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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.

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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

Fig. 1. Examples of large water bodies that have experienced recent increases in frequencies, magnitudes and duration of CyanoHABs. Left to right, starting at top: Neuse River Estuary, North Carolina, USA; Lake Volkerak, the Netherlands; Lake Taihu, China; St. Johns River, Florida, USA (courtesy of J. Burns); Lake Ponchartrain, Louisiana, USA (courtesy of J. Burns); Baltic Sea-Gulf of Finland (courtesy of Finnish Border Patrol and Institute of Marine Research, Helsinki, Finland).

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 N_2-fixing genera *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Nodularia*, the non-N_2-fixing genera *Microcystis* and *Planktothrix*, and the largely benthic N_2-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

Table 1. Toxins produced by cyanobacteria.

Toxin	Produced by
Neurotoxins	
Anatoxin-a	*Anabaena*, *Aphanizomenon*, *Oscillatoria* (*Planktothrix*)
Homo-Anatoxin-a	
Anatoxin-a(s)	*Anabaena*, *Oscillatoria* (*Planktothrix*)
Paralytic shellfish poisons (saxitoxins)	*Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, Lyngbya
Liver toxins	
Cylindrospermopsin	*Aphanizomenon*, *Cylindrospermopsis*, Umezakia
Microcystins	*Anabaena*, *Aphanocapsa*, *Hapalosiphon*, *Microcystis*, *Nostoc*, *Oscillatoria* (*Planktothrix*)
Nodularins	*Nodularia* (brackish to saline waters)
Contact irritant-dermal toxins	
Debromoaplysiatoxin, lyngbyatoxin	*Lyngbya* (marine)
Aplysiatoxin	*Schizothrix* (marine)

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

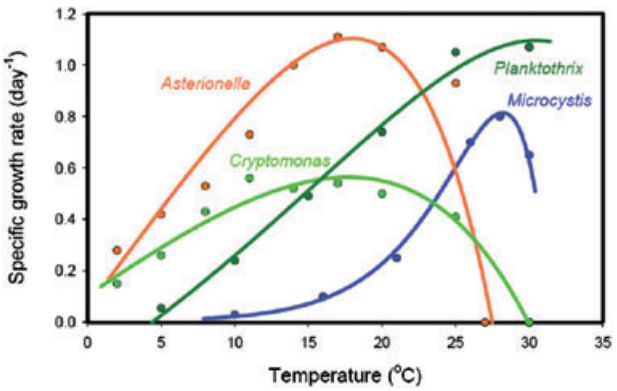

Fig. 2. Temperature dependence of the specific growth rates of the cyanobacteria *Microcystis aeruginosa* (Reynolds, 2006) and *Planktothrix agardhii* (Foy *et al.*, 1976), the diatom *Asterionella formosa* (Butterwick *et al.*, 2005) and the cryptophyte *Cryptomonas marssonii* (Butterwick *et al.*, 2005). The data are from controlled laboratory experiments using light-saturated and nutrient-saturated conditions. Solid lines are least-squares fits of the data to the temperature response curve of Chen and Millero (1986).

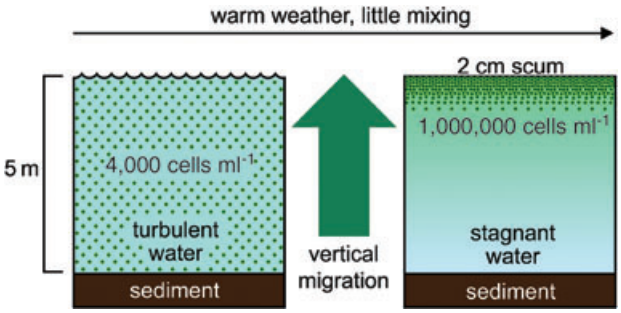

Fig. 3. The formation of dense surface blooms (scums). When the water is turbulent, for instance, in cold waters with intense wind mixing, the cyanobacteria are evenly distributed over the water column (left). However, when temperatures increase and there is little wind mixing, the water column becomes stagnant and buoyant cyanobacteria will float upwards forming dense scums at the water surface (right).

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 CO_2 to support photosynthetic growth, to the extent that the rate of CO_2 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 CO_2 will restrict the availability of free CO_2. If and when this occurs, buoyant cyanobacteria have a distinct advantage over subsurface phytoplankton populations, as surface-dwelling organisms can directly intercept CO_2 from the atmosphere, thereby minimizing carbon limitation of photosynthetic growth and taking advantage of rising atmospheric CO_2 levels (Paerl and Ustach, 1982) (Fig. 3). Recent research has shown that increasing levels of atmospheric CO_2 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 CO_2 consumption and thereby elevates pH. Several cyanobacterial bloom species are capable of sustained growth under the alkaline conditions resulting from active photosynthesis and CO_2 withdrawal during

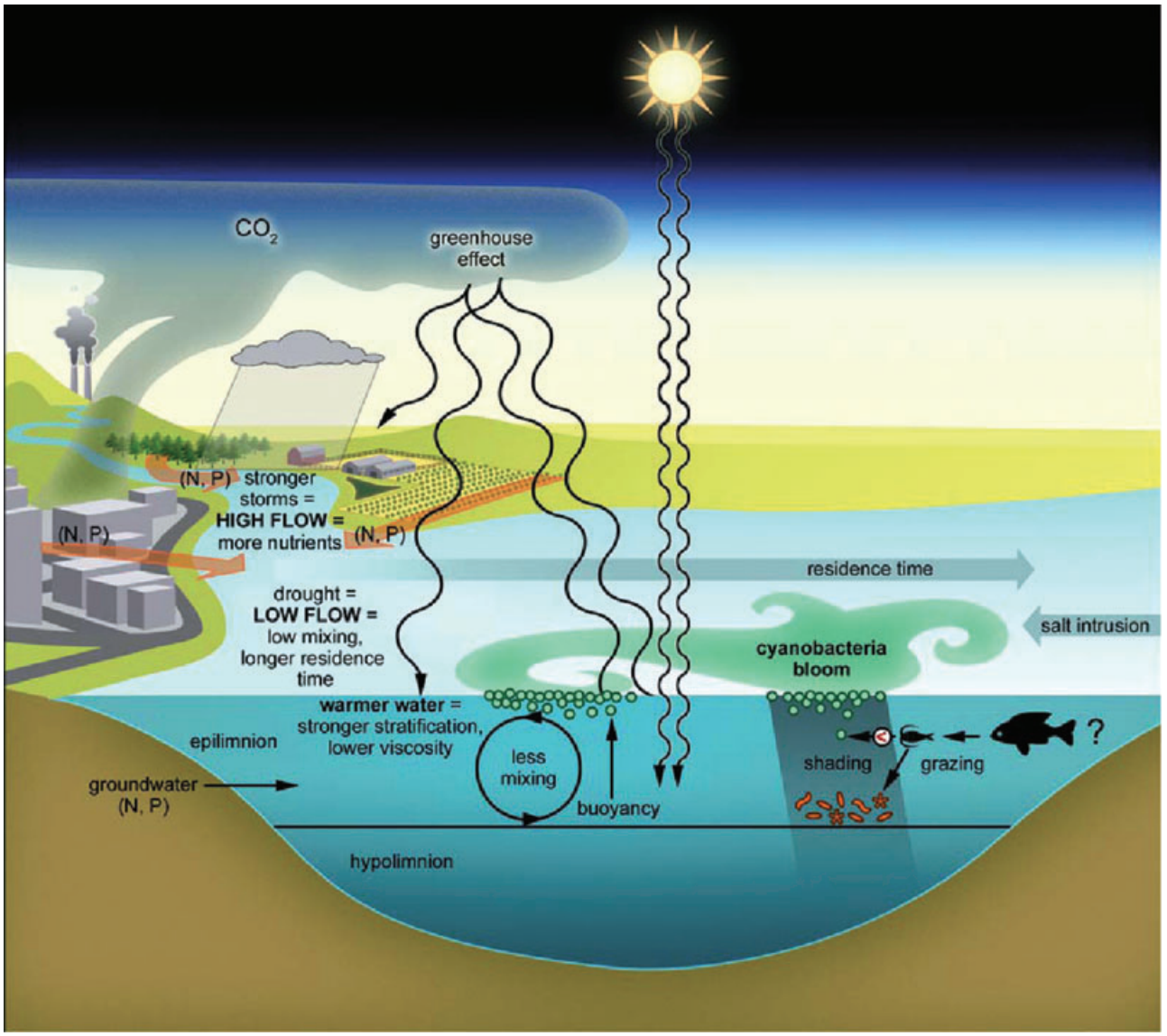

Fig. 4. Conceptual figure, illustrating the environmental controls of cyanobacterial bloom dynamics, and the direct and indirect effects of climate change on these dynamics.

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 aphanizominoides* 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 *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 (Matthiensen *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.

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 Hinze 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 *Microcystis* after closure of the Volkerak estuary by the Philipsdam in the Dutch delta area (Verspagen *et al.*, 2006).

Invasive species

Some cyanobacterial species show remarkable recent expansion of their geographical ranges, such as the planktonic N_2 fixer *Cylindrospermopsis raciborskii* and the benthic filamentous N_2-fixing genus *Lyngbya*. *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 *C. raciborskii* (Carmichael, 2001). The copper sulfate had caused lysis of the *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, *Cylindrospermopsis* was described as a tropical and subtropical species. However, *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). *Cylindrospermopsis raciborskii* was first identified in the USA in 1955, in Wooster Lake, Kansas. Researchers believe *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 Southeast 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 *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 aplysiatoxins 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:

- Dedicated monitoring of cyanobacteria-dominated ecosystems during the next decades, using traditional sampling coupled to online real-time techniques (e.g. smart buoys), and remote sensing.
- 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 CO_2 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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References

Albay, M., Matthiensen, A., and Codd, G.A. (2005) Occurrence of toxic blue-green algae in the Küçükçekmece Lagoon (Istanbul, Turkey). *Environ Toxicol* **20:** 227–284.

Briand, J.F., Leboulanger, C., Humbert, J.F., Bernard, C., and Dufour, P. (2004) *Cylindrospermopsis raciborskii* (*Cyanobacteria*) invasion at mid-latitudes: selection, wide physiological tolerance, or global warming? *J Phycol* **40:** 231–238.

Butterwick, C., Heaney, S.I., and Talling, J.F. (2005) Diversity in the influence of temperature on the growth rates of freshwater algae, and its ecological relevance. *Freshwater Biol* **50:** 291–300.

Caldeira, K., and Wickett, M.E. (2004) Anthropogenic carbon and ocean pH. *Nature* **425:** 365.

Carmichael, W.W. (2001) Health effects of toxin producing cyanobacteria: the 'CyanoHABS'. *Hum Ecol Risk Assess* **7:** 1393–1407.

Castenholz, R.W., and Garcia-Pichel, F. (2000) Cyanobacterial responses to UV radiation. In *The Ecology of Cyanobacteria*. Whitton, B.A., and Potts, M. (eds). Dordrecht, the Netherlands: Kluwer Academic Publishers, pp. 591–611.

Chapman, A.D., and Schelske, C.L. (1997) Recent appearance of *Cylindrospermopsis Cyanobacteria*) in five hypereutrophic Florida lakes. *J Phycol* **33:** 191–195.

Chen, C.T., and Millero, F.J. (1986) Precise thermodynamic properties for natural waters covering only the limnological range. *Limnol Oceanogr* **31:** 657–662.

Chen, Y.W., Qin, B.Q., Teubner, K., and Dokulil, M.T. (2003) Long-term dynamics of phytoplankton assemblages: *Microcystis*-domination in Lake Taihu, a large shallow lake in China. *J Plankton Res* **25:** 445–453.

Chorus, I. (ed.) (2001) *Cyanotoxins: Occurrence, Causes, Consequences*. Berlin: Springer-Verlag.

Codd, G.A. (1995) Cyanobacterial toxins: occurrence, properties and biological significance. *Water Sci Technol* **32:** 149–156.

Coles, J.F., and Jones, R.C. (2000) Effect of temperature on photosynthesis-light response and growth of four phytoplankton species isolated from a tidal freshwater river. *J Phycol* **36:** 7–16.

Cowell, B.C., and Botts, P.S. (1994) Factors influencing the distribution, abundance and growth of *Lyngbya wollei* in central Florida. *Aquat Bot* **49:** 1–17.

Cowell, B.C., and Dawes, C.L. (2004) Growth and nitrate-nitrogen uptake by the cyanobacterium *Lyngbya wollei*. *J Aquat Plant Man* **42:** 69–71.

Cox, P.A., Banack, S.A., and Murch, S.J. (2003) Biomagnification of cyanobacterial neurotoxins and neurodegenerative disease among the Chamorro people of Guam. *Proc Natl Acad Sci USA* **100:** 13380–13383.

De Senerpont Domis, L.N., Mooij, W.M., and Huisman, J. (2007) Climate-induced shifts in an experimental phytoplankton community: a mechanistic approach. *Hydrobiologia* **584:** 403–413.

De Stasio, B.T., Hill, D.K., Jr, Kleinhans, J.M., Nibbelink, N.P., and Magnuson, J.J. (1996) Potential effects of global climate change on small north-temperate lakes: physics, fish, and plankton. *Limnol Oceanogr* **41:** 1136–1149.

Dortch, Q., Peterson, T.D., Achee, S., and Furr, K.L. (2001) Phytoplankton, cyanobacterial blooms, and N_2 fixation in years with and without Mississippi River diversions. In *Coastal Hypoxia: Consequences for Living Resources and Ecosystems, Volume 58*. Turner, R.E., Justic, D., Dortch, Q., and Rabalais, N.N. (eds). Washington, D.C.: American Geophysical Union, pp. 37–48.

Dumont, H.E. (1998) The Caspian lake: history, biota, structure, and function. *Limnol Oceanogr* **43:** 44–52.

Elliott, J.A., Jones, I.D., and Thackeray, S.J. (2006) Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake. *Hydrobiologia* **559:** 401–411.

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

Fogg, G.E. (1969) The physiology of an algal nuisance. *Proc R Soc Lond B Biol Sci* **173:** 175–189.

Foy, R.H., Gibson, C.E., and Smith, R.V. (1976) The influence of daylength, light intensity and temperature on the growth rates of planktonic blue-green algae. *Eur J Phycol* **11:** 151–163.

Guo, L. (2007) Doing battle with the green monster of Lake Taihu. *Science* **317:** 1166.

Hense, I. (2007) Regulative feedback mechanisms in

cyanobacteria-driven systems: a model study. *Mar Ecol Prog Ser* **339:** 41–47.

Hense, I., and Beckmann, A. (2006) Towards a model of cyanobacteria life cycle: effects of growing and resting stages on bloom formation of N_2-fixing species. *Ecol Model* **195:** 205–218.

Hewson, I., O'Neil, J.M., and Dennison, W.C. (2001) Virus-like particles associated with *Lyngbya majuscula* (*Cyanophyta*; *Oscillatoriacea*) bloom decline in Moreton Bay, Australia. *Aquat Microb Ecol* **25:** 207–213.

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

Huisman, J.M., Matthijs, H.C.P., and Visser, P.M. (2005) *Harmful Cyanobacteria*. Springer Aquatic Ecology Series 3. Dordrecht, the Netherlands: Springer.

Hutchinson, G.E. (1957) *A Treatise on Limnology. V. 1, Geology, Physics and Chemistry*. New York, NY, USA: Wiley.

Ibelings, B.W., Mur, L.R., and Walsby, A.E. (1991) Diurnal changes in buoyancy and vertical distribution in populations of *Microcystis* in two shallow lakes. *J Plank Res* **13:** 419–436.

Ibelings, B.W., Vonk, M., Los, H.F.J., Van der Molen, D.T., and Mooij, W.M. (2003) Fuzzy modeling of cyanobacterial surface waterblooms: validation with NOAA-AVHRR satellite images. *Ecol Appl* **13:** 1456–1472.

Izaguirre, G., and Taylor, W.D. (2004) A guide to geosmin- and MIB-producing cyanobacteria in the United States. *Water Sci Technol* **49:** 19–24.

Jacquet, S., Briand, J.F., Leboulanger, C., Avois-Jacquet, C., Oberhaus, L., Tassin, B., *et al.* (2005) The proliferation of the toxic cyanobacterium *Planktothrix rubescens* following restoration of the largest natural French lake (Lac du Bourget). *Harmful Algae* **4:** 651–672.

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

Kahru, M., Leppänen, J.-M., and Rud, O. (1993) Cyanobacterial blooms cause heating of the sea surface. *Mar Ecol Prog Ser* **101:** 1–7.

Kanoshina, I., Lips, U., and Leppänen, J.-M. (2003) The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Harmful Algae* **2:** 29–41.

Kaplan, A., Schwarz, R., Lieman-Hurwitz, J., and Reinhold, L. (1991) Physiological and molecular aspects of the inorganic carbon-concentrating mechanism in *Cyanobacteria*. *Plant Physiol* **97:** 851–855.

Kardinaal, W.E.A., Janse, I., Kamst-van Agterveld, M., Meima, M., Snoek, J., Mur, L.R., *et al.* (2007a) *Microcystis* genotype succession in relation to microcystin concentrations in freshwater lakes. *Aquat Microb Ecol* **48:** 1–12.

Kardinaal, W.E.A., Tonk, L., Janse, I., Hol, S., Slot, P., Huisman, J., and Visser, P.M. (2007b) Competition for light between toxic and nontoxic strains of the harmful cyanobacterium *Microcystis*. *Appl Environ Microbiol* **73:** 2939–2946.

Karl, D., Michaels, A., Bergman, B., Capone, D., Carpenter, E., Letelier, R., *et al.* (2002) Dinitrogen fixation in the world's oceans. *Biogeochemistry* **57/58:** 47–98.

Knoll, A.H. (2003) *Life on a Young Planet: The First Three Billion Years of Evolution on Earth*. Princeton, NJ, USA: Princeton University Press.

Kromkamp, J., and Walsby, A.E. (1990) A computer model of buoyancy and vertical migration in cyanobacteria. *J Plank Res* **12:** 161–183.

Lehman, P.W., Boyer, G., Hall, C., Waller, S., and Gehrts, K. (2005) Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Bay Estuary, California. *Hydrobiologia* **541:** 87–99.

Maeda, H., Kawai, A., and Tilzer, M.M. (1992) The water bloom of cyanobacterial picoplankton in Lake Biwa, Japan. *Hydrobiologia* **248:** 93–103.

Matthiensen, A., Beattie, K.A., Yunes, J.S., Kaya, K., and Codd, G.A. (2000) [D-Leu(1)]microcystin-LR, from the cyanobacterium *Microcystis* RST 9501 and from a *Microcystis* bloom in the Patos Lagoon estuary, Brazil. *Phytochemistry* **55:** 383–387.

Mazur-Marzec, H., Zeglinska, L., and Plinski, M. (2005) The effect of salinity on the growth, toxin production, and morphology of *Nodularia spumigena* isolated from the Gulf of Gdansk, southern Baltic Sea. *J Appl Phycol* **17:** 171–179.

Moisander, P.H., McClinton, E., III, and Paerl, H.W. (2002) Salinity effects on growth, photosynthetic parameters, and nitrogenase activity in estuarine planktonic cyanobacteria. *Microb Ecol* **43:** 432–442.

Neilan, B.A., Sakert, M.L., Fastner, J., Törökné, A., and Burns, B.P. (2002) Phylogeography of the invasive cyanobacterium *Cylindrospermopsis raciborskii*. *Mol Ecol* **12:** 133–140.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437:** 681–686.

Osborne, N.J.T., Webb, P.M., and Shaw, G.R. (2001) The toxins of *Lyngbya majuscula* and their human and ecological health effects. *Environ Int* **27:** 381–392.

Padisák, J. (1997) *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. *Archiv für Hydrobiol Suppl* **107:** 563–593.

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

Paerl, H.W. (1990) Physiological ecology and regulation of N_2 fixation in natural waters. *Adv Microb Ecol* **11:** 305–344.

Paerl, H.W. (2008) Nutrient and other environmental controls of harmful cyanobacterial blooms along the freshwater-marine continuum. *Adv Exp Med Biol* **619:** 216–241.

Paerl, H.W., and Fulton, R.S. (2006) Ecology of harmful cyanobacteria. In *Ecology of Harmful Marine Algae*. Graneli, E., and Turner, J. (eds). Berlin, Germany: Springer-Verlag, pp. 95–107.

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

Paerl, H.W., and Ustach, J.F. (1982) Blue-green algal scums: an explanation for their occurrence during freshwater blooms. *Limnol Oceanogr* **27:** 212–217.

Paerl, H.W., Tucker, J., and Bland, P.T. (1983) Carotenoid enhancement and its role in maintaining blue-green algal (*Microcystis aeruginosa*) surface blooms. *Limnol Oceanogr* **8:** 847–857.

Peeters, F., Straile, D., Lorke, A., and Livingstone, D.M. (2007) Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Glob Change Biol* **13:** 1898–1909.

Pinckney, J.L., and Paerl, H.W. (1998) Lake ice algal phototroph community composition and growth rates, Lake Bonney, dry valley lakes, Antarctica. *Antarct J US Rev* **1996:** 215–216.

Potts, M., and Whitton, B.A. (2000) *The Biology and Ecology of Cyanobacteria*. Oxford, UK: Blackwell Scientific Publications.

Rai, A.N., Bergman, B., and Rasmussen, U. (2000) *Cyanobacteria in Symbioses*. Boca Raton, FL, USA: Kluwer Publications.

Reynolds, C.S. (1987) Cyanobacterial water blooms. *Adv Bot Res* **13:** 67–143.

Reynolds, C.S. (2006) *The Ecology of Phytoplankton (Ecology, Biodiversity and Conservation)*. Cambridge, UK: Cambridge University Press.

Rinta-Kanto, J.M., Ouellette, A.J.A., Boyer, G.L., Twiss, M.R., Bridgeman, T.B., and Wilhelm, S.W. (2005) Quantification of toxic *Microcystis* spp. during the 2003 and 2004 blooms in western Lake Erie using quantitative real-time PCR. *Environ Sci Technol* **39:** 4198–4205.

Robarts, R.D., and Zohary, T. (1987) Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *NZ J Mar Freshwater Res* **21:** 391–399.

Robson, B.J., and Hamilton, D.P. (2003) Summer flow event induces a cyanobacterial bloom in a seasonal Western Australian estuary. *Mar Freshwater Res* **54:** 139–151.

Ryan, E.F., Hamilton, D.P., and Barnes, G.E. (2003) Recent occurrence of *Cylindrospermopsis raciborskii* in Waikato lakes of New Zealand. *NZ J Mar Freshwater Res* **37:** 829–836.

Saker, M.L., Nogueira, I.C., Vasconcelos, V.M., Neilan, B.A., Eaglesham, G.K., and Pereira, P. (2003) First report and toxicological assessment of the cyanobacterium *Cylindrospermopsis raciborskii* from Portuguese freshwaters. *Ecotoxicol Environ Saf* **55:** 243–250.

Scheffer, M. (1998) *Ecology of Shallow Lakes*. London, UK: Chapman and Hall.

Schopf, J.W. (2000) The fossil record: tracing the roots of the cyanobacterial lineage. In *The Ecology of Cyanobacteria*. Whitton, B.A., and Potts, M. (eds). Dordrecht, the Netherlands: Kluwer Academic Publishers, pp. 13–35.

Stomp, M., Huisman, J., Vörös, L., Pick, F.R., Laamanen, M., Haverkamp, T., and Stal, L.J. (2007) Colourful coexistence of red and green picocyanobacteria in lakes and seas. *Ecol Lett* **10:** 290–298.

Stüken, A., Rücker, J., Endrulat, T., Preussel, K., Hemm, M., Nixdorf, B., *et al.* (2006) Distribution of three alien cyanobacterial species (*Nostocales*) in northeast Germany: *Cylindrospermopsis raciborskii*, *Anabaena bergii* and *Aphanizomenon aphanizomenoides*. *Phycologia* **45:** 696–703.

Suikkanen, S., Laamanen, M., and Huttunen, M. (2007) Long-term changes in summer phytoplankton communities of the open northern Baltic Sea. *Estuar Coast Shelf Sci* **71:** 580–592.

Tonk, L., Bosch, K., Visser, P.M., and Huisman, J. (2007) Salt tolerance of the harmful cyanobacterium *Microcystis aeruginosa*. *Aquat Microb Ecol* **46:** 117–123.

Tucker, S., and Pollard, P. (2005) Identification of cyanophage Ma-LBP and infection of the cyanobacterium *Microcystis aeruginosa* from an Australian subtropical lake by the virus. *Appl Environ Microbiol* **71:** 629–635.

Uwins, H.K., Teasdale, P., and Stratton, H. (2007) A case study investigating the occurrence of geosmin and 2-methylisoborneol (MIB) in the surface waters of the Hinze Dam, Gold Coast, Australia. *Water Sci Technol* **55:** 231–238.

Van Hannen, E.J., Zwart, G., van Agterveld, M.P., Gons, H.J., Ebert, J., and Laanbroek, H.J. (1999) Changes in bacterial and eukaryotic community structure after mass lysis of filamentous cyanobacteria associated with viruses. *Appl Environ Microbiol* **65:** 795–801.

Van den Hove, L. (2001) Tropisch blauwwier in Nederland aangetroffen. *H2O* **34:** 12–13.

Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., *et al.* (2002) History and timing of human impact on Lake Victoria, East Africa. *Proc R Soc Lond B Biol Sci* **269:** 289–294.

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

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

Via-Ordorika, L., Fastner, J., Hisbergues, M., Dittmann, E., Erhard, M., Komárek, J., *et al.* (2004) Distribution of microcystin-producing and non-microcystin producing *Microcystis* in European freshwater bodies: detection of microcystins and *mcy* genes in single colonies. *Syst Appl Microbiol* **27:** 592–602.

Visser, P.M., Ibelings, B.W., and Mur, L.R. (1995) Autumnal sedimentation of *Microcystis* spp. as result of an increase in carbohydrate ballast at reduced temperature. *J Plankt Res* **17:** 919–933.

Visser, P.M., Passarge, J., and Mur, L.R. (1997) Modelling vertical migration of the cyanobacterium *Microcystis*. *Hydrobiologia* **349:** 99–109.

Walsby, A.E. (1975) Gas vesicles. *Annu Rev Plant Physiol* **26:** 427–439.

Walsby, A.E., Hayes, P.K., Boje, R., and Stal, L.J. (1997) The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytol* **136:** 407–417.

Walsby, A.E., Schanz, F., and Schmid, M. (2006) The Burgundy-blood phenomenon: a model of buoyancy change explains autumnal waterblooms of *Planktothrix rubescens* in Lake Zurich. *New Phytol* **169:** 109–122.

Welker, M., Šejnohová, S., Némethová, D., von Döhren, H.,

Jarkovský, J., and Maršálek, B. (2007) Seasonal shifts in chemotype composition of *Microcystis* sp. communities in the pelagial and the sediment of a shallow reservoir. *Limnol Oceanogr* **52:** 609–619.

Wiedner, C., Rücker, J., Brüggemann, R., and Nixdorf, B. (2007) Climate change affects timing and size of populations of an invasive cyanobacterium in temperate regions. *Oecologia* **152:** 473–484.