Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate

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ABSTRACT

Climate change scenarios predict that rivers, lakes, and reservoirs will experience increased temperatures, more intense and longer periods of thermal stratification, modified hydrology, and altered nutrient loading. These environmental drivers will have substantial effects on freshwater phytoplankton species composition and biomass, potentially favouring cyanobacteria over other phytoplankton. In this Review, we examine how several cyanobacterial eco-physiological traits, specifically, the ability to grow in warmer temperatures; buoyancy; high affinity for, and ability to store, phosphorus; nitrogen-fixation; akinete production; and efficient light harvesting, vary amongst cyanobacteria genera and may enable them to dominate in future climate scenarios. We predict that spatial variation in climate change will interact with physiological variation in cyanobacteria to create differences in the dominant cyanobacterial taxa among regions. Finally, we suggest that physiological traits specific to different cyanobacterial taxa may favour certain taxa over others in different regions, but overall, cyanobacteria as a group are likely to increase in most regions in the future.

1. Introduction

Cyanobacterial blooms present major challenges for the management of rivers, lakes and reservoirs. Blooms have adverse impacts on aquatic ecosystems and human health, with wide-ranging economic and ecological consequences (Hallegraeff, 1993; Mur et al., 1999). The increased frequency and intensity of blooms have been attributed to anthropogenic changes, principally nutrient over-enrichment and river regulation (Anderson et al., 2002). More recently, it has been predicted that a changing climate associated with rising levels of atmospheric CO_2 will increase the occurrence of blooms (Beardall et al., 2009; Paerl and Huisman, 2009; Paul, 2008), or at least favour cyanobacterial dominance of phytoplankton communities (Mooij et al., 2005). Decision support trees for bloom formation (e.g., Oliver and Ganf, 2000), as well as numerical model predictions that allow testing of multiple stressors (e.g., Trolle et al., 2011), suggest that there may be synergistic interactions amongst an array of environmental drivers to promote cyanobacterial blooms.

Why would cyanobacteria, and not other phytoplankton, be favoured under future climatic conditions? It is possible that cyanobacteria have several physiological characteristics that may be acting in concert to allow them to dominate in a changed climate. Alternatively, there may be physiological attributes of different cyanobacterial taxa that may leave them vulnerable under some conditions expected with climate change. An improved understanding of the interactions amongst both the environmental drivers that are predicted to change in different regions and cyanobacterial physiology is crucial for developing management strategies to mitigate or avoid the potential of more frequent blooms under future climate scenarios (Brookes and Carey, 2011; Paerl et al., 2011).

1.1. Bloom increases and effects

Cyanobacterial blooms are not a new phenomenon and have been occurring for centuries in both marine and freshwater systems (Codd et al., 1994; Fogg et al., 1973; Hayman, 1992; Paerl, 2008). Since the 1960s, however, there has been a dramatic global increase in the number of publications and reports of cyanobacterial blooms (Anderson et al., 2002; Carmichael, 2008; Hallegraeff, 1993; Hamilton et al., 2009; Paerl and Huisman, 2008; Van Dolah, 2000), primarily in freshwater and estuarine environments (Paerl, 1988). While increased reports may to some extent be due to increased monitoring efforts (Sellner et al., 2003), there is substantial evidence that blooms are increasing not only in frequency, but also in biomass, duration and distribution (Anderson et al., 2002; Glibert et al., 2005; Hallegraeff, 1993; Smayda, 1990). Furthermore, it has been hypothesised that cyanobacteria may continue to increase in response to global climate change (Mooij et al., 2005; Paerl et al., 2011; Paerl and Huisman, 2009).

The proliferation of cyanobacteria can have numerous consequences. In addition to risks to human and animal health (Chorus and Bartram, 1999; Ibelings and Chorus, 2007), there may also be substantial economic costs for water treatment and losses in tourism, property values, and business (Dodds et al., 2009; Steffensen, 2008). With a global distribution, escalating bloom occurrence and worldwide concern (Lundholm and Moestrup, 2006), it is important to review the evidence for the likelihood of cyanobacterial increases with climate change and how this may be related to cyanobacterial eco-physiology. Cyanobacteria have an extensive evolutionary history, and fossil evidence indicates that they were abundant over 2.5 billion years ago (Summons et al., 1999), and may have emerged as early as 3.5 billion years ago (Schopf, 2000). They are the earliest-known oxygen-producing organisms, and have key roles in global primary production and nitrogen-fixation (Chorus and Bartram, 1999). The lengthy history and variable environmental conditions under which cyanobacteria evolved have resulted in the adaptation of some cyanobacterial taxa to extreme environments, and collectively they are widely dispersed across the globe (Badger et al., 2006). They exist across a multitude of hot, cold, alkaline, acidic and terrestrial environments, and can proliferate to be the dominant primary producers in freshwater, estuarine, and marine ecosystems (Chorus and Bartram, 1999; Mur et al., 1999). Our focus in this Review is on freshwater and estuarine cyanobacteria.

2. Anticipated changes to temperatures, stratification, nutrient loading, and hydrology

Over the past century, global mean surface air temperatures have increased by $0.74 \pm 0.18\ ^{\circ}C$ (Trenberth et al., 2007). This warming trend is expected to continue, with higher latitudes warming more than lower latitudes (Solomon et al., 2007). Warming will be strongest in winter for northern areas in Europe and North America and most of Asia, and warming is predicted to be stronger in summer for the southern areas of Europe and North America. Seasonal differences in South America are not projected to substantially change (Solomon et al., 2007). Of particular relevance for cyanobacterial blooms is the prediction that heat waves will become more frequent, more intense, and will last longer (Meehl et al., 2007).

Climate warming is expected to have a profound effect on the onset (earlier), strength (stronger) and duration (longer) of stratification of lakes (De Stasio et al., 1996; Peeters et al., 2002), even to the extent that some polymictic lakes may become dimictic, dimictic lakes may become warm monomictic, and monomictic lakes may become oligomictic (Gerten and Adrian, 2002). Variation in temperature on a diel scale is anticipated to become smaller, since daily minimum temperatures will likely increase more strongly than daily maximum temperatures. Hence, climate warming increases the likelihood that microstratification occurring during the day will be maintained during the night (Hanson et al., 2008).

Both deep and shallow lakes are expected to exhibit increased stratification, which can have large effects on phytoplankton biomass and community structure (Pomati et al., in press). For example, the water column stability of the deep peri-alpine Lake Zurich, Switzerland has increased by more than 20% over the past three decades (Livingstone, 2003). In shallow lakes, microstratification can resist turbulent mixing to reduce the mixing depth to a shallow mixed layer near the water's surface (Denman and Gargett, 1983). Wilhelm and Adrian (2008) determined the mixing regime of shallow, polymictic Lake Müggelsee (Germany) over a period of four years, and found that heat waves in 2003 and 2006 resulted in extended stratified periods that lasted up to two months.

Under future scenarios of modified hydrology, it is expected that nutrient loading will be increasingly variable, with regional differences. Across almost all regions, precipitation variability will increase in the future, and when precipitation events do occur, their intensity will be increased (Parry et al., 2007; Solomon et al., 2007). Warmer climates are predicted to experience higher precipitation extremes, and droughts will increase at low latitudes and mid-latitude continental interiors due to both decreased precipitation and increased evapotranspiration (Jeppesen et al., 2007; Parry et al., 2007). By the end of the 21st century, the distribution of the global land surface in extreme drought is predicted to increase from 1 to 3 % at the present day to 30% (Burke et al., 2006). Similarly, the incidence of extreme droughts every 100 years and mean drought duration are expected to increase by factors of two and six, respectively, by the 2090s (Burke et al., 2006).

Opposite to low-latitude regions, temperate and high-latitude regions are predicted to experience increased mean precipitation and the highest increase in precipitation

intensity, primarily in the winters (Meehl et al., 2005; Parry et al., 2007). Runoff in the high latitudes of North America and Eurasia is expected to increase by 10–40 % by 2050, whereas runoff will decrease in the Mediterranean, southern Africa, western USA, and northern Mexico by 10–30 %. Cumulatively, however, the areas with decreased runoff will expand between the late 20th century and 2050 (Milly et al., 2002). Taken altogether, these changes are likely to have large effects on nutrient delivery to lakes, reservoirs and rivers as rainfall distribution and runoff characteristics change.

In response to these climatic changes, many lake physical and chemical characteristics will change, potentially synergistically, which will subsequently affect phytoplankton communities (e.g., Pomati et al., in press). While there are large regional differences in the expected climatic changes, we expect that in most scenarios different cyanobacterial taxa will likely be able to dominate under increasingly variable conditions.

3. Cyanobacterial evolution and adaptations

Cyanobacteria possess a range of unique and highly-adaptable eco-physiological traits (Litchman et al., 2010). These traits, which can be specific at the genus level, include: 1) the ability to grow in warmer temperatures; 2) buoyancy, due to gas vesicle production; 3) high affinity for, and ability to store, phosphorus; 4) nitrogen-fixation; 5) akinete production and associated life history characteristics; and 6) light capture at low intensities and a range of wavelengths. Cyanobacteria possess many other unique eco-physiological traits (e.g., toxin production), however, we chose to focus on the traits listed above because we predict that these cyanobacterial characteristics may allow adaptation specific to the climate changes that we expect in future conditions (and that we are already experiencing). These climate changes include higher temperatures (Parry et al., 2007), stronger and longer periods of stratification (Jeppesen et al., 2007), and modified hydrology (i.e., changed flows, more intense storms but reduced frequency, which will create sporadic nutrient delivery; Jeppesen et al., 2007, 2011).

Below, we evaluate how different traits may interact with a changing climate to allow cyanobacteria to dominate aquatic systems. Cyanobacteria are a diverse group, ranging in size from unicellular picoplankton to multicellular macroscopic colonies. Consequently, no cyanobacterium possesses all of the traits listed above, so the response of cyanobacteria to changes in the environment will likely vary greatly among genera, which makes it harder to generalise the expected outcome of different climate change scenarios. Similarly, different geographical regions are predicted to experience varying climatic changes, which will affect the environmental drivers that interact with cyanobacterial physiological traits. Finally, there are several other factors that contribute to the success of cyanobacteria in freshwater systems, such as grazing resistance, that may be affected by climate change. Cyanobacterial taxa are considered to be poor quality food for zooplankton grazers (e.g., Daphnia sp.) because of the morphology of their filaments and colonies, which clog filtering appendages (Arnold, 1971; Lampert, 1982, 1987), their toxins (Fulton and Paerl, 1987; Lampert, 1981, 1982), and

because they lack certain required fatty acids, sterols, and nutrients (Ahlgren et al., 1990; Brett et al., 2006; Gulati and Demott, 1997; Holm and Shapiro, 1984). The effect of climate change on grazing resistance falls outside the scope of this paper, but we refer interested readers to reviews by Visser et al. (2005) or Ibelings and Havens (2008).

3.1. Direct and indirect effects of increasing temperatures

Temperature is an all-pervasive environmental parameter that affects the metabolism, growth, reproduction, and survival of living organisms, as well as the interactions among species (Ibelings et al., 2011; Kingsolver, 2009). Warmer temperatures will also result in a number of indirect effects (Dale et al., 2006), including increasing stratification and enhanced internal nutrient loading, that are likely to favour at least some cyanobacterial taxa (Boyd and Doney, 2002; De Stasio et al., 1996).

With an increase in water temperatures to values approaching physiological optima for a wide range of phytoplankton species, more phytoplankton will grow and replicate faster, at least until warming raises the water temperature beyond the optimal temperature for growth. Optimal temperatures and the degree to which growth rate increases with temperature, as determined by the rate of change in the rate-limiting anabolic process, differ greatly between phytoplankton species. As a consequence, climate warming will result in shifts in phytoplankton community composition (e.g., Winder et al., 2008), including shifts between cyanobacteria. Reynolds (1989, 2006) compiled literature data on the effect of temperature on phytoplankton growth under controlled conditions. The temperature at which maximum replication rates occurred for cyanobacteria varied from just over 20 °C for *Aphanizomenon flos-aquae* and *Planktothrix agardhii*, to 28 °C for *Microcystis aeruginosa*, and even 41 °C for *Synechococcus* sp. (Reynolds, 1989, 2006). The rate of acceleration, commonly measured as Q_{10} (acceleration over a 10 °C step, generally 10–20 °C) for *Synechococcus* sp. was ~2.6, whereas for *M. aeruginosa* it was ~9.6, the highest value recorded for all of the cyanobacterial or eukaryotic phytoplankton species in the assembled data. Based upon these data, *M. aeruginosa* will have a clear physiological advantage over other phytoplankton when water temperatures increase above 20 °C. For larger phytoplankton with a low surface area to volume ratio, which includes many bloom-forming, colonial cyanobacterial genera (e.g., *Anabaena*, *Aphanizomenon*), temperature dependence of growth tends to be controlled more by nutrient uptake and rates of intracellular assimilation than by photosynthetic rates (Foy et al., 1976; Konopka and Brock, 1978; Reynolds, 2006).

In contrast to the data presented above from Reynolds (2006), Lürling et al. (in press) tested – but rejected – the hypothesis that cyanobacteria have higher optimum growth temperatures and higher growth rates at their optimum temperature when compared to chlorophytes (green algae). Lürling et al. (in press) ran a controlled experiment with eight cyanobacteria (including *M. aeruginosa*, *Cylindrospermopsis raciborskii*, and *P. agardhii*) and eight green algae at six different temperatures (20 °C–35 °C), and found no significant difference in optimum temperatures for growth between the two taxonomic groups

(optimum temperatures for both were ~29 °C). However, while the green algae grew faster at the lowest experimental temperature (20 °C), the mean growth rates at the optimal temperature (29 °C) were not significantly different, indicating that the cyanobacteria benefited more than the chlorophytes from an increase in temperature. Nevertheless, the data also suggest that increasing temperatures, at least in regards to their effect on replication rates, do not offer cyanobacteria a clear advantage over their competitors, even at their optimal growth temperature. Data from Lürling et al. (in press) also provide a warning against simplification, as there were considerable differences in response to temperature increases among different cyanobacterial species and even among strains. For example, Lürling et al. (in press) found that the Q_{10} for *M. aeruginosa* CYA140 was ~4.3, while the Q_{10} of *M. aeruginosa* PCC7941 was only ~2.1 (calculations by the authors based upon data in Lürling et al., in press). The former value was the highest Q_{10} of all phytoplankton tested, lending support to Reynolds (2006)' view that *M. aeruginosa* exhibits an exceptionally high Q_{10}. The latter value, however, is well within the range for most cyanobacteria (1.8—4.3), and even chlorophytes (1.1—3.7) (Lürling et al., in press). Finally, it is important to realise that both datasets (Reynolds, 2006; Lürling et al., in press) were obtained under laboratory conditions where nutrients and light were saturating for growth. Light-limited growth rates of *P. agardhii*, for example, have been shown to be independent of temperature (Post et al., 1985; Robarts and Zohary, 1987).

In natural systems, it has been shown that warmer water temperatures do favour cyanobacterial dominance in phytoplankton communities (Kosten et al., 2012). Similarly, it has been proposed that warmer temperatures will mean earlier and longer potential bloom periods, as well as lead to possible range expansions (Dale et al., 2006; Moore et al., 2008; Wiedner et al., 2007). If the direct effects of warming on cyanobacteria are limited, as suggested in the above paragraph (i.e., in regards to replication rates and Q_{10} values), consequently, indirect effects must underlie the observations on increased occurrence of cyanobacterial blooms with ongoing climate warming (Paerl and Huisman, 2008).

In the literature there appear to be conflicting opinions about the relative importance of the direct versus indirect effects of lake warming on cyanobacteria (direct effects examine differences in Q_{10} and replication rates, while indirect effects focus on how temperatures modify the environment in ways that indirectly affect cyanobacteria; e.g., via stratification). Jöhnk et al. (2008) presented model output showing that increased water temperatures favour cyanobacteria directly through increased growth rates. Paerl and Huisman (2008) reached a similar conclusion on the basis of temperature-dependent growth rates from the literature: while the growth rates of most eukaryotic taxa decline at temperatures exceeding 20 °C, cyanobacterial growth rates for many taxa, including *M. aeruginosa* and *P. agardhii*, continue to increase. Others posit that cyanobacteria may only benefit indirectly from temperature increases, especially from enhanced water column stability, and not the direct effects of climate warming (Wagner and Adrian, 2009). Contrary to their expectations, Moss et al. (2003) found that an increase in temperatures of 3 °C above ambient conditions did not result in an increase in cyanobacteria in mesocosm experiments, perhaps because the

mesocosms allowed only for the direct, and not indirect, effects of lake warming on cyanobacterial dominance. More work is clearly needed to determine the relative importance of the indirect versus direct effects of increased temperatures on cyanobacteria in freshwater systems.

3.2. Buoyancy

Many species of planktonic cyanobacteria produce gas vesicles, which provide buoyancy and allow access to well-lit surface waters (Walsby, 1994). This buoyancy can be offset with ballast arising from photosynthetic carbohydrate production and other cell constituents (Utkilen et al., 1985). The regulation of buoyancy, which allows migration in stratified lakes between illuminated surface waters and nutrient-rich bottom waters (Ganf and Oliver, 1982), occurs as cells accumulate carbohydrates when exposed to light and respire these products of photosynthesis in the dark (Kromkamp and Walsby, 1990). Under prolonged irradiance, gas vesicles may collapse under turgor pressure (Kinsman et al., 1991).

As described above, changes in climate, such as increased temperatures, prolonged droughts and longer water residence times (De Stasio et al., 1996), are predicted to promote cyanobacterial bloom establishment by increasing the strength and duration of stratification (Boyd and Doney, 2002; Paerl and Huisman, 2008). Furthermore, increased nutrient loading from storm events can synergistically interact with climate-driven effects to increase stratification, further strengthening the competitive advantage of buoyancy-regulating cyanobacteria (Jones et al., 2005). Rinke et al. (2010) demonstrated that the increased phytoplankton biomass resulting from eutrophic conditions increased light attenuation and surface temperatures relative to oligotrophic conditions, thereby strengthening stratification. Thus, buoyant cyanobacteria can themselves modify their environment to promote further blooms by increasing water temperatures and stratification (Kumagai et al., 2000; Rinke et al., 2010).

The buoyancy strategies of cyanobacteria, which are a function of gas vesicle volume, the rate of change in dense cellular constituents, and colony size, play a significant role in their ability to dominate their habitats. *Microcystis* sp. can form large colonies that float rapidly to the surface, but as with *Anabaena* sp., these colonies can be mixed through the surface mixed layer with wind (Bormans et al., 1999; Brookes et al., 1999, 2002; Ibelings et al., 1991). Hence, these two cyanobacterial genera may be well adapted to a regime with stronger stratification and a reduced mixing depth. *Microcystis* sp. and *Anabaena* sp.'s fast flotation velocity (Walsby et al., 1991) allows them to efficiently track the near-surface mixed layer (Humphries and Lyne, 1988), as demonstrated by Ibelings et al. (1991) in the Dutch lake Vinkeveen. If there is increased stratification and reduced turbulence, then *Microcystis* sp. colonies will be larger and their buoyancy will be enhanced during vertical migration cycles (O'Brien et al., 2004). Another cyanobacterium, *Planktothrix rubescens*, maintains its vertical position in part because its small filaments have a low sinking or floating velocity (Walsby, 2005), and also because the tight coupling between carbohydrate accumulation and gas vesicle-mediated buoyancy maintains filaments close to the depth supporting neutral buoyancy (Walsby et al., 2004). Jacquet et al. (2005) suggested that the

recent increase of *P. rubescens* in pre-alpine lakes undergoing re-oligotrophication (Ernst et al., 2009) may be because the cyanobacterium can take advantage of the earlier onset of stratification caused by increased temperatures.

Motile or buoyant species may also be able to combine light harvesting near the surface with uptake of nutrients in the hypolimnion. According to Bormans et al. (1999), there is little evidence that buoyant cyanobacteria are capable of exploiting these spatially separated resources. However, Wagner and Adrian (2009) argue that in relatively shallow lakes, such as Lake Müggelsee (maximum depth = 8 m), cyanobacterial migration is sufficient to allow access to the hypolimnion where nutrient concentrations are elevated. Ganf and Oliver (1982) also found that *M. aeruginosa* and *Anabaena spiroides* were able to migrate 12 m to access light and nutrients, despite substantial density barriers. Hence, fast-migrating genera (e.g., *Microcystis*, *Anabaena*) may benefit from the climate-induced strengthening of stratification by gaining a competitive advantage over other non-migrating or slow-migrating phytoplankton. While increased stratification is predicted to favour buoyancy-regulating cyanobacteria in comparison to non-buoyant algae in most environmental conditions (Huisman et al., 2004), Wagner and Adrian (2009) found that certain thresholds needed to be exceeded for bloom-forming cyanobacteria (especially *Aphanizomenon*, *Anabaena*, and *Microcystis* sp.) to dominate: stratification periods in Lake Müggelsee needed to be longer than 3 weeks and exhibit a Schmidt stability index exceeding 44 g cm^{-2} within a critical total phosphorus (TP) range of 70—215 μg L^{-1} (Wagner and Adrian, 2009).

The short-term buoyancy response to light, where carbohydrate is accumulated and respired, is nested within a longer-term response that is a function of both the cyanobacterium's previous nutrient and light history (Brookes and Ganf, 2001) and these resources' effects on gas vesicle production and cell metabolism. The rate of gas vesicle production relative to growth, which dilutes the gas vesicle pool per cell, can decrease as nitrogen becomes limiting (Brookes and Ganf, 2001; Klemer, 1978; Klemer et al., 1982). Konopka et al. (1987) showed that gas vesicle volume increased in phosphate-limited *Aphanizomenon flos-aquae* but that the filaments remained non-buoyant while P-limitation persisted. Similarly, Brookes et al. (2000) observed considerably fewer gas vesicles in P-limited *M. aeruginosa* cells relative to P-replete cells.

In contrast to the reduction in buoyancy that accompanies gas vesicle dilution in nitrogen-limited cultures, nitrogen-replete *M. aeruginosa* colonies can show persistent buoyancy (Brookes and Ganf, 2001). There are several examples in which a proportion of cyanobacterial cells maintained at high light failed to lose buoyancy (Walsby et al., 1989), for which excess nutrients was invoked as the mechanism maintaining persistent buoyancy (Brookes et al., 1999). Eutrophic conditions in freshwater ecosystems, which are expected to occur more frequently in regions that will experience increased nutrient loading and changed hydrology, could lead to 'over-buoyancy' and surface accumulations of cyanobacteria.

Gas vesicle strength is related to the depth of the water body in which the cyanobacteria are found. For example, *P. rubescens* from Lake Zurich (maximum depth = 143 m) has narrower and stronger gas vesicles than found in any other freshwater cyanobacteria (Bright and Walsby, 1999), which may have evolved to withstand the high hydrostatic pressures experienced during deep winter mixing. Thus, deep mixing may select for species with strong gas vesicles able to withstand deep mixing without collapsing. Modifications to the mixing regime that may occur if winters become milder and turnover less frequent (Gerten and Adrian, 2002) could potentially open up new habitat for species with weaker gas vesicles that were previously outcompeted. Similarly, if lakes experience dramatic decreases in water levels under future scenarios of modified hydrology and drought, cyanobacteria with weaker gas vesicles may proliferate.

Decreasing water temperatures in the autumn is a central factor in the loss of buoyancy and resultant sinking of many cyanobacteria to the sediments (Visser et al., 2005). The temperature at which *Microcystis* sp. colonies have been observed to lose buoyancy has been shown to range from 12 to 18 °C (Visser et al., 1995 and references therein). The loss of buoyancy as water temperatures decrease is not due to the weakening and collapse of gas vesicles, but rather to the accumulation of carbohydrate ballast, caused by a difference in temperature sensitivity between respiration and photosynthesis (Thomas and Walsby, 1986). Warmer waters in autumn may delay the sinking of cyanobacteria that have formed blooms, but it is likely to be a strongly strain-dependent effect, as demonstrated by the wide range of temperatures that triggered *Microcystis* sp. sinking (Visser et al., 1995). Experiments with *M. aeruginosa* in water that was warmed from 15 °C to 20 and 28 °C demonstrated that buoyancy became constitutive at higher temperatures, with cells remaining buoyant throughout the light period (Kromkamp et al., 1988). Hence, lake warming may result in additional buoyancy that sustains prolonged blooms.

The high degree of variability in catchment hydrology, nutrient loading and hydrodynamics that lakes will experience makes it difficult to predict how the buoyancy of different cyanobacterial groups will be impacted by climate change. However, general conclusions can be made. Increased stratification will favour the fast-migrating buoyant cyanobacteria. As nutrient loading and stratification increase, there will tend to be a shift towards buoyant species that can access both the well-lit surface waters and hypolimnetic nutrient pool. High nocturnal temperatures will act to maintain a shallower surface mixed layer, causing cells to not mix as deeply during night, which will enable them greater access to light during day. These changes may shift the balance between competing cyanobacteria. For example, in Lake Ijsselmeer, The Netherlands, *Microcystis* is commonly the dominant cyanobacterial genus unless summers are exceptionally warm and stable, at which point *P. agardhii* dominates because of shallow mixing over extended periods (Ibelings, 1992). Higher water temperatures persisting into autumn may mean that the loss of buoyancy and mass-sedimentation of cyanobacterial populations that normally occurs will be delayed.

3.3. Luxury phosphorus uptake and storage

In many freshwater systems, phosphorus (P) is a limiting nutrient (Schindler, 1974, 1977; Schindler et al., 2008). Cyanobacteria, however, have been shown to overcome this

limitation by at least two mechanisms: they produce phosphatases, enzymes that hydrolyse phosphate from organic solutes that then can be taken up (Coleman, 1992) and they have the ability to sequester luxury P intracellularly (reviewed in Healey, 1982). Luxury P uptake into storage can increase the P cell quota from 0.2 to 0.4% of ash-free dry mass to $\geq$3% of ash-free dry mass, almost 8—16 times the minimum quota (Reynolds, 2006). As a result, cyanobacteria can theoretically double three to four times without having to uptake any additional P (Reynolds, 2006), which provides a large competitive advantage in P-limiting environments.

Different cyanobacterial genera vary in their ability to access organic P with phosphatases and to store luxury P. Whitton et al. (1991) found significant differences among 50 cyanobacterial strains (10 genera) in their ability to access P from various organic molecules. For example, the Rivulariaceae tested (*Calothrix, Dichothrix*, and *Gloeotrichia*) produced significantly higher P yields than filamentous non-Rivulariaceae (*Anabaena, Fischerella, Lyngbya,* and *Tolypothrix*) from most organic molecules. *Gloeotrichia*, in particular, exhibited significantly higher extracellular phosphomonoesterase (PMEase) activity than any other genus tested (Whitton et al., 1991). Similar differences in luxury P storage ability may exist among cyanobacteria, which could favour certain taxa over others during periods of P deficiency. For example, *Anacystis* may be less able to take up luxury P than *Anabaena*, *Plectonema*, or *Synechococcus* (Healey, 1982).

Paradoxically, cyanobacteria are able to dominate in both low and high P conditions. In low nutrient conditions, cyanobacteria's high affinity for P allows them to outcompete other phytoplankton (e.g., Posselt et al., 2009). Increased P results in higher concentrations of phytoplankton biomass, which is the best predictor for cyanobacterial dominance in lakes (Downing et al., 2001). Cyanobacteria benefit indirectly from high phytoplankton conditions, potentially because of the low light and CO_2 concentrations that result from high levels of production (reviewed in Hyenstrand et al., 1998). Cyanobacteria are superior competitors for light (but with noted differences among taxa, see Section 3.6), and can create higher turbidity per unit P than any other phytoplankton group, thereby excluding their competitors (Scheffer et al., 1997). At low CO_2 levels, cyanobacteria can become dominant because they generally have better CO_2 uptake kinetics than other phytoplankton (Shapiro, 1997). As a result, cyanobacteria can reduce CO_2 concentrations to levels that allow them to persist but exclude other phytoplankton (Shapiro, 1997). Finally, when phytoplankton are high, buoyant cyanobacteria can shade out competitors by forming surface scums (see Sections 3.2 and 3.6 on buoyancy and photoacclimation, respectively), further strengthening their dominance at high P conditions.

As described above, the hydrology of low-latitude and continental mid-latitude regions will be characterised by oscillating periods of drought and flooding by the end of the 21st century. When the associated effects of warmer temperatures are also taken into account, we expect that low-latitude and continental mid-latitude inland waters will experience greater thermal stratification, lower water levels during drought periods, less ice cover, and pulsed nutrient loads (Jeppesen et al., 2007; Parry et al., 2007). During long periods of stratification, P limitation in the epilimnion will

increase while the hypolimnion may experience anoxia and consequently increased P concentrations due to internal recycling from the sediments (Nürnberg, 1984, 1988; Nürnberg et al., 1986). Cyanobacteria may be able to overcome the epilimnetic P limitation during stratification due to their internal nutrient storage (Istvánovics et al., 1993; Pettersson et al., 1993), while phytoplankton without luxury P uptake may not be able to persist during low nutrient periods. For example, *Gloeotrichia echinulata* is able to outcompete other phytoplankton in nutrient-limited conditions because it absorbs additional P in the sediments so as to not require any additional P uptake for its own metabolism or reproduction after it recruits into the water column (Istvánovics et al., 1993). *G. echinulata*'s P uptake and storage may explain why the cyanobacterium is able to dominate nutrient-limited lakes across the northeastern U.S. (Carey et al., 2008). Despite lower precipitation overall in low to mid-latitudes, high-intensity episodic storm events are predicted to increase in these regions (Parry et al., 2007). Because of their anticipated increased severity (Parry et al., 2007), these storms may be more effective at triggering mixing, which could result in the release of large concentrations of hypolimnetic P to the epilimnion (Søndergaard et al., 2003). The release of hypolimnetic P during mixing events caused by storms may also be coupled with large external loads of P entering lakes through surface runoff (Jeppesen et al., 2007). During these periods of increased nutrient loading due to storms, we expect that the high levels of P will lead to higher primary production and may favour cyanobacteria, as seen with anthropogenic eutrophication. We predict that small cyanobacteria with large surface area to volume ratios and high nutrient uptake rates may especially benefit (Finkel et al., 2009). Finally, lower water levels during drought periods and less ice cover may also promote cyanobacteria because lower lake levels may concentrate and increase nutrient concentrations, and longer ice-free periods extend the cyanobacterial growing season (Peeters et al., 2007).

In temperate and high-latitude regions, which are predicted to experience increased mean precipitation and the greatest increase in precipitation intensity, cyanobacteria may also dominate. Jeppesen et al. (2007) found that in Danish lakes, the higher external P loads caused by runoff would be greater than the predicted water volume increase, resulting in net higher nutrient concentrations in aquatic ecosystems. The increased precipitation intensity in winter will increase flows, erosion, and nutrient delivery in the spring while lower flows in the summer will compound the stratification and drought conditions described above (Jeppesen et al., 2007). These three drivers- increased nutrient concentrations, greater erosion and discharge due to high precipitation intensity, and summer drought- are all predicted to favour cyanobacteria with rapid nutrient uptake and P luxury storage.

3.4. Nitrogen-fixation

Nitrogen-fixation (N-fixation) is a physiological adaptation of some species of cyanobacteria that can provide them with a competitive advantage when available sources of N in the water column are strongly depleted (Oliver and Ganf, 2000; Wood et al., 2010). Dissolved inorganic forms of N, primarily

nitrate and ammonium, are preferentially assimilated by phytoplankton, although dissolved organic N has occasionally been shown to constitute an additional component of N nutrition for some cyanobacteria (Berman, 1997). Utilisation of gaseous N_2 via N-fixation is energetically expensive because of its requirement to both break the triple bond linking N_2 molecules during the formation of ammonium and to maintain the nitrogenase enzyme essential to catalyse the reaction. However, energetic investments in N-fixation and maintenance of heterocysts in freshwater N-fixing cyanobacteria may be offset by the competitive advantage provided to them in severely N-deficient environments (Oliver and Ganf, 2000). In freshwater environments, N-fixation is generally accomplished by heterocysts, specialised cells that prevent the incursion of oxygen from surrounding water and neighbouring vegetative cells, which would otherwise inactivate the activity of nitrogenase. Heterocystous cyanobacteria occur in pelagic freshwater and brackish environments but rarely in the ocean (Paerl, 1996).

Non-heterocystous strategies of N-fixation are best known in the marine cyanobacteria Trichodesmium sp. (Berman-Frank et al., 2003) but can also occur in freshwater and brackish cyanobacteria by temporal separation of N-fixation. For example, nitrogenase activity at night in some species of Lyngbya can be separated from the oxygen-producing photosynthetic activity that would otherwise inactivate nitrogenase during the day (Stal et al., 2010). Species of Lyngbya are known to form toxic blooms in marine or brackish-water environments and some species (e.g., Lyngbya wollei) also form large benthic mats that can be dislodged and form surface blooms in lake environments, often in association with storm-driven mixing (Bridgeman and Penamon, 2010).

Like many other physiological processes specific to cyanobacteria, there are several hypotheses about how increases in water temperature will affect rates of N-fixation in vivo (e.g., Miyamato et al., 1979). In a warmer climate, enzymatically-controlled processes such as N-fixation might be expected to increase at a rate approximating cyanobacterial growth rate responses to temperature (i.e., a Q_{10} of ≥ 1.8; Reynolds, 2006). Staal et al. (2003) showed that Q_{10} values for N-fixation of heterocystous strains of Nodularia spumigena and Anabaena sp., inferred from nitrogenase activity rates, were indeed >1.8 and commonly close to 2.0 in the light. They found for 21 different heterocystous species that rates of N-fixation in the light were 2.5–4 times higher in the light than in the dark, and that there was substantially greater temperature dependence of N-fixation in the light (Staal et al., 2003). Further work is required to understand if, and the extent to which, temperature dependence of N-fixation may enhance the competitiveness of this group of cyanobacteria in a warmer climate. There are also a number of indirect effects of temperature on N-fixation. For example, an increase in water temperature will reduce the solubility of oxygen and nitrogen in water, and may result in adaptation of the heterocyst by decreasing cell wall thickness and permeability (Staal et al., 2003). This response has been hypothesised to reduce the competitiveness of heterocystous over non-heterocystous cyanobacteria, but is probably unlikely to supplant the dominance of heterocystous N-fixing cyanobacteria in freshwater and brackish environments.

The availability of dissolved inorganic N is critical to the occurrence of N-fixation, both for heterocystous (e.g.,

Anabaena, Aphanizomenon, and Planktothrix) and non-heterocystous genera (e.g., Lyngbya). Heterocysts have been shown to differentiate rapidly in vivo as nitrate concentrations decrease below ~30 μg L^{-1} (Agawin et al., 2007) and their proliferation has also been shown to precede the rapid increase in vegetative cells associated with blooms, when the relative abundance of heterocysts can decrease rapidly (Wood et al., 2010). Changes in N loading therefore need to be considered when assessing changes in N-fixation under a future climate. Nitrogen loading from lake catchments may potentially either increase or decrease with climate change, driven primarily by geographic heterogeneity of rainfall and temperature-induced changes in soil and vegetation dynamics (Jeppesen et al., 2007), but it will also be strongly influenced by human activities relating to changes in land use and intensification in cultivated catchments (Jeppesen et al., 2011). In this context it is relevant to consider that human activities have already profoundly altered the global N cycle through massive escalation of N-fixation and application of synthetic N fertilisers for both crop production for human food and pasture production to support greater numbers of domesticated animals (Vitousek et al., 1997). Increases in N loading are not only specific to cultivated catchments, however, because with more than twice the amount of reactive N circulating in the biosphere due to human activities, atmospheric N deposition has alleviated N-limitation of phytoplankton in lakes that would otherwise be largely unaffected by human activities (Elser et al., 2010). Greater availability of inorganic N species arising from increases in atmospheric and terrestrial inputs and storm-driven N loading to freshwater systems could reduce the occurrence of N-fixation.

Despite the increase in N loading from cultivation and atmospheric deposition in many catchments, there is not yet, to the best of our knowledge, any evidence that a link exists between N loading and changes in occurrence of N-fixing cyanobacteria. Several factors may offset the expected net alleviation of N-limitation by increased anthropogenic N loading. For example, within lakes there can be changes in the way that N is transformed and utilised, including observed increases in N losses due to denitrification as N loads increase in association with greater percentages of the catchment in pasture (Bruesewitz et al., 2011). Climate change is likely to increase the duration of water column stratification, which may favour N-fixing, buoyancy-regulating cyanobacteria as inorganic N-species are depleted from surface waters over extended growing seasons (Jeppesen et al., 2011). Both of these examples would promote cyanobacteria capable of N-fixation, even if nutrient loading increases with greater storm intensity. Thus, the interplay of nutrient availability and increases in water temperature will be critical to the future occurrence and proliferation of N-fixing cyanobacteria.

Considerations of how N-fixation may be altered by climate change could be assisted with models of N-fixation that explicitly include water temperature. The models that currently exist (e.g., Hense and Beckmann, 2006; Howarth et al., 1999; Levine and Lewis, 1987; Stal and Walsby, 1998) tend to be more specifically targeted to a species level and are based primarily on substrate limitation (e.g., by light and nitrogen). These models offer limited insight into the complexity of N-fixation in natural ecosystems. Most other models of

cyanobacteria populations have been directed either at non N-fixing cyanobacteria (Robson and Hamilton, 2004) or have not explicitly included N-fixation (e.g., Howard et al., 1996). The complexity involved in modelling N-fixation, even at the scale of chemostats (Agawin et al., 2007), indicates that challenges remain to incorporating the major processes relevant to N-fixation in models that operate at the lake ecosystem scale, including a need for fundamental process information on N-fixation in different species of cyanobacteria at different temperatures and N concentrations.

3.5. Akinete production and life cycle attributes

Some taxa within the Nostocaceae, Rivulariaceae and Stigonemataceae families of cyanobacteria (which include, but are not limited to, the genera of *Anabaena*, *Cylindrospermopsis*, *Gloeotrichia*, and *Nodularia*) can produce akinetes, or thick-walled resting cells (Nichols and Adams, 1982). Akinete differentiation typically occurs during unfavourable growth conditions and is triggered by changes in light, nutrients, temperature and potentially desiccation (reviewed in Kaplan-Levy et al., 2010). Akinete metabolism is very low or undetectable, allowing the cells to survive in bottom sediments for extended periods of time until germination occurs under favourable growth conditions (Adams and Duggan, 1999). Akinete development may ensure the long-term survival of cyanobacterial populations (Whitton, 1987), as akinetes can survive temperatures up to 55 °C (Yamamoto, 1976), and are viable up to 64 and potentially >100 years after deposition (Livingstone and Jaworski, 1980; Wood et al., 2009) and after desiccation on land for six winter months (Forsell, 1998). Akinete germination can be activated by increasing light, temperatures, nutrients, or dissolved oxygen (or a combination of these factors; Kaplan-Levy et al., 2010).

Under future climate scenarios, cyanobacteria that produce akinetes may have an advantage in withstanding increasingly variable conditions. For example, cyanobacterial populations that form akinetes could be better adapted to intermittent nutrient availability that may be caused by altered precipitation regimes and changes in light intensity and quality due to increased turbidity from storm-induced erosion. In regions that will experience increased drought conditions, akinete-forming cyanobacteria can potentially persist even if water bodies dry up seasonally (Paerl et al., 2011). In general, cyanobacteria exhibit high tolerance to desiccation by producing polyhydroxy saccharides that protect cellular macromolecules from denaturation (Potts, 1994), allowing them to survive alternating drought and wet conditions.

Microcystis sp. do not form akinetes; rather, they overwinter in a vegetative state (Verspagen et al., 2005). Successful overwintering is crucial for *Microcystis* sp. because the sediment provides an inoculum for population growth in the following spring. Model simulations indicate that *Microcystis* sp. blooms may be reduced by as much as 50% if the size of the benthic inoculum is reduced (Verspagen et al., 2005). A study by Brunberg and Blomqvist (2002) on overwintering under different environmental conditions indicates that a reduction in the snow cover on ice-covered lakes would reduce overwintering *Microcystis* sp. populations. We expect that warmer temperatures may increase *Microcystis* sp. recruitment from the sediments, as has been observed for other cyanobacterial taxa (e.g., Karlsson-Elfgren et al., 2004), and may allow *Microcystis* sp. to overwinter in the water column. However, Verspagen et al. (2006) found that increasing temperatures also increase *Microcystis* sp. mortality rate, and overwintering in the water column may increase the light and temperature fluctuations cells are exposed to, decreasing their survival (Brunberg and Blomqvist, 2002). Consequently, decreasing ice cover and rising temperatures in temperate and high-latitude regions may potentially favour other, akinete-forming, cyanobacterial genera over *Microcystis*.

3.6. Photosynthesis

In this section, we explore photosynthesis and photo-acclimation in cyanobacteria and whether the direct and indirect effects of climate change may affect the competition for light between cyanobacteria and their phytoplankton competitors. Cyanobacteria are reputed to be strong competitors for light due to their accessory pigmentation and the structural organisation of their light-harvesting antenna (e.g., Osborne and Raven, 1986). Laboratory experiments demonstrated that the picoplanktonic cyanobacterium *Synechocystis* sp. attenuated light to lower levels than any other tested species and readily outcompeted other phytoplankton species when light was limiting (Passarge et al., 2006). However, Huisman et al. (1999) found that *Microcystis* sp. were not particularly strong competitors for light in a well-mixed environment, as did Reynolds (2006), who found that *Microcystis* sp. had the poorest light efficiency (by examining the steepness of the initial slope of growth vs. irradiance curves) of 19 phytoplankton species tested. The differences in light interception among different species were mostly due to morphological characteristics: slender, attenuated forms − like that of filamentous cyanobacterial species − were superior to large colonial species at harvesting light (Reynolds, 2006). Huisman et al. (1999) concluded that the observed dominance of cyanobacteria in eutrophic waters cannot be explained (solely) by competition for light.

Overall, we hypothesise that the indirect effects of climate warming (i.e., the strengthening stability of the water column) will have a bigger impact on the competition for light among cyanobacterial taxa and with other phytoplankton than the direct effect of warmer water temperatures. The ability of phytoplankton to acclimate to higher water temperatures and photosynthesise is dependent on changes in the fluidity of the thylakoid membranes, which occurs by changing the lipid composition of the membranes (Herrero and Flores, 2008). Increased temperatures as a result of climate change may affect photosynthetic electron transport in cyanobacterial photosystems, photoacclimation, and the maximum rates of photosynthesis (e.g., Post et al., 1985; Wu et al., 2009). As a result, cyanobacterial photosynthesis may not actually be affected by warmer temperatures during bloom periods or other times when photosynthetic rates are limited because temperature does not have a large effect on the overall efficiency of photosynthesis (Post et al., 1985).

By comparison, the indirect effect of stronger thermal stability on photosynthesis may alter dominance among

cyanobacterial taxa and other phytoplankton. Field observations show that when mixing is strong and buoyant phytoplankton do not have a competitive advantage, *Microcystis* sp. arc outcompeted by superior competitors for light such as *P. agardhii* (see Scheffer et al., 1997) or *C. raciborskii* (O'Brien et al., 2009; Wu et al., 2009). *P. agardhii* has a higher affinity for light than *Microcystis* sp. and if its biomass is sufficiently concentrated during bloom periods, it can shade out competitors, including *Microcystis* sp. (Scheffer et al., 1997). If climate warming stimulates blooms, thereby reducing light availability in the water column, a genus such as *Planktothrix* would benefit. *Microcystis*, however, is adapted to alternating periods of mixing and quiescence and is highly buoyant, potentially favouring the genera under climate scenarios of increased water column stability. When mixing subsides, buoyant colonies can rapidly float up into the near-surface mixed layer and benefit from enhanced access to light. This short-term benefit may have long-term consequences, however, because the time spent at or near the lake surface determines the risk of photoinhibition (described below). Consequently, *Microcystis* may face a trade-off in lakes with strongly enhanced water column stability.

Photoacclimation is the phenotypic adjustment to changes in the availability of light, most notably up or downsize regulation of cellular pigment contents, but also in electron chain components or Calvin cycle enzymes (Falkowski and LaRoche, 1991; MacIntyre et al., 2002). The role of photoacclimation is not just to maximise the rate of photosynthetic carbon assimilation, but also to protect the cells against damage from an excess of energy (Schagerl and Mueller, 2006; Zonneveld, 1998). *Synechococcus* sp., for example, are able to grow under full sunlight but only when acclimated gradually to the extreme conditions (MacIntyre et al., 2002). Photoinhibition of photosynthesis will occur if cells are exposed to an irradiance level that is much higher than what they were acclimated to, causing light stress if irradiance is in excess to what can be used directly in photosynthesis (Powles, 1984). Under these conditions, safe dissipation of the excess excitation energy is required to protect the photosystems from long-term damage (Niyogi, 2000).

Surface bloom formation by buoyant cyanobacteria after a period of intensive mixing will dramatically increase irradiance and can cause severe photoinhibition, even in nutrient-replete cells (Ibelings, 1996; Ibelings and Maberly, 1998). The effect of photoinhibition can be extremely detrimental because cyanobacteria synthesise new gas vesicles during periods of deep mixing (and ensuing low irradiance; Konopka et al., 1987). Once mixing subsides, the now over-buoyant colonies can no longer reduce their buoyancy and will become trapped at the surface (Walsby et al., 1991). Photoinhibition sets in quickly and can induce long-lasting cellular damage (Abeliovich and Shilo, 1972; Zohary and Pais-Madeira, 1990). Ibelings et al. (1994) directly compared *M. aeruginosa* and the green alga *Scenedesmus protuberans* to high (and fluctuating) irradiance, mimicking natural light regimes in lakes. They found that buoyant *M. aeruginosa* was more sensitive to photoinhibition than its green algal competitor. Photoinhibition that is invoked promptly protects cells from potentially much more damaging effects, i.e., it is a mechanism for the long-term protection of photosystem 2 (PS2) (Oquist et al., 1992). Photoinhibition that is quickly activated may protect PS2, but during relatively short periods of high irradiance under wind-mixed conditions, *M. aeruginosa* apparently depresses its rate of photosynthesis while *S. protuberans* maintains uninhibited photosynthesis. It appears that *M. aeruginosa* is not as well adapted to fluctuating light as its eukaryotic competitors and is thus unable to benefit from the saturating irradiance levels that are temporarily available when mixing takes cells to the upper layers of the water column.

Others have also found that mixing not only prevents surface bloom formation but also arrests the growth of bloom-forming species (e.g., Reynolds et al., 1983). This re-emphasises the dependence of buoyant *Microcystis* sp. on a water column that is at least partially stable, enabling the colonies to be maintained in a shallow near-surface mixed layer where light fluctuations are reduced and where irradiance levels are usually consistently high. In a changing climate with stronger and longer periods of water column stability, the buoyancy-dependent niche of *Microcystis* sp. would be strengthened, even in relatively shallow lakes. However, if stability gets too strong and mixing subsides, *Microcystis* biomass would accumulate in surface scums, possibly causing population losses.

The combination of extreme conditions – high irradiance, depleted carbon, and elevated temperatures (Ibelings, 1996; Ibelings and Maberly, 1998) – makes it likely that scums should be considered as net loss factors for buoyant bloom-forming genera, which are costly for slow growing specialists like *Microcystis*. Finally, whether lake warming would indeed promote blooms of taxa like *Microcystis* sp. may critically depend on the degree of water column stability and lake morphometry.

4.   Conclusion

Incorporating cyanobacterial physiology into bloom predictions is essential to understand how freshwater and brackish cyanobacteria will respond to climate changes. Fundamentally, cyanobacteria are an extremely diverse group with different sets of traits, and will respond to different aspects of climate change (e.g., increased stratification, altered nutrient availability). For example, *Microcystis* sp. do not fix N but have a relatively high Q_{10} (however, see discussion in this paper), while *Anabaena* sp. fix N but have a lower Q_{10}, and both genera have efficient buoyancy regulation and migration in stable water columns. We would then predict that in warmer waters *Microcystis* may be favoured, but that its competitive advantage may be compromised if N becomes limiting due to altered nutrient delivery. There will most likely also be regional differences in which cyanobacterial taxa dominate, depending on how future climate, hydrology, and nutrient loading vary geographically. Taken together, however, we believe that trade-offs in cyanobacterial physiology among species will overall promote cyanobacterial dominance over other phytoplankton in most future climate scenarios.

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