Climate Change and Microbial Ecology
Current Research and Future Trends

Edited by

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Abstract
Cyanobacteria are the earth's oldest oxygenic phototrophs, and they have had major impacts on shaping its biosphere. Their long evolutionary history (~3.5 billion years ago) has enabled them to adapt to geochemical and climatic changes and recent anthropogenic modifications of aquatic environments, including nutrient over-enrichment (eutrophication), water diversions, withdrawal and salinization. Eutrophication has promoted a worldwide proliferation of cyanobacterial blooms that is harmful to ecological and animal (including human) health. In addressing steps needed to stem and reverse this troubling trend, both nitrogen and phosphorus input constraints are probably needed. Cyanobacteria exhibit optimal growth rates and bloom potentials at relatively high water temperatures; hence global warming plays a key interactive role in their expansion and persistence. Additional manifestations of climatic change, including increased vertical stratification, salinization, and intensification of storms and droughts and their impacts on nutrient delivery and flushing characteristics of affected water bodies, play synergistic roles in promoting bloom frequency, intensity, geographic distribution and duration. Rising temperatures cause shifts in critical nutrient thresholds at which cyanobacterial blooms can develop; thus, nutrient reductions for blooms control may need to be more aggressively pursued in response to climatic changes taking place worldwide. Cyanobacterial bloom control must consider both nitrogen and phosphorus loading dynamics within the context of altered thermal and hydrologic regimes associated with climate change.

Introduction
Cyanobacteria are the earth's oldest known prokaryotic oxygenic phototrophs, having appeared over 2.5 billion years ago (Schopf, 2000). They have witnessed major biogeochemical and climatic changes, including extreme swings in irradiance (visible and UV light) and temperature (ice ages as well as warm periods), rising oxygen levels (in large part due their own photosynthetic activities) and major changes in chemical composition during the evolution of the earth's atmosphere (Schopf, 2000). They have witnessed periods of high and low nutrient (nitrogen, phosphorus, minor elements) abundance, and a great deal of variability in climatic conditions, including extremely wet and dry periods, combined with major changes in the earth's surface temperature. In addition, geophysical processes such as volcanism and continental drift have altered their habitats and have exerted eco-physiological stresses over a wide range of time scales.

As a major phylogenetic group, cyanobacteria have 'seen it all' when considering potential physical-chemical impacts and their biotic ramifications on earth. This is probably a key reason why cyanobacteria exhibit an extremely broad geographic distribution, ranging from polar to tropical regions, from subsurface aquatic to alpine habitats (Potts and Whitton, 2000). They can be found in virtually all terrestrial and aquatic habitats, ranging from deserts to tropical rain forests and from the ultraoligotrophic open ocean to hypereutrophic lakes (Potts and Whitton, 2000; Whitton, 2012). Over geological and biological time scales, cyanobacteria reveal a remarkable ability to both counter extreme climatic conditions as well as thrive under them.
Diverse cyanobacterial taxa exhibit widespread adaptations to climatic extremes, including the formation of heat and desiccation-tolerant resting cells, or akinetes, cysts, the presence of photoprotective and desiccation-resistant sheaths and capsules, a wide array of photoprotective (including UV protective) cellular pigments, the ability to glide and (in planktonic environments) use buoyancy regulation to adjust and optimize their position in the water column in response to irradiance and nutrient gradients (Potts and Whitton, 2000; Reynolds, 2006). They have also developed a wide array of physiological adaptations to periodic nutrient deplete conditions, including the ability to convert or 'fix' atmospheric nitrogen (N₂) into biologically available ammonia (Gallion, 1992), sequester (by chelation) iron (Wilhelm and Trick, 1994), store phosphorus, nitrogen and other essential nutrients (Healy, 1982; Reynolds, 2006), and produce metabolites that enhance their ability to counter potentially adverse conditions in their immediate environment, including photooxidation, and serve yet to be discovered protectives and adaptive functions (Pael and Millie, 1996; Huisman et al., 2005; Pael and Otten, 2013a,b). Cyanobacteria have a diverse suite of mutualistic and symbiotic associations with prokaryotic and eukaryotic microbes, plants and animals, that help ensure their (as well as their partners') survival in environments too hostile for individual members to survive in (Pael, 1982, 1986).

It should therefore come as no great surprise that a rich 'playbook' of ecological strategies aimed at surviving and at times thriving as massive growths or 'blooms' under these conditions has enabled cyanobacteria to take advantage of recent human alterations of aquatic environments; including nutrient over-enrichment (eutrophication), hydrologic alterations due to water withdrawal (for drinking, irrigation, industrial use) from streams, rivers and lakes, dam/reservoir, artificial waterway, lagoon and marina construction, and alterations of a variety of benthic and planktonic habitats (Fig. 1.1).

Climatic variability and change have been features of the earth's atmosphere and biosphere ever since the evolution of life and cyanobacterial diversification. Key features of climate change and their potential impacts on cyanobacterial activity, community structure and function that will be discussed in this chapter include changes in temperature and precipitation, and the combination of these factors I will discuss these impacts and their ramifications for cyanobacterial eco-physiology, habitats and community composition and function, with an emphasis on potential impacts on biogeochemical cycling, water quality and trophodynamics along the freshwater to marine continuum.

The cyanobacterial 'players'
In aquatic ecosystems, cyanobacteria exist in three major morphologically distinct groups (Fig 1.2):

1. Coccolid cells, ranging from solitary (e.g. Synechococcus, Chroococcus) (<3 mm diameter), largely non-N₂-fixing coccolid to avoid cyanobacterial genera, make up an important, and at times dominant (>50%), fraction of freshwater, estuarine and marine phytoplankton biomass (Kuosa, 1991; Sánchez-Baracaldo et al., 2008; Gaulke et al., 2010). Other coccolid forms are aggregated in colonies that are widespread and sometimes dominate as 'blooms' (e.g Microcystis) in planktonic and benthic environments over a wide range of trophic states (ultraoligotrophic to hypertrophic) (Fig. 1.1). Most of these genera do not fix nitrogen, and hence are dependent on combined nitrogen supplies. Some genera (e.g Microcystis) can produce secondary metabolites that are toxic to inhabitants and consumers, ranging from zooplankton to fish to humans.

2. Filaments of mostly undifferentiated cells. This group mostly comprises non-N₂-fixing genera (e.g Oscillatoria, Planktothrix); however, some N₂-fixing genera also exist (e.g Lyngbya, Trichodesmium), and these genera can at times dominate, as blooms, in benthic and planktonic environments.

3. Filaments with highly differentiated, biochemically specialized, N₂-fixing cells called heterocysts (Wolk, 1996) Heterocystous cyanobacteria are considered morphologically most advanced because heterocysts appear to be an adaptation to
Figure 1.1 Cyanobacterial blooms, viewed for space and in the field. (a) NASA SeaWIFS image of a *Trichodesmium* spp. bloom in the tropical Atlantic Ocean (Courtesy NASA). (b) ASTER-TERRA image of a *Lyngbya* sp. bloom in Lake Atitlán, Guatemala (Courtesy NASA). (c) MODIS image of *Microcystis*-dominated blooms in the Western Basin of Lake Erie and southern region of Saginaw Bay, Laurentian Great Lakes during the summer of 2009 (Courtesy NASA and NOAA Coastwatch-Great Lakes). (d) Bloom of the benthic Cyanobacterium *Lyngbya wollei* at Silver Glen Springs, Florida (Photo, Hans Paerl). (e) View of a *Microcystis*-dominated bloom in Meiliang Bay, Lake Taihu during summer 2009 (Photo, Hans Paerl). (f) Hans Paerl sampling the Taihu bloom during 2007. (g) A *Trichodesmium* sp. bloom in South Pacific Ocean waters near Fiji (Photo, courtesy Ryan Paerl). (h) Mixed *Microcystis*, *Anabaena*, and *Aphanizomenon* sp. bloom in the St. Johns River, Florida, summer 1999 (Photo, courtesy John Burns). (i) Aircraft view of an *Anabaena* bloom on the St. Johns River (Photo, courtesy Bill Yates/CIPIX). (j) A benthic *Lyngbya* sp. bloom floating to the surface of Weeki Wachee Springs, Florida during summer 2003 (Photo, Hans Paerl). (k) A marine *Lyngbya* sp. bloom attached to a reef near Puerto Rico (Photo Courtesy, Valerie Paul). (l) Mixed *Microcystis* and *Anabaena* bloom at a development near the Indian River Lagoon, Florida (Photo, John Burns).
ambient oxygen-rich conditions (Wolk, 1996), which the cyanobacteria brought about during their proliferation on earth. There are numerous bloom-forming genera in this group (e.g., *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Nodularia*). In addition to planktonic bloom formers, benthic filamentous genera (*Calothrix*, *Rivularia*, *Scytonema*, *Lyngbya*, *Oscillatoria*) can undergo explosive growths as epiphytes, mats and biofilms (Fig. 1.1). Each group contains species that produce secondary metabolites that can be toxic to a variety of animal consumers, ranging from zooplankton to fish to mammals, including humans (Carmichael 1997, 1998; Paerl and Otten, 2013).

**Climate change, cyanobacterial ecology and dominance**

While there is a rich literature showing a clear link between nutrient (nitrogen, phosphorus, trace metals) availability and the composition, distribution and abundance of cyanobacterial taxa in aquatic ecosystems (Vincent, 1987; Potts and Whitton, 2000; Huisman *et al.*, 2005; Paerl and Fulton, 2006), climate change plays an additional modulating role. Rising global temperatures, altered precipitation patterns and changes in hydrologic properties (i.e. freshwater discharge or flushing rates) of water bodies strongly influence growth rates, composition and bloom dynamics of cyanobacteria (Jöhnk *et al.*, 2008; Paerl and Huisman, 2008, 2009; Paerl *et al.*, 2011a,b; Paul, 2008; Kosten
et al., 2012). Warmer temperatures favour surface bloom-forming cyanobacterial genera because as procaryotes, they tend to show a strong preference for relatively warm conditions, and their maximal growth rates occur at relatively high temperatures; often in excess of 25°C (Foy et al., 1976; Robarts and Zohary, 1987; Butterwick et al., 2005) (Fig. 1.3). At these elevated temperatures, cyanobacteria can outcompete eukaryotic algae (Weyhenmeyer, 2001; Elliot, 2010). Specifically, as the growth rates of the eukaryotic taxa reach their maxima or decline in response to warming, cyanobacterial growth rates reach their optima (Fig. 1.3).

Warmer surface waters are also prone to more intense vertical stratification. The strength of vertical stratification depends on the density difference between the relatively warm surface layer and the cold water beneath (Fig. 1.4). In marine systems, salinity gradients also induce stratification. As mean temperatures rise, winters will begin to stratify earlier in the spring, and stratification will persist longer into the fall (Stüken et al., 2006; Peeters et al., 2007; Suikkanen et al., 2007; Wiedner et al., 2007; Wagner and Adrian, 2009). Northern lakes, rivers and estuarine ecosystems have shown warming of surface waters, leading to earlier ‘ice out’ and later ‘ice on’ periods and stronger vertical temperature stratification. This has extended both the periodicity and range of cyanobacterial species, especially bloom-forming ones. Evidence for this can be obtained from lakes in northern Europe and North America, some of which no longer have ice on them during winter months (Wiedner et al., 2007; Wagner and Adrian, 2009).

Even in the polar regions relatively small increases in warming can have significant impacts on the activities, biogeochemical cycling and trophodynamics associated with cyanobacterial communities. Along the margins of the Antarctic continent, cyanobacteria are found associated with exposed soils, glaciers, ice shelves, frozen lakes and stream beds, where they are often comprise most of the ecosystem biomass (Vincent, 1988). These communities are most commonly found as desiccated, frozen mats comprising both coccoïd and filamentous genera. However, during the Austral summer, there is a brief ‘window’ (usually several weeks to a month) during which surface temperatures are high enough to melt the ice, allowing cyanobacteria

![Figure 1.3 Relationships between temperature and specific growth rates of cyanobacterial species and eukaryotic phytoplankton in three different taxonomic groups (chlorophytes, dinoflagellates and diatoms). The dashed line is for comparison of optimal cyanobacterial growth temperature with temperature-growth relationships in other groups. Data points are 5°C running bin averages of percent maximum growth rates from three or four species within each group. Fitted lines are third order polynomials and are included to emphasize the shape of the growth versus temperature relationship. Figure adapted from Paerl et al. (2011a). Data sources and per cent maximum growth rates of individual species are provided in Paerl et al. (2011a).]
and associated microflora access to liquid water. Virtually all the photosynthetic activity (primary production), nutrient cycling and trophic transfer is confined to this ice-free period (Vincent, 1988; Priscu, 1998; Priscu et al., 1998). Global warming will likely have a positive effect on the cyanobacterial communities by providing an extended window of liquid water conditions. In addition to increasing habitat availability, polar cyanobacteria are also highly responsive to warmer temperatures (Vincent and Quesada, 2012). Clearly, these effects have ramifications for nutrient and carbon cycling in the aquatic and terrestrial ecosystems experiencing this manifestation of warming.

In the extensive Arctic tundra environments, warming has likewise been documented, to the extent that near-surface permafrost is thawing and the temporal extent to which liquid water persists in these environments is increasing. Cyanobacterial communities are already abundant in surface soils, wetlands, stream and lakes comprising these environments (Vincent, 2000). The opportunities for these communities to increase their productivity, abundance and distributions are clearly increasing, given longer periods of ice-free, hydrated conditions.

In both Arctic and Antarctic environments it is likely that warming habitats are opening up to cyanobacterial and associated microbial expansion. This includes the polar seas, which at present contain undetectable or sparse populations of cyanobacteria, in contrast to most of the world ocean (Vincent and Quesada, 2012). The overall biogeochemical and trophic importance of this ramification of climate change needs to be addressed. It could have a highly significant impact on carbon and nutrient cycling as well as greenhouse gas fluxes between the atmosphere and the massive amount of terrestrial,
wetland and aquatic surface area characterizing these regions.

Another symptom of climatic changes potentially impacting cyanobacterial communities is increasing variability and more extremeness in precipitation amounts and patterns. Storm events, including tropical cyclones, nor'easters, and summer thunderstorms, are becoming more extreme, and have higher amounts and intensities of rainfall (Webster, 2005; IPCC, 2007; 2012; Holland and Webster, 2007; Allan and Soden, 2008; Bender et al., 2010). Conversely, droughts are becoming more severe and protracted (Trenberth, 2005). These events cause large changes in hydrologic variability, i.e. wetter wet periods and drier dry periods. This has led to more episodic ‘flashy’ discharge periods in which large amounts of nutrients are captured and transported in runoff events that can lead to rapid and profound nutrient enrichment of receiving waters. If such events are followed by periods of extended drought in which freshwater flow decreases dramatically and residence time of receiving waters increases, conditions favouring cyanobacterial dominance and bloom formation will greatly improve. This will be particularly effective if it is accompanied by warming, since as a phytoplankton group, cyanobacteria have relatively slow growth rates at moderate temperatures (Butterwick et al., 2005) (Fig. 1.3); which would increase in a warmer regime (Paul, 2008; Paerl and Paul, 2011). The combination of episodic loads of nutrients (e.g. spring runoff period), followed by a protracted warm (summer), low discharge period (long residence time) can promote cyanobacterial growth and bloom potentials in geographically diverse regions (Paerl et al., 2011a).

Examples of this sequence of events include the Swan River and Estuary (Australia), Hartbeespoort Dam (South Africa), the Neuse River Estuary (North Carolina, USA), the Potomac River (Chesapeake Bay, USA), and Lake Taihu (China) (Paerl et al., 2011a). Attempts to regulate discharge of rivers and lakes by dams and sluices may increase residence time, and thus further enhance cyanobacterial bloom proliferation.

Higher amounts of freshwater runoff can also lead to enhanced vertical density stratification (reduced vertical mixing) in waters having appreciable salinity, including estuarine and coastal waters as well as saline lakes and rivers, by allowing relatively light freshwater lenses to establish themselves on top of heavier (denser) saltwater. The resultant enhanced vertical stratification will favour phytoplankton capable of vertical migration to position themselves at physically–chemically optimal depths (Paerl and Huisman, 2009). Bloom-forming cyanobacteria are capable of rapidly altering their buoyancy in response to varying light, temperature and nutrient regimes, by periodically forming blooms in surface waters (Walsby et al., 1997). Surface blooms are inhospitable to grazers and eukaryotic taxa that cannot handle the excessive irradiance in these waters. Many bloom taxa have photoprotective pigments, enabling them persist as surface blooms (Paerl et al., 1983), while subsurface algal taxa will be shaded by surface blooms, leaving them in suboptimal light conditions (Fig. 1.4).

More extensive summer droughts, rising sea levels, and increased use of freshwater for agricultural irrigation can lead to salinization, and this phenomenon has increased worldwide. Numerous cyanobacterial genera are salt-tolerant, even though they may be most common to freshwater ecosystems (probably because they are nutrient enriched). These genera include the N₂ fixers Anabaena, Anabaenopsis and Nodularia and some species of Lyngbya and Oscillatoria, as well as non-N₂-fixing genera, including Microcystis, Oscillatoria, Phormidium and picoplanktonic genera (Synechococcus, Chroococcus). Some strains of Microcystis aeruginosa remain unaffected by salinities up to 10, nearing 30% of that of seawater (Tonk et al., 2007), and in Patos Lagoon, Brazil, it can thrive under ‘mixohaline’ conditions. Some Anabaena and Anabaenopsis species can withstand salinities up to 15 (Montagnoli et al., 2004), while the common Baltic Sea bloom-former Nodularia spumigena can tolerate salinities exceeding 20 (Mazur-Marsec et al., 2005; Moisander et al., 2002). These salt-tolerant species are common to brackish systems; presumably spurred on by a combination of nutrient overenrichment, climatically or anthropogenically driven (i.e. water withdrawal) salinization.

Examples of cyanobacterial expansion in a climatically changing world

Over the past several decades, field studies have demonstrated the expansion of cyanobacterial
taxa in response to changing climatic (thermal and hydrological) conditions. It should be noted that in certain cases, such as altered hydrology, the drivers cannot be solely attributed to climate change, but rather reflect the complex interactions of human alteration of hydrology as well as changing rainfall patterns.

**Cylindrospermopsis raciborskii**

The filamentous, bloom-forming and toxin-producing diazotroph *Cylindrospermopsis raciborskii* has undergone recent expansion of its geographical range (Fig. 1.5). Its expansion initially gained widescale attention following an outbreak of severe hepatitis-like disease on Palm Island (Australia), the so-called 'Palm Island mystery disease' (Carmichael, 2001). This outbreak followed treatment of a local water supply reservoir in Australia, with copper sulfate. Epidemiological studies confirmed the linkage between the 'mystery disease' and the newfound presence of *Cylindrospermopsis* (Carmichael, 2001). Lysis of the *Cylindrospermopsis* bloom released the highly stable toxin into the water supply.

*Cylindrospermopsis* has traditionally been described as a tropical/subtropical genus (Padisak, 1997). However, *C. raciborskii* was documented in Europe during the 1930s, and showed a progressive colonization from Greece and Hungary towards higher latitudes near the end of the 20th century (Padisak, 1997). It was described in France in 1994, and in the Netherlands in 1999, and it is now widespread in lakes in northern Germany (Stuken et al., 2006; Wiedner et al., 2007), and has also been detected in Canada (Hamilton et al., 2005). *C. raciborskii* was noted in Florida almost 35 years ago, after which it aggressively proliferated throughout lakes and rivers (Chapman and Schelske, 1997). It is now present throughout the US in reservoirs, lakes, rivers and even oligohaline estuarine waters experiencing various degrees of eutrophication and loss of water clarity (Paerl and Fulton, 2006; Calandriano and Paerl, 2011). This combination is significant because *C. raciborskii* is adapted to low light conditions (high turbidity) typifying eutrophic waters. It also prefers water temperatures above 20°C, and survives adverse conditions using specialized vegetative resting cells (akinetes). This scenario hints of a link to eutrophication and global warming. The activation of akinetes in this and other heterocystous species (e.g. *Aphanizomenon ovalisporum*) is strongly temperature regulated (Cires et al., 2012). Increases in ambient temperatures may therefore play an important role in the geographic dispersal strategy, and potential expansion of this and other akinete-forming genera (*Anabaena, Anabaenopsis, Nodularia*).

![Figure 1.5 Map showing the geographic expansion of the harmful (toxic) cyanobacterial species *Cylindrospermopsis raciborskii*. Expansion is best documented in Europe, North America and Australia, where populations have expanded both in response to altered hydrologic regimes (e.g. droughts and poor flushing in Australian reservoirs) and warming (northerly directions in Europe and North America).]
Lyngbya spp.

Blooms of the filamentous, non-heterocystous, toxin-producing bloom former Lyngbya spp. have become increasingly common and problematic in nutrient-enriched freshwater and marine ecosystems; including those that have experienced human disturbances such as dredging, municipal waste inputs and the discharge of nutrient-laden agricultural runoff (Watkinson et al., 2005; Osborne et al., 2007). Lyngbya is a ubiquitous genus, with various species occurring in planktonic and benthic habitats. *L. majuscula* (marine-benthic) and *L. wolsei* (freshwater-benthic and planktonic) are opportunistic invaders. Following large climatic and hydrologic perturbations such as tropical cyclones, *L. wolsei* has proven to be an aggressive initial colonizer of perturbed systems (Paerl, 2012; Paerl and Fulton, 2006). Lyngbya blooms can proliferate as dense, attached or floating mats that shade other primary producers, which enables it to dominate the system by effectively outcompeting them for light (Fig. 1.6). As is the case with *Cylindrospermopsis* and *Microcystis*, this genus benefits from both human and climate-induced environmental change.

Managing cyanobacterial bloom dynamics in a climatically changing world

Cyanobacterial growth and bloom formation thrive on the synergistic interactions between human- and climatically altered physical-chemical alterations of aquatic ecosystems. This presents a formidable challenge to water quality managers because ecosystem

![Figure 1.6 Examples of expanding freshwater (left) and coastal marine (right) blooms of benthic Lyngbya spp. blooms. Left hand side: (a) Lyngbya spp. bloom in Silver Spring, Florida. (b) Close-up photograph of Lyngbya aggregates covering freshwater macrophytes. (c) Photomicrograph of dominant Lyngbya species forming the bloom. Right hand side: (d) Lyngbya spp. bloom covering a seagrass bed, near Sanibel Island, Florida. (e) Close-up photograph of Lyngbya aggregates clinging to seagrass leaves. (d) Photomicrograph of Lyngbya sp. responsible for the bloom. Photographs by Hans Paerl.](image-url)
level, physical, chemical and biotic regulatory variables often co-occur and interact synergistically and/or antagonistically to control the activities (N, fixation, photosynthesis) and growth of harmful (toxic, food web disrupting, hypoxia-generating) bloom-forming cyanobacteria, or CyanoHABs (Paerl, 1988; Paerl and Millie, 1996) (Fig. 1.4). How to best address this challenge?

Nutrient input reductions are the most obvious targets, which can be altered and as such should be a central part of any CyanoHAB mitigation strategies in both freshwater and marine environments (Figs. 1.4 and 1.7). We have long been aware that phosphorus input reduction is an effective means of reducing cyanobacterial dominance in aquatic, and especially freshwater, ecosystems. However, there are increasing instances where nitrogen input reductions are also needed. This is especially the case in eutrophic, CyanoHAB susceptible, lakes, rivers, estuaries and coastal waters which are capable of assimilating more nitrogen and increasing their trophic state (Paerl and Scott, 2010; Paerl, 2013). A key management priority is establishing nitrogen and phosphorus input thresholds (e.g., total maximum daily loads; TMDLs), below which CyanoHABs can be controlled in terms of magnitude, temporal and spatial coverage (Paerl, 2013). The ratios of nitrogen to phosphorus inputs should be considered when developing these thresholds. Ideal input ratios are those that do not favour CyanoHAB species over more desirable taxa, but there does not appear to be a universal ratio- above or below – which CyanoHABs can be consistently and reliably controlled. For this reason, total nutrient loads and concentrations need to be considered in CyanoHAB management (Paerl and Scott, 2010; Scott et al., 2013). For example, it is generally thought that total molar N/P ratios above ~15 discourage CyanoHAB dominance (Smith, 1983; Smith and Schindler, 2009). However, if the nutrient load and internal concentrations of nitrogen or phosphorus are extremely high (i.e., above saturation levels), a ratio approach for reducing CyanoHABs is not likely to be effective (Paerl and Otten, 2013a).

There are many ways to reduce nutrient inputs on a lake or larger ecosystem scale (see Smith and Schindler, 2009; US EPA, 2011). Nutrient inputs have been classified as point source and non-point source. Point sources are often associated with well-defined and identifiable discharge sites; therefore, these nutrient inputs are relatively easy to control. Targeting point sources is often attractive, because they can account for a highly significant share of phosphorus and nitrogen loading, they are readily identifiable, accessible, and hence from a regulatory perspective, easiest to control. The major challenge that remains in many watersheds is targeting and controlling non-point sources, which in many instances are the largest sources of nutrients; hence, their controls are likely to play a critical role in mitigating CyanoHABs in the context of human and climatically driven environmental changes currently taking place.

Phosphorus management

Phosphorus inputs to aquatic ecosystems are dominated by (1) non-point source surface runoff, (2) point sources such as effluents from wastewater treatment plants, industrial and municipal discharges, and (3) subsurface drainage from septic systems and groundwater. Among these, point sources have been the focus of phosphorus reductions. In agricultural and urban watersheds, non-point source and subsurface phosphorus inputs are of increasing concern. Increased phosphorus fertilizer use, generation and discharge of animal waste, soil disturbance and erosion, conversion of forests and grasslands to row-crop and other intensive farming operations, and the proliferation of septic systems accompanying human population growth are rapidly increasing non-point phosphorus loading (Sharpley et al., 2010). In agricultural and urban watersheds, non-point sources can account for at least 50% of annual phosphorus loading (Sharpley et al., 2010). Because of the diffuse nature of these loadings, they are more difficult to identify and address from a nutrient management perspective. They are also very susceptible to mobilization due to an increase in episodic rainfall events, including nor’easters and tropical cyclones.

The manner in which phosphorus is discharged to phosphorus-sensitive waters pays a role in CyanoHAB proliferation and management. Considerations include (1) total annual (i.e., chronic) phosphorus loading, (2) shorter-term seasonal and event-based pulse (i.e., acute) phosphorus loadings, (3) particulate versus dissolved phosphorus loading, and (4) inorganic versus organic phosphorus loading. In terms of overall ecosystem phosphorus
budgets and long-term responses to phosphorus loadings (and reductions), annual phosphorus inputs are of fundamental importance. When and where phosphorus enrichment occurs can determine the difference between bloom-plagued versus bloom-free conditions. For example, if a large spring phosphorus discharge event precedes a summer of dry, stagnant (stratified) conditions in a relatively long residence time water body, the spring phosphorus load will be available to support summer bloom development and persistence. Effective exchange and cycling between the water column and bottom sediments can retard phosphorus transport and hence retain phosphorus (Wetzel, 2001) (Fig. 14). As a result, acute phosphorus inputs due to high flow events and periods may be retained longer than would be estimated based on water flushing time alone. As such, water bodies exhibit both rapid biological responses to and a ‘memory’ for acute phosphorus loads.

Unlike nitrogen, which can exist in dissolved, particulate and gaseous forms, phosphorus exists only in dissolved ionic and particulate forms in natural waters. Therefore, the main concern is with dissolved versus particulate forms of inorganic and organic phosphorus. Dissolved inorganic phosphorus (DIP) exists as orthophosphate (PO$_4^{3-}$), which is readily assimilated by all CyanoHAB taxa. Cyanobacteria can accumulate and store assimilated phosphorus intracellularly as polyphosphates; which can be available for subsequent use during times of phosphorus depletion (Healy, 1982). Dissolved organic phosphorus (DOP) can also be a significant fraction of the total dissolved phosphorus pool. DOP can be assimilated by bacteria, microalgae and cyanobacteria, although not as rapidly as PO$_4^{3-}$ (Lean, 1973). A large fraction of the assimilated DOP is microbially recycled to DIP, enhancing phosphorus availability. The role of particulate phosphorus (as inorganic or organic forms) in aquatic production and nutrient cycling dynamics is less well understood. Particulate phosphorus (PP) may provide a source of DIP and DOP via desorption and leaching, and it may serve as a ‘slow release’ source of DIP. In this manner, a fraction of PP can serve as a source of biologically available phosphorus and hence play a role in CyanoHAB control. On the ecosystem-scale, sedimented PP serves as an important source of stored phosphorus for subsequent release, especially during hypoxic/anoxic periods. It is therefore essential to include both dissolved and particulate phosphorus when managing phosphorus inputs, especially under hydrologically variable conditions predicted with climate change.

**Nitrogen management**

Nitrogen exists in multiple dissolved, particulate and gaseous forms. Many of these forms are biologically available and readily exchanged within and between the water column and sediments (Galloway et al., 2004). In addition, biological nitrogen (N$_2$) fixation and denitrification control the exchange between inert gaseous atmospheric N$_2$ and biologically available combined nitrogen forms. Combined forms of nitrogen include dissolved inorganic nitrogen (DIN; including ammonium (NH$_4^+$), nitrate (NO$_3^-$) and nitrite (NO$_2^-$)), dissolved organic nitrogen (DON; e.g. amino acids and peptides, urea, organo-nitrates), and particulate organic nitrogen (PON; polypeptides, proteins, organic detritus). These forms can be supplied from non-point and point sources. Non-point sources include surface runoff, atmospheric deposition and groundwater, while point sources are dominated by municipal, agricultural and industrial wastewater. In rural and agricultural settings, non-point nitrogen inputs tend to dominate (>50% of total nitrogen loading), while in urban centres, point sources often dominate (US EPA, 2011). All sources contain diverse organic and inorganic nitrogen species in dissolved and particulate forms; representing a mixture of biologically available DIN, DON and PON.

Nitrogen inputs are dynamic, reflecting land use, population and economic growth and hydrologic conditions (Galloway et al., 2002). The means and routes by which human nitrogen sources impact eutrophication are changing (US EPA, 2011). Among the most rapidly growing (amount and geographic scale) sources of human nitrogen loading include surface runoff, groundwater and atmospheric deposition. Atmospheric nitrogen loading is also an often-overlooked but expanding source of nitrogen input to nitrogen-sensitive waters (Paerl et al., 2002; US EPA, 2011). As with phosphorus, nitrogen input and cycling dynamics are sensitive to patterns and intensities of precipitation, freshwater flow, which control mobilization in the watershed and discharge to nitrogen-sensitive waters.
The interactions of physical, biological and nutrient controls of cyanobacteria in a climatically changing world

Physical factors
Physical factors, including altering turbulence, vertical mixing and hydrological flushing, play key roles of cyanobacterial blooms in aquatic ecosystems. It is well known that vertical stability (thermal or salt stratification), and long water replacement (residence or flushing) times favour cyanobacteria over eukaryotic phytoplankton; hence disruption of these conditions can, under certain circumstances and in specific systems modulate cyanobacterial bloom dynamics (Figs. 1.4 and 1.7). Vertical mixing devices, bubblers and other means of breaking down destratification have proven effective in controlling outbreaks and persistence of CyanoHABs in relatively small impoundments such as farm and fish ponds (Visser et al., 1996; Huisman et al., 2005). These devices have limited applicability in large lake, estuarine and coastal waters however, because they cannot exert their forces over such large areas and volumes.

Increasing the flushing rates, and thereby decreasing water residence time (or water age), can be effective in reducing or controlling bloom taxa; mainly because cyanobacteria exhibit relatively slow growth rates, relative to eukaryotes. Horizontal flushing, by increasing the water flow through lakes or estuaries, can reduce the time for cyanobacterial bloom development (Maier et al., 2004). While these approaches can yield positive results (i.e. suppression of CyanoHAB intensity), hydrological changes can be quite expensive and restricted to relatively small water bodies.

Water quality managers must ensure that the flushing water is relatively low in nutrient content, so as not to worsen the enrichment problem, especially in large water bodies, which tend to have a long ‘memory’ for nutrient inputs. For example, in hypereutrophic Lake Taihu, China, efforts to reduce Microcystis-dominated blooms by flushing this large lake with nearby Yangtze River water, which reduced the lake’s overall residence time from ~1 year to ~200 days, have not had a significant impact on reducing blooms, largely because Yangtze River water is exceedingly high in dissolved nitrogen and phosphorus compounds. Furthermore, the inflow pattern of Yangtze River water has altered the circulation regime of Taihu, and entrained or ‘trapped’ blooms in the lake’s northern bays, where they are most intense to begin with (Qin et al., 2010). Lastly, few catchments have the luxury of being able to use precious water resources normally reserved for drinking or irrigation water for flushing purposes. This is especially true of regions where freshwater runoff is limited and/or is periodically impacted by droughts (Paerl et al., 2011a).

Non-nutrient chemical controls
Chemical treatments have been used to control cyanobacterial blooms. These include the applications of algaecides, the most common of which is copper sulfate. Copper sulfate is effective, but it can be toxic to a wide variety of plant and animal species and its residue in the sediments is problematic as a legacy pollutant. More recently, hydrogen peroxide (Matthijs et al., 2013) has been shown to be an effective algicide. It is an attractive alternative to copper sulfate because it is selective for cyanobacteria (vs eukaryotic algae and higher plants) and poses no serious long-term pollution problem. Both of these treatments are restricted to fairly small impoundments.

An alternative (to algaecides) chemical approach is to employ precipitation of phosphorus, thereby keeping it ‘locked up’ in the sediments (Fig 1.4). One treatment, called Phoslock, uses a bentonite clay infused with the rare earth element lanthanum (Robb et al., 2003). The lanthanum ions are electrostatically bound to the bentonite, while also strongly binding to phosphate anions. The bound phosphate then settles out of the water column and the thin layer (~1 mm) of Phoslock on the sediment surface forms a barrier to phosphate diffusing out of the sediments (Robb et al., 2003). Phoslock has been shown to work well in small reservoirs, where it can lead to phosphorus-limited conditions that can control CyanoHAB production (Robb et al., 2003). Additionally, the thin Phoslock layer increases the critical erosional velocity of fine-grained surficial sediments, which should reduce the frequency of resuspension events and associated pulse nutrient loading (although, this will largely be effective in relatively small, deep lakes). Sediment stabilization and reduced phytoplankton biomass may also aid restoration of macrophyte communities in shallow, eutrophic systems where light limitation and low
root anchoring capacity of fine-grained, organic-rich sediments often synergistically determine CyanohAB dominance. Shallow lakes in which wind-driven sediment resuspension may be a common feature may not be good candidates for precipitation techniques like Phoslock.

**Altering sediment dynamics**

Even when external nutrient inputs are reduced, the legacy of eutrophication in sediments can perpetuate high internal nutrient loads and provide a steady inoculum of algal spores or cysts that can continue to fuel CyanohABs (Petersen, 1982; Cronberg, 1982; Robb et al., 2003). Therefore, either removing sediments or capping them so that sediment-water column exchange of nutrients and algal cells is restricted has been used to control CyanohABs (Fig. 14).

Sediment removal involves expensive dredging, disturbance of lake bottoms, which can lead to additional nutrient (and potentially toxic substances) release and destruction of benthic flora and fauna (Petersen, 1982). There are examples of successful eradication of CyanohABs using this approach, e.g. Lake Trummen, Sweden, a small (∼1 km², mean depth 1.6 m) lake that experienced CyanohAB related water quality degradation in response to domestic sewage and industrial nutrient inputs during the mid-1900s (Cronberg, 1982). Suction dredging the upper half-metre of sediments during a two-year period led to highly significant decreases in nutrient concentrations and CyanohABs (Cronberg, 1982). The Lake Trummen success can largely be attributed to its small, easily manipulatable size, and the ability to effectively target reductions of external nutrient loads from its small (13 km²) watershed, following dredging. In other sediment dredging efforts on sections of large lakes, results have been far less successful or not noticeable at all (e.g. Lake Taihu, China)

**Biological controls**

Biological controls include a number of approaches to change the aquatic food web to increase grazing pressure on cyanobacteria or to reduce recycling of nutrients. Biomanipulation approaches can include introducing fish and benthic filter feeders capable of consuming cyanobacteria, or introduction of lytic bacteria and viruses. The most common biomanipulation approaches are intended to increase the abundance of herbivorous zooplankton by removing zooplanktivorous fish or introducing piscivorous fish. Alternatively, removal of benthivorous fish can reduce resuspension of nutrients from the bottom sediments. Questions have been raised about the long-term efficacy of curtailing cyanobacterial blooms by increasing grazing pressure, because this may lead to dominance by ungrazeable or toxic strains (McQueen, 1990; Ghadouani et al., 2003). Presently, biomanipulation is viewed as one component of an integrated approach to water quality management in circumstances in which nutrient reductions alone are insufficient to restore water quality (Moss et al., 1996; Scheffer, 1998; Elser, 1999; Jeppesen et al., 2007a,b). Otherwise, nutrient management is the most practical, economically feasible, environmentally friendly, long-term option.

In an overwhelming number of cases, nutrient input reductions are the most direct, simple, and ecologically/economically feasible cyanobacterial management strategy; this is especially true for ecosystems experiencing effects of climate change, including warming and/or increased hydrological variability and extremes. Nutrient input reductions that can decrease cyanobacterial competitive abilities, possibly combined with physical controls (in systems that are amenable to those controls) are often the most effective strategies. Nutrient (specifically nitrogen) treatment costs can be prohibitive however, in which case, alternative nutrient removal strategies may prove attractive; including construction of wetlands, cultivation and stimulation of macrophytes, stocking of herbivorous (and specifically cyanobacteria consuming) fish and shellfish species.

**Conclusions**

Cyanobacteria are globally distributed and their activities and relative roles in production and nutrient cycling dynamics are controlled by a complex, set of environmental variables that are heavily influenced by human and climatic perturbations. Their long evolutionary history has enabled them to structurally and functionally diversify, which in turn has enabled them to adapt to short-term (i.e. diurnal, seasonal, decadal) and longer term (geological) environmental perturbations and more gradual changes. Because they have experienced major and
extreme climatic shifts over these time scales, they are well suited to deal with and take advantage of various climatic changes that we are now experiencing, including warming, altered rainfall patterns and amounts, resultant changes in freshwater runoff, flushing and vertical stratification.

In addition to climatically driven environmental changes known to influence cyanobacterial growth and dominance, the most significant anthropogenically influenced factors include (1) nutrient (especially nitrogen and phosphorus) enrichment, (2) hydrological changes, including freshwater diversions, the construction of impoundments such as reservoirs, water use for irrigation, drinking, flood control, all of which affect water residence time or flushing rates, (3) biological alterations of aquatic ecosystems, including manipulations of grazers (from zooplankton to fish), and lastly (4) the discharge of xenobiotic compounds e.g. heavy metals, herbicides and pesticides, industrial and domestic chemicals, antibiotics and other synthetic growth regulators, all of which affect phytoplankton community growth and composition.

Effective long-term management of CyanohABS must address the above-mentioned suites of environmental factors, along with knowledge of the ecological and physiological adaptations that certain taxa possess to circumvent controls derived from our knowledge of these factors. Examples include (1) the ability of N₂-fixing taxa to exploit nitrogen-limited conditions, (2) the ability of certain buoyant taxa to counteract mixing and other means of man-induced destratification aimed at minimizing cyanobacterial dominance, (3) specific mutualistic and symbiotic associations that cyanobacteria have with other microorganisms, higher plants and animals, which may provide clues as to the roles toxins and other chemical factors play in shaping biotic community structure and function.

In an overwhelming number of cases, nutrient input reductions are the most direct, simple, and ecologically/economically feasible cyanobacterial management strategy; this is especially true for ecosystems experiencing effects of climate change, including warming and/or increased hydrologic variability and extremes (Fig. 1.7). Nutrient input reductions that can decrease cyanobacterial competitive abilities, possibly combined with physical controls (in systems that are amenable to those controls) are often the most effective strategies. Nutrient (specifically nitrogen) treatment costs can be prohibitive however, in which case alternative nutrient removal strategies may prove attractive; including construction of wetlands, cultivation and stimulation of macrophytes, stocking of herbivorous (and specifically cyanobacteria consuming) fish and shellfish species.

Water quality managers will have to accommodate the hydrological and physical-chemical effects of climatic change in their strategies. Given the competitive advantages (over eukaryotic algae) that cyanobacteria enjoy in a more climatically extreme period we are now experiencing, efforts aimed at control and management of cyanobacteria will need to be flexible enough to incorporate this extremeness. For example, nutrient input reductions aimed at stemming eutrophication and cyanobacterial bloom potentials will need to be carefully gaged and potentially changed to accommodate higher cyanobacterial growth potentials due to warming and increasing bloom potentials due to stronger vertical stratification and positive nutrient cycling feedbacks.

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![Figure 1.7 Conceptual diagram, showing human and climatic factors affecting cyanobacterial growth responses, aquatic ecosystem responses and ecological effects. The role of physical manipulations and nutrient (nitrogen and phosphorus) input constraints on mitigating negative ecological effects are also shown.](image-url)
Lastly, without a comprehensive strategy to reduce greenhouse gas emissions, future warming trends and their impacts on aquatic ecosystems will likely only lead to further expansion and dominance of these ecosystems by cyanobacteria.

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