Minireview

Climate change: a catalyst for global expansion of harmful cyanobacterial blooms

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Summary

Cyanobacteria are the Earth's oldest known oxygen-evolving photosynthetic microorganisms, and they have had major impacts on shaping our current atmosphere and biosphere. Their long evolutionary history has enabled cyanobacteria to develop survival strategies and persist as important primary producers during numerous geochemical and climatic changes that have taken place on Earth during the past 3.5 billion years. Today, some cyanobacterial species form massive surface growths or 'blooms' that produce toxins, cause oxygen depletion and alter food webs, posing a major threat to drinking and irrigation water supplies, fishing and recreational use of surface waters worldwide. These harmful cyanobacteria can take advantage of anthropogenically induced nutrient over-enrichment (eutrophication), and hydrologic modifications (water withdrawal, reservoir construction). Here, we review recent studies revealing that regional and global climatic change may benefit various species of harmful cyanobacteria by increasing their growth rates, dominance, persistence, geographic distributions and activity. Future climatic change scenarios predict rising temperatures, enhanced vertical stratification of aquatic ecosystems, and alterations in seasonal and interannual weather patterns (including droughts, storms, floods); these changes all favour harmful cyanobacterial blooms in eutrophic waters. Therefore, current mitigation and water management strategies, which are largely based on nutrient input and hydrologic controls, must also accommodate the environmental effects of global warming.

Introduction

Cyanobacteria are the Earth's oldest known oxygen-producing organisms, with fossil remains dating back ~3.5 billion years (Schopf, 2000). Their proliferation during the Precambrian period is largely responsible for the modern-day, oxygen-enriched atmosphere, and subsequent evolution of higher plant and animal life (Knoll, 2003). Today, the cyanobacteria exhibit remarkable ecophysiological adaptations, including the ability to thrive in aquatic environments undergoing human-induced and naturally induced environmental change (Huisman et al., 2005; Paerl and Fulton, 2006). They can dominate a wide variety of ecosystems, ranging from oligotrophic oceans to eutrophic lakes, and from the tropics to polar regions (Pinckney and Paerl, 1998; Potts and Whitton, 2000; Stomp et al., 2007). They also occur as endosymbionts in diatoms, sponges, corals, lichens, ferns, and a variety of other organisms (Rai et al., 2000). Moreover, cyanobacteria are the only known oxygenic phototrophs capable of atmospheric nitrogen fixation, which has assured access to a virtually unlimited pool of nitrogen not available to their competitors (Paerl, 1990; Karl et al., 2002).

Human-induced environmental changes, most notably nutrient over-enrichment (particularly nitrogen and phosphorus) associated with urban, agricultural and industrial development, have led to accelerated rates of primary production, or eutrophication. This favours periodic proliferation and dominance by cyanobacteria in many freshwater and brackish ecosystems (Fogg, 1969; Huisman et al., 2005; Paerl and Fulton, 2006). Mass development of cyanobacteria, as harmful algal blooms (CyanoHABs), increases the turbidity of eutrophied lakes, reservoirs, lagoons and brackish waters (e.g. Baltic Sea) (Fig. 1). This, in turn, suppresses the establishment and growth of aquatic macrophytes and thereby negatively affects the underwater habitat for many invertebrates and fish species (Scheffer, 1998). Furthermore, dense cyanobacterial
blooms may cause night-time oxygen depletion, which can result in fish kills. Cyanobacterial blooms can also cause distinct odour problems by the production of geosmin and other musty chemicals (Izaguirre and Taylor, 2004; Uwins et al., 2007).

Lastly, some cyanobacterial bloom species produce toxic peptides and alkaloids, which are a major threat to the use of freshwater ecosystems and reservoirs for drinking water, irrigation, fishing and recreational purposes (Codd, 1995; Carmichael, 2001; Chorus, 2001). Ingestion of these cyanotoxins causes widespread and serious animal and human health problems, including liver, digestive and skin diseases, neurological impairment, and death (Carmichael, 2001; Cox et al., 2003; Huisman et al., 2005). Common toxin-producing cyanobacteria include the planktonic N₂-fixing genera Anabaena, Aphanizomenon, Cylindrospermopsis, Nodularia, the non-N₂-fixing genera Microcystis and Planktothrix, and the largely benthic N₂-fixing genus Lyngbya (Table 1).

Cyanobacterial blooms are currently a great threat to the ecological integrity and sustainability of some of the world’s largest and most resource-rich water bodies, including Lake Victoria in Africa (Verschuren et al., 2002), Lakes Erie and Michigan in US-Canada (Rinta-Kanto et al., 2005), Lake Okeechobee and Lake Ponchartrain in the USA (Paerl and Fulton, 2006), Lake Taihu in China (Guo, 2007), Lake Biwa in Japan (Maeda et al., 1992), the Baltic Sea in Northern Europe (Kanoshina et al., 2003; Suikkanen et al., 2007), the Caspian Sea in west Asia (Dumont, 1998), and many other ecologically and economically important lakes, rivers and estuaries (Huisman et al., 2005; Paerl and Fulton, 2006).

While there are well-established connections between nutrient enrichment and the predominance of cyanobacterial blooms (Fogg, 1969; Reynolds, 1987; Paerl, 1988), there are other environmental changes taking place that may play additional roles in promoting the recent upsurge and expansion of such blooms. In particular, there could...
be a link with global warming (Paerl and Huisman, 2008). Here, we review recent evidence that, in eutrophic waters, climate change provides a potent catalyst for the further expansion of cyanobacterial blooms on a global scale.

Influence of a changing climate on cyanobacterial blooms

Temperature effects

Rising temperatures favour CyanoHABs in several ways. As a group, cyanobacteria generally exhibit optimal growth rates at relatively high temperatures, usually in excess of 25°C (Robarts and Zohary, 1987; Coles and Jones, 2000). At these elevated temperatures, cyanobacteria compete most effectively with eukaryotic primary producers, such as diatoms, chlorophytes, cryptophytes and dinoflagellates (Elliott et al., 2006; De Senerpont Domis et al., 2007; Jöhnk et al., 2008). That is, as the growth rates of these eukaryotic taxa decline, cyanobacterial growth rates reach their optima (Fig. 2). This is exemplified by the temperature dependence of cyanobacterial blooms worldwide (Robarts and Zohary, 1987; Paerl, 1990; Kanoshina et al., 2003; Fernald et al., 2007), and the northward (in the northern hemisphere) and southward (in the southern hemisphere) spread of invasive species originating from the subtropics like Cylindrospermopsis (Padisák, 1997; Ryan et al., 2003; Wiedner et al., 2007).

In addition to the direct effects of rising temperatures on cyanobacterial growth, warming of surface waters also intensifies vertical stratification. The strength of vertical stratification depends on the density difference of water in the surface mixed layer (epilimnion) and in the deeper waters (hypolimnion). The density of water is a function of temperature, with a maximum density at ~4°C in freshwater ecosystems, and a quadratic decline with temperature above 4°C (Chen and Millero, 1986). As a result, rising temperatures reduce the density of the epilimnion, thereby strengthening the vertical stratification of aquatic ecosystems. Also, global warming lengthens the period of stratification. There is a tendency for many lakes in the temperate zone to stratify earlier in spring, the stratification is maintained throughout summer, and destratification of lakes is postponed to later in autumn (De Stasio et al., 1996; Peeters et al., 2007).

Many cyanobacterial species are able to uniquely exploit stratified conditions. In contrast to eukaryotic phytoplankton species, some bloom-forming cyanobacteria can form gas vesicles, which allow for buoyancy regulation (Walsby, 1975; Walsby et al., 1997). In turbulent waters with intense wind mixing, buoyancy does not provide much of an advantage as vertical mixing will distribute the cyanobacteria over the entire water column (Fig. 3). However, when temperatures increase and there is little wind mixing, the water column becomes stagnant and buoyant cyanobacteria will float upwards. This leads to the accumulation of dense surface blooms at the water surface (Fig. 3). The accumulation of large numbers of cells may lead to very

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<th>Table 1. Toxins produced by cyanobacteria.</th>
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<td>Cylindrospermopsin</td>
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<td>Nodularins</td>
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<td>Contact irritant-dermal toxins</td>
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<td>Debrisoquine-sulfotoxin, lyngbyatoxin</td>
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high toxin concentrations. As a consequence, the cyanotoxin concentrations in dense surface blooms are often several orders of magnitude higher than the toxin concentrations in the surrounding waters.

Cyanobacterial surface blooms have a distinct competitive advantage over other phytoplankton. Surface blooms take advantage of high levels of irradiance at the water surface to optimize their photosynthetic needs (Paerl et al., 1983; Huisman et al., 2004). Several taxa contain photoprotective accessory pigments (e.g., carotenoids, scytonemins) that ensure long-term survival under extremely high irradiance conditions (Paerl et al., 1983; Castenholz and Garcia-Pichel, 2000). Simultaneously, surface blooms cast shade upon non-buoyant eukaryotic phytoplankton deeper down in the water column, thereby suppressing their competitors (Huisman et al., 2004; Jöhnk et al., 2008) (Fig. 3). Most bloom-forming cyanobacteria can regulate their vertical position in strongly stratified waters, by counterbalancing the buoyancy of cellular gas vesicles by the accumulation of ballast in the form of carbohydrates (Kromkamp and Walsby, 1990; Visser et al., 1995; 1997). This enables bloom-forming taxa to migrate up and down, periodically obtaining nutrients from deeper waters, while subsequently returning to the surface as blooms (Fig. 4). Owing to its buoyancy regulation, the toxin-producing red cyanobacterium Planktothrix rubescens can form large populations at 10–20 m depth in stratified lakes, which may float up to the surface during autumn to form spectacular red surface blooms known as the ‘Burgundy blood phenomenon’ (Walsby et al., 2006). Enhanced vertical stratification during warm years has favoured the dominance of buoyant cyanobacteria in a wide variety of aquatic ecosystems (Kanoshina et al., 2003; Jacquet et al., 2005; Fernald et al., 2007; Jöhnk et al., 2008).

Rising temperatures not only strengthen vertical stratification, but also decrease the viscosity of water (Hutchinson, 1957). According to Stokes’ Law, the vertical velocity attained by small organisms such as cyanobacteria and other phytoplankton is inversely proportional to viscosity (Reynolds, 2006). Therefore, rising temperatures decrease the water’s resistance to vertical migration of phytoplankton. This will facilitate the formation of surface blooms by buoyant cyanobacteria, and will favour rapid vertical adjustment of migrating cyanobacteria to optimize their nutrient and light acquisition. Conversely, sinking diatoms suffer higher sedimentation losses when viscosity is reduced. These opposite responses further enhance the competitive advantage of buoyant cyanobacteria over sinking diatoms in stratified water bodies (Jöhnk et al., 2008).

It has even been shown that dense surface blooms of cyanobacteria may locally increase water temperatures, through the intense absorption of light by their photosynthetic and photoprotective pigments. In remote sensing studies, Kahru and colleagues (1993) found temperatures of surface blooms in the Baltic Sea to be at least 1.5°C above ambient waters. Another remote sensing study by Ibelings and colleagues (2003) documented that the surface temperature within cyanobacterial blooms in Lake IJsselmeer, the Netherlands, was 3°C higher than in surrounding surface waters. This could represent an important positive feedback mechanism, whereby buoyant cyanobacteria locally enhance surface temperatures, which in turn favours their own competitive dominance over eukaryotic phytoplankton (Hense, 2007).

Carbon dioxide effects

Dense algal blooms exhibit a strong demand for CO₂ to support photosynthetic growth, to the extent that the rate of CO₂ supply can at times limit the rate of algal biomass production (Paerl and Ustach, 1982; Ibelings et al., 1991). High rates of photosynthesis and hence high demand for CO₂ will restrict the availability of free CO₂. If and when this occurs, buoyant cyanobacteria have a distinct advantage over subsurface phytoplankton populations, as surface-dwelling organisms can directly intercept CO₂ from the atmosphere, thereby minimizing carbon limitation of photosynthetic growth and taking advantage of rising atmospheric CO₂ levels (Paerl and Ustach, 1982) (Fig. 3). Recent research has shown that increasing levels of atmospheric CO₂ may lead to acidification of both freshwater and marine surface waters (Caldeira and Wickett, 2004; Orr et al., 2005). In systems with dense cyanobacterial blooms, however, this effect is likely to be negated by increased bloom activity, which enhances CO₂ consumption and thereby elevates pH. Several cyanobacterial bloom species are capable of sustained growth under the alkaline conditions resulting from active photosynthesis and CO₂ withdrawal during
blooms, by using bicarbonate (HCO$_3^-$) as their carbon source (Kaplan et al., 1991).

**Rising salinities**

Summer droughts, rising sea levels and increased use of freshwater for agricultural irrigation have led to rising salinities in many parts of the world. Increased salination threatens the freshwater supply in many countries. It also has major impacts on freshwater plankton communities with repercussions for water quality and use. One such impact is increased vertical density stratification, which would benefit buoyant cyanobacteria known to take advantage of such stratification (Walsby et al., 1997; Huisman et al., 2004). In addition, some species of the common cyanobacterial genera *Anabaena*, *Microcystis* and *Nodularia* are quite salt tolerant, sometimes more tolerant than eukaryotic freshwater phytoplankton species. For instance, the growth rate of toxic strains of *Microcystis aeruginosa* remains unaffected by salinities ranging from 0 up to 10 g l$^{-1}$, which is 30% of the salinity of seawater (Tonk et al., 2007). Temporary salinity fluctuations of up to 15–20 g l$^{-1}$ may still allow survival of toxic *Microcystis* strains, but causes salt stress leading to leakage of cells and excretion of the toxin microcystin (Tonk et al., 2007). Likewise, *Anabaena aphanizomenoides* can withstand salt levels up to 15 g l$^{-1}$, while *Anabaenopsis* and toxic *Nodularia spumigena* even tolerate...
salinities of 20 g l\(^{-1}\) (Moisander et al., 2002). Laboratory experiments indicate that the nodularin content of \textit{Nodularia} correlates positively with salinity (Mazur-Marzec et al., 2005). The high salt tolerance of these ‘freshwater’ cyanobacteria is reflected by increasing numbers of blooms in brackish waters, for example, in the Baltic Sea in Scandinavia (Kanoshina et al., 2003; Suikkanen et al., 2007), the Caspian Sea in west Asia (Dumont, 1998), the Küçükçekmece Lagoon in Turkey (Albay et al., 2005), the Patos Lagoon in Brazil (Matthiessen et al., 2000), the Swan River Estuary in Australia (Robson and Hamilton, 2003), the San Francisco Bay Delta in California (Lehman et al., 2005) and Lake Ponchartrain in Louisiana (Dortch et al., 2001). Thus, increased salination of freshwater and brackish waters may favour cyanobacteria over other freshwater phytoplankton species. This, in turn, exposes other aquatic organisms and human users of these waters for recreation or fishing to elevated concentrations of cyanobacterial toxins.

\textbf{Changes in hydrology and the watershed}

Global warming and associated changes in local climate affect patterns, intensities and duration of precipitation and droughts. These hydrologic changes may further enhance cyanobacterial dominance. For example, larger and more intense precipitation events will increase nutrient enrichment of water bodies from enhanced surface runoff and groundwater discharge. Freshwater discharge to downstream waters would also increase, which in the short term may prevent blooms through enhanced flushing. However, as the discharge subsides and water residence time increases, its nutrient load will be captured by receiving water bodies, eventually promoting their bloom potential. This scenario will most likely occur if elevated winter–spring rainfall and flushing events are followed by protracted periods of drought, a sequence that has been increasingly observed this decade (mid-1990s–mid-2000s) (Paerl and Huisman, 2008). Examples include the Swan River and Hinz Dam in Australia (Uwins et al., 2007), Hartbeespoortdam in South Africa, the Neuse River Estuary in North Carolina and the Potomac Estuary in Maryland, USA (Paerl and Fulton, 2006). This sequence of events may also have been responsible for massive cyanobacterial blooms in large lake ecosystems serving key drinking water, fisheries and recreational needs, such as Lake Taihu and other large lakes in China (Chen et al., 2003; Guo, 2007), Lake Erie in the USA, Lake Victoria and Lake George in Africa (Paerl and Fulton, 2006), and also in parts of the Baltic Sea (Kahru et al., 1993; Suikkanen et al., 2007). Attempts to control fluctuations in the discharge of rivers and lakes by dams and sluices may increase the residence time, and thereby further aggravate cyanobacteria-related ecological and human health problems. This is exemplified by the development of mass blooms of \textit{Microcystis} after closure of the Volkerak estuary by the Philipsdam in the Dutch delta area (Verspagen et al., 2006).

\textbf{Invasive species}

Some cyanobacterial species show remarkable recent expansion of their geographical ranges, such as the planktonic N\(_2\) fixer \textit{Cylindrospermopsis raciborskii} and the benthic filamentous N\(_2\)-fixing genus \textit{Lyngbya}. \textit{Cylindrospermopsis} gained major attention for its role in the Palm Island ‘mystery disease’ (Carmichael, 2001). In November 1979, an outbreak of a severe hepatitis-like illness was described for 138 children and 10 adults on Palm Island, Australia. The outbreak occurred 3 days after the major water supply was treated with copper sulfate to control a cyanobacterial bloom. A subsequent epidemiological study of the incident confirmed the linkage between the ‘mystery disease’ and a thus far unknown toxin produced by \textit{C. raciborskii} (Carmichael, 2001). The copper sulfate had caused lysis of the \textit{Cylindrospermopsis} bloom, which released its toxins into the water supply. The toxin is now known as cylindrospermopsin, and has also been found in a number of other cyanobacteria.

Originally, \textit{Cylindrospermopsis} was described as a tropical and subtropical species. However, \textit{C. raciborskii} appeared in Europe during the 1930s, and showed a progressive colonization from Greece and Hungary towards higher latitudes near the end of the 20th century (Padisák, 1997). It was first described in France in 1994 (Briand et al., 2004), in Portugal in the late 1990s (Saker et al., 2003), in the Netherlands in 1999 (Van den Hove, 2001), and it is now also widespread in lakes in northern Germany (Stüken et al., 2006). \textit{Cylindrospermopsis raciborskii} was first identified in the USA in 1955, in Wooster Lake, Kansas. Researchers believe \textit{C. raciborskii} may have arrived in Florida almost 35 years ago, after which it aggressively proliferated in lake and river systems throughout central Florida (Chapman and Schelske, 1997). Subsequently, it has spread throughout US South-east and Midwest reservoirs and lakes, especially those undergoing eutrophication accompanied by a loss of water clarity (Paerl, 2008). In addition, it has proliferated in the southern hemisphere, having recently been reported in New Zealand (Ryan et al., 2003), and spreading throughout Australian reservoirs (Neilan et al., 2002). The mechanisms of invasion and proliferation are under examination. However, it is known that \textit{C. raciborskii}, which is typically dispersed throughout the water column, is adapted to low-light conditions encountered in many turbid, eutrophic waters (Padisák, 1997). It also prefers water temperature conditions in excess of 20°C, and survives adverse conditions using specialized resting cells.
called akinetes. These bloom characteristics suggest a link to eutrophication and global warming.

Filamentous toxin-producing cyanobacteria of the genus Lyngbya have likewise exhibited remarkable invasive abilities in a range of aquatic ecosystems, including streams, rivers, lakes, reservoirs, estuarine and coastal waters. Nutrient enrichment has been implicated in their expansion (Cowell and Botts, 1994; Cowell and Dawes, 2004; Paerl and Fulton, 2006). Lyngbya species often form periphytic or benthic mats, although some species, such as L. birgei, are planktonic. Lyngbya outbreaks have been associated with human health problems. The marine species Lyngbya majuscula is commonly known as ‘fireweed’ or ‘mermaid’s hair’. It is widely associated with contact dermatitis, where the initial burning symptoms give way to blister formation and peeling of the skin (Osborne et al., 2001). Lyngbya majuscula produces a large suite of bioactive compounds (Table 1), including the dermatoxic alysiatoxins and lyngbyatoxin A, as well as the potent neurotoxins kalkitoxin and antillatoxin. In freshwater environments, Lyngbya wollei has been associated with the production of paralytic shellfish-poisoning toxins (Carmichael, 2001; Osborne et al., 2001).

Lyngbya blooms are increasingly common in nutrient-enriched waters, including those that have experienced human disturbance such as dredging, inputs of treated municipal waste, and the discharge of nutrient-laden freshwater through coastal canals (Paerl and Fulton, 2006). In these eutrophying waters, both L. majuscula (marine) and L. wollei (freshwater) are opportunistic invaders when environmental conditions permit. Following large climatic and hydrological perturbations such as hurricanes, L. wollei is a aggressive initial colonizer of well-flushed freshwater systems (Paerl and Fulton, 2006). Lyngbya blooms can proliferate as dense floating mats that shade other primary producers, enabling Lyngbya to dominate the system by effectively competing for light. As is the case with Cylindrospermopsis and Microcystis, cyanobacteria of the Lyngbya genus can thus take advantage of both eutrophication and climate change.

Towards a research agenda for the 21st century

In order to gain a better understanding of the interactive roles that human activities and climatic changes play in controlling CyanohAB dynamics on the ecosystem scale, the following set of research and assessment priorities emerge:

• Studies of the annual life cycle of cyanobacteria (Verspagen et al., 2004; Hense and Beckmann, 2006), with special emphasis on the impacts of climatic variables on different phases of the life cycle (Wiedner et al., 2007).
• Laboratory and field assays testing temperature and dissolved inorganic carbon responses of cyanobacterial species and strains under varying nutrient loading scenarios.
• Studies of the development of cyanobacterial surface blooms, and their dependence on mixing processes in aquatic ecosystems (Walsby et al., 1997; Huisman et al., 2004; Jöhnk et al., 2008).
• Studies of the selection of toxic versus non-toxic strains within cyanobacterial species, and their seasonal succession (Via-Ordorika et al., 2004; Kardinaal et al., 2007a; Welker et al., 2007). For example, it has recently been shown that competition among toxic versus non-toxic strains is a major determinant of the overall toxicity of Microcystis blooms, and is strongly affected by the length of the spring–summer period and light availability (Kardinaal et al., 2007b).
• Studies of viral infections, which may lead to mass lysis of cyanobacteria within a few days (Van Hannen et al., 1999; Hewson et al., 2001; Tucker and Pollard, 2005). This begs the question of whether the viral–cyanobacterial interactions depend on temperature, and perhaps could respond strongly to climate change. Clearly, more research is needed in this area.
• Studies of the potential predators of cyanobacteria (e.g. large zooplankton species, zebra mussels), and their responses to climate change.
• Assessments of the impacts of human and natural hydrological modifications (reservoir construction, dams, diversions, droughts, storms and floods) on cyanobacterial bloom potentials, persistence and geographic expansion.

Concluding remarks

Accelerating anthropogenic nutrient loading, rising temperatures, enhanced vertical stratification and increased atmospheric CO₂ supplies are likely to favour cyanobacterial dominance in a wide range of aquatic ecosystems (Fig. 4). The expansion of harmful cyanobacteria has serious consequences for human drinking and irrigation water supplies, fisheries and recreational resources. This has ramifications for water management, as current controls of cyanobacterial blooms, which are largely based on the reduction of nutrient inputs, will also be affected by climatic change. In addition to nutrient reduction, water authorities will have to accommodate the hydrological and physicochemical effects of climatic change in their management strategies, with particular focus on surface water heating, density stratification, freshwater runoff, residence
time, possible salination and the availability of inorganic carbon.

The sensitivity and adaptation of cyanobacteria to climatic change, combined with their ecophysiological flexibility, are in large part products of a long evolutionary history, which has served this group of photosynthetic pioneers well. In a sense, cyanobacteria ‘have seen it all’ as far as global climatic extremes are concerned. In particular, this group appears well adapted to and able to take advantage of an increasingly warmer world. From a management perspective, a key climatic control we can exert to reduce the rate and extent of global warming is curbing greenhouse gas emissions. Without taking this essential step, it is likely that future warming trends and resultant physicochemical changes in a broad spectrum of aquatic ecosystems will continue to play into the hands of this rapidly expanding group of nuisance species.

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