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HORIZONS

Predicting the effects of climate change on freshwater cyanobacterial blooms requires consideration of the complete cyanobacterial life cycle

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To date, most research on cyanobacterial blooms in freshwater lakes has focused on the pelagic life stage. However, examining the complete cyanobacterial life cycle—including benthic life stages—may be needed to accurately predict future bloom dynamics. The current expectation, derived from the pelagic life stage, is that blooms will continue to increase due to the warmer temperatures and stronger stratification associated with climate change. However, stratification and mixing have contrasting effects on different life stages: while pelagic cyanobacteria benefit from strong stratification and are adversely affected by mixing, benthic stages can benefit from increased mixing. The net effects of these potentially counteracting processes are not yet known, since most aquatic ecosystem models do not incorporate benthic stages and few empirical studies have tracked the complete life cycle over multiple years. Moreover, for many regions, climate models project both stronger stratification *and* increased storm-induced mixing in the coming decades; the net effects of those physical processes, even on the pelagic life stage, are not yet understood. We therefore recommend an integrated research agenda to study the dual effects of stratification and mixing on the complete cyanobacterial life cycle—both benthic and pelagic stages—using models, field observations and experiments.

KEYWORDS: complex life history; cyanobacteria; mixing; population dynamics; recruitment; stratification

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INTRODUCTION

Surface aggregations of cyanobacteria (blooms) are increasing in many freshwater systems worldwide, threatening ecosystem services fundamental to society (Paerl & Huisman, 2008; Taranu *et al.*, 2015; Ho *et al.*, 2019). To date, most studies of freshwater cyanobacteria have focused on this conspicuous stage of their life history. However, the pelagic focus overlooks the fact that in temperate and boreal lakes, cyanobacteria are generally not present in the water column year-round (Fig. 1). Instead, a large part of the life cycle is spent in the benthos, on or near the sediment (Fryxell, 1983; Reynolds, 2006; Poulickova *et al.*, 2008; Kaplan-Levy *et al.*, 2010). Subsequent recruitment from the benthos to the open water pelagic zone inoculates blooms (Reynolds, 1972; Hansson *et al.*, 1994; Perakis *et al.*, 1996; Brunberg & Blomqvist, 2003; Padisak, 2003; Stahl-Delbanco *et al.*, 2003; Kravchuk *et al.*, 2006; Torres & Adámek, 2013). Similar benthic-pelagic coupling is also implicated in marine and estuarine harmful algal blooms, including red tides (e.g. Boero *et al.*, 1996; Steidinger, 2010).

Although previous papers have suggested that knowledge of cyanobacterial life cycles is required for effective bloom prediction and management (e.g. Hellweger *et al.*, 2008; Hense & Beckmann, 2010; Suikkanen *et al.*, 2010), we still do not have a good understanding of the environmental conditions in which recruitment from benthic life stages is critical to pelagic population dynamics. When quantified, cyanobacterial recruitment on average contributes <1 to 2% of the pelagic population (reviewed by Tan, 2012)—yet can sometimes account for up to 60% of the pelagic population (reviewed by Carey *et al.*, 2014). Further, eliminating recruitment could result in 50% smaller blooms (Verspagen *et al.*, 2005). A predictive understanding of when, where, and why benthic life stages matter to bloom formation could lead to novel management strategies to diminish benthic survival or recruitment, as has been explored by some researchers (e.g. Visser *et al.*, 1996; Baker, 1999; Tsujimura, 2004; Verspagen *et al.*, 2006; Tan, 2012; Jia *et al.*, 2014; Chen *et al.*, 2016a; Visser *et al.*, 2016; Wu *et al.*, 2017).

In this Horizons article, we urge researchers to consider the *complete* cyanobacterial life cycle to meet the pressing challenges of predicting and managing cyanobacterial blooms against a backdrop of ongoing global change. First, we review what is known about cyanobacterial life cycles, including how lake thermal stratification and its converse, mixing, have contrasting impacts on benthic versus pelagic life stages. We then explore how these differential responses might alter the current expectation that climate change will continue to increase cyanobacterial blooms (e.g. Paerl & Huisman, 2008) and conclude by proposing a research agenda to advance our understanding of cyanobacterial life history and when it matters to bloom prediction and forecasting. Although our focus is primarily on temperate and boreal lakes that exhibit summer thermal stratification, we also consider waterbodies of other mixing regimes and climates in the proposed research agenda.

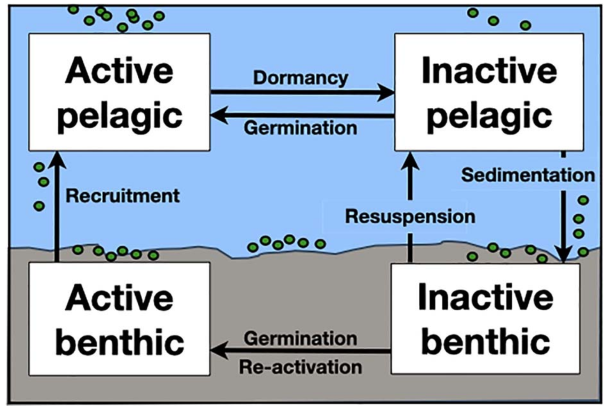

Fig. 1. Schematic for a generalized cyanobacterial life cycle; details vary among taxa.

QUICK PRIMER ON CYANOBACTERIAL BENTHIC-PELAGIC COUPLING

Cyanobacterial life cycles are complex, with key ecological constraints in each habitat impacting the transitions between habitats (Fig. 1). Cyanobacterial population growth within the water column is generally enhanced by warm temperatures, high light and nutrient availability, and thermal stability (e.g. Paerl, 1988; Huisman & Hulot, 2005; Reynolds, 2006; Jöhnk *et al.*, 2008; Wagner & Adrian, 2009).

When pelagic conditions for cyanobacteria deteriorate, e.g. due to cooling water temperatures in the autumn in temperate and boreal environments, many cyanobacterial taxa actively exit the water column (Fig. 1). Their transition to the benthos happens via one of two mechanisms. First, in true dormancy, cyanobacteria produce specialized cells called akinetes while still in the water column; the colonies (with akinetes) then senesce and sink to the sediment, forming a "seed bank" (Nichols & Adams, 1982; Gyllstrom & Hansson, 2004; Suikkanen *et al.*, 2010). Cyanobacterial genera with true dormancy include *Aphanizomenon*, *Cylindrospermopsis*, *Dolichospermum* and *Gloeotrichia* (Adams & Duggan, 1999; Karlsson-Elfgren & Brunberg, 2004; Reynolds, 2006; Rücker *et al.*, 2009; Wood *et al.*, 2009; Kaplan-Levy *et al.*, 2010; Kovacs *et al.*, 2012). Akinetes are highly resistant to environmental stressors, including desiccation, and can either germinate immediately (e.g. Rother & Fay, 1977; Lynch & Shapiro, 1981; Cmiech *et al.*, 1984) or persist for months to decades (Livingstone & Jaworski, 1980; Rasanen *et al.*, 2006; Wood *et al.*, 2009), providing a “storage effect” against adverse conditions (Warner & Chesson, 1985; Caceres, 1997) and facilitating invasion into new lakes (e.g. Padisak, 2003; Rücker *et al.*, 2009; Ramm *et al.*, 2017).

Alternatively, instead of producing akinetes, taxa such as *Microcystis* and *Planktothrix* lower their metabolic activity and sink to overwinter on or near the sediments as (mostly) inactive vegetative cells (Fallon & Brock, 1981; Reynolds *et al.*, 1981; Tsujimura *et al.*, 2000; Brunberg & Blomqvist, 2002; Poulickova *et al.*, 2004; Ihle *et al.*, 2005; Sabart *et al.*, 2015; Wang *et al.*, 2018). In some environments, few of these inactive vegetative cells persist through the winter due to mortality, burial and other loss processes (e.g. Baker, 1999; Wang *et al.*, 2018). In others, cells can persist for years (although not decades) before returning to the water column (Caceres & Reynolds, 1984; Bostrom *et al.*, 1989; Brunberg, 1995; Brunberg & Blomqvist, 2003).

Return of benthic life stages to the water column occurs both passively and via buoyancy regulation with gas vesicles (Fig. 1). Passive recruitment occurs when physical processes or bioturbation resuspend benthic akinetes or inactive vegetative colonies, which then become active in the water column (Stahl-Delbanco & Hansson, 2002; Verspagen *et al.*, 2004; Yamamoto, 2010; Gu, 2012; Karlson *et al.*, 2012; Chen *et al.*, 2016b). By contrast, favorable environmental conditions in the benthos can trigger akinete germination or the resumption of metabolic activity by inactive benthic stages. The newly active cyanobacteria then enter the water column after photosynthetic rates are sufficient to promote gas vesicle production, enabling buoyancy (Preston *et al.*, 1980; Trimbee & Harris, 1984b; Karlsson-Elfgren *et al.*, 2003; Carey *et al.*, 2008). Importantly, the conditions triggering the *in situ* transition from the inactive benthic stage to the active stage are incompletely understood, in part because most studies examine only a few environmental drivers for limited time periods. Moreover, when the same drivers have been studied using both observational and experimental approaches, responses differ across taxa and lakes (Tables S1 and S2). In addition, our understanding of spatial and temporal heterogeneity in recruitment patterns within and among lakes remains limited.

DIFFERENT LIFE STAGES HAVE CONTRASTING RESPONSES TO STRATIFICATION AND MIXING

Regardless of these gaps in current understanding, work to date strongly suggests that cyanobacterial benthic and pelagic stages can respond very differently to the same environmental drivers due to the inherent differences in their habitat and life strategy. For well-studied taxa such as *Aphanizomenon*, *Dolichospermum* and *Microcystis*, cyanobacterial sensitivity to lake stratification and mixing depends on the life stage and whether the mixing is occurring in the water column or at the sediment–water interface.

In the pelagic life stage, the general expectation is that thermal stratification is “good” and mixing is “bad” for cyanobacterial growth and reproduction, especially in deep lakes (M_1 in Fig. 2). Stratification gives buoyant cyanobacteria a competitive advantage (Walsby, 1994), as their ability to regulate their vertical position also enables them to access nutrients elsewhere in the water column (reviewed by Cottingham *et al.*, 2015) and shade out competitors (Carey *et al.*, 2012). Conversely, mixing events break up surface aggregations of cyanobacteria (reviewed in Zhao *et al.*, 2017; Xiao *et al.*, 2018). Mixing events strong enough to disrupt stratification can cause premature loss of active cyanobacteria from the water column because the greater pressures at depth cause gas vesicles to collapse or they transport cells/colonies below the compensation depth (e.g. Walsby, 1994; Visser *et al.*, 1996; Huisman *et al.*, 2004). After gas vesicle collapse, cells are no longer able to control their buoyancy and sink to the benthos (Oliver & Walsby, 1984; Kinsman *et al.*, 1991). Even if cells do not immediately senesce, light limitation and colder temperatures at depth usually result in losses that exceed reproduction (Huisman & Hulot, 2005). These mechanisms explain why increased thermal stability driven by climatic warming is implicated as a leading cause of increasing cyanobacterial blooms (e.g. Jöhnk *et al.*, 2008; Wagner & Adrian, 2011; Carey *et al.*, 2012)—as well as why some lake managers deploy epilimnetic mixing systems to control cyanobacteria (reviewed by Visser *et al.*, 2016; Xiao *et al.*, 2018; Lofton *et al.*, 2019).

However, mixing can have positive impacts on benthic cyanobacterial life stages (M_2 in Fig. 2). For example, mixing at the sediment–water interface triggers the return of benthic cyanobacteria to the water column either passively via physical resuspension by sediment mixing (Reynolds *et al.*, 1981; Thomas & Walsby, 1986; MacIntyre & Melack, 1995; Verspagen *et al.*, 2004; Misson *et al.*, 2011; Sejnohova & Marsalek, 2012) or ebullition (Delwiche *et al.*, 2020), or by stimulating germination and active recruitment (Stahl-Delbanco *et al.*, 2003; Karlsson-Elfgren *et al.*, 2004; Rengefors

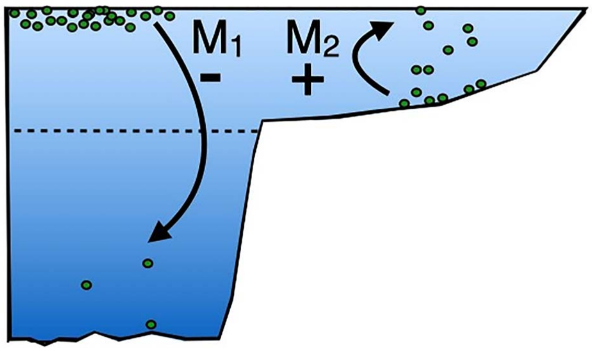

Fig. 2. Graphical depiction of the core hypothesized mechanisms: mixing events that disrupt stratification have an adverse effect on pelagic cyanobacteria (M_1), while mixing in shallow water stimulates recruitment from benthic life stages back into the water column (M_2). Both mechanisms are at work in deep lakes, whereas only M_2 would operate in shallow lakes. The net effect of these opposing processes on pelagic population size is not yet known, but is expected to differ among cyanobacterial taxa as a function of lake type, location, and time of year, as explained in the text. The dotted line represents the thermocline.

et al., 2004; Misson & Latour, 2012). We reviewed the literature on the environmental factors determining reactivation, germination and recruitment (Tables S1 and S2) and found reports demonstrating positive effects of mixing on recruitment for multiple genera, including *Aphanizomenon* (Trimbee & Harris, 1984a; Hansson *et al.*, 1994), *Dolichospermum* (Reynolds, 1972; Rengefors *et al.*, 2004; Bertos-Fortis *et al.*, 2016), *Microcystis* (Reynolds *et al.*, 1981; Stahl-Delbanco *et al.*, 2003; Verspagen *et al.*, 2004; Ihle *et al.*, 2005; Verspagen *et al.*, 2005; Misson *et al.*, 2011; Misson & Latour, 2012; Su *et al.*, 2016), *Nodularia* (Bertos-Fortis *et al.*, 2016) and *Gloeotrichia* (Forsell & Pettersson, 1995; Karlsson-Elfgren *et al.*, 2003, 2004, 2005; Rengefors *et al.*, 2004; Carey *et al.*, 2014). Moreover, macrophyte presence, which decreases mixing in shallow waters (e.g. Gebrehiwot *et al.*, 2017), is associated with lower phytoplankton recruitment (reviewed by Villena & Romo, 2007). If mixing indeed facilitates the transition from benthic to pelagic habitats—thereby stimulating blooms—it may explain the equivocal success of bloom management via epilimnetic mixing systems (Visser *et al.*, 2016; Lofton *et al.*, 2019).

Based on M_1 and M_2 (Fig. 2), we predict that cyanobacterial taxa that depend strongly on both recruitment and gas vesicles for bloom formation will be positively affected by mixing at the sediment–water interface in both shallow and deep lakes, but negatively affected (at least in the short-term) by the disruption of summer stratification by water column mixing. However, the *net* consequences of mixing events for cyanobacterial populations are difficult to predict, especially given different dormancy strategies, physiological traits that affect success in the water column, lake morphometry, stochasticity in the timing of mixing events relative to plankton phenology, and other factors. As such, a careful consideration of all of these effects, and the time scales over which they manifest (e.g. Wilson *et al.*, 2016), is needed to make accurate predictions of how cyanobacteria may change in the future.

INTERSECTIONS OF CYANOBACTERIAL LIFE HISTORY AND CLIMATE CHANGE

The effects of climate change on stratification and mixing (e.g. MacKay *et al.*, 2009; Woolway *et al.*, 2019) are already having, and will continue to have, profound influences on aquatic biota in temperate and boreal lakes, including cyanobacteria (Stockwell *et al.*, 2020). The timing, duration and strength of thermal stratification are changing in lakes and reservoirs globally due to increasing air temperatures (Lehman, 2002; O'Reilly *et al.*, 2003; O'Reilly *et al.*, 2015; Woolway & Merchant, 2019). For pelagic cyanobacterial populations that are "seeded" by mixing events that stimulate recruitment, changes to the temporal dynamics of stratification could have important consequences for summer blooms, especially in deep lakes. However, this possibility has not yet been fully explored.

Moreover, the predicted changes in stratification are not unidirectional, as many global climate change scenarios also predict increased high-intensity storms in both mid-latitude and tropical regions (Christensen, 2007; Hayhoe *et al.*, 2007; Field *et al.*, 2012; Havens *et al.*, 2016; Prein *et al.*, 2017). To date, however, the potential consequences of increased storms have not been investigated as extensively as changes in water temperature and stratification (but see Stockwell *et al.*, 2020). In deep stratified lakes, more storms will increase episodic water column mixing (see e.g. Jennings *et al.*, 2012; Klug *et al.*, 2012; De Eyto *et al.*, 2016; Woolway *et al.*, 2018) during otherwise thermally-stable summers. While this mixing may disrupt pelagic cyanobacterial populations in the short term via M_1 in Fig. 2, it may also increase recruitment via M_2 or stimulate pelagic cyanobacteria over days to weeks due to increased nutrients from runoff, resuspended sediments or entrained hypolimnetic water. By contrast, in polymictic lakes, the positive effects of storms on recruitment or nutrient availability (e.g. Zhu *et al.*, 2014; Havens *et al.*, 2016) could be offset by increased hydraulic flushing rates that remove pelagic cyanobacteria, particularly in systems with short residence times (Havens *et al.*, 2016; Richardson *et al.*, 2018, 2019).

Thus, the interplay between two key physical aspects of climate change—stronger thermal stratification and increased intense storms—is likely to have both negative and positive effects on cyanobacteria, with effects that differ for benthic and pelagic life stages (e.g. Hense & Beckmann, 2006; Jager & Diehl, 2014) and among lakes. Notably, although the impacts of different aspects of climate change are beginning to be addressed for pelagic cyanobacteria in temperate systems (e.g. Taranu *et al.*, 2012; Rigosi *et al.*, 2014; Richardson *et al.*, 2018, 2019), none of these studies has considered benthic life stages or recruitment. To develop robust predictions of how cyanobacteria respond to the physical effects of climate change, we need to better understand how these drivers interact with cyanobacterial traits (*sensu* Litchman & Klausmeier, 2008; Kruk *et al.*, 2010). For example, differences in dormancy strategies (i.e. akinetes vs. inactive vegetative cells, as described above), accessory photosynthetic pigments (e.g. Glibert, 2016), buoyancy (e.g. floating velocity, Xiao *et al.*, 2018) and sensitivity to increased temperature (e.g. Lurling *et al.*, 2013) may modulate responses to different aspects of climate change. Further, lake-specific characteristics such as morphometry, watershed characteristics and water chemistry may amplify or diminish climate change impacts (e.g. Richardson *et al.*, 2018). For example, cooler overnight air temperatures increase convective mixing in the littoral zone, potentially stimulating both nutrient cycling and passive recruitment (MacIntyre & Melack, 1995), but the impact of this mechanism likely varies with the proportion of a lake comprising littoral habitat and degree of seasonal change in air temperature.

RESEARCH AGENDA

A comprehensive research agenda is required to advance our understanding of how stratification and mixing impact the complete cyanobacterial life cycle. Some of this work is already underway, yet we need concerted efforts to integrate across taxa, lakes and geographic regions to identify emergent trends that may not be evident within any one system (Burford *et al.*, 2020). Specific research needs include:

Simulation models. Simulation models that capture the dynamic impacts of physical and chemical processes on both benthic and pelagic life stages are needed to answer two key questions: (1) What are the net effects of stratification and mixing on cyanobacterial populations, especially bloom formation? and (2) Under a suite of realistic climate and management scenarios, will cyanobacterial blooms increase or decrease? Understanding how diverse taxa and lakes might be impacted by different scenarios can only be achieved through extensive studies using models with different levels of complexity to see whether findings are consistent across modeling approaches and lakes (Sommer *et al.*, 2012; Hipsey *et al.*, 2015). Some individual-based cyanobacterial population models have included benthic stages (e.g. Hense & Beckmann, 2006; Hellweger *et al.*, 2008) and the effects of mixing on pelagic phytoplankton have been explored previously (e.g. Huisman *et al.*, 2004; Jöhnk *et al.*, 2008; Blottière *et al.*, 2014; Zhao *et al.*, 2017). However, to our knowledge, no lake ecosystem simulation model incorporates recruitment from benthic life stages as a contributor to pelagic populations. Addition of recruitment to simulation models such as PROTECH (Elliott *et al.*, 1999; Gray *et al.*, 2019) and the General Lake Model coupled with the Aquatic EcoDynamics modules (GLM-AED2, Hipsey *et al.*, 2019) would allow for wide-scale exploration of potential scenarios of the strength of stratification; the type, frequency, intensity and duration of mixing; interactions with other environmental drivers; and lake management. The mixing scenarios should be informed by both climate change predictions, specifically those related to temperature, wind and the frequency and intensity of storm events, as well as managers' needs with respect to anticipated water uses. All models should be parameterized from observations and experiments conducted across a wide range of lakes, as described below, and specifically include core environmental drivers likely to determine growth and survival during each life stage (e.g. light, temperature and mixing; Tables S1 and S2).

Field observations. Field observations of how mixing events of varying magnitude and duration impact both the pelagic and the benthic life stage of important bloom-forming taxa in a broad array of lakes are necessary to parameterize the models for different taxa and lakes. In particular, observational data on recruitment for more taxa over multiple years, especially in tropical lakes and polymictic lakes, are urgently needed to better understand the effects of mixing on cyanobacterial life histories. Simultaneous collection of data on interacting environmental drivers—including temperature, light, mixing, nutrients and dissolved oxygen—allows for correlative identification of potential drivers of pelagic population dynamics (e.g. Zhu *et al.*, 2014; Yang *et al.*, 2016) and recruitment (e.g. Carey *et al.*, 2014). To date, however, most cyanobacterial recruitment studies have been conducted over just one or two summer stratified seasons in temperate regions (Carey *et al.*, 2014); studies that run year-round or across many years, and in boreal or tropical regions, remain rare. In particular, cyanobacteria in tropical regions pose major management concerns, yet much less is known about the drivers of tropical blooms (reviewed by Mowe *et al.*, 2015). Consequently, it remains unknown how mixing events may affect tropical cyanobacterial life histories. Newer technologies such as FlowCAMs coupled with taxonomic identification via machine learning may expedite the tedious work of identification via microscopy (e.g. Thomas *et al.*, 2018; Hrycik *et al.*, 2019), though to our knowledge such approaches have not yet been used in recruitment studies.

Experiments. Because of the difficulty of identifying causal drivers from observational data, laboratory or field mesocosm experiments that manipulate the intensity and duration of mixing can be used to isolate the effects of mixing on both benthic and pelagic life stages (see, for example, the studies of mixing in Table S2). As with the other research approaches, experiments will need to be conducted for multiple taxa, in lakes with different morphometries and seasonal regimes. Field mesocosm experiments have the benefit of generally providing more realistic conditions than smaller scale lab culture experiments (e.g. Wang *et al.*, 2018, but see Park *et al.*, 2018), though field studies can be logistically challenging and lose realism after longer durations of time (Burford *et al.*, 2020). In some lakes, it may be possible to manipulate stratification and mixing using engineered systems, enabling the testing of model predictions at the whole-lake scale (Jungo *et al.*, 2001; Cantin *et al.*, 2011; Read *et al.*, 2011; Chen *et al.*, 2018; Lofton *et al.*, 2019).

CONCLUSION

Bloom-forming freshwater cyanobacteria sequentially occupy the benthic and pelagic zones in temperate and boreal lakes, but typically only the pelagic life stage is studied. Because stratification and mixing can have opposing effects on the benthic and pelagic life stages of cyanobacteria, a more complete understanding of all stages of the cyanobacterial life cycle will enable plankton researchers to better predict how ongoing climate change will affect the frequency, intensity and duration of cyanobacterial blooms.

AUTHOR CONTRIBUTIONS

The core ideas in this manuscript evolved over many years of collaboration among all co-authors. C.C.C. and K.L.C. outlined the paper, performed the literature review for Tables S1 and S2, and wrote the first draft; all authors edited and approved the submitted version.

DATA ARCHIVING

Not applicable.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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REFERENCES

Adams, D. G. and Duggan, P. S. (1999) Heterocyst and akinete differentiation in cyanobacteria. *New Phytol.*, **144**, 3–33.

Baker, P. D. (1999) Role of akinetes in the development of cyanobacterial populations in the lower Murray River, Australia. *Mar. Freshw. Res.*, **50**, 265–279.

Bertos-Fortis, M., Farnelid, H. M., Lindh, M. V., Casini, M., Andersson, A., Pinhassi, J. and Legrand, C. (2016) Unscrambling cyanobacteria community dynamics related to environmental factors. *Front. Microbiol.*, **7**, 625.

Blottière, L., Rossi, M., Madricardo, F. and Hulot, F. D. (2014) Modeling the role of wind and warming on *Microcystis aeruginosa* blooms in shallow lakes with different trophic status. *Theor Ecol*, **7**, 35–52.

Boero, F., Belmonte, G., Fanelli, G., Piraino, S. and Rubino, F. (1996) The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends Ecol. Evol.*, **11**, 177–180.

Bostrom, B., Pettersson, A. K. and Ahlgren, I. (1989) Seasonal dynamics of a cyanobacteria-dominated microbial community in surface sediments of a shallow, eutrophic lake. *Aquat Sci*, **51**, 153–178.

Brunberg, A. K. (1995) Microbial activity and phosphorus dynamics in eutrophic lake-sediments enriched with *Microcystis* colonies. *Freshwater Biol*, **33**, 541–555.

Brunberg, A. K. and Blomqvist, P. (2002) Benthic overwintering of *Microcystis* colonies under different environmental conditions. *J. Plankton Res.*, **24**, 1247–1252.

Brunberg, A. K. and Blomqvist, P. (2003) Recruitment of *Microcystis* (Cyanophyceae) from lake sediments: the importance of littoral inocula. *J. Phycol.*, **39**, 58–63.

Burford, M. A., Carey, C. C., Hamilton, D. P., Huisman, J., Paerl, H. W., Wood, S. A. and Wulff, A. (2020) Perspective: advancing the research agenda for improving understanding of cyanobacteria in a future of global change. *Harmful Algae*. doi: 10.1016/j.hal.2019.04.004 101601.

Caceres, C. E. (1997) Temporal variation, dormancy, and coexistence: a field test of the storage effect. *P Natl Acad Sci USA*, **94**, 9171–9175.

Caceres, O. and Reynolds, C. S. (1984) Some effects of artificially-enhanced anoxia on the growth of *Microcystis aeruginosa* Kutz Emend-Elenkin, with special reference to the initiation of its annual growth cycle in lakes. *Arch Hydrobiol*, **99**, 379–397.

Cantin, A., Beisner, B. E., Gunn, J. M., Prairie, Y. T. and Winter, J. G. (2011) Effects of thermocline deepening on lake plankton communities. *Can. J. Fish. Aquat. Sci.*, **68**, 260–276.

Carey, C. C., Cottingham, K. L., Weathers, K. C., Ewing, H. A. and Greer, M. L. (2014) Spatial and temporal variability in the recruitment of the cyanobacterium *Gloeotrichia echinulata* in an oligotrophic lake. *Freshw Sci*, **33**, 577–592.

Carey, C. C., Ibelings, B. W., Hoffmann, E. P., Hamilton, D. P. and Brookes, J. D. (2012) Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Res.*, **46**, 1394–1407.

Carey, C. C., Weathers, K. C. and Cottingham, K. L. (2008) *Gloeotrichia echinulata* blooms in an oligotrophic lake: helpful insights from eutrophic lakes. *J. Plankton Res.*, **30**, 893–904.

Chen, C., Yang, Z., Kong, F. X., Zhang, M., Yu, Y. and Shi, X. L. (2016a) Growth, physiochemical and antioxidant responses of overwintering benthic cyanobacteria to hydrogen peroxide. *Environ. Pollut.*, **219**, 649–655.

Chen, N., Liu, L., Chen, M. S., Li, Y. F., Xing, X. G. and Lv, Y. Y. (2016b) Effects of benthic bioturbation on phytoplankton in eutrophic water: a laboratory experiment. *Fund Appl Limnol*, **188**, 25–39.

Chen, S. Y., Carey, C. C., Little, J. C., Lofton, M. E., Mcclure, R. P. and Lei, C. W. (2018) Effectiveness of a bubble-plume mixing system for managing phytoplankton in lakes and reservoirs. *Ecol. Eng.*, **113**, 43–51.

Christensen, J. H. *et al.* (2007) Regional climate projections. In Solomon, S. *et al.* (eds.), *Climate Change 2007: The Physical Science Basis Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, England, pp. 847–940.

Cmiech, H. A., Reynolds, C. S. and Leedale, G. F. (1984) Seasonal periodicity, heterocyst differentiation and sporulation of planktonic Cyanophyceae in a shallow lake, with special reference to *Anabaena solitaria*. *British Phycological Journal*, **19**, 245–257.

Cottingham, K. L., Ewing, H. A., Greer, M. L., Carey, C. C. and Weathers, K. C. (2015) Cyanobacteria as biological drivers of lake nitrogen and phosphorus cycling. *Ecosphere*, **6**, 1. doi: 10.1890/ES14-00174.1.

De Eyto, E., Jennings, E., Ryder, E., Sparber, K., Dillane, M., Dalton, C. and Poole, R. (2016) Response of a humic lake ecosystem to an extreme precipitation event: physical, chemical, and biological implications. *Inland Waters*, **6**, 483–498.

Delwiche, K., Gu, J., Hemond, H. and Preheim, S. P. (2020) Vertical transport of sediment-associated metals and cyanobacteria by ebullition in a stratified lake. *Biogeosciences*, **17**, 3135–3147.

Elliott, J. A., Irish, A. E., Reynolds, C. S. and Tett, P. (1999) Sensitivity analysis of PROTECH, a new approach in phytoplankton modelling. *Hydrobiologia*, **414**, 45–51.

Fallon, R. D. and Brock, T. D. (1981) Overwintering of *Microcystis* in Lake Mendota. *Freshwater Biol*, **11**, 217–226.

Field, C. B., Barros, V., Stocker, T. F., Qin, D., Dokken, D. J., Ebi, K. L., Mastrandrea, M. D., Mach, K. J. *et al.* (2012) *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, England.

Forsell, L. and Pettersson, K. (1995) On the seasonal migration of the cyanobacterium *Gloeotrichia echinulata* in Lake Erken, Sweden, and its influence on the pelagic population. *Mar. Freshw. Res.*, **46**, 287–293.

Fryxell, G. A. (1983) *Survival Strategies of the Algae*, Cambridge University Press, Cambridge, England.

Gebrehiwot, M., Kifle, D., Stiers, I. and Triest, L. (2017) Phytoplankton functional dynamics in a shallow polymictic tropical lake: the influence of emergent macrophytes. *Hydrobiologia*, **797**, 69–86.

Glibert, P. M. (2016) Margalef revisited: a new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology. *Harmful Algae*, **55**, 25–30.

Gray, E., Elliott, J. A., Mackay, E. B., Folkard, A. M., Keenan, P. O. and Jones, I. D. (2019) Modelling lake cyanobacterial blooms: disentangling the climate-driven impacts of changing mixed depth and water temperature. *Freshwater Biol*, **64**, 2141–2155.

Gu, Z. D. (2012) Life Cycle of Bloom-forming cyanobacteria and its influencing factors. *Appl Mech Mater*, Vols. **209-211**, 1227–1230.

Gyllstrom, M. and Hansson, L. A. (2004) Dormancy in freshwater zooplankton: induction, termination and the importance of benthic-pelagic coupling. *Aquat Sci*, **66**, 274–295.

Hansson, L. A., Rudstam, L. G., Johnson, T. B., Soranno, P. and Allen, Y. (1994) Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake. *Can. J. Fish. Aquat. Sci.*, **51**, 2825–2833.

Havens, K., Paerl, H., Phlips, E., Zhu, M., Beaver, J. and Srifa, A. (2016) Extreme weather events and climate variability provide a lens to how shallow lakes may respond to climate change. *Watermark*, **8**, 229.

Hayhoe, K., Wake, C. P., Huntington, T. G., Luo, L. F., Schwartz, M. D., Sheffield, J., Wood, E., Anderson, B. *et al.* (2007) Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynam.*, **28**, 381–407.

Hellweger, F. L., Kravchuk, E. S., Novotny, V. and Gladyshev, M. I. (2008) Agent-based modeling of the complex life cycle of a cyanobacterium (*Anabaena*) in a shallow reservoir. *Limnol. Oceanogr.*, **53**, 1227–1241.

Hense, I. and Beckmann, A. (2006) Towards a model of cyanobacteria life cycle - effects of growing and resting stages on bloom formation of N-2-fixing species. *Ecol. Model.*, **195**, 205–218.

Hense, I. and Beckmann, A. (2010) The representation of cyanobacteria life cycle processes in aquatic ecosystem models. *Ecol. Model.*, **221**, 2330–2338.

Hipsey, M. R., Bruce, L. C., Boon, C., Busch, B., Carey, C. C., Hamilton, D. P., Hanson, P. C., Read, J. S. *et al.* (2019) A General Lake Model (GLM 3.0) for linking with high-frequency sensor data from the Global Lake Ecological Observatory Network (GLEON). *Geosci. Model Dev.*, **12**, 473–523.

Hipsey, M. R., Hamilton, D. P., Hanson, P. C., Carey, C. C., Coletti, J. Z., Read, J. S., Ibelings, B. W., Valesini, F. J. *et al.* (2015) Predicting the resilience and recovery of aquatic systems: a framework for model evolution within environmental observatories. *Wat Resources Res*, **51**, 7023–7043.

Ho, J. C., Michalak, A. M. and Pahlevan, N. (2019) Widespread global increase in intense lake phytoplankton blooms since the 1980s. *Nature*, **574**, 667–670.

Hrycik, A. R., Shambaugh, A. and Stockwell, J. D. (2019) Comparison of FlowCAM and microscope biovolume measurements for a diverse freshwater phytoplankton community. *J. Plankton Res.*, **41**, 849–864.

Huisman, J. and Hulot, F. D. (2005) Population dynamics of harmful cyanobacteria. In Huisman, J., Matthijs, H. C. P. and Visser, P. M. (eds.), *Harmful Cyanobacteria*, Springer, The Netherlands, pp. 143–176.

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

Ihle, T., Jahnichen, S. and Benndorf, J. (2005) Wax and wane of *Microcystis* (Cyanophyceae) and microcystins in lake sediments: a case study in Quitzdorf Reservoir (Germany). *J. Phycol.*, **41**, 479–488.

Jager, C. G. and Diehl, S. (2014) Resource competition across habitat boundaries: asymmetric interactions between benthic and pelagic producers. *Ecol Monogr*, **84**, 287–302.

Jennings, E., Jones, S. E., Arvola, L., Staehr, P. A., Gaiser, E., Jones, I. D., Weathers, K. C., Weyhenmeyer, G. A. *et al.* (2012) Effects of weather-related episodic events in lakes: an analysis based on high-frequency data. *Freshwater Biol*, **57**, 589–601.

Jia, Y., Yang, Z., Su, W., Johnson, D. and Kong, F. (2014) Controlling of cyanobacteria bloom during bottleneck stages of algal cycling in shallow Lake Taihu (China). *J. Freshwater Ecol.*, **29**, 129–140.

Jöhnk, K. D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P. M. and Stroom, J. M. (2008) Summer heatwaves promote blooms of harmful cyanobacteria. *Glob. Chang. Biol.*, **14**, 495–512.

Jungo, E., Visser, P. M., Stroom, J. and Mur, L. R. (2001) Artificial mixing to reduce growth of the blue-green alga *Microcysti*s in Lake Nieuwe Meer, Amsterdam: an evaluation of 7 years of experience. *Water Supply*, **1**, 17–23.

Kaplan-Levy, R. N., Hadas, O., Summers, M. L., Rucker, J. and Sukenik, A. (2010) Akinetes: dormant cells of cyanobacteria. In Lubzens, E., Cerda, J. and Clark, M. S. (eds.), *Dormancy and Resistance in Harsh Environments*, Springer, Heidelberg, pp. 5–27.

Karlson, A. M. L., Nascimento, F. J. A., Suikkanen, S. and Elmgren, R. (2012) Benthic fauna affects recruitment from sediments of the harmful cyanobacterium *Nodularia spumigena*. *Harmful Algae*, **20**, 126–131.

Karlsson-Elfgren, I. and Brunberg, A. K. (2004) The importance of shallow sediments in the recruitment of *Anabaena* and *Aphanizomenon* (Cyanophyceae). *J. Phycol.*, **40**, 831–836.

Karlsson-Elfgren, I., Hyenstrand, P. and Rydin, E. (2005) Pelagic growth and colony division of *Gloeotrichia echinulata* in Lake Erken. *J. Plankton Res.*, **27**, 145–151.

Karlsson-Elfgren, I., Rengefors, K. and Gustafsson, S. (2004) Factors regulating recruitment from the sediment to the water column in the bloom-forming cyanobacterium *Gloeotrichia echinulata*. *Freshwater Biol*, **49**, 265–273.

Karlsson-Elfgren, I., Rydin, E., Hyenstrand, P. and Pettersson, K. (2003) Recruitment and pelagic growth of *Gloeotrichia echinulata* (Cyanophyceae) in Lake Erken. *J. Phycol.*, **39**, 1050–1056.

Kinsman, R., Ibelings, B. W. and Walsby, A. E. (1991) Gas vesicle collapse by turgor pressure and its role in buoyancy regulation by *Anabaena flos-aquae*. *J. Gen. Microbiol.*, **137**, 1171–1178.

Klug, J. L., Richardson, D. C., Ewing, H. A., Hargreaves, B. R., Samal, N. R., Vachon, D., Pierson, D. C., Lindsey, A. M. *et al.* (2012) Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. *Environ. Sci. Technol.*, **46**, 11693–11701.

Kovacs, A. W., Toth, V. R. and Voros, L. (2012) Light-dependent germination and subsequent proliferation of N-2-fixing cyanobacteria in a large shallow lake. *Annales De Limnologie-International Journal of Limnology*, **48**, 177–185.

Kravchuk, E. S., Ivanova, E. A. and Gladyshev, M. I. (2006) Seasonal dynamics of akinetes of *Anabaena flos-aquae* in bottom sediments and water column of small Siberian reservoir. *Aquat Ecol*, **40**, 325–336.

Kruk, C., Huszar, V. L. M., Peeters, E., Bonilla, S., Costa, L., Lurling, M., Reynolds, C. S. and Scheffer, M. (2010) A morphological classification capturing functional variation in phytoplankton. *Freshwater Biol*, **55**, 614–627.

Lehman, J. T. (2002) Mixing patterns and plankton biomass of the St. Lawrence Great Lakes under climate change scenarios. *J. Great Lakes Res.*, **28**, 583–596.

Litchman, E. and Klausmeier, C. A. (2008) Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol. Syst.*, **39**, 615–639.

Livingstone, D. and Jaworski, G. H. M. (1980) The viability of akinetes of blue-green algae recovered from the sediments of Rostherne Mere. *British Phycological Journal*, **15**, 357–364.

Lofton, M. E., Mcclure, R. P., Chen, S., Little, J. C. and Carey, C. C. (2019) Wholeecosystem experiments reveal varying responses of phytoplankton functional groups to epilimnetic mixing in a eutrophic reservoir. *Watermark*, **11**, 222.

Lurling, M., Eshetu, F., Faassen, E. J., Kosten, S. and Huszar, V. L. M. (2013) Comparison of cyanobacterial and green algal growth rates at different temperatures. *Freshwater Biol*, **58**, 552–559.

Lynch, M. and Shapiro, J. (1981) Predation, enrichment, and phytoplankton community structure. *Limnol. Oceanogr.*, **26**, 86–102.

MacIntyre, S. and Melack, J. M. (1995) Vertical and horizontal transport in lakes: linking littoral, benthic, and pelagic habitats. *J N Am Benthol Soc*, **14**, 599–615.

MacKay, M. D., Neale, P. J., Arp, C. D., Domis, L. N. D., Fang, X., Gal, G., Johnk, K. D., Kirillin, G. *et al.* (2009) Modeling lakes and reservoirs in the climate system. *Limnol. Oceanogr.*, **54**, 2315–2329.

Misson, B. and Latour, D. (2012) Influence of light, sediment mixing, temperature and duration of the benthic life phase on the benthic recruitment of *Microcystis*. *J. Plankton Res.*, **34**, 113–119.

Misson, B., Sabart, M., Amblard, C. and Latour, D. (2011) Involvement of microcystins and colony size in the benthic recruitment of the cyanobacterium *Microcystis* (Cyanophyceae). *J. Phycol.*, **47**, 42–51.

Mowe, M. A. D., Mitrovic, S. M., Lim, R. P., Furey, A. and Yeo, D. C. J. (2015) Tropical cyanobacterial blooms: a review of prevalence, problem taxa, toxins and influencing environmental factors. *J Limnol*, **74**, 205–224.

Nichols, J. M. and Adams, D. G. (1982) Akinetes. In Carr, N. G. and Whitton, B. A. (eds.), *The Biology of Cyanobacteria*, University of California Press, Berkeley, CA, pp. 387–402.

O'Reilly, C. M., Alin, S. R., Plisnier, P. D., Cohen, A. S. and Mckee, B. A. (2003) Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature*, **424**, 766–768.

O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D. *et al.* (2015) Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.*, **42**, 2015GL066235.

Oliver, R. L. and Walsby, A. E. (1984) Direct evidence for the role of light-mediate gas vesicle collapse in the buoyancy regulation of *Anabaena flos-aquae* (cyanobacteria). *Limnol. Oceanogr.*, **29**, 879–886.

Padisak, J. (2003) Estimation of minimum sedimentary inoculum (akinete) pool of Cylindrospermopsis raciborskii: a morphology and life-cycle based method. *Hydrobiologia*, **502**, 389–394.

Paerl, H. W. (1988) Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol. Oceanogr.*, **33**, 823–847.

Paerl, H. W. and Huisman, J. (2008) Climate: blooms like it hot. *Science*, **320**, 57–58.

Park, C. H., Park, M. H., Kim, K. H., Park, J. H., Kwon, D. R., Kim, N. Y., Lim, B. J. and Hwang, S. J. (2018) Akinete germination chamber: an experimental device for cyanobacterial akinete germination and plankton emergence. *Harmful Algae*, **72**, 74–81.

Perakis, S. S., Welch, E. B. and Jacoby, J. M. (1996) Sediment-to-water blue-green algal recruitment in response to alum and environmental factors. *Hydrobiologia*, **318**, 165–177.

Poulickova, A., Hasler, P. and Kitner, M. (2004) Annual cycle of *Planktothrix agardhii* (Gom.) ANAGN. & KOM. Nature population. *Int Rev Hydrobiol*, **89**, 278–288.

Poulickova, A., Lysakova, M., Hasler, P. and Lelkova, E. (2008) Fishpond sediments - the source of palaeoecological information and algal "seed banks". *Nova Hedwigia*, **86**, 141–153.

Prein, A. F., Liu, C. H., Ikeda, K., Trier, S. B., Rasmussen, R. M., Holland, G. J. and Clark, M. P. (2017) Increased rainfall volume from future convective storms in the US. *Nature Climate Change*, **7**, 880–884.

Preston, T., Stewart, W. D. P. and Reynolds, C. S. (1980) Bloom-forming cyanobacterium *Microcystis aeruginosa* overwinters on sediment surface. *Nature*, **288**, 365–367.

Ramm, J., Rücker, J., Knie, M. and Nixdorf, B. (2017) Lost in the dark: estimation of the akinete pool for the recruitment of Nostocales populations (cyanobacteria) in a temperate deep lake. *J. Plankton Res.*, **39**, 392–403.

Rasanen, J., Kauppila, T. and Vuorio, K. (2006) Sediment and phytoplankton records of the cyanobacterial genus anabaena in boreal Lake Pyhajarvi. *Hydrobiologia*, **568**, 455–465.

Read, J. S., Shade, A., Wu, C. H., Gorzalski, A. and Mcmahon, K. D. (2011) "Gradual entrainment Lake inverter" (GELI): a novel device for experimental lake mixing. *Limnology and Oceanography: Methods*, **9**, 14–28.

Rengefors, K., Gustafsson, S. and Stahl-Delbanco, A. (2004) Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profundal sediments. *Aquat. Microb. Ecol.*, **36**, 213–226.

Reynolds, C. S. (1972) Growth, gas vacuolation and buoyancy in a natural population of a planktonic blue-green alga. *Freshwater Biol*, **2**, 87–106.

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

Reynolds, C. S., Jaworski, G. H. M., Cmiech, H. A. and Leedale, G. F. (1981) On the annual cycle of the blue-green alga *Microcystis aeruginosa* Kutz Emend Elenkin. *Philos T R Soc B*, **293**, 419–477.

Richardson, J., Feuchtmayr, H., Miller, C., Hunter, P. D., Maberly, S. C. and Carvalho, L. (2019) Response of cyanobacteria and phytoplankton abundance to warming, extreme rainfall events and nutrient enrichment. *Glob. Chang. Biol.*, **25**, 3365–3380.

Richardson, J., Miller, C., Maberly, S. C., Taylor, P., Globevnik, L., Hunter, P., Jeppesen, E., Mischke, U. *et al.* (2018) Effects of multiple stressors on cyanobacteria abundance vary with lake type. *Glob. Chang. Biol.*, **24**, 5044–5055.

Rigosi, A., Carey, C. C., Ibelings, B. W. and Brookes, J. D. (2014) The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. *Limnol. Oceanogr.*, **99**, 99–114.

Rother, J. A. and Fay, P. (1977) Sporulation and the development of planktonic blue-green algae in two Salopian meres. *Proc R Soc Lond B*, **196**, 317–332.

Rücker, J., Tingwey, E. I., Wiedner, C., Anu, C. M. and Nixdorf, B. (2009) Impact of the inoculum size on the population of Nostocales cyanobacteria in a temperate lake. *J. Plankton Res.*, **31**, 1151–1159.

Sabart, M., Misson, B., Jobard, M., Bronner, G., Donnadieu-Bernard, F., Duffaud, E., Salençon, M.-J., Amblard, C. *et al.* (2015) Genetic diversity along the life cycle of the cyanobacterium *Microcystis*: highlight on the complexity of benthic and planktonic interactions. *Environ. Microbiol.*, **17**, 901–911.

Sejnohova, L. and Marsalek, B. (2012) Microcystis. In Whitton, B. A. (ed.), *Ecology of Cyanobacteria II: Their Diversity in Space and Time*, Springer, New York, pp. 195–228.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B. W., Jeppesen, E., Lurling, M. *et al.* (2012) Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. *Annu. Rev. Ecol. Syst.*, **43**, 429–448.

Stahl-Delbanco, A. and Hansson, L. A. (2002) Effects of bioturbation on recruitment of algal cells from the "seed bank" of lake sediments. *Limnol. Oceanogr.*, **47**, 1836–1843.

Stahl-Delbanco, A., Hansson, L. A. and Gyllstrom, M. (2003) Recruitment of resting stages may induce blooms of *Microcysti*s at low N: P ratios. *J. Plankton Res.*, **25**, 1099–1106.

Steidinger, K. A. (2010) Research on the life cycles of harmful algae: a commentary. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **57**, 162–165.

Stockwell, J. D., Doubek, J. P., Adrian, R., Anneville, O., Carey, C. C., Carvalho, L., De Senerpont Domis, L. N., Dur, G. *et al.* (2020) Storm impacts on phytoplankton community dynamics in lakes. *Glob. Chang. Biol.*, **26**, 2756–2784.

Su, Y. P., You, X. J., Lin, H., Zhuang, H. R., Weng, Y. and Zhang, D. Y. (2016) Recruitment of cyanobacteria from the sediments in the eutrophic Shanzi Reservoir. *Environ. Technol.*, **37**, 641–651.

Suikkanen, S., Kaartokallio, H., Hallfors, S., Huttunen, M. and Laamanen, M. (2010) Life cycle strategies of bloom-forming, filamentous cyanobacteria in the Baltic Sea. *Deep Sea Research Part II-Topical Studies in Oceanography*, **57**, 199–209.

Tan, X. (2012) Physiological and ecological characteristics in the life cycle of bloom-forming cyanobacteria. *Journal of Food Agriculture & Environment*, **10**, 929–934.

Taranu, Z. E., Gregory-Eaves, I., Leavitt, P. R., Bunting, L., Buchaca, T., Catalan, J., Domaizon, I., Guilizzoni, P. *et al.* (2015) Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. *Ecol. Lett.*, **18**, 375–384.

Taranu, Z. E., Zurawell, R. W., Pick, F. and Gregory-Eaves, I. (2012) Predicting cyanobacterial dynamics in the face of global change: the importance of scale and environmental context. *Glob. Chang. Biol.*, **18**, 3477–3490.

Thomas, M. K., Fontana, S., Reyes, M. and Pomati, F. (2018) Quantifying cell densities and biovolumes of phytoplankton communities and functional groups using scanning flow cytometry, machine learning and unsupervised clustering. *PLoS One*, **13**, e0196225.

Thomas, R. H. and Walsby, A. E. (1986) The effect of temperature on recovery of buoyancy by *Microcystis*. *J. Gen. Microbiol.*, **132**, 1665–1672.

Torres, G. S. and Adámek, Z. (2013) Factors promoting the recruitment of benthic cyanobacteria resting stages: a review. *Croatian J Fisheries*, **71**, 182–186.

Trimbee, A. M. and Harris, G. P. (1984a) Phytoplankton population dynamics of a small reservoir: effect of intermittent mixing on phytoplankton succession and the growth of blue-green algae. *J. Plankton Res.*, **6**, 699–713.

Trimbee, A. M. and Harris, G. P. (1984b) Phytoplankton population dynamics of a small reservoir: use of sedimentation traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green algae. *J. Plankton Res.*, **6**, 897–918.

Tsujimura, S. (2004) Reduction of germination frequency in *Anabaena* akinetes by sediment drying: a possible method by which to inhibit bloom formation. *Water Res.*, **38**, 4361–4366.

Tsujimura, S., Tsukada, H., Nakahara, H., Nakajima, T. and Nishino, M. (2000) Seasonal variations of *Microcystis* populations in sediments of Lake Biwa. *Japan. Hydrobiologia*, **434**, 183–192.

Verspagen, J. M. H., Passarge, J., Johnk, K. D., Visser, P. M., Peperzak, L., Boers, P., Laanbroek, H. J. and Huisman, J. (2006) Water management strategies against toxic *Microcystis* blooms in the Dutch delta. *Ecol. Appl.*, **16**, 313–327.

Verspagen, J. M. H., Snelder, E. O. F. M., Visser, P. M., Huisman, J., Mur, L. R. and Ibelings, B. W. (2004) Recruitment of benthic *Microcystis* (Cyanophyceae) to the water column: internal buoyancy changes or resuspension? *J. Phycol.*, **40**, 260–270.

Verspagen, J. M. H., Snelder, E. O. F. M., Visser, P. M., Johnk, K. D., Ibelings, B. W., Mur, L. R. and Huisman, J. (2005) Benthic-pelagic coupling in the population dynamics of the harmful cyanobacterium *Microcystis*. *Freshwater Biol*, **50**, 854–867.

Villena, M. J. and Romo, S. (2007) Effects of nutrients, fish, charophytes and algal sediment recruitment on the phytoplankton ecology of a shallow lake. *Int Rev Hydrobiol*, **92**, 626–639.

Visser, P. M., Ibelings, B. W., Bormans, M. and Huisman, J. (2016) Artificial mixing to control cyanobacterial blooms: a review. *Aquat Ecol*, **50**, 423–441.

Visser, P. M., Ibelings, B. W., Vanderveer, B., Koedood, J. and Mur, L. R. (1996) Artificial mixing prevents nuisance blooms of the cyanobacterium Microcystis in Lake Nieuwe Meer, the Netherlands. *Freshwater Biol*, **36**, 435–450.

Wagner, C. and Adrian, R. (2009) Cyanobacteria dominance: quantifying the effects of climate change. *Limnol. Oceanogr.*, **54**, 2460–2468.

Wagner, C. and Adrian, R. (2011) Consequences of changes in thermal regime for plankton diversity and trait composition in a polymictic lake: a matter of temporal scale. *Freshwater Biol*, **56**, 1949–1961.

Walsby, A. E. (1994) Gas vesicles. *Microbiol. Rev.*, **58**, 94–144.

Wang, C. B., Feng, B., Tian, C. C., Tian, Y. Y., Chen, D., Wu, X. Q., Li, G. B. and Xiao, B. D. (2018) Quantitative study on the survivability of *Microcystis* colonies in lake sediments. *J. Appl. Phycol.*, **30**, 495–506.

Warner, R. R. and Chesson, P. L. (1985) Coexistence mediated by recruitment fluctuations - a field guide to the storage effect. *Am. Nat.*, **125**, 769–787.

Wilson, R. S., Hardisty, D. J., Epanchin-Niell, R. S., Runge, M. C., Cottingham, K. L., Urban, D. L., Maguire, L. A., Hastings, A. *et al.* (2016) A typology of time-scale mismatches and behavioral interventions to diagnose and solve conservation problems. *Conserv. Biol.*, **30**, 42–49.

Wood, S. A., Jentzsch, K., Rueckert, A., Hamilton, D. P. and Cary, S. C. (2009) Hindcasting cyanobacterial communities in Lake Okaro with germination experiments and genetic analyses. *FEMS Microbiol. Ecol.*, **67**, 252–260.

Woolway, R. I. and Merchant, C. J. (2019) Worldwide alteration of lake mixing regimes in response to climate change. *Nat. Geosci.*, **12**, 271–276.

Woolway, R. I., Merchant, C. J., Van Den Hoek, J., Azorin-Molina, C., Nõges, P., Laas, A., MacKay, E. B. and Jones, I. D. (2019) Northern hemisphere atmospheric stilling accelerates lake thermal responses to a warming world. *Geophys. Res. Lett.*, **46**, 11983–11992.

Woolway, R. I., Simpson, J. H., Spiby, D., Feuchtmayr, H., Powell, B. and Maberly, S. C. (2018) Physical and chemical impacts of a major storm on a temperate lake: a taste of things to come? *Clim. Change*, **151**, 333–347.

Wu, Y. H., Wang, F. W., Xiao, X., Liu, J. Z., Wu, C. X., Chen, H., Kerr, P. and Shurin, J. (2017) Seasonal changes in phosphorus competition and allelopathy of a benthic microbial assembly facilitate prevention of cyanobacterial blooms. *Environ. Microbiol.*, **19**, 2483–2494.

Xiao, M., Li, M. and Reynolds, C. S. (2018) Colony formation in the cyanobacterium *Microcystis*. *Biol. Rev.*, **93**, 1399–1420.

Yamamoto, Y. (2010) Contribution of bioturbation by the red swamp crayfish Procambarus clarkii to the recruitment of bloom-forming cyanobacteria from sediment. *J Limnol*, **69**, 102–111.

Yang, Y., Pettersson, K. and Padisák, J. (2016) Repetitive baselines of phytoplankton succession in an unstably stratified temperate lake (Lake Erken, Sweden): a long-term analysis. *Hydrobiologia*, **764**, 211–227.

Zhao, H., Zhu, W., Chen, H., Zhou, X., Wang, R. and Li, M. (2017) Numerical simulation of the vertical migration of *Microcystis* (cyanobacteria) colonies based on turbulence drag. *J Limnol*, **76**, 190–198.

Zhu, M. Y., Paerl, H. W., Zhu, G. W., Wu, T. F., Li, W., Shi, K., Zhao, L. L., Zhang, Y. L. *et al.* (2014) The role of tropical cyclones in stimulating cyanobacterial (*Microcystis* spp.) blooms in hypertrophic Lake Taihu, China. *Harmful Algae*, **39**, 310–321.