhang, R., Zhang, L. & Chen, G. (2014). Differences in growth, pigment composition and photosynthetic rates of two phenotypes *Microcystis aeruginosa* strains under high and low iron conditions. *Biochemical Systematics and Ecology* **55**, 112–117.

Wang, Y. W., Zhao, J., Li, J. H., Li, S. S., Zhang, L. H. & Wu, M. (2011). Effects of calcium levels on colonial aggregation and buoyancy of *Microcystis aeruginosa*. *Current Microbiology* **62**, 679–683.

Watanabe, M. (1996). Isolation, cultivation and classification of bloom-forming *Microcystis* in Japan. *Toxic Microcystis* **2**, 13–34.

*Weller, D. (2011). Detection, identification and toxigenicity of cyanobacteria in New Zealand lakes using PCR-based methods. *New Zealand Journal of Marine and Freshwater Research* **45**, 651–664.

*Wiedner, C., Rücker, J., Stüken, A., Preussel, K., Fastner, J., Chorus, I. & Nixdorf, B. (2007). *Cylindrospermopsis raciborskii and Cylindrospermopsin in Lakes of the Berlin Area: Occurrences, Causes and Consequences*. Kompetenzzentrum Wasser Berlin, Berlin.

*Wilk-Woźniak, E., Solarz, W., Najberek, K. & Pociecha, A. (2016). Alien cyanobacteria: an unsolved part of the "expansion and evolution" jigsaw puzzle? *Hydrobiologia* **764**, 65–79.

*Willame, R., Jurczak, T., Iffly, J.-F., Kull, T., Meriluoto, J. & Hoffmann, L. (2005). Distribution of hepatotoxic cyanobacterial blooms in Belgium and Luxembourg. *Hydrobiologia* **551**, 99–117.

*Willén, E., Ahlgren, G., Tilahun, G., Spoof, L., Neffling, M.-R. & Meriluoto, J. (2011). Cyanotoxin production in seven Ethiopian Rift Valley lakes. *Inland Waters* **1**, 81–91.

Willis, A., Chiovitti, A., Dugdale, T. M. & Wetherbee, R. (2013). Characterization of the extracellular matrix of *Phaeodactylum tricornutum* (Bacillariophyceae): structure, composition, and adhesive characteristics. *Journal of Phycology* **49**, 937–949.

Willis, A., Posselt, A. J. & Burford, M. A. (2017). Variations in carbon-to-phosphorus ratios of two Australian strains of *Cylindrospermopsis raciborskii*. *European Journal of Phycology* **52**, 303–310.

Wilson, A. E., Wilson, W. A. & Hay, M. E. (2006). Intraspecific variation in growth and morphology of the bloom-forming cyanobacterium *Microcystis aeruginosa*. *Applied and Environmental Microbiology* **72**, 7386–7389.

Wingender, J., Neu, T. R. & Flemming, H.-C. (1999). *Microbial Extracellular Polymeric Substances*. Springer-Verlag Berlin Heidelberg, New York, Germany.

*Wiśniewska, M. & Paczuska, B. (2015). Long-term changes in the dynamics and structure of cyanobacteria in Koronowo Reservoir. *Oceanological and Hydrobiological Studies* **44**, 127–138.

*Wood, S. A. (2004). *Bloom forming and toxic cyanobacteria in New Zealand species diversity and distribution, cyanotoxin production and accumulation of microcystins in selected freshwater organisms*: PhD Thesis, Massey University, Palmerston North.

Wood, S. A., Maier, M. Y., Puddick, J., Pochon, X., Zaiko, A., Dietrich, D. R. & Hamilton, D. P. (2017). Trophic state and geographic gradients influence planktonic cyanobacterial diversity and distribution in New Zealand lakes. *FEMS Microbiology Ecology* **93**, fiw234.

*Wu, J.-T., Hsu, Y.-B. & Kow, L.-C. (2015). Resilience of a phytoplankton community after disturbance in a subtropical reservoir: a case study in Feitsui Reservoir, Taiwan. *Ecological Indicators* **52**, 284–291.

Wu, X., Kong, F. & Zhang, M. (2011). Photoinhibition of colonial and unicellular *Microcystis* cells in a summer bloom in Lake Taihu. *Limnology* **12**, 55–61.

Wu, X., Wu, Z. & Song, L. (2011). Phenotype and temperature affect the affinity for dissolved inorganic carbon in a cyanobacterium *Microcystis*. *Hydrobiologia* **675**, 175–186.

Wu, Z., Gan, N., Huang, Q. & Song, L. (2007). Response of *Microcystis* to copper stress - do phenotypes of *Microcystis* make a difference in stress tolerance? *Environmental Pollution* **147**, 324–330.

*Wu, Z., Shi, J. & Li, R. (2009). Comparative studies on photosynthesis and phosphate metabolism of *Cylindrospermopsis raciborskii* with *Microcystis aeruginosa* and *Aphanizomenon flos-aquae*. *Harmful Algae* **8**, 910–915.

Wu, Z. & Song, L. (2008). Physiological comparison between colonial and unicellular forms of *Microcystis aeruginosa* Kütz. (cyanobacteria). *Phycologia* **47**, 98–104.

Xiao, M., Willis, A., Burford, M. A. & Li, M. (2017). Review: a meta-analysis comparing cell-division and cell-adhesion in *Microcystis* colony formation. *Harmful Algae* **67**, 85–91.

Xu, F., Zhu, W., Xiao, M. & Li, M. (2016*a*). Interspecific variation in extracellular polysaccharide content and colony formation of *Microcystis* spp. cultured under different light intensities and temperatures. *Journal of Applied Phycology* **28**, 1533–1541.

Xu, S., Sun, Q., Zhou, X., Tan, X., Xiao, M., Zhu, W. & Li, M. (2016*b*). Polysaccharide biosynthesis-related genes explain phenotype-genotype correlation of *Microcystis* colonies in Meiliang Bay of Lake Taihu, China. *Scientific Reports* **6**, 35551.

Xu, S., Peng, Q. & Li, M. (2014). Morphospecies and genospecies of *Microcystis* during blooms in eutrophic Lake Taihu (China) in autumn. *Biochemical Systematics and Ecology* **57**, 322–327.

Yamamoto, Y. & Nakahara, H. (2009). Seasonal variations in the morphology of bloom-forming cyanobacteria in a eutrophic pond. *Limnology* **10**, 185–193.

Yamamoto, Y. & Shiah, F.-K. (2010). Variation in the growth of *Microcystis aeruginosa* depending on colony size and position in colonies. *Annales de Limnologie-International Journal of Limnology* **46**, 47–52.

Yamamoto, Y., Shiah, F.-K. & Chen, Y.-L. (2011). Importance of large colony formation in bloom-forming cyanobacteria to dominate in eutrophic ponds. *Annales de Limnologie-International Journal of Limnology* **47**, 167–173.

Yang, Z. & Kong, F. (2012). Formation of large colonies: a defense mechanism of *Microcystis aeruginosa* under continuous grazing pressure by flagellate *Ochromonas* sp. *Journal of Limnology* **71**, 61–66.

Yang, Z. & Kong, F. (2013). Abiotic factors in colony formation: effects of nutrition and light on extracellular polysaccharide production and cell aggregates of *Microcystis aeruginosa*. *Chinese Journal of Oceanology and Limnology* **31**, 796–802.

Yang, Z., Kong, F. & Shi, X. (2005). Effects of filtered lake water on colony formation and growth rate in *Microcystis aeruginosa* of different physiological phases. *Journal of Freshwater Ecology* **20**, 425–429.

Yang, Z., Kong, F., Shi, X. & Cao, H. (2006). Morphological response of *Microcystis aeruginosa* to grazing by different sorts of zooplankton. *Hydrobiologia* **563**, 225–230.

Yang, Z., Kong, F., Shi, X., Zhang, M., Xing, P. & Cao, H. (2008). Changes in the morphology and polysaccharide content of *Microcystis aeruginosa* (Cyanobacteria) during *Flagellate* grazing. *Journal of Phycology* **44**, 716–720.

Yang, Z., Kong, F., Yang, Z., Zhang, M., Yu, Y. & Qian, S. (2009). Benefits and costs of the grazer-induced colony formation in *Microcystis aeruginosa*. *Annales de Limnologie-International Journal of Limnology* **45**, 203–208.

Yang, Z., Kong, F., Zhang, M., Yang, Z., Yu, Y. & Qian, S. (2009). Effect of filtered cultures of flagellate *Ochromonas* sp. on colony formation in *Microcystis aeruginosa*. *International Review of Hydrobiology* **94**, 143–152.

Yasumoto, K., Nishigami, A., Kasai, F., Kusumi, T. & Ooi, T. (2006). Isolation and absolute configuration determination of aliphatic sulfates as the *Daphnia* kairomones inducing morphological defense of a phytoplankton. *Chemical and Pharmaceutical Bulletin* **54**, 271–274.

Yoshida, T., Ayabe, Y., Yasunaga, M., Usami, Y., Habe, H., Nojiri, H. & Omori, T. (2003). Genes involved in the synthesis of the exopolysaccharide methanolan by the obligate methylotroph *Methylobacillus* sp strain 12S. *Microbiology* **149**, 431–444.

Yoshida, T., Hairston, N. G. & Ellner, S. P. (2004). Evolutionary trade–off between defence against grazing and competitive ability in a simple unicellular alga, *Chlorella vulgaris*. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 1947–1953.

Yunes, J. S., Salomon, P., Matthiensen, A., Beattie, K., Raggett, S. & Codd, G. (1996). Toxic blooms of cyanobacteria in the Patos lagoon estuary, southern Brazil. *Journal of Aquatic Ecosystem Stress and Recovery* (Formerly Journal of Aquatic Ecosystem Health) **5**, 223–229.

*Zarenezhad, S., Sano, T., Watanabe, M. M. & Kawachi, M. (2012). Evidence of the existence of a toxic form of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) in Japan. *Phycological Research* **60**, 98–104.

*Zhang, H., Boegman, L., Scavia, D. & Culver, D. A. (2016). Spatial distributions of external and internal phosphorus loads in Lake Erie and their impacts on phytoplankton and water quality. *Journal of Great Lakes Research* **42**, 1212–1227.

Zhang, M., Kong, F., Tan, X., Yang, Z., Cao, H. & Xing, P. (2007). Biochemical, morphological, and genetic variations in *Microcystis aeruginosa* due to colony disaggregation. *World Journal of Microbiology and Biotechnology* **23**, 663–670.

Zhang, M., Shi, X., Yu, Y. & Kong, F. (2011). The acclimative changes in photochemistry after colony formation of the cyanobacteria *Microcystis aeruginosa*. *Journal of Phycology* **47**, 524–532.

*Zhang, W., Lou, I., Ung, W. K., Kong, Y. & Mok, K. M. (2017). Application of PCR and real-time PCR for monitoring cyanobacteria, *Microcystis* spp. and *Cylindrospermopsis raciborskii*, in Macau Freshwater Reservoir. *Frontiers of Earth Science* **8**, 291–301.

Zhao, L., Lu, L., Li, M., Xu, Z. & Zhu, W. (2011). Effects of Ca and Mg levels on colony formation and EPS content of cultured *M. aeruginosa*. *Procedia Environmental Sciences* **10**, 1452–1458.

*Zhong, F., Gao, Y., Yu, T., Zhang, Y., Xu, D., Xiao, E., He, F., Zhou, Q. & Wu, Z. (2011). The management of undesirable cyanobacteria blooms in channel catfish ponds using a constructed wetland: contribution to the control of off-flavor occurrences. *Water Research* **45**, 6479–6488.

Zhu, W., Li, M., Dai, X. & Xiao, M. (2015). Differences in vertical distribution of *Microcystis* morphospecies composition in a shallow hypertrophic lake (Lake Taihu, China). *Environmental Earth Sciences* **73**, 5721–5730.

Zhu, W., Li, M., Luo, Y., Dai, X., Guo, L., Xiao, M., Huang, J. & Tan, X. (2014). Vertical distribution of *Microcystis* colony size in Lake Taihu: its role in algal blooms. *Journal of Great Lakes Research* **40**, 949–955.

Zhu, W., Zhou, X., Chen, H., Gao, L., Xiao, M. & Li, M. (2016). High nutrient concentration and temperature alleviated formation of large colonies of *Microcystis*: evidence from field investigations and laboratory experiments. *Water Research* **101**, 167–175.

*Zohary, T., Pais-Madeira, A. M., Robarts, R. & Hambright, K. D. (1996). Interannual phytoplankton dynamics of a hypertrophic African lake. *Archiv für Hydrobiologie* **136**, 105–126.

## 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.

(*Received 3 August 2017; revised 16 January 2018; accepted 24 January 2018; published online 22 February 2018*)