

The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change

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ABSTRACT

Cyanobacteria are the most ancient phytoplankton on the planet and form harmful algal blooms in freshwater, estuarine, and marine ecosystems. Recent research suggests that eutrophication and climate change are two processes that may promote the proliferation and expansion of cyanobacterial harmful algal blooms. In this review, we specifically examine the relationships between eutrophication, climate change and representative cyanobacterial genera from freshwater (*Microcystis*, *Anabaena*, *Cylindrospermopsis*), estuarine (*Nodularia*, *Aphanizomenon*), and marine ecosystems (*Lyngbya*, *Synechococcus*, *Trichodesmium*). Commonalities among cyanobacterial genera include being highly competitive for low concentrations of inorganic P (DIP) and the ability to acquire organic P compounds. Both diazotrophic (= nitrogen (N₂) fixers) and non-diazotrophic cyanobacteria display great flexibility in the N sources they exploit to form blooms. Hence, while some cyanobacterial blooms are associated with eutrophication, several form blooms when concentrations of inorganic N and P are low. Cyanobacteria dominate phytoplankton assemblages under higher temperatures due to both physiological (e.g. more rapid growth) and physical factors (e.g. enhanced stratification), with individual species showing different temperature optima. Significantly less is known regarding how increasing carbon dioxide (CO₂) concentrations will affect cyanobacteria, although some evidence suggests several genera of cyanobacteria are well-suited to bloom under low concentrations of CO₂. While the interactive effects of future eutrophication and climate change on harmful cyanobacterial blooms are complex, much of the current knowledge suggests these processes are likely to enhance the magnitude and frequency of these events.

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1. Introduction

While cyanobacterial harmful algal blooms have been reported in the scientific literature for more than 130 years (Francis, 1878), in recent decades, the incidence and intensity of these blooms, as well as economic loss associated with these events has increased in both fresh and marine waters (Chorus and Bartram, 1999; Carmichael, 2001, 2008; Hudnell, 2008; Heisler et al., 2008; Hoagland et al., 2002; Paerl, 2008; Paul, 2008; Paerl and Huisman, 2008). Recently, there have been discoveries of previously unidentified cyanobacterial toxins, such as amino β-methylamino-1-alanine (BMAA), and of new genera of cyanobacteria capable of producing previously described toxins (Cox et al., 2003, 2005, 2009; Cox, 2009; Brand, 2009; Kerbrat et al., 2011). To date, factors identified as contributing towards the global expansion of

harmful cyanobacterial blooms have included increased nutrient inputs, the transport of cells or cysts via anthropogenic activities, and increased aquaculture production and/or overfishing that alters food webs and may permit harmful species to dominate algal communities (GEOHAB, 2001; HARRNESS, 2005; Heisler et al., 2008). It has also been shown that an increase in surface water temperatures due to changing global climate could play a role in the proliferation of cyanobacterial blooms (Peperzak, 2003; Paerl and Huisman, 2008; Paul, 2008). Importantly, there is consensus that harmful algal blooms are complex events, typically not caused by a single environmental driver but rather multiple factors occurring simultaneously (Heisler et al., 2008). Finally, an improved ability to detect and monitor harmful cyanobacterial blooms, and their toxins as well as increased scientific and public awareness of these events has also led to better documentation of these events (GEOHAB, 2001; HARRNESS, 2005; Sivonen and Börner, 2008).

There have been several reviews of the intensification and global expansion of harmful cyanobacterial blooms in terms of

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both abundance, geographic extent, and effects on ecosystem health, as well as factors that may be facilitating this expansion (Paerl, 1988, 1997; Paerl and Millie, 1996; Soranno, 1997; Carmichael, 2001; Saker and Griffiths, 2001; Landsberg, 2002; Codd et al., 2005a,b; Huisman and Hulot, 2005; see multiple papers in Hudnell, 2008). The purpose of this review is to: (1) Highlight important findings of the last decade of harmful cyanobacterial bloom research in fresh, estuarine and marine environments; and (2) Describe how factors associated with eutrophication and climate change affect some of the most widely studied harmful cyanobacterial bloom genera.

2. Background

Cyanobacteria are prokaryotes but have historically been grouped with eukaryotic “algae” and at varying times have been referred to as: blue–greens, blue–green algae, *Myxophyceae*, *Cyanophyceae* and *Cyanophyta* (Carmichael, 2008). More recently cyanobacteria that form harmful blooms have been termed “CyanoHABs” (Carmichael, 2001, 2008; Paerl, 2008) or “cyanobacterial blooms” (Hudnell et al., 2008).

2.1. Toxins

Many genera of cyanobacteria are known to produce a wide variety of toxins and bioactive compounds, which are secondary metabolites (i.e. compounds not essential to the cyanobacteria for growth or its own metabolism) (Sivonen and Jones, 1999). Toxins generally refer to compounds that cause animal and human poisonings or health risks, and bioactive compounds refer to compounds that can have antimicrobial and cytotoxic properties and are often of interest in pharmaceutical and as research tools (Codd et al., 2005a,b). While many of these compounds have recognized toxic effects, the impact and long term effects of many of these compounds is unknown (Tonk, 2007).

Hepatotoxins are globally the most prevalent cyanobacterial toxins followed by neurotoxins (Sivonen and Jones, 1999; Klisch and Häder, 2008; Sivonen and Börner, 2008). Hepatotoxins include: (1) microcystins, (2) nodularins, and (3) cylindrospermopsins. The three most commonly produced types of cyanobacterial neurotoxins are: (1) anatoxin-a, (2) anatoxin-a (S), and (3) saxitoxins. As noted above, Cox et al. (2003, 2005) recently described the presence of the neurotoxic compound, BMAA in nearly all cyanobacteria they tested (Table 1). It has been hypothesized that BMAA may be a possible cause of the amyotrophic lateral sclerosis parkinsonism–dementia complex (ALS-PDC; Cox et al., 2003, 2009; Murch et al., 2004; Cox, 2009). As such, the discovery that this compound is potentially produced by a broad range of cyanobacteria greatly increases the potential for human exposure (Sivonen and Börner, 2008; Brand, 2009). Indeed,

in the Baltic Sea, an ecosystem whose primary production is dominated by cyanobacteria, BMAA has been measured in significant quantities in both fish and shellfish (Jonasson et al., 2010).

2.2. Nutrients

Of all of the potential environmental drivers behind harmful algal and cyanobacterial blooms, the one that has received the most attention among the global scientific community has been anthropogenic nutrient pollution. Research indicates that cultural eutrophication associated with the increased global human population has stimulated the occurrences of harmful algal blooms (Anderson, 1989; Hallegraeff, 1993; Burkholder, 1998; Anderson et al., 2002; Glibert et al., 2005; Glibert and Burkholder, 2006; Heisler et al., 2008). As bodies of freshwater become enriched in nutrients, especially phosphorus (P), there is often a shift in the phytoplankton community towards dominance by cyanobacteria (Smith, 1986; Trimbee and Prepas, 1987; Watson et al., 1997; Paerl and Huisman, 2009). Examples of these changes are the dense blooms often found in newly eutrophied lakes, reservoirs, and rivers previously devoid of these events (Fogg, 1969; Reynolds and Walsby, 1975; Reynolds, 1987; Paerl, 1988, 1997). Empirical models predict that in temperate ecosystems, summer phytoplankton communities will be potentially dominated by cyanobacteria at total phosphorus (TP) concentrations of ~ 100 – $1000 \mu\text{g L}^{-1}$ (Trimbee and Prepas, 1987; Jensen et al., 1994; Watson et al., 1997; Downing et al., 2001).

One reason that P often controls the proliferation of freshwater ecosystems is that many cyanobacteria that bloom in warm waters have the ability to fix nitrogen (N; Paerl, 1988; Paerl et al., 2001). Since many of the bloom forming cyanobacteria genera are not diazotrophic and the proliferation of some blooms may be limited by N (Gobler et al., 2007; Davis et al., 2010), it has been hypothesized both N and P may control harmful cyanobacterial blooms (Paerl et al., 2008; Paerl and Huisman, 2009). While research on cyanobacterial blooms has traditionally considered inorganic N and P pools as being accessed by cyanobacteria or total N and P pools for understanding the trophic state of ecosystems, recent research has demonstrated that organic N and P may be important nutrient sources for cyanobacteria. Much of the soluble N and P pools in most aquatic environments are comprised of organic compounds (Franko and Heath, 1979; Seitzinger and Sanders, 1997; Kolowitz et al., 2001) and many cyanobacteria can utilize various forms of dissolved and particulate organic N and P (Glibert and Bronk, 1994; Paerl, 1988; Paerl and Millie, 1996; Pinckney et al., 1997; Berman and Chava, 1999; Glibert and O'Neil, 1999; Davis et al., 2010). Since neither inorganic nutrient pools nor nutrients ratios typically are able to sufficiently explain the extended duration of dense cyanobacterial blooms (Heisler et al.,

Table 1
Major cyanobacterial bloom toxins.

Toxin group	Primary target organ in mammals	Cyanobacterial genera
Microcystins	Liver	<i>Microcystis</i> , <i>Anabaena</i> , <i>Planktothrix</i> (<i>Oscillatoria</i>), <i>Nostoc</i> , <i>Hapalosiphon</i> , <i>Anabaenopsis</i> , <i>Trichodesmium</i> , <i>Synechococcus</i> , <i>Snowella</i>
Nodularian	Liver	<i>Nodularia</i>
Cylindrospermopsin	Liver	<i>Cylindrospermopsis</i> , <i>Umezakia</i> , <i>Aphanizomenon</i> , <i>Lyngbya</i> , <i>Raphidiopsis</i> , <i>Anabaena</i>
Anatoxin-a	Nerve synapse	<i>Anabaena</i> , <i>Planktothrix</i> (<i>Oscillatoria</i>), <i>Aphanizomenon</i> , <i>Phormidium</i> , <i>Raphidiopsis</i>
Anatoxin-a(S)	Nerve synapse	<i>Anabaena</i>
Saxitoxins	Nerve axons	<i>Anabaena</i> , <i>Planktothrix</i> (<i>Oscillatoria</i>), <i>Aphanizomenon</i> , <i>Lyngbya</i> , <i>Cylindrospermopsis</i> , <i>Scytonema</i>
Palytoxins	Nerve axons	<i>Trichodesmium</i>
Aplysiatoxins	Skin	<i>Lyngbya</i> , <i>Schizothrix</i> , <i>Planktothrix</i> (<i>Oscillatoria</i>)
Lyngbyatoxin-a	Skin, gastro-intestinal tract	<i>Lyngbya</i>
Lipopolysaccharides	Irritant; affects exposed tissue	All
BMAA	Nerve synapse	All

Sources: Chorus and Bartram (1999), Li et al. (2001a), Codd et al. (2005a,b), Humpage (2008), Klisch and Häder (2008), Smith et al. (2011).

2008; Paerl, 2008), research of these events must consider the impacts of all nutrient species, including micro-nutrients. Iron (Fe) has also been found to be an important micro-nutrient in determining cyanobacterial bloom abundance, especially for diazotrophs, given that the enzyme nitrogenase has a high Fe requirement (Kustka et al., 2003). The recent expansion of molecular investigations of cyanobacteria has permitted a clearer understanding of the manner in which harmful cyanobacterial bloom species respond to all nutrients at the cellular level. Importantly, there are diverse responses to nutrient sources and concentrations among cyanobacterial blooms species that will be highlighted in this review.

2.3. Climate change

The sum of research conducted regarding the evolutionary history, ecophysiology, and *in situ* dynamics of cyanobacteria suggests that they will thrive under the conditions predicted for global climate change (Paul, 2008; Paerl and Huisman, 2009). The details of how specific genera of cyanobacteria may respond to climate change, however, are less clear. This review will focus on the specific effects of temperature and concomitant changes in stratification, as well as the effect of CO₂ and pH on multiple freshwater, estuarine, and marine cyanobacteria genera.

2.3.1. Temperature

The burning of fossil fuels and subsequent rise in atmospheric carbon dioxide has caused the earth's surface temperature to increase by approximately 1 °C during the 20th century, with most of the increase having occurred during the last 40 years (IPCC, 2007). In the current century, global temperatures are expected to increase an additional 1.5–5 °C (Houghton et al., 2001; IPCC, 2007). Natural communities of phytoplankton have been and will continue to be influenced by these increases in temperature as algal growth rates are strongly, but differentially, temperature dependent (Eppeley, 1972; Goldman and Carpenter, 1974; Raven and Geider, 1988). As temperatures approach and exceed 20 °C, the growth rates of freshwater eukaryotic phytoplankton generally stabilize or decrease while growth rates of many cyanobacteria increase, providing a competitive advantage (Canale and Vogel, 1974; Peperzak, 2003; Paerl and Huisman, 2009).

Beyond the direct effects on cyanobacterial growth rates, rising temperatures will change many of the physical characteristics of aquatic environments in ways that may be favorable for cyanobacteria. For instance, higher temperatures will decrease surface water viscosity and increase nutrient diffusion towards the cell surface, an important process when competition for nutrients between species occurs (Vogel, 1996; Peperzak, 2003). Secondly, since many cyanobacteria can regulate buoyancy to offset their sedimentation, a decrease in viscosity will preferentially promote the sinking of larger, non-motile phytoplankton with weak buoyancy regulation mechanisms (e.g. diatoms) giving cyanobacteria a further advantage in these systems (Wagner and Adrian, 2009; Paerl and Huisman, 2009). Thirdly, insular heating will increase the frequency, strength, and duration of stratification. This process will generally reduce the availability of nutrients in surface waters favoring cyanobacteria that regulate buoyancy to obtain nutrients from deeper water, or that are diazotrophic. Consistent with the sum of these observations, cyanobacteria tend to dominate phytoplankton assemblages in eutrophic, freshwater environments during the warmest periods of the year, particularly in temperate ecosystems (Paerl, 1988; Paerl et al., 2001; Paerl and Huisman, 2008; Paul, 2008; Liu et al., 2011). For all of these reasons, it has generally been concluded that cyanobacterial blooms may increase in distribution, duration and intensity, as global temperatures rise (Paerl and Huisman, 2009; Paul, 2008). The precise response of

individual cyanobacterial taxa to rising temperatures will be diverse and has not been reviewed in detail to date.

2.3.2. Carbon dioxide and pH

The combustion of fossil fuels during the past two centuries has significantly increased concentrations of atmospheric carbon dioxide (CO₂), a trend that is projected to continue in the coming decades (IPCC, 2007). Atmospheric CO₂ concentrations that had previously increased at a rate of 1% per year in the 20th century are now increasing ~3% per year and may exceed 800 ppm by the end of this century (IPCC, 2007; Füssel, 2009). Aquatic chemistry will be strongly altered by this rising CO₂ as levels of both pH and carbonate ions will decline (Cao and Caldeira, 2008).

The pH of aquatic water bodies is intimately linked to the speciation of dissolved inorganic carbon (DIC) (e.g. CO₂; carbonic acid H₂CO₃; bicarbonate HCO₃⁻; or carbonate CO₃²⁻) and the pH of most systems (7.5–8.1) maintains inorganic carbon primarily in the form of HCO₃⁻. The buffering capacity of marine ecosystems maintains the pH and speciation of inorganic DIC in a smaller range than those typically observed in freshwaters. Many lakes are supersaturated with CO₂ (Cole et al., 1994; Maberly, 1996) due to terrestrial C inputs and sediment respiration (Cole et al., 1994). The pH and speciation of inorganic carbon in lakes can vary widely on a scale from daily (diel), to episodic, to seasonal (Maberly, 1996; Qui and Gao, 2002) with diel variations in productive lakes as high as 2 pH units and 60 μmol DIC L⁻¹ (Maberly, 1996). The large, diel drawdown in DIC associated with algal blooms in eutrophic lakes may cause phytoplankton to become ephemerally C-limited. It has been hypothesized that surface-dwelling cyanobacteria may have an advantage over other phytoplankton due to their closer proximity to atmospheric CO₂ that may rapidly diffuse into surface waters and promote their growth when water column CO₂ concentrations are drawn down by dense blooms (Paerl and Huisman, 2009). Alternatively, there is evidence that low DIC environments may favor cyanobacteria. Several studies have reported that cyanobacteria out-compete eukaryotic algae under high pH and low CO₂ conditions (Shapiro and Wright, 1990; Oliver and Ganf, 2000; Qui and Gao, 2002). Furthermore, some cyanobacteria decrease cell division rates in response to lower pH conditions (Shapiro and Wright, 1990; Whitton and Potts, 2000; Czerny et al., 2009). However, laboratory and field studies have demonstrated that other cyanobacteria respond to increased CO₂ with increased cell division rates, carbon fixation, or both (Hein and Sand-Jensen, 1997; Burkhardt et al., 1999; Hinga, 2002; Yang and Gao, 2003; Riebesell, 2004; Barcelos e Ramos et al., 2007; Fu et al., 2007, 2008; Hutchins et al., 2007; Levitan et al., 2007; Riebesell et al., 2007; Kranz et al., 2009).

There are a number of phylogenetically distinct ways phytoplankton take up, transport, or convert CO₂ and HCO₃⁻ (Raven, 1997; Kaplan and Reinhold, 1999; Beardall and Giordano, 2002; Badger and Price, 2003; Reinfelder, 2011). Nearly all, eukaryotic algae and all cyanobacteria possess carbon-concentrating mechanisms (CCMs; Giordano et al., 2005). Cyanobacteria have evolved pathways for the active inorganic carbon uptake and partition their ribulose biphosphate carboxylase-oxygenase (Rubisco) into micro-compartments known as carboxysomes that generate a high concentration of CO₂ around the Rubisco enzyme (Badger et al., 2002). It has been demonstrated that CCMs in cyanobacteria are more efficient than other algae or higher plants at low CO₂ concentrations (Badger and Price, 2003; Badger et al., 2006) and that this heightened efficiency may facilitate their dominance under low CO₂ conditions (Price et al., 2008). Considered in the context of climate change, increases in atmospheric concentrations of CO₂ could have a more beneficial impact on species that, unlike cyanobacteria, possess inferior CCMs, do not contain any CCMs, and/or rely primarily on CO₂ transport (Fu et al., 2007). While this



Fig. 1. Major CHAB genera from (A) freshwater: (1) *Anabaena* (photo: Michele Burford); (2) *Microcystis* (photo: Glenn MacGregor); (3) *Cylindrospermopsis* (photo: Glenn MacGregor); (B) estuarine: (4) *Nodularia* (photo: Hans Paerl); (5) *Aphanizomena* (photo: Christina Esplund-Lindquist); (C) marine environments: (6) *Lynbya* (photo: Judy O'Neil); (7) *Trichodesmium* (photo: Judy O'Neil); and (8) *Synechococcus* (photo: Florida Fish & Wildlife Institute-FWRI).

might suggest that globally rising CO_2 may diminish the intensity of cyanobacterial blooms, little is known regarding how increases in the concentration of CO_2 will impact cell physiology and growth rates of individual cyanobacteria genera. Changing CO_2 conditions may also effect the strain composition within a cyanobacterial community. One study addressed this question using competition experiments with toxic versus non-toxic strains of cyanobacteria at high CO_2 availability; which resulted in a competitive advantage of the non-toxic strain (Van de Waal et al., 2011). Below we will discuss what is known in regard to potential climate change effects for each of the major harmful cyanobacterial bloom genera across the fresh to marine spectrum.

2.3.3. Salinity

Climate change may also affect salinity in estuaries and freshwater systems due to rising sea-level: an increase in drought frequency and duration in some regions and concomitant increase in dessication; or in other areas, increases in precipitation due to storms. This may cause shifts in phytoplankton species composition (Ahmed et al., 1985; Moisaner et al., 2002; Bordalo and Vieira, 2005). Although many eukaryotic phytoplankton cannot tolerate changes in salinity, a number of cyanobacterial species have very euryhaline tolerances. Therefore changes in salinity may affect both community composition as well as potential toxin concentrations and distribution (Laamanen et al., 2002; Orr et al., 2004; Tonk et al., 2007).

3. Freshwater environments

As noted above, freshwater harmful algal blooms are predominantly caused by pelagic cyanobacteria (Carmichael, 2001, 2008).

As such, this review will focus on the role of eutrophication and climate change in the occurrence of three of the most prevalent pelagic cyanobacterial bloom forming genera in this environment, *Anabaena*, *Microcystis*, and *Cylindrospermopsis* (Fig. 1A).

3.1. *Anabaena*

Anabaena is a ubiquitous freshwater genus found throughout the world, but typically prevalent in lentic waterbodies such as lakes, reservoirs, cease-to-flow rivers and weir pools. *Anabaena* is a filamentous, akinete-forming diazotroph in the order Nostocales. Some species of this genera produce the toxins microcystins (MCYs), anatoxin-a and anatoxin-a(S) and cylindrospermopsin (CYN), while others, principally *Anabaena circinalis*, produces a saxitoxin (STX). The gene cluster responsible for anatoxin biosynthesis has recently been described for *Anabaena* (Rantala-Yilnen et al., 2011), the characterization of the gene clusters responsible for saxitoxin biosynthesis (*stx*; Mihali et al., 2009) and microcystin biosynthesis (*mcyA – I*; Rouhiainen et al., 2004) in *Anabaena* have allowed for the distinction between strains that can and cannot produce STX (Al-Tebrineh et al., 2010) and MCY (Rouhiainen et al., 2004). As a diazotroph, *Anabaena* has been functionally classified as tolerant of low nitrogen conditions, but sensitive to mixing and low light, utilizing buoyancy regulation to counteract this sensitivity (Reynolds et al., 2002). Like a number of other cyanobacterial genera, it is tolerant of low CO_2 concentrations, as it relies on the enzyme, carbonic anhydrase, to access bicarbonate (Shiraiwa and Miyachi, 1985). There are two main HAB-forming species typically reported in the scientific literature – *A. circinalis* and *A. flos-aquae*. Recent studies of *Anabaena* have focused principally on two main aspects: the life cycle; and the role

of physical conditions, namely light, stratification, salinity and water flow regimes in promoting growth. There have also been advances in the understanding of the life cycle of *Anabaena*, particularly focused on factors causing akinete formation and germination (Tsujimura and Okubo, 2003; Karlsson-Elfgren and Brunberg, 2004; Faithfull and Burns, 2006; Thompson et al., 2009). The role of nutrients, and the interaction with physical conditions, has also received some attention.

3.1.1. Potential nutrient effects

Anabaena is diazotrophic under low dissolved inorganic nitrogen conditions (Fogg, 1942). Many papers have examined this capacity in both field and laboratory studies, and demonstrated that this physiological ability permits *Anabaena* to outcompete non-nitrogen fixers in N depauperate waters (e.g. Kangatharalingam et al., 1991; Chan et al., 2004; Wood et al., 2010) and even other diazotrophs such as *Aphanizomenon* (DeNobel et al., 1997).

Since *Anabaena* is a diazotroph, P appears to be a key limiting nutrient for surface blooms of this genus. Limitation by P may also promote akinete production, a strategy for ensuring that populations can recover when P becomes available again (Olli et al., 2005). Recently an agent-based model of the life cycle of *Anabaena* determined that soon after germination, populations get most of their nutrients from the sediment bed (Hellweger et al., 2008). This may give *Anabaena* a competitive advantage over other non-akinetes forming genera, at least in the early stages of bloom formation, until P becomes depleted or cells move into surface waters. Furthermore, Rapala et al. (1997) found that both growth rate and intracellular MCY concentrations of two *Anabaena* isolates increased with increasing P concentrations. However, increases in DIN (e.g. nitrate) did not yield a significant increase in growth rate and had differing effects on the production of various microcystin congeners. An additional strategy available to *Anabaena* (and other cyanobacterial species) is the ability to utilize organic forms of N and P. Recently genes putatively encoding alkaline phosphatase analogs have been identified in *Anabaena* (Luo et al., 2010).

3.1.2. Potential climate change effects

It has been proposed that increasing temperature will benefit cyanobacteria, both directly and indirectly by increasing thermal stratification (Paerl and Huisman, 2008) and there is evidence these processes will specifically promote *Anabaena*. Strong stratification that minimizes the availability of remineralized nutrients in surface waters should favor diazotrophs such as *Anabaena* and also specifically favors *Anabaena* physiology due to its ability to control buoyancy in the water column (Oliver, 1994). Consistent with this concept, Brookes et al. (1999) reported that *Anabaena* forms blooms under thermally stratified conditions due to the ability to regulate its buoyancy, and access sufficient light for growth and McCausland et al. (2005) specifically demonstrated that stable conditions indicative of diurnal stratification promote growth of *A. circinalis*. A recent study in a German lake showed that *Anabaena* may benefit from increased thermal stratification as a result of temperature increases, although, this appeared to be linked to their ability to regulate their buoyancy and access nutrients in the hypolimnion rather than a direct temperature effect (Wagner and Adrian, 2009). Studies of *A. circinalis* populations in the lower Murray River, Australia, exposed to persistent stratification were shown to grow faster than under diurnally stratified or mixed conditions (Westwood and Ganf, 2004a). Additionally, Westwood and Ganf (2004b) found that blooms were unlikely to form when periods of diurnal stratification were less than 1 week. Finally, temperature will also have differential physiological impacts on phytoplankton and a recent laboratory study found that increasing water temperatures from 18 to 23 °C increased *Anabaena* photosynthetic performance in comparison

with the cyanobacteria *Microcystis* and *Arthrospira* (Giordanino et al., 2011).

Flow conditions affect stratification in cease-to-flow river systems, and therefore changes in rainfall patterns, and hence runoff to rivers, will have an impact on this. Studies have identified critical discharges to control *A. circinalis* blooms in the Barwon-Darling River, Australia (Mitrovic et al., 2003, 2006). Researchers found that there was a 12% probability of *A. circinalis* blooms exceeding 15,000 cells mL⁻¹ under typical flow conditions in the Murray River and threshold flow rates were described to reduce probability of blooms (Maier et al., 2004). Modeling studies of a thermally stratified reservoir with regular blooms of *A. circinalis* have shown that they can be controlled by the use of aerators or surface mixers (Lewis et al., 2004). *Anabaena* is purported to grow in both fresh- and brackish waters and a recent study of *Anabaena* in field experiments demonstrated that both growth and toxin production were higher at lower salinity (Engström-Öst and Mikkonen, 2011). As such, higher flow rates within river systems connected to estuaries may move *Anabaena* blooms into the brackish portions of estuaries.

These studies highlight the potential effect of climate change driven effects on rainfall patterns, and hence flow regimes. In southeast Australia, the combination of a predicted decrease in rainfall coupled with increases in air temperature and evaporation is modeled to give rise to measurable increases in *Anabaena* bloom occurrence and duration (Viney et al., 2007).

3.2. Microcystis

Microcystis is one of the most common bloom formers in freshwater systems on every continent except Antarctica (Fristachi and Sinclair, 2008). This genus can produce a suite of potentially harmful compounds including MCYs, anatoxin-(a), and BMAA (Fristachi and Sinclair, 2008). Not all *Microcystis* cells produce MCY as bloom populations of *Microcystis* are typically comprised of MCY-producing (MCY+) and non-MCY producing (MCY-) strains that are distinguishable only via molecular quantification of the MCY synthetase gene operon (*mcyA – J*; Tillett et al., 2000) and a molecular marker for the total *Microcystis* population, such as the 16S rRNA gene (Kurmayer and Kutzenberger, 2003; Davis et al., 2009). This method of distinguishing between these sub-populations has been used in laboratory and field studies during the past decade (e.g. Rinta-Kanto et al., 2005; Davis et al., 2010; Van de Waal et al., 2011; Wood et al., 2011). There is evidence that indicates that global change to aquatic ecosystems such as rising temperatures, nutrient loads, and CO₂ concentrations will affect the dominance and toxicity of *Microcystis*.

3.2.1. Potential nutrient effects

Historically, P has been considered the primary limiting nutrient in freshwater ecosystems (Likens, 1972; Schindler, 1977; Wetzel, 2001; Kalff, 2002; Paerl, 2008). There is evidence to suggest, however, that N may be equally or more important than P in the occurrence of toxic, non-diazotrophic cyanobacteria blooms, such as *Microcystis*. Laboratory studies have shown that increasing N concentrations will generally increase the growth and toxicity of *Microcystis* (Watanabe and Oishi, 1985; Codd and Poon, 1988; Orr and Jones, 1998). Furthermore, experiments have established positive relationships between DIN supply, MCY production, and MCY content in toxic strains of *Microcystis* (Utkilen and Gjølme, 1995; Orr and Jones, 1998; Long et al., 2001). Field studies of *Microcystis* have also found that blooms are often associated with high levels of N (Jacoby et al., 2000; Gobler et al., 2007; Davis et al., 2010; Liu et al., 2011; Te and Gin, 2011; Paerl et al., 2011).

Nutrients can also differentially affect the relative abundance of MCY+ and MCY– *Microcystis* strains. Laboratory experiments have shown that MCY– strains of *Microcystis* require lower nutrient concentrations to achieve maximal growth rates compared to MCY+ strains whereas MCY+ strains yield higher growth rates than MCY– strains at high N concentrations (Vézé et al., 2002). Consistent with this trend, field studies have shown that bloom populations of *Microcystis* shifted from dominance of MCY+ strains to MCY– strains as inorganic N concentrations declined through the summer (Davis et al., 2010). Several other studies have observed a similar seasonal succession of *Microcystis* populations (Briand et al., 2004; Fastner et al., 2001; Welker et al., 2007) or have noted the dominance of MCY– strains during the peak of *Microcystis* bloom event (Welker et al., 2003, 2007; Kardinaal et al., 2007). Since inorganic nutrient levels are generally reduced when algal blooms occur (Sunda et al., 2006), the predominance of MCY– strains during this period may be a function of their ability to outcompete MCY+ strains when nutrient levels are lower (Vézé et al., 2002). Consistent with this hypothesis, during field-based, incubation experiments, MCY+ strains were more frequently stimulated by higher concentrations of N than their MCY– counterparts (Davis et al., 2009, 2010). Microcystin is a N-rich compound (10 N atoms per molecule) and studies have found that microcystin can represent up to 2% of cellular dry weight of *Microcystis* (Nagata et al., 1997). Additionally, toxic *Microcystis* strains have N requirements associated with the enzymes involved in the synthesis of MCY (Tillett et al., 2000) as well as with additional light-harvesting pigments they may possess (Hesse and Kohl, 2001). Although the precise mechanism is unclear, toxic *Microcystis* cells seem to have a higher N requirement than non-toxic cells (Vézé et al., 2002; Davis et al., 2010).

Studies have shown that some forms of DON can be utilized by *Microcystis* blooms. Field studies conducted by Takamura et al. (1987) and Présing et al. (2008) using ^{15}N -labeled nitrogenous compounds demonstrated that *Microcystis* was able to take up nitrate, ammonium, and urea. During a study of a New York lake where *Microcystis* represented more than 98% of the $>20\ \mu\text{m}$ phytoplankton population, this size-fraction displayed flexibility in N assimilation, obtaining the majority of its N from nitrate, ammonium or urea on different occasions, as well as some of its N from glutamic acid (Davis, 2009). Uptake rates of ammonium and urea by the $>20\ \mu\text{m}$ size plankton community were significantly correlated with ambient concentrations of these nutrients ($P < 0.05$) suggesting that N utilization by *Microcystis* was dependent on nutrient availability. The $>20\ \mu\text{m}$ phytoplankton group also obtained significantly more of its total N from organic compounds than did smaller plankton ($<20\ \mu\text{m}$), emphasizing the importance of organic N as a source of nutrition for *Microcystis*. In support of this hypothesis, Berman and Chava (1999) found that non-axenic cultured *Microcystis aeruginosa* consistently grew best using urea as a N source. Additionally, Dai et al. (2009) found that a Chinese strain of *M. aeruginosa* was able to utilize amino acids, such as alanine, leucine, and arginine to support growth and toxin production. Furthermore, genes associated with the uptake and utilization of urea and amino acids have been identified in *M. aeruginosa* (Kaneko et al., 2007; Frangeul et al., 2008). Given that *Microcystis* can efficiently utilize both organic and inorganic species of N, successful bloom mitigation strategies will need to target reductions in both N sources.

Phosphorus loading can favor the dominance of cyanobacteria within phytoplankton communities (Fogg, 1969; Smith, 1986; Downing et al., 2001) and may also specifically promote the density and/or toxicity of *Microcystis*. For example, Utkilen and Gjørlme (1995) found that an increase in P concentrations can lead to an increase in MCY content of *Microcystis* cells. Until recently, most field work conducted relating the toxicity of cyanobacteria

blooms to P have been correlative field studies which found MCY to be both positively and negatively correlated with various P pools (Wicks and Thiel, 1990; Kotak et al., 1995; Lahti et al., 1997; Rinta-Kanto et al., 2009). Recent field studies in North America examining MCY+ and MCY– strains of *Microcystis* suggest that MCY+ strains of *Microcystis* dominated the community during times of elevated inorganic P (DIP) concentrations whereas MCY– strains became more abundant when DIP concentrations were depleted (Davis et al., 2010). Consistent with this trend, MCY+ strains were enhanced by experimental P loading more frequently than MCY– strains (Davis et al., 2009, 2010). These findings parallel the work of Vézé et al. (2002) who reported that the growth rates of MCY+ *Microcystis* cultures exceeded MCY– strains under high orthophosphate concentrations. Since some MCY+ have more light-harvesting pigments than MCY– strains (Hesse and Kohl, 2001), the RNA and DNA required for the synthesis of both light-harvesting pigments and microcystin by MCY+ strains may represent a significant P requirement not present in MCY– strains.

Recent genomic sequencing of two strains of *Microcystis* (Kaneko et al., 2007; Frangeul et al., 2008) has revealed an array of genes involved in the utilization of P including two high affinity phosphate binding proteins (*pstS* and *sphX*) and a putative alkaline phosphatase (*phoX*). Subsequent sequence analyses among 10 clones of *M. aeruginosa* has demonstrated that these genes are present and conserved within the species and are strongly up-regulated (50–400-fold) by low DIP conditions ($<2\ \mu\text{M}$) but not by organic P sources (Harke et al., 2011). Since *Microcystis* dominates phytoplankton assemblages in summer when levels of DIP are often low (Bertram, 1993; Wilhelm et al., 2003) and/or dominate lakes with low DIP and high organic P (Heath et al., 1995; Vanderploeg et al., 2001; Raikow et al., 2004), this species may rely on *pstS*, *sphX*, and *phoX* to efficiently transport DIP and exploit organic sources of P to form blooms.

3.2.2. Potential climate change effects

Microcystis grows and photosynthesizes optimally at, or above, $25\ ^\circ\text{C}$ (Konopka and Brock, 1978; Takamura et al., 1985; Robarts and Zohary, 1987; Reynolds, 2006; Jöhnk et al., 2008; Paerl and Huisman, 2008, 2009) and within an ecosystem setting, *Microcystis* has been shown to out-compete species of eukaryotic algae at even higher temperatures ($\geq 30\ ^\circ\text{C}$; Fujimoto et al., 1997). Temperature effects on stratification may further promote this genus. For example, like many bloom-forming cyanobacteria, *Microcystis* can alter its position in the water column by regulating gas vesicle production (Walsby, 1975; Walsby et al., 1997) and negatively buoyant carbohydrate stores (Kromkamp and Walsby, 1990; Visser et al., 1995, 1997). Since strong stratification generally favors the proliferation of buoyancy regulating cyanobacteria (Kanoshina et al., 2003; Jacquet et al., 2005; Fernald et al., 2007; Jöhnk et al., 2008), increasing water temperatures that simultaneously increase stratification will further promote the dominance of cyanobacteria such as *Microcystis* (Paerl and Huisman, 2009). Beyond stratification, warmer temperatures also decrease water viscosity, a change that may increase the sedimentation rate of eukaryotic algae and further strengthen the competitive advantage of *Microcystis*.

Although theoretical studies have predicted that *Microcystis* and other bloom forming cyanobacteria will dominate under higher temperatures, information regarding how subpopulations of *Microcystis* will be affected by changes in water temperature has been scarce. Davis et al. (2009) conducted surveys and temperature manipulation experiments in multiple ecosystems across the temperate northeast USA and found that *Microcystis* became the dominant phytoplankton species present at all six study sites as temperatures reached their annual maximum. During field-based experiments, a $\sim 4\ ^\circ\text{C}$ increase in temperatures yielded significantly

higher growth rates for the MCY+ cells in most experiments, while the growth rates of MCY– cells were enhanced by higher temperature in only a third of experiments conducted (Davis et al., 2009). Consistent with these trends, Kim et al. (2005) found that toxic *Microcystis* strains cultured at 25 °C had more *mcyB* transcripts than cultures reared at 20 °C. Collectively these studies suggest that higher temperatures not only promote *Microcystis* blooms but may favor the proliferation of MCY+ strains, and/or strains with more MCY synthetase gene operons.

Changes in salinities due to changes in drought/storm cycles may affect *Microcystis* distribution and toxin production, since toxin production can increase with salinity. For instance, *Microcystis* PCC 7806 has high salt tolerance compared to most other freshwater phytoplankton (Tonk et al., 2007). This suggests that in freshwater ecosystems exposed to increasing salinity *Microcystis* may gain an advantage over other phytoplankton species with lower salt tolerances and may become more toxic (Robson and Hamilton, 2003).

The impacts of rising CO₂ concentrations on cyanobacterial blooms is an area of research that has not, to date, been explored in great detail and as described above, their precise response to these conditions is uncertain. A recent study investigating the impacts of increased CO₂ concentrations on competition between MCY+ and MCY– strains of *Microcystis* found MCY+ strains dominated at low CO₂ concentrations, whereas MCY– strains were more abundant under elevated CO₂ concentrations (Van de Waal et al., 2011). The authors note that prior studies have found that MCYs could play a role in the acquisition of CO₂ at low concentrations (Jähnichen et al., 2001, 2007). Furthermore, another study found elevated concentrations of MCYs in the carboxysomes of cyanobacteria (Gerbersdorf, 2006). Given that previous research has demonstrated that elevated temperature favors MCY+ *Microcystis* strains (Davis et al., 2009) the response of this harmful cyanobacterial bloom species to future climate change scenarios that include temperature and CO₂ concentrations is difficult to predict. Further research into the response of *Microcystis* to changes in CO₂ concentrations alone, and in conjunction with other global change parameters, is needed to better understand these interactions.

3.3. *Cylindrospermopsis*

The cyanobacterium *Cylindrospermopsis* is a solitary, filamentous diazotroph. It was once thought to be a strictly tropical/subtropical species being first identified in Java in 1912 (Komárková, 1998). In the past decade there has been a substantial expansion in its geographical range across every continent, except Antarctica: Australia/Oceania (Hawkins et al., 1985; Wood and Stirling, 2003), North America (Chapman and Schelske, 1997; Hamilton et al., 2005; Hong et al., 2006), South America (Branco and Senna, 1996; Bouvy et al., 2006; Figueredo and Giani, 2009), Europe (Fastner et al., 2003; Saker et al., 2003; Briand et al., 2004; Monteiro et al., 2011), Africa (Dufour et al., 2006; Mohamed, 2007) and Asia (Chonudomkul et al., 2004). *Cylindrospermopsis* was first deemed a harmful bloom species after a toxic bloom event in 1979 caused acute hepato-enteritis and renal damage among more than 150 people on Palm Island, off the coast of North Queensland, Australia (Hawkins et al., 1985; Carmichael, 2001). The structure of cylindrospermopsin (CYN), the toxin responsible, was determined in 1992 (Ohtani et al., 1992), when the mystery of the so-called “Palm Island disease” was resolved (Griffiths and Saker, 2003). Subsequently, it has been shown that other cyanobacteria including *Umezakia natans* (Harada et al., 1994), *Aphanizomenon ovalisporum* (Shaw et al., 1999; Carmichael, 2001), *Lyngbya wollei* (Seifert et al., 2007), *Raphidiopsis mediterranea* (McGregor et al., 2011), and *Anabaena lapponica* (Spoof et al., 2006) also are capable of producing CYN.

Although, *Cylindrospermopsis raciborskii* can be found on almost every continent, like most cyanobacterial bloom species the ability to produce CYN is not universal. *C. raciborskii* has CYN producing (CYN+) and non-CYN producing (CYN–) strains identifiable by the presence or absence of the CYN biosynthesis gene cluster (*cyrA* – *cyrO*; Mihali et al., 2008). Lagos et al. (1999) found that Brazilian strains of *C. raciborskii* do not produce CYN although some strains do produce the neurotoxin, saxitoxin. Also, previous studies have found that European and Asian *C. raciborskii* strains can be toxic to mice but do not contain any of the known cyanotoxins (Fastner et al., 2003; Saker et al., 2003). While there have been accounts of CYN being associated with systems containing *Cylindrospermopsis* in North America (Burns, 2008) and Italy (Messineo et al., 2010), no North American or European strain has been found to produce CYN or contain the CYN synthesis genes (Neilan et al., 2003; Kellmann et al., 2006; Yilmaz et al., 2008). Therefore, only Australian (Hawkins et al., 1985; Ohtani et al., 1992), New Zealand (Wood and Stirling, 2003) and some Asian (Li et al., 2001b; Chonudomkul et al., 2004) strains of *C. raciborskii* have been found to produce CYN with Australian and New Zealand strains also producing the CYN analogue, deoxy-cylindrospermopsin (Norris et al., 1999; Wood and Stirling, 2003).

3.3.1. Potential nutrient effects

C. raciborskii is a diazotroph, but low DIN conditions are not a prerequisite for blooms. A microcosm experiment examined the competition between *C. raciborskii* and another diazotroph, *Anabaena* spp. found that *C. raciborskii* was a stronger competitor for DIN than *Anabaena* (Moisander et al., 2008). Studies have shown that under DIN replete conditions, DIN uptake rates were higher than N fixation rates for *C. raciborskii*-dominated waters (Présing et al., 1996; Burford et al., 2006). Since diazotrophy is an energetically costly biochemical process, it is not surprising that ammonium is preferentially used, when available. Laboratory studies have confirmed that *C. raciborskii* growth rates were fastest when N was supplied as ammonium, followed by nitrate, then urea (Saker et al., 1999; Hawkins et al., 2001; Saker and Neilan, 2001). It has been proposed that activation of N₂-fixation was dependent on the N content of the cells (Spröber et al., 2003). Therefore, *C. raciborskii* seems to display a flexible N strategy: when DIN concentrations are sufficient, this source is used, and during periods of depletion, N₂-fixation is employed.

Little is known about the effect of N on CYN production. Several studies have investigated the impact of different sources of DIN on CYN content of Australian isolates of *C. raciborskii* and found that the highest intracellular CYN content (reported as % of freeze-dried weight) were in the cultures devoid of a fixed N source and lowest in cultures grown with saturating concentrations of ammonium (Saker et al., 1999; Saker, 2000; Saker and Neilan, 2001). This contrasts with patterns of growth rates that were highest in the presence of ammonium and the lowest in the absence of a fixed N source (Saker et al., 1999; Saker and Neilan, 2001). Mihali et al. (2008) hypothesized that increased intracellular CYN content in the absence of fixed N was due to the flanking of the CYN biosynthesis gene cluster in the *C. raciborskii* genome by *hyp* gene homologs associated with the maturation of hydrogenases. Since the *hyp* gene cluster is controlled by the global N regulator (*ntcA*; activates the transcription of the N assimilation genes) in another cyanobacterium, *Nostoc* sp. strain PCC73102, it is plausible that the *hyp* genes and, therefore, the CYN biosynthesis gene cluster are under the same regulation in *C. raciborskii* (Mihali et al., 2008).

Phosphorus appears to play an important role in the dominance of, and CYN production by, *C. raciborskii*. This species blooms in reservoirs and lakes when phosphate concentrations are below detection limits (Padisák and Istvanovics, 1997; Burford and O'Donohue, 2006). Istvánovics et al. (2000) showed that a

European strain of *C. raciborskii* had a high P affinity and storage capacity, and consistent with this finding, field studies have concluded *C. raciborskii* dominance may be related to its superior DIP scavenging ability under stratified, low DIP concentrations (Padisák, 1997; Shafik et al., 2001; Antenucci et al., 2005; Posselt et al., 2009). Furthermore, a recent laboratory study showed that *C. raciborskii* grows faster under P limitation when there is sufficient supply of DIN (Kenesi et al., 2009). Other studies have found that CYN concentrations have been positively correlated with total P concentrations (Wiedner et al., 2008) and that CYN production rates are positively correlated with *C. raciborskii* growth rates in P-limited cultures during exponential growth (P. Orr, personal communication). In a manner similar to *Microcystis*, the recent sequencing of an Australian strain of *C. raciborskii* (Stucken et al., 2010) allowed for identification of genes associated with P uptake and utilization that may be related to its ability to persist under low P conditions. *C. raciborskii* contains the genes to utilize inorganic and organic P including high affinity phosphate binding proteins (*pstS*, *sphX*), phosphonate uptake (*phnC,D,E*) and metabolism (*phnG-M,X,W*), and phosphorus ester metabolism (*phoA*). In laboratory cultures, *C. raciborskii* has been shown to utilize DOP, giving it an advantage over algae that do not utilize this P source in low DIP environments (Posselt, 2009).

3.3.2. Potential climate change effects

The growth response of *C. raciborskii* to temperature has been examined using multiple strains isolated from both temperate and tropical areas (Briand et al., 2004; Chonudomkul et al., 2004). In studies of subtropical and tropical reservoirs in Australia, *C. raciborskii* was found to be chronically dominant in tropical reservoirs, but only bloomed during summer in the subtropics (Bouvy et al., 2000; McGregor and Fabbro, 2000; Burford and O'Donohue, 2006; Burford et al., 2007). Studies have also found that *C. raciborskii* dominates temperate systems at higher temperatures (i.e. summer months; Hamilton et al., 2005; Conroy et al., 2007). *C. raciborskii* displays positive net growth from 20 to 35 °C, with maximum rates at ~30 °C (Saker and Griffiths, 2000). This temperature tolerance explains the capacity of *C. raciborskii* to invade both temperate and tropical areas of the world as well as its seasonality in sub-tropical and temperate ecosystems (e.g. Chapman and Schelske, 1997; Fastner et al., 2003; Briand et al., 2004; Hong et al., 2006; Messineo et al., 2010). It has been proposed that cyanobacteria will increasingly dominate freshwater systems due to global warming (Padisák, 1997; Paerl and Huisman, 2008) and the high temperature optima for maximal growth in *C. raciborskii* indicates this species is one of the most likely cyanobacteria to benefit from climatic warming. Consistent with this hypothesis, Wiedner et al. (2007) has shown that growth initiation of *C. raciborskii* is controlled by temperature in German lakes and has proposed that the invasion of *C. raciborskii* into these lakes is the result of global climate change.

Temperature has been found to play a key role in the production of CYN, although there seems to be a “disconnect” between optimal growth temperature and optimal CYN production temperature for *C. raciborskii*. Saker and Griffiths (2000) found that cell toxicity was highest at 20 °C, but that optimal growth occurred between 25 and 30 °C. Moreover, they found a negative correlation between temperature and CYN production between 20 and 35 °C with no CYN production at 35 °C despite continued growth at this temperature. This and other studies suggest that although maximum *C. raciborskii* growth rates occur at higher temperatures (25–35 °C; Saker and Griffiths, 2000; Briand et al., 2004), these temperatures produce cells with lower CYN content.

Although it has been hypothesized that enhanced stratification will lead to more sustained cyanobacterial blooms (Paerl and Huisman, 2008, 2009), this hypothesis may be less applicable to *C.*

raciborskii. *C. raciborskii* often blooms in stratified, deeper reservoirs (>15 m) (McGregor and Fabbro, 2000). Severe blooms of *C. raciborskii* occurred in a subtropical reservoir during periods of low rainfall, and when the water column was more stable (Harris and Baxter, 1996). It was concluded that vertical stratification provided a competitive advantage for *C. raciborskii* over other algal species likely due to its superior DIP scavenging ability under stratified, low DIP concentrations (Antenucci et al., 2005; Burford and O'Donohue, 2006). Interestingly, the installation of a destratification unit in this reservoir designed to reduce stratification did not mitigate *C. raciborskii* blooms but rather yielded earlier bloom initiation and a longer persistence of blooms (Antenucci et al., 2005; Burford and O'Donohue, 2006). This is likely due to the ability of cells to photoadapt to dark and fluctuating light conditions (O'Brien et al., 2009). Laboratory studies have shown that *C. raciborskii* has low light requirements for optimal growth (Shafik et al., 2001; Briand et al., 2004; Dyble et al., 2006). Consistent with this finding, *C. raciborskii*, is not positively buoyant, but does have very low rates of sinking (Kehoe, 2010). Collectively, these findings suggest strong stratification is not a requisite condition for *C. raciborskii* blooms.

4. Estuarine environments

There are several genera of euryhaline cyanobacteria that bloom in estuarine environments with a range of salinities (Paerl, 1988; Stal and Zehr, 2008). The site of perhaps the most widely studied estuarine cyanobacterial blooms is the Baltic Sea, one of the largest brackish water bodies in the world. This system has been experiencing an acceleration of anthropogenic nutrient inputs from a densely populated (~80 million people) watershed in recent decades (Larsson et al., 1985; Elmgren, 2001). Blooms of diazotrophic cyanobacteria are common during the summer months in the Baltic (Edler, 1979; Stal et al., 2003) sometimes covering >100,000 km² (Kahru, 1997). It has been hypothesized that these blooms have been regular features of this ecosystem since 7000 years before present, when the Baltic Sea first became a brackish water body (Bianchi et al., 2000). In contrast, Zillén and Conley (2010) argue that the Baltic Sea did not experience these events until the recent emergence of anthropogenic P loading and deep water hypoxia during summer. Regardless, cyanobacterial blooms have been documented in all basins of the central Baltic Sea and in the Gulf of Finland (Karjalainen et al., 2007) and are becoming more frequent and intense in most areas (Kahru et al., 1994; Finni et al., 2001; Poutanen and Nikkilä, 2001; Mazur-Marzec et al., 2006) including the Bothnian Sea where, until recently, these events had been rare (Niemi, 1979; Kahru et al., 1994).

The three primary bloom-forming cyanobacterial genera in the Baltic Sea are *Nodularia*, *Aphanizomenon*, and *Anabaena* (Fig. 1B). The sole producer of cyanotoxins in the Baltic was thought to be *Nodularia* as *Aphanizomenon* had been reported to be non-toxic (Sivonen et al., 1989; Repka et al., 2004). Karlsson et al. (2005) suspected that *Anabaena* produced MCYs and recent studies have confirmed this (Halinen et al., 2007). Since *Anabaena* has been discussed above and since *Nodularia* spp., which produces the hepatotoxin nodularin, is the main toxin producing and best-studied cyanobacterium found in this system, this review will focus primarily on the impacts of continued eutrophication and climatic change on this cyanobacterium but will also consider competition between this genera and *Aphanizomenon*.

4.1. *Nodularia*

Nodularia spp. blooms occur in brackish waters worldwide (Sellner, 1997; Bolch et al., 1999; Moisander and Pearl, 2000) and

N. spumigena was the species responsible for the first well documented bloom of a toxic cyanobacterial species in the world (Francis, 1878). Komarek et al. (1993) differentiated strains of *Nodularia* from the Baltic Sea by multiple ecological and morphological factors including the presence of gas vesicles, the dimensions and shapes of vegetative cells, heterocytes, akinetes, and the size and shape of trichomes. However, it was later shown that morphological features did not accurately differentiate *Nodularia* strains in the Baltic (Barker et al., 1999). It is currently believed that there are only three species of *Nodularia* in the Baltic Sea, one planktonic, *N. spumigena*, and two benthic (*N. sphaerocarpa* and *N. harveyana*; Laamanen et al., 2001; Janson and Granéli, 2002; Lyra et al., 2005). The latter two are relatively uncommon and found only in coastal habitats (Lyra et al., 2005). *Nodularia spumigena* produces nodularin (NOD), which can have severe negative impacts when ingested by terrestrial vertebrates (Rinehart et al., 1988; Runnegar et al., 1988; Eriksson et al., 1990) including the promotion of liver tumors and acts directly as a liver carcinogen (Carmichael et al., 1988; Sivonen et al., 1989), due to inhibition of protein phosphatases (Ohta et al., 1994). Nodularin can compromise up to 2% of cellular dry weight of *N. spumigena* (Komarek et al., 1993).

Similar to many cyanotoxins, NOD is synthesized non-ribosomally by a multifunctional enzyme complex consisting of both peptide synthetase and polyketide synthase modules as well as tailoring enzymes (*ndaA* – I; Moffitt and Neilan, 2004). Koskenniemi et al. (2007) developed a qPCR assay for *Nodularia* spp. and found that *ndaF* gene copies were strongly correlated with NOD concentrations in the Baltic Sea, a finding that parallels those for *Microcystis*, MCY, and the *mcyD* gene in North America (Davis et al., 2009, 2010). *N. spumigena* is the only known NOD-producing, bloom-forming *Nodularia* species in the Baltic Sea (Sivonen et al., 1989; Kononen et al., 1996; Stal et al., 2003; Krüger et al., 2009). In this section we discuss the potential impacts of eutrophication and climate change on the growth and NOD production of *Nodularia* spp. in general, and *N. spumigena*, in particular.

4.1.1. Nutrients

Eutrophication and resulting hypoxia associated with stratification strongly influence the ecology of the Baltic Sea ecosystem (HELCOM, 2007). Over geological time, prolonged periods of hypoxia in the Baltic Sea have paralleled warmer climatic conditions (Zillén et al., 2008). Hypoxia enhances P fluxes from sediments, decreasing N:P ratios and favoring blooms of diazotrophic cyanobacteria (Vahtera et al., 2007). Continued increases in global temperatures are likely to promote longer periods of stratification and hypoxia and, increased fluxes of N and P from sediments (Wulff et al., 2007). As described below, this could lead to more prolonged and intense cyanobacterial blooms in the Baltic.

Availability of phosphorus affects the spatial and temporal distribution of cyanobacteria in the Baltic Sea (Niemi, 1979). Summer stratification promotes hypoxia, P-fluxes, and, as a consequence, blooms of diazotrophic cyanobacteria in the Baltic (Fonselius, 1978; Lindahl et al., 1980; Stockner and Shortreed, 1988). Furthermore, in shallower areas of the Baltic Sea, wind-driven re-suspension of P from bottom sediments (Blomqvist and Larsson, 1994; Heiskanen and Leppänen, 1995) as well as P from terrestrial sources and river discharge (Stepanovskas et al., 2000, 2002) may facilitate bloom formation. Of the three primary bloom forming cyanobacteria in the Baltic, *Nodularia* appears to be best adapted to low-P conditions (Uehlinger, 1981; Wallström et al., 1992; DeNobel et al., 1997), whereas *Aphanizomenon* may be a better competitor for higher levels of available P (Wallström, 1988; Grönlund et al., 1996; Kononen et al., 1996; Kononen and Leppänen, 1997). Another study found that *Aphanizomenon* populations were dependent on ample P concentrations; whereas

Nodularia seemed to grow well at a range of P concentrations (Vahtera et al., 2007). This may be due to *Nodularia*'s ability to rapidly utilize pulses of P as well as a high P storage capacity (Mur et al., 1999; Vahtera et al., 2007) although this has been debated (Larsson et al., 2001; Kangro et al., 2007). Collectively, these findings suggest management plans aimed towards reducing P loads may favor a shift in dominance among cyanobacteria from *Aphanizomenon* to *Nodularia*.

Like most microbes, *Nodularia* can produce alkaline phosphatase (APase) to utilize the monophosphate esters when orthophosphate is depleted. *Nodularia* is well-adapted to take advantage of organic P as it has a lower substrate half-saturation constants (K_M) and higher $V_{max}:K_M$ ratio of the APase enzyme than *Aphanizomenon* suggesting it has a higher affinity for organic P (Degerholm et al., 2006). Compared to other phytoplankton in the Baltic, *N. spumigena* populations had a higher percentage of cells displaying APase activity and were superior competitors for DOP (Vahtera et al., 2010). The ability of *Nodularia* to efficiently utilize DOP is consistent with the hypothesis that reductions in DIP may promote a succession of cyanobacterial communities towards this genus.

Availability of phosphorus has been shown to affect NOD production in *Nodularia*. Expression of the *nda* gene cluster increased in response to DIP starvation (Jonasson et al., 2008) but measurements of intracellular and extracellular NOD indicated that levels did not vary significantly with P depletion (Repka et al., 2001; Jonasson et al., 2008), suggesting the existence of a post-transcriptional control of NOD production. Interestingly, Lehtimäki et al. (1994, 1997) reported that high P concentration yielded higher NOD production while Repka et al. (2001) found that *Nodularia* biomass increased with increasing P while NOD concentrations did not. Lastly, Lehtimäki et al. (1994) found that NOD– strains of *Nodularia* grew better than NOD+ strains at low P concentrations which suggests that, in a manner similar to *Microcystis*, synthesis of this hepatotoxin represents an additional P burden for NOD+ cells (Vézic et al., 2002; Davis et al., 2009, 2010). Clearly, the role of P in NOD production is not yet fully understood.

Marine primary production is generally considered to be N limited (Paerl, 1988) and since *Nodularia* spp. are diazotrophic, their dynamics are controlled primarily by temperature, salinity and P (Granéli et al., 1990; Plinski and Józwiak, 1999; Stal et al., 2003) but not N. Supporting this view, Vuorio et al. (2005) found that *N. spumigena* biomass decreased with increased fixed N concentrations while Jonasson et al. (2008) found the expression of the *nda* gene cluster decreased with increasing ammonium concentrations. Conversely, when ammonium concentrations were low, NDA synthesis genes, as well as N_2 -fixation genes, were upregulated (Jonasson et al., 2008). Vintila and El-Shehawey (2010) concluded that Baltic strains of *N. spumigena* are not efficient at utilizing DIN. Consistent with these findings, stratified conditions induced by the late summer water temperatures lead to N depletion (low DIN:DIP ratios) and favored the growth of diazotrophic cyanobacteria such as *Nodularia* spp. (Niemi, 1979; Kononen et al., 1996; Stal et al., 1999).

4.1.2. Potential climate change effects

Studies have found that *Nodularia* spp. typically grows optimally at temperatures between 20 and 25 °C (Lehtimäki et al., 1994, 1997), whereas its primary cyanobacterial competitor, *Aphanizomenon* spp., grows faster at lower temperatures (16–22 °C; Lehtimäki et al., 1994, 1997). High temperatures (25–30 °C) promoted the growth and NDA production by NDA+ *Nodularia* spp. (Lehtimäki et al., 1997; Hobson and Fallowfield, 2003), whereas NDA– strains of *Nodularia* grew better than NDA+ strains at lower temperatures (Lehtimäki et al., 1994). Therefore, continued climatic warming will likely promote greater abundances and toxin synthesis by NDA+ *Nodularia* populations in the Baltic Sea.

To date, there has only been a single investigation of the effects of increasing CO₂ on *Nodularia* spp. Czerny et al. (2009) found that *N. spumigena* exposed to higher CO₂ concentrations displayed reduced cell division rates and N₂-fixation rates and hypothesized that *N. spumigena* is well-adapted to the low CO₂/high pH conditions that develop during dense blooms in the poorly buffered brackish Baltic (Thomas and Schneider, 1999). This hypothesis is consistent with several other studies that reported cyanobacteria can out-compete eukaryotic algae under high pH and low CO₂ conditions (Shapiro and Wright, 1990; Oliver and Ganf, 2000). Hence, rising CO₂ concentrations may reduce the severity of *N. spumigena* blooms by causing a shift in dominance to species that are positively affected by the increased CO₂ concentrations. Given the scarcity of research on this topic and that expected higher temperatures will favor the growth of *N. spumigena* (see above) further research is required to better understand the possible trajectories of this genera in the face of climate change.

5. Marine environment

The prevalence of cyanobacterial blooms in aquatic environments generally follows the hierarchy of freshwater > estuarine/brackish > marine systems (Fristachi and Sinclair, 2008). Dinoflagellates have often been the more commonly studied marine HAB, possibly due in part to their acute effects on human health (Yasumoto and Murata, 1993; Wang, 2008). In contrast, the harmful effects of marine cyanobacteria may be subtler and/or more chronic (e.g., BMAA). The most conspicuous marine cyanobacterial bloom formers that will be the foci of this review are filamentous, colonial members of the genera *Lyngbya*, and *Trichodesmium* and the coccoid cyanobacteria *Synechococcus* (Fig. 1C).

5.1. *Lyngbya*

Cyanobacteria of the genus *Lyngbya* are generally benthic species growing attached to seagrasses, macroalgae, corals and sediment. They also can form dense surface blooms when they episodically detach from their benthic substrates buoyed by gas vesicles and bubbles trapped within their filaments after active photosynthesis, especially under calm stratified conditions. This acts as a means of dispersal, and can also cause serious economic and health issues when blooms wash up on beaches necessitating cleanup of rotting, malodorous biomass (Watkinson et al., 2005; Albert et al., 2005; O'Neil and Dennison, 2005).

Lyngbya occur in many environments along the fresh to marine continuum with over 70 species described (Cronberg et al., 2003). The two most commonly reported bloom species are the freshwater/to brackish species *L. wollei* and the marine species *Lyngbya majuscula*, *Lyngbya confervoides*, *Lyngbya polychroa* (Paerl et al., 2008; Sharp et al., 2009), and *Lyngbya bouillonii* (Hoffmann and Demoulin, 1991; Hoffmann, 1999) have also been reported to often grow over corals (Paul et al., 2005). Recently, the lesser known freshwater species *Lyngbya hieronymusii* and/or *Lyngbya robusta* have been forming blooms in Lake Atitlan, Guatemala (Rejmánková et al., 2011). Cyanobacteria taxonomy is often imprecise, particularly in the case of the polyphyletic characteristics of the *Lyngbya* genera (Speziale and Dyck, 1992; Engene et al., 2011a, 2011b), and while improvements in classification have been made (Anagnostidis and Komárek, 1985, 1988, 1990; Komárek and Anagnostidis, 1989, 2005), including the recent reclassification of some *Lyngbya* species to the genus *Moorea* (Engene et al., 2011b), it is clear molecular analyses are necessary, and will assist in reclassifications

(Komárek and Golubic, 2005; Komárek, 2006; Engene et al., 2011a). The ambiguity of *Lyngbya* taxonomy and inherent problems in morphological identification are highlighted in recent work by Jones et al. (2011) who have sequenced the genome of *L. majuscula* “3D”, which has been in culture for 15 years, and was originally isolated from Curacao. In addition to finding a complex network of genes that suggests an enhanced ability to adapt to shifting conditions in dynamic coastal marine environments, this study also had the surprising result of not finding *nif* genes for N₂ fixation, despite multiple studies of this species across the world reporting it as being diazotrophic (Jones, 1990; Dennison et al., 1999; Lundgren et al., 2003; Elmetri and Bell, 2004; O'Neil and Dennison, 2005). Additionally, other researchers have specifically identified *nif* genes in *L. majuscula* (Joyner et al., 2008). It has been suggested that this may reflect “strain differences” (Engene et al., 2010) or co-mingling of different cyanobacteria or mis-identification of similar looking cyanobacteria (Jones et al., 2011). Clearly, this illustrates the need for better understanding of cyanobacteria taxonomy and refining of techniques to match morphological and molecular identifications (Engene et al., 2011a, 2011b).

The toxins produced by *Lyngbya* spp. seem to vary significantly not only by geographic location, but by environmental conditions and growth stage (Osborne et al., 2001; Capper et al., 2006). The fresh water species *L. wollei* is capable of producing saxitoxin (Onodera et al., 1997; Mihali et al., 2011) as well as cylindrospermopsin (Seifert et al., 2007). *L. majuscula*, the most commonly reported marine species, is found mainly in tropical waters and produces several demotoxic alkaloids, neurotoxins, as well as a plethora of bioactive compounds with natural product uses (Osborne et al., 2001; Nogle and Gerwick, 2002; Gerwick et al., 2008; Tan, 2007; Jones et al., 2011; Engene et al., 2011a), with 50 new bioactive peptides reported since 2007 alone (Liu and Rein, 2010). The sheer number of natural products isolated from the species *L. majuscula* alone, has prompted a re-examination of this genus and there are taxonomic reassignments that have currently been proposed (Engene et al., 2011a,b).

There have been several detailed reviews of toxins associated with *L. majuscula* (Moore, 1981; Osborne et al., 2001) which include Lyngbyatoxin-A (LTA), and debromoaplysiatoxin (DTA). Deleterious effects of these compounds include asthma-like symptoms and severe dermatitis in humans (Osborne et al., 2001, 2007). These compounds have also been implicated in tumor promotion in green sea turtles which may ingest *L. majuscula* growing epiphytically on seagrasses (Arthur et al., 2006, 2008). Additionally, one human fatality has been attributed to the presence of LTA in ingested green turtle meat (Yasumoto, 1998). More recently new microcolins, lyngbyamides and barbamides (see review Liu et al., 2011) have been identified in addition to previously reported bioactive deterrents to fish and invertebrate grazing (Pennings et al., 1996; Nagle et al., 1998; Capper et al., 2005, 2006; Capper and Paul, 2008).

Blooms of *L. majuscula* were first reported as toxic in Hawaii, USA, in the 1950s through the 1970s (Banner, 1959; Moikeha and Chu, 1971; Hashimoto et al., 1976). Large blooms have been reported since the late 1990s in several locations in Australia, most severely in Moreton Bay, Queensland off the coast of the city of Brisbane, resulting in severe dermatitis and asthma-like symptoms in fisherman (Dennison et al., 1999; Watkinson et al., 2005; Albert et al., 2005; O'Neil and Dennison, 2005). Blooms have also been reported in more pristine locations such as Shoalwater Bay, Queensland (Arthur et al., 2006), and on the Great Barrier Reef, at Hardy Reef (Albert et al., 2005). Most recently, blooms have been occurring in various locations in Western Australia in the Peel-Harvey Estuary near Perth and in Roebuck Bay, near Broome (Deeley, 2009) as well as in the Northern Territory in Darwin

Harbour (Drewry et al., 2010). Potential causes include increased nutrient input from groundwater (Environmental Protection Authority, 2008) and tidal creeks (Drewry et al., 2010). Blooms have also been reported in various locations in Florida (Paerl et al., 2008; Paul et al., 2005; Sharp et al., 2009). The Caribbean and the South Pacific have been active spots for *Lyngbya* isolates for natural products chemistry (e.g. Tan, 2007, 2010; Gerwick et al., 2008; Engene et al., 2011a).

5.1.1. Potential effects of nutrients

Many *Lyngbya* species are reportedly diazotrophs (Jones, 1990; Dennison et al., 1999; Elmetri and Bell, 2004; Lundgren et al., 2003; cf. Jones et al., 2011), fixing dinitrogen mainly at night. However, it appears to be very flexible in its N acquisition strategies, and can grow on inorganic as well as organic (urea) forms of N (O'Neil et al., 2004), similar to other diazotrophic cyanobacteria such as *Cylindrospermopsis*. Also, similar to other diazotrophs, *Lyngbya* growth and productivity is often stimulated by P (Elmetri and Bell, 2004; Watkinson et al., 2005; Ahern et al., 2006a, 2008). In addition to taking up nutrients from the water column, its benthic habitat permits utilization of redox-based, diel phosphorus and iron fluxes from sediments at night when fixation is at maximal capacity (Watkinson et al., 2005). Ammonium fluxes from the sediments are also observed at night, and given the flexible physiology of *L. majuscula*, it may switch between the most energetically efficient N source, ammonium, and N fixation, depending on availability (O'Neil et al., 2004; Paerl et al., 2008).

Blooms of *L. majuscula* have increased in abundance, severity, and duration in tropical and subtropical regions around the globe in the past several decades and in many instances blooms have been linked to anthropogenic eutrophication. In Australia, for example, *L. majuscula* had not been a conspicuous bloom former in 35 years of nearly daily observation on Hardy Reef, located offshore of the Whitsunday Islands along the Great Barrier Reef. However, *L. majuscula* began overgrowing branching corals, and benthic calcareous macroalgal species (e.g., *Udotea*; *Penicillus*) a few months after the installation of a tourist helicopter platform in the reef lagoon (Albert et al., 2005). The platform became a roost for hundreds of sea-birds, causing a concentrated source of guano-derived N and P, pooling at low tide, and it was hypothesized that this was stimulating *L. majuscula* productivity (Albert et al., 2005). Similarly, a lesser known freshwater species, *L. robusta*, began forming blooms in Lake Atitlan, Guatemala in 2008 after years of sustained nutrient inputs and increased runoff from tropical storm activity that increased P levels and decreased N:P ratios (Rejmánková et al., 2011).

Lyngbya, like other diazotrophs such as *Trichodesmium*, seems to be particularly sensitive to the availability of iron (Fe), a component of the nitrogenase enzyme responsible for nitrogen fixation (Kustka et al., 2003). It has been suggested that blooms of *L. majuscula* in Moreton Bay may be due in part to anthropogenic disturbance via industry and land development of Fe rich acid-sulphate soils, causing increased mobilization of iron from the terrestrial to aquatic environments (Pointon et al., 2008; Albert et al., 2005; Ahern et al., 2006b, 2007, 2008). Recently it has been demonstrated that *L. majuscula* can use superoxide radicals to obtain bio-available Fe by reducing Fe bound to organic ligands (Rose et al., 2005; Rose and Waite, 2006), which may partially explain its persistence in organic-rich waters such the Deception Bay region of Moreton Bay (Albert et al., 2005; Ahern et al., 2007). Addition of P, Fe and N have also been shown to increase productivity, N₂-fixation and some secondary metabolites in *L. majuscula* in bioassays (Elmetri and Bell, 2004) as well as in field studies in Guam (Kuffner and Paul, 2001) and Florida (Paerl et al., 2008), showing a consistency in factors affecting this species over broad geographic ranges.

5.1.2. Potential climate change effects

L. majuscula occurs in tropical and sub-tropical environments and grows at maximal rates between 24 and 30 °C (Watkinson et al., 2005). The high temperature requirements for *L. majuscula* are similar to those reported for other cyanobacteria (Robarts and Zohary, 1987; Paul, 2008; Paerl and Huismann, 2008, 2009). Projected temperature increases this century (IPCC, 2007) may increase the bloom persistence and duration of *L. majuscula* where they already occur, as well as increase its geographic range. This has already been observed in Moreton Bay, where small populations of *L. majuscula* now persist through winter months (C. Roelfsema UQ, personal communication). Its northern range on the East Coast of the US may be expanding with extensive blooms during summer months observed recently in Provincetown Massachusetts (J.M. O'Neil, personal observation.) and Penobscott Bay Maine (K.A. Studholme UMCES, personal communication).

Beyond affecting growth, temperature and physical factors in the environments where blooms occur, may also influence secondary metabolite accumulation in cyanobacteria. (Watanabe and Oishi, 1985; Sivonen, 1990; Rapala et al., 1997; Lehtimäki et al., 1994; Paul, 2008). While temperature has not been directly linked to increased toxin production in *L. majuscula*, maximum toxin concentrations typically occur at the peak of bloom abundances that often coincide with temperature and growth maxima (Osborne, 2004). Given that bloom initiation of *L. majuscula* is in the benthos, periods of higher temperatures and water column stability, coincide with higher benthic light penetration and thus increase growth and productivity for *L. majuscula* (Watkinson et al., 2005). These changes may also directly or indirectly change other physiological features such as toxin production. For instance, it has been demonstrated that concentrations of the bioactive compound pitipeptolide A in *L. majuscula* increase under high light levels (Pangilinan, 2000, as cited in Paul, 2008). To date, no study has examined the effects of increasing CO₂ on *Lyngbya*.

5.2. *Trichodesmium*

Trichodesmium a colonial non-heterocystous filamentous member of the Oscillatoriales, is the most abundant bloom forming cyanobacteria in the marine pelagic environment with a pan-global distribution in oligotrophic waters of tropical and subtropical oceans (Capone et al., 1997; LaRoche and Breitbart, 2005). Blooms generally occur in stable clear water columns with low nutrient concentrations and high light penetration. Water column stability and the natural buoyancy of *Trichodesmium* colonies (due to strong gas vesicles) aid in the development of vast, conspicuous, surface blooms (Paerl, 1988; Capone et al., 1997). Blooms hundreds of kilometers in length have been observed in the Pacific (Kuchler and Jupp, 1988), Arabian Sea and Indian Ocean as well as the Caribbean and Gulf of Mexico (Capone et al., 1997). Such massive aggregations of biomass have significant impacts on nutrient cycling and ecosystem trophodynamics (Furnas et al., 1993; Karl et al., 2002). *Trichodesmium* has relatively slow growth rates (doubling times of 3–5 days) which may be an adaptation for exploiting the high energy, but low nutrient conditions of the oligotrophic open oceans where blooms tend to form (Capone et al., 1997; Stal and Zehr, 2008). *Trichodesmium* is generally outcompeted when it washes into coastal environments, but can thrive for periods of days to weeks causing large coastal blooms in tropical regions. When these blooms decay in enclosed coastal environments, they can leach nutrients, organic matter, and water soluble toxins, consequently causing localized anoxia, fish kills and mortality in marine organisms, including aquaculture species (Negri et al., 2004).

Trichodesmium has been widely studied due to its important role in biogeochemical cycling (Capone et al., 1997). The toxic nature of *Trichodesmium* blooms, on the other hand, has received considerably less attention (Kerbrat et al., 2010, 2011) despite anecdotal evidence of its deleterious effects, including dermatitis in Belize called “pica pica” (Villareal, 1995) and asthma-like symptoms in Brazil, called “Tamarande Fever” (Sato et al., 1963; Volterra and Conti, 2000). Similarly, beaches along the length of Queensland, Australia are often closed due to *Trichodesmium* blooms that cause skin irritations, asthma-like symptoms and headaches (Stewart et al., 2007). A neurotoxic factor from *Trichodesmium* was first investigated by Hawser et al. (1991) in the Caribbean which was found to negatively impact zooplankton and prawn communities (Hawser et al., 1992; Guo and Tester, 1994; Preston et al., 1988). Further, ciguatera-like toxic effects were noted (Hahn and Capra, 1992), and compounds extracted from mackerel implicated in ciguatera-like poisonings in Queensland, Australia. These compounds were indistinguishable from those found in *T. erythraeum* (Endean et al., 1993) with similar findings more recently in New Caledonia (Kerbrat et al., 2010). In the last decade, MCY-LR (Ramos et al., 2005) and a MCY-like cyclic peptide (Shaw et al., 2004) have also been isolated from *T. erythraeum*. More recently, analogs of MCY, cylindrospermopsin, and saxitoxin produced by *Trichodesmium* have been reported off the coast of Brazil (Proença et al., 2009), which will require lab studies to confirm.

Researchers in New Caledonia following up on the earlier “ciguatera-like” toxin findings, made the breakthrough isolation and identification of palytoxin and its derivative 42-hydroxypalytoxin (PLTXs) from both *T. erythraeum* and *T. thiebautii*. These compounds were not previously known to be produced by cyanobacteria, and had originally been isolated from the marine zooxanthid *Palythoa* and the marine dinoflagellate *Ostreopsis* (Kerbrat et al., 2011). This is a significant finding, in that human intoxications such as cluetoicism (which has symptoms that include: digestive disorders, paralysis, tachycardia, convulsions and respiratory distress) which occurs from eating plantivorous fish, could be cyanobacterial in origin, rather than previously being solely associated with *Ostreopsis* (Kerbrat et al., 2011). Researchers have also found other benthic cyanobacteria responsible for local intoxication from the same lagoonal regions in New Caledonia including *Hormothonium lyngbyaceus*, *Oscillatoria*, and *Phormidium* (Laurent et al., 2008). More information is needed to better understand effects of cyanobacterial toxins on ecosystem trophodynamics and human health.

5.2.1. Nutrients

Trichodesmium as a N₂ fixer, thrives in low nutrient environments, and is often limited by Fe or P (Sañudo-Wilhelmy et al., 2001; Karl et al., 2002; Mills et al., 2004; Bell et al., 2005). Colonies can assimilate multiple species of N, including organic forms such as urea and amino acids (Glibert and Bronk, 1994; Mulholland and Capone, 2001). *Trichodesmium* is capable of exploiting a variety of P sources including inorganic phosphate, phosphomonoesters, and phosphonate compounds (Dyhrman et al., 2006). Given its diazotrophic nature, and adaptations for growth on a range of P sources at low levels, eutrophication in terms of N and P would not be expected to promote *Trichodesmium* blooms. Iron, however, has been speculated to be able to increase *Trichodesmium* blooms on large basin scales when large dust storms, from the Sahara deposit Fe-rich particles as far as the Caribbean (Prospero, 1999, 2006; Lenes et al., 2001; Prospero and Lamb, 2003). Therefore, conditions such as “desertification” (Takeda and Tsuda, 2005) due to climate change, drought or anthropogenic influences such as land clearing, that increase transport and deposition of Fe-rich aeolian dust may result in increases in *Trichodesmium* and other cyanobacteria

blooms (Lenes et al., 2001; Pointon et al., 2008). There is some indication that organic N derived from large Fe-driven *Trichodesmium* blooms can then in turn provide a N source from N₂-fixation for other phytoplankton in the region including the red-tide dinoflagellate HAB species *Karenia brevis* in the Gulf of Mexico (Lenes et al., 2001; Walsh and Steidinger, 2001; Mulholland et al., 2006; Lenes and Heil, 2010).

5.2.2. Potential climate change effects

Trichodesmium is a tropical species that grows above 20 °C and thus may expand its range in the face of globally increasing temperatures (Hutchins et al., 2007; Stal and Zehr, 2008). Recently large blooms of *Trichodesmium* occurred in the vicinity of the Canary Islands when sea-surface temperature exceeding 27.5 °C promoted increased stratification. Blooms had not previously been recorded within this northwest African upwelling system (Ramos et al., 2005; Paul, 2008). Breitbarth et al. (2007) demonstrated that the correlation of *Trichodesmium* blooms with temperature were due to temperature-enhanced diazotrophic growth and suggested that the range and timing of *Trichodesmium* blooms may expand in the future. Higher temperatures will also increase stratification, shoal the mixed layer, and suppress the upwelling of nitrate (Doney, 2006), further promoting the growth of diazotrophic organisms such as *Trichodesmium*.

There have been several recent studies demonstrating that *Trichodesmium* experiences increased productivity, N₂-fixation and/or growth under higher pCO₂ levels (Barcelos e Ramos et al., 2007; Hutchins et al., 2007; Levitan et al., 2007, 2010a, 2010b, 2010c; Kranz et al., 2010a, 2009, 2011). *Trichodesmium* may be chronically C limited under bloom conditions, when high rates of photosynthesis increase pH, as well as physical boundary layer limitation (Kranz et al., 2010b). Therefore, under high light intensities and high CO₂ levels, *Trichodesmium* shifts more energy to nitrogen fixation, rather than towards acquiring carbon (Hutchins et al., 2007). Collectively, findings regarding both temperature and CO₂ and *Trichodesmium* suggest this cyanobacterium may be one of the “winners” in projected climate change scenarios (Hutchins et al., 2007, 2009).

5.3. *Synechococcus*

While *Synechococcus* is a cosmopolitan open ocean cyanobacterium (Zwirgmaier et al., 2008), it also forms harmful blooms in multiple ecosystems including Florida Bay, USA (Walters et al., 1992; Boesch et al., 1993; Fourqurean and Robblee, 1999; Sunda et al., 2006). These blooms cover large areas (100's of square km) and can last for months. Negative ecosystem impacts include anoxic events and increased light attenuation (Phlips and Badylak, 1996; Phlips et al., 1999), which has reduced the distribution of seagrass beds and corals communities (Hall et al., 1999). The blooms are also detrimental to fish (Boesch et al., 1993; Chasar et al., 2005), sponges (Butler et al., 1994; Peterson et al., 2006; Wall et al., 2011), and spiny lobsters (Butler et al., 1995). *Synechococcus* blooms are also known to inhibit zooplankton grazing (Goleski et al., 2010) due to the production of extracellular polysaccharides and/or cellular toxins such as MCY (Mitsui et al., 1989; Phlips et al., 1999; Carmichael and Li, 2006). The discovery of a haline strain of microcystin-producing *Synechococcus* is significant as production of this toxin has previously only been described in freshwater strains (Carmichael and Li, 2006).

5.3.1. Nutrients

Originally, nutrient loading had been hypothesized as a prime cause of *Synechococcus* blooms in Florida Bay (Phlips et al., 1999) and has been the focus of water quality management and restoration efforts there (Boesch et al., 1993). However, reigning

algal paradigms support the concept that increased levels of nutrients generally relieve the nutrient stress, and favor the growth of larger phytoplankton (Raven and Kubler, 2002), suggesting that other factors could be contributing to the blooms of small ($\sim 1 \mu\text{m}$) *Synechococcus* cells, including low predation rates. Consistent with this hypothesis, experimental inorganic nutrient loading to bloom waters in Florida Bay significantly decreased the relative abundance of *Synechococcus* in the plankton (Goleski et al., 2010), suggesting that nutrient loading is likely to discourage these blooms. *Synechococcus* blooms in Florida Bay are known to exploit organic matter for growth (Glibert et al., 2004; Boyer et al., 2006) and are therefore more likely to dominate under low inorganic nutrient conditions. These conclusions are also consistent with the notion that the primary niche of picocyanobacteria is oligotrophic, open ocean environments (Agawin et al., 2000).

5.3.2. Potential climate change effects

Regarding climate change, *Synechococcus* achieves maximal growth rates at higher temperatures ($\sim 30^\circ\text{C}$) than other cyanobacteria (Moore et al., 1995) and thus will potentially be promoted by future climatic warming. This is consistent with the strong temperature dependence of *Synechococcus* in coastal environments (Waterbury et al., 1986; Agawin et al., 1998; Gobler et al., 2002). *Synechococcus* dominance may potentially be further promoted by warming-enhanced stratification that minimizes inorganic nutrient fluxes to the upper mixed layer and maximizes the importance of use of organic nutrient compounds. High temperatures are likely to co-occur with high CO_2 in the future. In laboratory studies, Fu et al. (2007) found that increasing temperatures from 20°C to 24°C increased *Synechococcus* growth rates and when combined with increasing CO_2 concentration (from 380 ppm to 750 ppm) growth rates were further enhanced. Further study is needed to fully clarify how future climate change may influence harmful blooms caused by *Synechococcus*.

6. Synthesis and future directions

As this review has demonstrated, cyanobacterial blooms are promoted by higher temperatures and are often associated with high levels of anthropogenic nutrient loads, particularly with regard to P. Paradoxically, however, most cyanobacteria are superior competitors for low levels of inorganic P and have highly refined strategies for accessing P from organic compounds. These seemingly contradictory observations suggest that blooms of cyanobacteria occur as a sequence of events in temperate ecosystems whereby blooms of other, non-cyanobacteria phytoplankton are likely to precede cyanobacterial blooms and drawdown orthophosphate concentrations to low levels, a condition under which most cyanobacteria seem to thrive. As the non-cyanobacteria phytoplankton are succeeded, die and/or are grazed, their biomass will be remineralized into organic forms which most cyanobacteria are well adapted to exploit. In tropical ecosystems, high temperatures promote the rapid microbial assimilation of orthophosphate even in the face of high P loads, keeping concentrations chronically low, and favoring blooms of cyanobacteria. Concurrently low levels of N will further favor cyanobacteria that are diazotrophic and/or generally display highly flexible N acquisition strategies. Since cyanobacterial blooms typically occur under low CO_2 conditions, future increases in CO_2 associated with climate change may suppress harmful cyanobacterial blooms, although research on this topic is in its infancy.

The response of cyanobacteria to both eutrophication and global climate change effects (Fig. 2) are topics that will require intense research focus in the future (Paul, 2008; Hudnell and Dortch, 2008; Hudnell, 2008). Given the potential increase in the frequency and toxicity of cyanobacterial blooms in response to both direct and indirect effects of changing climatic conditions (Fig. 2), water management agencies will have to incorporate the changing physical and chemical conditions of watersheds into

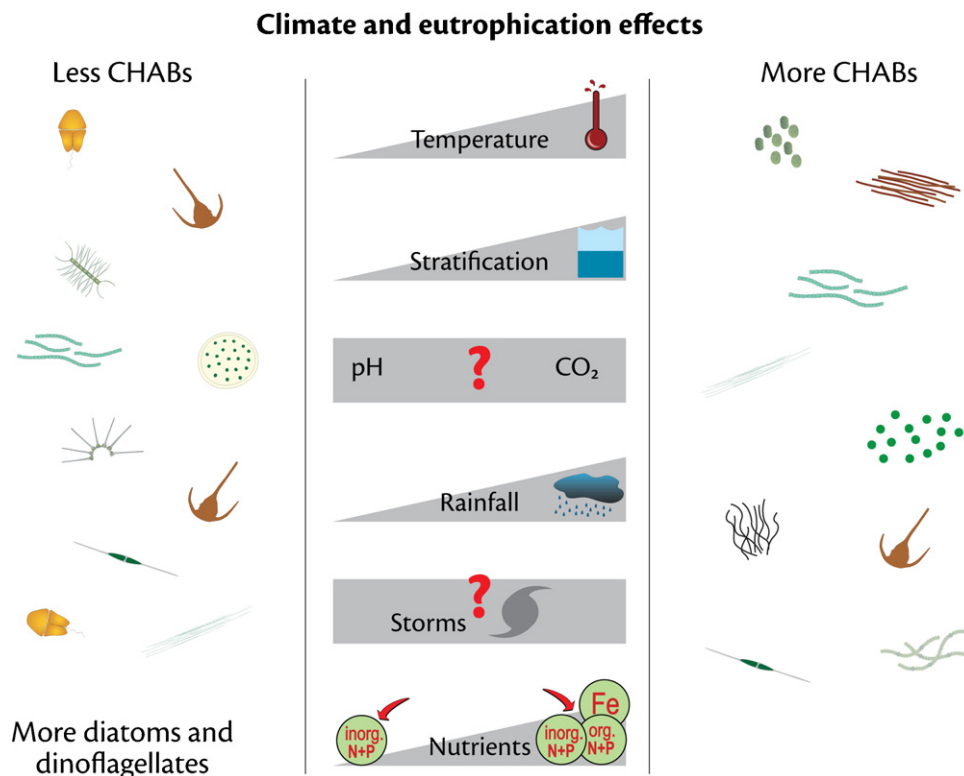


Fig. 2. Eutrophication and potential effects of climate change on Cyanobacterial Harmful Algal bloom (CHAB) abundance.

remediation/management strategies which, to date, have primarily focused on nutrient reduction. As discussed in this review, increased warming of surface waters will impact the viscosity and stratification of water columns. This will have a direct impact on the duration of hypoxic conditions in bottom waters of systems (i.e. Baltic Sea; Lake Erie, USA), nutrient cycling within the hypoxic zones (i.e. P, Fe) as well as have a significant impact on competition within the plankton community in surface waters and, therefore, must be considered in future management plans. Furthermore, changing climatic conditions will potentially alter rainfall patterns and thus the delivery of nutrients into aquatic ecosystems. Two scenarios are possible in different regions: (1) storms and rainfall will increase, lead to enhanced freshwater delivery of nutrients and decreased residence time, which may or may not stimulate harmful cyanobacterial blooms or other HAB species, depending on the physical factors including light and temperature; or (2) While such increased flow could initially suppress blooms by decreased residence times, increased turbidity and a reduction in stratification, subsequent drought periods with increased residence times and internal cycling of nutrients which could yield larger, more sustained harmful cyanobacterial bloom events. This pattern has already been seen in multiple systems worldwide (Paerl and Huisman, 2009). Therefore, the impacts of changing rainfall patterns must also be considered by water managers. To date, dissolved organic nutrients have rarely been considered in management/remediation strategies, although it has been well documented that cyanobacteria have flexible N and P acquisition strategies which include the uptake and utilization of organic compounds (see sections above). As nutrient loading of many systems worldwide increases, management agencies should consider reducing organic nutrient loads within remediation strategies.

As this review highlights, there have been a multitude of laboratory and field studies investigating many aspects of harmful cyanobacterial bloom ecology. One knowledge gap regarding cyanobacterial blooms is how CO₂ concentrations will impact these events within an ecosystem setting where harmful cyanobacterial bloom species are competing with other phytoplankton; most cyanobacteria – CO₂ studies have considered the cyanobacterial response only. Another outstanding issue is the focus of many studies on a single environmental variable (temperature or nutrients or CO₂ concentrations). Since changes in climatic conditions will not occur independently of each other, but rather simultaneously, it will be important to consider how the interactions of temperature, CO₂ and nutrients will impact the ecology of harmful cyanobacteria and their toxins as well as eukaryotic algal competitors. Given the vast amount of genomic sequencing that has been performed with cyanobacteria to date, genomic and molecular approaches will increasingly answer many of these key ecological questions, as well those associated with toxin production, and cyanobacteria phylogeny. Further, just as bottom-up controls of harmful cyanobacterial blooms will be impacted by future climatic changes so too will the top-down controls (i.e. grazing communities). Therefore, studies investigating the impacts of future climatic changes on higher trophic levels as they impact and are impacted by cyanobacterial blooms are warranted. Lastly, in addition to effects on biogeochemical cycles, food web dynamics, and ecosystem function, cyanobacterial blooms have the potential to significantly affect human health. The possibility of the wide-spread production of newly identified toxins such as BMAA, and the ability of a wider variety of species to produce known toxins, provides ample incentive for increased research and management of these organisms.

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