Climate change: Links to global expansion of harmful cyanobacteria

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Abstract
Cyanobacteria are the Earth's oldest (~3.5 bya) oxygen evolving organisms, and they have had major impacts on shaping our modern-day biosphere. Conversely, biospheric environmental perturbations, including nutrient enrichment and climatic changes (e.g. global warming, hydrologic changes, increased frequencies and intensities of tropical cyclones, more intense and persistent droughts), strongly affect cyanobacterial growth and bloom potentials in freshwater and marine ecosystems. We examined human and climatic controls on harmful (toxic, hypoxia-generating, food web disrupting) bloom-forming cyanobacteria (CyanoHABs) along the freshwater to marine continuum. These changes may act synergistically to promote cyanobacterial dominance and persistence. This synergy is a formidable challenge to water quality, water supply and fisheries managers, because bloom potentials and controls may be altered in response to contemporaneous changes in thermal and hydrologic regimes. In inland waters, hydrologic modifications, including enhanced vertical mixing and, if water supplies permit, increased flushing (reducing residence time) will likely be needed in systems where nutrient input reductions are neither feasible nor possible. Successful control of CyanoHABs by grazers is unlikely except in specific cases. Overall, stricter nutrient management will likely be the most feasible and practical approach to long-term CyanoHAB control in a warmer, stormier and more extreme world.

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1. Introduction
Cyanobacteria (blue-green algae) are the Earth's oldest known oxygen-producing organisms, with fossil remains dating back ~3.5 billion years (Schopf, 2000). Cyanobacterial proliferation during the Precambrian period is largely responsible for the modern-day, oxygen-enriched atmosphere, and subsequent evolution of higher plant and animal life (Schopf, 2000; Whitton and Potts, 2000). This long evolutionary history has served cyanobacteria well, for it has enabled them to develop diverse and highly effective ecophysiological adaptations and strategies for ensuring survival and dominance in aquatic environments undergoing natural and human-induced environmental change (Hallock, 2005; Huisman et al., 2005; Paerl and Fulton, 2006; Paul, 2008). Today, they enjoy a remarkably broad geographic distribution, ranging from polar to tropical regions in northern and southern hemispheres, where they are capable of dominating planktonic and benthic primary production in diverse habitats.
As a “microalgal” group, the cyanobacteria exhibit highly efficient nutrient (N, P, Fe and trace metal) uptake and storage capabilities, and they are the only oxygenic phototrophs capable of utilizing atmospheric dinitrogen (N₂) as a nitrogen source to support growth via N₂ fixation (Fogg, 1969; Gallon, 1992). Furthermore, many planktonic genera are capable of rapid vertical migration by altering their buoyancy, allowing them to exploit deeper, nutrient-rich waters while also taking advantage of radiant-rich conditions near the surface (Ibelings et al., 1991; Walsby et al., 1997; Reynolds, 2006). Lastly, some genera have formed symbioses (as endosymbionts) in diatoms, sponges, corals, lichens, ferns, and mutualistic associations with a variety of other organisms which provide protection and enhance nutrient cycling and availability in nutrient-deplete waters (Paerl and Pinckney, 1996; Carpenter, 2002; Rai et al., 2002).

Over the past several centuries, human nutrient overenrichment (particularly nitrogen and phosphorus) associated with urban, agricultural and industrial development, has promoted accelerated rates of primary production, or eutrophication. Eutrophication favors periodic proliferation and dominance of harmful blooms of cyanobacteria (CyanoHABs), both in planktonic (Fogg, 1969; Steinberg and Hartmann, 1988; Huisman et al., 2005; Paerl and Fulton, 2006) and benthic (Baker et al., 2001; Dasey et al., 2005; Wood et al., 2006; Izaguirre et al., 2007; Elmetri and Bell, 2004; Albert et al., 2005; Ahern et al., 2007; Paerl et al., 2008) environments.

In freshwater ecosystems, P availability has traditionally been viewed as a key factor limiting CyanoHAB proliferation (Schindler, 1975; Schindler et al., 2008), and excess P (relative to N) loading has been identified as favoring CyanoHABs (Smith, 1983; Watson et al., 1997; Downing et al., 2001). The emphasis on P controls is based on the N₂ fixing capabilities of some CyanoHAB genera, which help satisfy cellular N-requirements under P-limited conditions (Paerl and Fulton, 2006). However, at the ecosystem level, only a fraction, usually far less than 50%, of primary and secondary production demands are met by N₂ fixation, even when P supplies are sufficient (Howarth et al., 1988; Lewis and Wurtsbaugh, 2008; Paerl and Scott, 2010). Hence, N₂ fixation appears to be controlled by factors in addition to P availability. Nutrient loading dynamics have changed substantially over the past several decades. While P reductions have been actively pursued, human population growth in watersheds has been paralleled by increased N loading, often at higher rates than P (Vitousek et al., 1997; Paerl and Scott, 2010). Excessive N loads are now as large a concern as P loads as stimulants of freshwater, estuarine and marine eutrophication and harmful algal (including cyanobacterial) blooms (Conley et al., 2009; Paerl, 2009; Ahn et al., 2011).

Mass development of CyanoHABs, increases turbidity and hence restricts light penetration in affected ecosystems (Figs. 1 and 2). This, in turn, suppresses the establishment and growth of aquatic macrophytes and benthic microalgae and

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**Fig. 1** – Examples of freshwater systems impacted by proliferating CyanoHABs Upper left, MODIS satellite image of surface cyanobacterial blooms in Lake Erie (US-Canadian Great Lakes) during July, 2007. (Courtesy of NASA and Coastwatch-Great Lakes). Upper right, Cyanobacterial (Aphanizomenon flos aquae) bloom on Lake Dianchi, Yunan Province, China, July 2006 (Courtesy of http://4.bp.blogspot.com/_KbJGi-TtEtQ/5VUNroO4aI/AAAAAAAAYE/iGR9zvvSPg/s400/Dianchi+Lake_China_Blue+Green+Algae+Bloom). Lower left, Cyanobacterial (Microcystis spp.) bloom in Lake Taihu, Jiangsu Province, China, photographed by author H. Paerl during a lake-wide bloom in July, 2007. Lower right, a CyanoHAB bloom (Microcystis and Anabaena spp.) on the lower St. Johns River, Florida during summer, 2005 (Courtesy of Bill Yates/CYPIX).
thereby negatively affects the underwater habitat for benthic flora and fauna (Jeppesen et al., 2007; Scheffer et al., 1997, Scheffer, 2004). CyanoHABs also cause nighttime oxygen depletion through respiration and bacterial decomposition of dense blooms, which can result in fish kills and loss of benthic infauna and flora (Paerl, 2004; Watkinson et al., 2005; Garcia and Johnstone, 2006; Paerl and Fulton, 2006). Persistence of CyanoHABs can lead to long-term loss of benthic habitat (c.f., Karlson et al., 2002). Lastly, numerous planktonic and benthic cyanobacterial bloom genera produce toxic peptides and alkaloids (Berry et al., 2008; Humpage, 2008; Liu and Rein, 2010). Ingestion of these cyanotoxins has been linked to liver, digestive and skin diseases, neurological impairment and even death (Chorus and Bartram, 1999; Carmichael, 2001; Humpage, 2008). Hence, toxic CyanoHABs are a major threat to the use of freshwater ecosystems and reservoirs for drinking water, irrigation, and freshwater and marine fishing and recreational purposes (Chorus and Bartram, 1999; Carmichael, 2001; Osborne et al., 2001, 2007).

Wide-distributed toxin-producing CyanoHABs include the planktonic N₂ fixing genera Anabaena, Aphanizomenon, Cylindrospermopsis, Nodularia, the non-N₂ fixing genera Microcystis and Planktothrix, and the benthic N₂ fixing genera Lyngbya, Hormothamnion and (some species of) Oscillatoria, and non-N₂ fixing genera Phormidium, Symploca, and Oscillatoria.

2. Influence of a changing climate on CyanoHAB proliferation

While the connection between eutrophication and CyanoHABs expansion is well-established (Fogg, 1969; Paerl, 1988; Reynolds, 2006; Paerl and Fulton, 2006), climatic changes have also been implicated (Briand et al., 2004; Elliott et al., 2005, 2006; Paerl and Huisman, 2008; Paul, 2008; Paerl et al., 2011a,b). In particular, global warming and associated hydrologic changes, both of which are well-documented (IPCC, 2007), strongly affect the physical–chemical environment and biological processes, most notably metabolism, growth rates and bloom formation (Fig. 3).

Warming can selectively promote cyanobacterial growth because as prokaryotes, their growth rates are optimized at relatively high temperatures (Robarts and Zohary, 1987; Butterwick et al., 2005; Watkinson et al., 2005). This provides...
CyanoHABs a distinct advantage under nutrient-enriched conditions, when competition with eukaryotic primary producers, including diatoms, chlorophytes, cryptophytes and dinoflagellates can be intense (Paerl et al., 2011a,b). Fig. 4 shows that as growth rates of these eukaryotic taxa level off or decline, cyanobacterial growth rates reach their optima and continue to remain high, even when temperatures exceed 25 °C.

Warming of surface waters intensifies vertical stratification in both freshwater and marine systems. Seasonal warming also lengthens the period of stratification. In freshwater systems, stratification tends to take place earlier in spring, the stratification is maintained throughout summer, and destratification is postponed to later in autumn (De Stasio et al., 1996; Peeters et al., 2007; Elliott et al., 2005; Elliott, 2010). Many CyanoHAB species are able to uniquely exploit stratified conditions. Most bloom-forming cyanobacteria contain gas vesicles which provide buoyancy (Walsby et al., 1997), enabling them to form dense surface blooms in stratified waters (Figs. 1 and 2), where they can take advantage of high levels of irradiance to optimize photosynthesis (Huisman et al., 2005).

CyanoHABs themselves may locally increase water temperatures, through the intense absorption of light by their photosynthetic and photoprotective pigments. Using remote sensing, Kahru et al. (1993) found temperatures of surface blooms in the Baltic Sea to be at least 1.5 °C above ambient waters, and Ibelings et al. (2003) noted that the surface temperatures within cyanobacterial blooms in Lake IJsselmeer, Netherlands, were higher than the surrounding surface waters. This represents a positive feedback mechanism, whereby buoyant cyanobacteria enhance surface temperatures, which promotes their competitive dominance over eukaryotic phytoplankton.

Surface-dwelling CyanoHAB taxa contain photoprotective accessory pigments (e.g. carotenoids) and UV-absorbing compounds (mycosporine-like amino acids (MAAs), scytomin) that ensure long-term survival under extremely high irradiance conditions (Paerl et al., 1983; Castenholz and Garcia-Pichel, 2000; Paul, 2008; Carreto and Carignan, 2011), while suppressing non-buoyant species through competition for light.

Other mechanisms surface-dwelling cyanobacteria have for dealing with UV stress include production of antioxidant enzymes, such as superoxide dismutase, catalase, and glutathione peroxidase, and antioxidant molecules, including
ascorbate, carotenoids, and tocopherols (Paerl et al., 1985; He and Häder, 2002; Xue et al., 2005). Cyanobacteria have been shown to adapt to UV radiation (280–315 nm) hours to days after exposure, even without the productions of MAAs. Protective mechanisms include enhanced DNA repair, induction of UVR (100–400 nm) resistant proteins and lipids, and upregulation of peptides and proteins (Castenholz and Garcia-Pichel, 2000). Carotenoids can help protect cyanobacterial surface blooms from UVR (Paerl et al., 1983). The beneficial effects of carotenoids may be indirect since they do not optimally absorb UVR, and they may primarily serve as antioxidants and inhibitors of free radical reactions (Castenholz and Garcia-Pichel, 2000). Planktonic cyanobacteria and motile species that occur in microbial mats can migrate vertically in the water column or within benthic mats to move away from UVR. Increasing temperatures, stronger stratification and longer bloom-susceptible periods will affect both the composition and successional patterns of cyanobacterial and eukaryotic algae in aquatic ecosystems. Longer bloom periods provide a wider “window” for the establishment and succession of CyanoHABs. For example, it has recently been shown that competition among toxic vs. non-toxic strains of the often-dominant CyanoHAB Microcystis is strongly affected by the length of the spring–summer period and light availability needed for supporting various strains (Kardinaal et al., 2007).

3. The link to carbon dioxide dynamics

A key driver of global warming is the rising level of the atmospheric greenhouse gas carbon dioxide (CO₂), which is emitted from accelerating rates of fossil fuel combustion and biomass burning (IPCC, 2007). In nutrient-enriched freshwater systems, dense CyanoHAB blooms exhibit high photosynthetic demands for CO₂; to the extent that ambient waters contain virtually no free CO₂, driving the pH up to 10 or higher; to the extent that the rate of CO₂ supply can at times control the rate of algal biomass production (Paerl and Ustach, 1982; Ibelings and Maberly, 1998; Huisman et al., 2005). When this occurs, buoyant CyanoHABs have a distinct advantage over sub-surface phytoplankton populations, since surface-dwelling taxa can directly intercept CO₂ from the atmosphere, thereby minimizing dissolved inorganic carbon (DIC) limitation of photosynthetic growth and taking advantage of rising atmospheric CO₂ levels (Paerl and Ustach, 1982). Rising levels of atmospheric CO₂ may lead to acidification of both freshwater and marine surface waters, a subject of current research (Doney, 2006; Keller, 2009). However, in CyanoHAB-impacted eutrophic systems, this effect is likely to be negated by the increased bloom activity, which enhances CO₂ consumption and elevates pH levels. In addition, some non-surface dwelling CyanohABs are capable of sustained growth under the high pH conditions resulting from active photosynthesis and CO₂ withdrawal during blooms, by being able to directly use bicarbonate (HCO₃⁻) as a DIC source (Shapiro, 1990; Kaplan et al., 1991; Badger and Price, 2003). Elevated CO₂ was shown experimentally to enhance growth, C:N ratios and N₂ fixation in the open ocean bloom-forming cyanobacterium Trichodesmium erythraeum (Levitan et al., 2007) and may similarly affect other N₂ fixing planktonic and benthic cyanobacteria.

4. Hydrologic changes associated with climatic change

Global warming and associated changes in climatic oscillations affect patterns, intensities and duration of precipitation and droughts, with ramifications for CyanoHAB dominance. For example, larger and more intense precipitation events mobilize nutrients on land and increase nutrient enrichment of receiving waters (Paerl et al., 2006; King et al., 2007). Freshwater discharge to downstream waters would also increase, which in the short-term may prevent blooms by flushing. However, as the discharge subsides and water residence time increases, its nutrient load will be captured and cycled by receiving water bodies, eventually promoting bloom potentials. This scenario will most likely occur if elevated winter–spring rainfall and flushing events are followed by protracted periods of drought. Examples include the Swan River and its estuary in Australia, Hartbeespoort dam reservoir, South Africa, the Neuse River Estuary, North Carolina, and the Potomac Estuary, Maryland, USA (Sellner et al., 1988; Robson and Hamilton, 2003; Huisman et al., 2005; Paerl, 2008). This sequence of events has also been responsible for massive CyanoHABs in large lake ecosystems serving key drinking water, fisheries and recreational needs (e.g. Lake Taihu and other large lakes in China, Lake Erie, US Great Lakes, Lake Victoria and Lake George, Africa) (Huisman et al., 2005; Qin et al., 2010; Paerl et al., 2011a,b), and regions of the Baltic Sea (Kahrul et al., 1993; Suikkanen et al., 2007). Attempts to control discharge of rivers and lakes by dams and sluices may increase the residence time, thereby further aggravating ecological and health problems associated with CyanoHABs (Burch et al., 1994; Rahman et al., 2005; Mitrovic et al., 2006).

5. Salinization

Increasing frequency and severity of droughts is causing more saline conditions in lake, reservoir, riverine and estuarine environments worldwide. In addition, rising sea levels, and ever-increasing demands on freshwater for drinking water and irrigation purposes have promoted increased levels of salinity. From a hydrologic perspective, this trend represents a positive feedback loop, since increased water withdrawal for human use threatens the freshwater supply because it is getting saltier as a result of those withdrawals. Many CyanoHAB taxa can counter such extremeness by surviving for long periods (up to many years) as dormant cysts in sediments, soils, or desiccated mats in arid regions (Potts, 1994). Increasing salinity levels also have major impacts on planktonic and benthic microalgal community structure and function. One impact of salinization is increased vertical density stratification, which would benefit buoyant CyanoHABs that can take advantage of such stratification (Visser et al., 1995; Walsby et al., 2006). In addition, some species of common CyanoHAB genera such as Anabaena, Anabaenopsis, Microcystis and Nodularia are quite salt tolerant, sometimes
more so than counterpart eukaryotic freshwater phytoplankton species (Fig. 5). For instance, the growth rate of toxic strains of Microcystis aeruginosa remains unaffected by salinities ranging from 0 g L\(^{-1}\) up to 10 g L\(^{-1}\), or 30% of seawater salinity (Tonk et al., 2007). Intermittent salinity fluctuations of up to 15–20 g L\(^{-1}\) may still allow survival of Microcystis populations, but cause salt stress, leading to leakage of cells and excretion of the toxin microcystin (Ross et al., 2006). Likewise, Anabaena aphanizominoides can withstand salt levels up to 15 g L\(^{-1}\), while Anabaenopsis and toxic Nodularia spumigena even tolerate salinities ranging from 0 g L\(^{-1}\) to more than 20 g L\(^{-1}\) (Moisander et al., 2002; Tonk et al., 2007) (Fig. 5. Laboratory experiments indicate that the nodularin content of Nodularia correlates positively with salinity (Mazur-Marzec et al., 2005). The high salt tolerance of these CyanoHABs is reflected by increasing reports of blooms in brackish waters, for example in the Baltic Sea (Northern Europe), Caspian Sea (west Asia), Patos Lagoon Estuary (Brazil), the Oued Mellah reservoir (Morocco), the Swan River Estuary (Australia), San Francisco Bay (California, USA), Lake Ponchartrain (Louisiana, USA), and the Kucukcekmece Lagoon (Turkey) (Paerl and Huisman, 2009; Akcaalan et al., 2009). The increased expansion of CyanoHABs into brackish and full-salinity waters potentially exposes other aquatic organisms and human users (recreational, fishing) of these waters to elevated concentrations of cyanobacterial toxins.

6. Grazer interactions

Cyanobacteria are generally considered to be relatively low preference foods for marine herbivores because of chemical and structural defenses and poor nutritional quality; however, there is considerable variability in the ability of different
grazers to consume and grow on cyanobacteria (Paerl et al., 2001; Paul et al., 2001; Landsberg, 2002; Sarnelle and Wilson, 2005; Camacho and Thacker, 2006; Berry et al., 2008; Wilson et al., 2006; Tillmanns et al., 2008). There is evidence that the natural products from cyanobacteria, which are mainly lipopeptides, peptides, depsipeptides and alkaloids, can serve as chemical defenses or may be toxic to grazers and competitors (Christoffersen, 1996; Paul et al., 2001, 2007; Landsberg, 2002; Berry et al., 2008). The chemical defenses of cyanobacteria may play a critical role in bloom formation and persistence by limiting the grazing activity of some potential consumers.

Hallock (2005) suggested that benthic marine cyanobacteria, which are resistant to strong solar radiation, warm temperatures, abundant nutrients, and many generalist grazers, may be useful indicators of stress conditions in reef ecosystems. Benthic cyanobacteria can be early colonizers of dead coral and disturbed substrates and are becoming increasingly well-established on coral reefs. Tsuda and Kami (1973) observed that low light penetration and selective browsing by herbivorous fishes on macroalgae removed potential competitors and favored the establishment of unpalatable benthic cyanobacteria in tropical lagoonal environments. Crude extracts and isolated secondary metabolites of several benthic marine cyanobacteria such as Lyngbya spp., have been shown to deter grazing by generalist herbivores such as fishes and sea urchins (reviewed by Paul et al. 2001, 2007).

In freshwater ecosystems, cyanobacterial blooms can have negative effects on large cladocerans such as Daphnia spp., which may be more susceptible to cyanobacterial toxins than some other grazers (Tillmanns et al., 2008). Negative physiological effects (DeMott et al., 1991; Rohrlack et al., 2001, 2005) and negative fitness consequences (Gustafsson et al., 2005) on zooplankton grazers such as Daphnia spp. have been observed; however, the physiological susceptibilities of different populations of zooplankton can vary considerably. Some populations of Daphnia galeata and Daphnia pulicaria exposed to chronically high abundance of cyanobacteria can adapt to being more tolerant of cyanobacteria in their diets (Haiden et al., 1999, 2001; Sarnelle and Wilson, 2005). Cyanobacteria and cyanotoxins can also inhibit feeding by other grazers, such as copepods and rotifers, in fresh and estuarine waters (Sellner et al., 1993; Paerl et al., 2001; Reinikainen et al., 2002).

Grazer interactions with cyanobacteria are highly species-specific; considerable intra- and interspecific variation in the effects of cyanobacteria and cyanobacterial toxins on consumers have been observed in experimental studies (Wilson and Hay, 2007; Tillmanns et al., 2008).

Additional complexity in zooplankton–cyanobacterial interactions can be observed when higher trophic levels, such as fishes that are zooplankton grazers, are included in observational and experimental studies. Zooplankton species that can control cyanobacteria, such as Daphnia spp. (Sarnelle, 1993; Tillmanns et al., 2008), are often the preferred food of planktivorous fishes in freshwater systems. Studies manipulating fish abundance often demonstrate a typical trophic cascade where planktivorous fishes reduce the abundance of zooplankton and increase the biomass of phytoplankton (Brett and Goldman, 1997; Vanni et al., 1997; Carpenter et al., 2001). Fish and zooplankton abundance also directly and indirectly affect nutrient dynamics in these lakes (Sarnelle, 1993; Vanni et al., 1997). Both consumers and nutrient availability can have pronounced effects on food webs, including phytoplankton biomass and community structure (Brett and Goldman, 1997). These complex factors coupled with climatic variation can drive successional patterns, phytoplankton and zooplankton dynamics in lake ecosystems (Blenckner et al., 2007).

Little is known about how temperature and other abiotic factors may play a role in specific trophic interactions. Temperature, light, and nutrients may have interactive effects on cyanobacterial growth and toxin production, with consequent effects on aquatic food webs. One laboratory study showed that increases in water temperature could increase the susceptibility of rotifers to toxic effects of anatoxin-a produced by Anabaena flos-aquae (Gilbert, 1996). Two planktonic rotifers were acclimated for many generations to low (12–14 °C), intermediate (19 °C), and high (25 °C) water temperatures, and reproductive rates of the rotifers were inhibited by the cyanobacterium and anatoxin-a. The negative effects of the cyanobacterium and the toxin increased with increasing temperature.

Studies have also shown correlations between climate variation, often related to the North Atlantic Oscillation (NAO), and spring plankton dynamics and clear water phases in shallow, polymeric European lakes (Gerten and Adrian, 2000; Scheffer et al., 2001; Abrantes et al., 2006; Blenckner et al., 2007). Clear water phases, caused by grazing of zooplankton on microalgae, were studied in 71 shallow Dutch lakes and were found to occur earlier when water temperatures were higher (Scheffer et al., 2001, Scheffer, 2004). Water temperatures were strongly related to the North Atlantic Oscillation (NAO) winter index. A simulation model of algae–zooplankton dynamics seemed to confirm the primary role of temperature in determining the probability and timing of the clear water phase. In a 42-year study of the small subalpine Castle Lake in northern California, increasing water temperatures were accompanied by increasing mean summer cyanobacteria biomass, whereas diatoms and other phytoplankton groups did not show significant trends with summer water temperatures (Park et al., 2004). Summer water temperature also had a significant positive correlation with biomass of Daphnia rosea, a relationship also reported for European lakes where warm winter air temperatures caused by the NAO enhanced spring Daphnia biomass and influenced the timing of the clear water phase (Strale and Adrian, 2000; Blenckner et al., 2007).

7. Evidence from aquatic ecosystems undergoing climatically-induced ecological change

Evidence from geographically-diverse aquatic ecosystems varying in size, morphology, salinity and hydrologic conditions, indicates that climatic change can act synergistically with anthropogenic nutrient enrichment to promote global expansion of CyanoHABs.

Kosten et al. (2011) conducted a survey of 143 lakes of varying trophic state situated along a latitudinal gradient from Northern Europe to Southern South America. They found that the percentage of total phytoplankton biomass attributable to...
cyanobacteria increased markedly with temperature. These authors also noted that temperature increases may lower the nutrient input thresholds at which blooms can be initiated and sustained; that is, at elevated temperatures, bloom-forming CyanoHABs can proceed at lower nutrient input rates and concentrations than when temperatures were relatively cooler. For example, in Northern Europe (N. Germany, Sweden, Finland) lakes that exhibit symptoms of long-term (decadal-scale) warming, including warmer surface water temperatures, stronger and more persistent vertical stratification, earlier melting of their ice covers and overall extended warm water conditions and longer growing seasons show increases in cyanobacterial dominance, bloom frequencies and persistence (Weyhenmeyer, 2001; Nöges et al., 2003; Wagner and Adrian, 2009; Feuchtmayr et al., 2009; Elliott, 2010).

These results expand on previous studies confined to lakes in tropical and subtropical waters that show a tendency toward domination by cyanobacteria, even when trophic states varied (Ganf and Horne, 1975; Talling, 1986; Lewis, 1987; Philips et al., 1997; Bouvy et al., 2000; Velzeboer et al., 2000; Komárkova and Tavera, 2003; Havens et al., 2003; Abrantes et al., 2006). Relatively high rates of N₂ fixation, a key indicator of cyanobacterial activity and an important biogeochemical process, are observed in tropical freshwater and marine systems as well (Horne and Viner, 1971; Capone, 1983; Capone et al., 2005). Overall, these studies show a strong positive relationship between mean annual temperature and cyanobacterial dominance, a trend originally observed by Robarts and Zohary (1987). There are exceptions to this, including high elevation (although cyanobacteria are common in some high altitude, low latitude lakes (e.g. Lake Titicaca, Peru-Bolivia) (Wurtsbaugh et al., 1985), high humic acid content and resultant acidic conditions (i.e. pH < 6), extremely oligotrophic (severe nutrient-limited), rapidly flushed (short residence time), and poorly-stratified (polymictic) conditions (Vincent, 1987). Interestingly, the proportion of cyanobacteria in both planktonic and benthic habitats of these systems increases as nutrient loading increases, which suggests synergism between elevated temperatures and nutrient enrichment.

Some of the CyanoHAB taxa typically associated with warmer water conditions, including the planktonic heterocystous N₂ fixer Cylindrospermopsis sp, and the benthic/planktonic non-heterocystous filamentous genus Lyngbya spp. (some species are known to fix N₂) have expanded into temperate regions (Stüken et al., 2006; Wiedner et al., 2007). Cylindrospermopsis was originally described as a tropical and subtropical species. However, Cylindrospermopsis raciborskii appeared in Europe during the 1930s, and showed a progressive colonization from Greece and Hungary toward higher latitudes near the end of the 20th century (Padišák, 1997). It was first described in France in 1994, in the Netherlands in 1999, and it is now also widespread in lakes in northern Germany (Stüken et al., 2006). C. raciborskii was first identified in the United States in 1955, in Wooster Lake, Kansas. 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). This CyanoHAB has spread throughout US Southeast and Midwest reservoirs and lakes, especially those undergoing eutrophication accompanied by a loss of water clarity (Chapman and Schelske, 1997). 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 (Padišák, 1997; Stüken et al., 2006). It also prefers water temperature conditions in excess of 20 °C, and survives adverse conditions using specialized resting cells, akinetes (Briand et al., 2004; Wiedner et al., 2007).

The filamentous toxin-producing CyanoHAB genus Lyngbya has 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 its expansion (Paerl and Fulton, 2006). Lyngbya species often form periphytic or benthic mats, although some species, such as Lyngbya 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” (Fig. 2). It is widely associated with contact dermatitis, where the initial burning symptoms give way to blister formation and peeling of the skin (Carmichael, 2001). L. majuscula produces a large suite of bioactive compounds, including the dermatoxoy alysiatoxins and lyngbyatoxin A (Osborne et al., 2001), and hundreds of other natural products (Paul et al., 2007; Liu and Rein, 2010). In freshwater environments, Lyngbya wollei has been associated with the production of paralytic shellfish poisoning (PSP) toxins (Carmichael, 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 et al., 2006, 2008). Both Lyngbya majuscula (marine) and Lyngbya wollei (freshwater) are opportunistic invaders when favorable environmental conditions exist (nutrient over-enrichment, poorly flushed conditions). Following large climatic and hydrologic perturbations such as hurricanes, L. wollei is an aggressive initial colonizer of flushed 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 (Fig. 2). As is the case with Cylindrospermopsis and Microcystis, this CyanoHAB can take advantage of both human and climate-induced environmental change.

Interestingly, expansion of some CyanoHAB genera has occurred even in some lakes that have experienced no recent increase in nutrient (N and P) loading, indicating that in certain cases increasing temperature may play an independent role in promoting geographic expansion of some CyanoHABs (Padišák, 1997; Stüken et al., 2006; Kosten et al., 2011). Most CyanoHAB-impacted lakes, rivers, estuaries and coastal waters, however, also have a recent history of increases in nutrient loading accompanying human population increases in their water- and airsheds (Huismans et al., 2005; Paerl et al., 2011a,b). These systems have, in general, shown increases in cyanobacterial dominance and production. They are also sensitive to the effects of regional warming. In central Florida
(USA), numerous lakes have experienced the co-occurring effect of nutrient over-enrichment and climate change, including larger oscillations between particularly active storm periods and extreme droughts, as well as long-term increases in mean seasonal and annual air temperatures (Philips et al., 1997; Havens et al., 2007).

China’s third largest lake, Taihu is situated in Jiangsu Province, China’s most rapidly-growing economic region (Fig. 1). Rapid increases in urbanization, agricultural production and industrial output have led to a significant increase in both N and P loading (Qin et al., 2007; Hai et al., 2010; Paerl et al., 2011a,b). This trend has led to a phytoplanktonic “state change”, from a largely diatom-dominated community in the 1960s and 1970s to what is now a CyanoHAB (Microcystis spp.) dominated community for much of the year (May through October) (Chen et al., 2003a,b; Qin et al., 2010). Increases in N and P loading have continued steadily since the 1960s, reflecting population growth in the Taihu Basin (Qin et al., 2007, 2010). Regional warming has also taken place, as shown in records kept by the Chinese Meteorological Bureau at nearby Shanghai and a recent rise in mean lake water temperatures (Qin et al., 2010) (Fig. 6). The recent increase in warming has occurred much faster than nutrient loading (Qin et al., 2010). Interestingly, bloom intensity or biomass, as measured by depth-integrated chlorophyll a concentrations, have also rapidly increased in parallel with air and water temperature increases (Fig. 6). Qin et al. (2010) concluded that these trophic changes were attributed to the combined effects of nutrient over-enrichment and a warming trend.

The shallow lakes of the Netherlands provide a long-term record of phytoplankton community changes accompanied by cultural eutrophication and climatic changes. Eutrophic conditions have been present for several centuries, following the reclaiming of land from the sea by the formation of sub sea-level polders (17th and 18th century), accompanied by agricultural expansion (rowcrop, cattle grazing and dairy operations), urbanization and industrialization. However, over the past 100 + years, this region has also experienced a rise in mean annual air temperatures. This has caused surface water warming, an increased potential for water column stratification and increased frequencies and magnitudes of buoyant, surface-dwelling CyanoHAB genera, especially non-N2 fixing genera such as Microcystis (indicative of N enrichment). Regional warming further promotes such blooms (Jöhnk et al., 2008).

Similarly, the Baltic Sea region, which has been impacted by anthropogenic nutrient enrichment and has exhibited symptoms of eutrophication for several centuries (Elmgren and Larsson, 2001), has also shown a recent warming trend, which has translated into changes in phytoplankton community composition favoring cyanobacterial dominance (Suikkanen et al., 2007). Paleolimnological evidence, including diagnostic pigment analyses of sediments (Bianchi et al., 2000) has indicated that cyanobacteria formed a significant fraction of phytoplankton biomass prior to the 20th century. However, the relative dominance and persistence of CyanoHABs may have increased in response to more favorable climatic conditions, especially warming (Suikkanen et al., 2007).

In efforts to protect the world’s drinking and irrigation waters, fisheries and recreational resources represented by these ecosystems, researchers and water quality/resource managers are faced with simultaneous, interactive “moving targets” that represent formidable challenges, including effects of 1) nutrient over-enrichment, 2) temperature increases, including changes in thermal stratification and 3) changes in freshwater discharge, flow (flushing) regimes and water residence time. Despite the diverse findings showing general trends in expansion of cyanobacterial blooms along latitudinal climatic gradients, there is substantial individuality.

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**Fig. 6** Changes in mean daily spring surface air temperature from March 1 to May 31 since 1951 at Shanghai Meteorological Station, Meteorological Bureau of China, changes in mean daily surface water temperature from March 1 to May 31 in Lake Taihu since 1995, and changes in annual mean surface chlorophyll a concentrations over a similar time frame (lake monitoring data were first systematically collected in 1995 and are from Qin et al., 2010). Lake Taihu is located approximately 100 km west of Shanghai, China.
in susceptibility among aquatic ecosystems due to differences in hydrography and geomorphology, hydraulic residence time, variable nutrient inputs and grazing pressures and seasonal and inter-annual rainfall. Therefore, there is good reason to examine susceptibility and needed management actions on a system-specific basis.

8. Future research and management ramifications and needs

Clearly, nutrient reduction strategies aimed at CyanoHAB control must take co-occurring climatic changes favoring CyanoHAB dominance into account. Specifically, nutrient concentration and loading thresholds below which CyanoHABs can be controlled may need to be revised, because they are changing due to the nutrient-climate change interactions taking place (Paerl et al., 2011a,b; Kosten et al., 2011). Critical nutrient loads above which CyanoHAB dominance is promoted under favorable hydrologic (reduced flushing and increased residence time) and temperature (increases) conditions may need to be revised downward in order to compensate for more favorable growth and competition (with eukaryotes) conditions. In all likelihood, these nutrient loading adjustments will be system-specific, because nutrient loading characteristics are often a unique product of the size, population density and development patterns/activities of watershed/airsheds and the area/morphometry/volume, hydrologic residence time, vertical mixing and optical properties of receiving waterways. Superimposed on this will be changes in seasonal temperature, irradiance, precipitation and wind conditions.

An additional set of factors that were not addressed in this article, but will need to be factored into determining and predicting changes in ecosystem-level sensitivity to CyanoHAB invasion, magnitudes and persistence, are changes in “top down” consumption (zooplankton and benthic grazing). These changes could at least in part be driven by climatic changes, including impacts of temperature regimes on grazer community structure and activity, as well as human activities, including habitat disturbances and alterations, introductions of exotic species, fishing pressure, and the construction of barriers such as dams, locks, and submerged structures (piers, jetties, artificial reefs, etc.).

The interactive nature of these complex and often nonlinear alterations in physical, chemical and biotic drivers/ perturbations of aquatic ecosystem function will require new quantitative approaches to detecting, quantifying, synthesizing and modeling impacts and effects. Furthermore, the synthesis and modeling product will help managers and decision makers account for and adjust their strategies for CyanoHAB control in response to future climate change and human impact scenarios. Lastly, management actions will need to be system-specific, due to the aforementioned complex interactions of controlling variables, which vary in individual water bodies. This is an unenviable but essential task as we strive to formulate effective, verifiable and accountable management strategies aimed at controlling CyanoHABs and protecting our precious water resources well into the 21st century.

9. Conclusions

Recent research and models, laboratory studies and field observations show that the combination of anthropogenic nutrient loading, rising temperatures, enhanced vertical stratification, and increased atmospheric CO2 supplies will favor cyanobacterial dominance in a wide range of aquatic ecosystems (Fig. 3). Cyanobacteria have efficient CO2 and nutrient uptake mechanisms, are well protected from light and UV radiation, and are highly adaptable, allowing them to take advantage of changing environmental conditions in aquatic environments. The expansion of CyanoHABs has serious consequences for human drinking and irrigation water supplies, fisheries and recreational resources. This has ramifications for water management. In addition to nutrient reduction, water authorities combating CyanoHABs will have to accommodate the hydrological and physical—chemical effects of climatic change in their management strategies, keeping in mind regional climatic and anthropogenically-driven changes taking place. In all likelihood, quantitative “fine tuning” of management strategies will need to be system-specific. A key general control we can exert to reduce the rate and extent of global warming however is curbing greenhouse gas emissions. Without this essential step, it is likely that future warming trends and resultant physical—chemical changes in a broad spectrum of aquatic ecosystems will play into the hands of this rapidly expanding group of nuisance species.

Acknowledgments

We thank A. Joyner, N. Hall and T. Otten for technical assistance and J. Huisman, J. Dyble Bressie, and A. Wilson for helpful discussions. This work was supported by the National Science Foundation (OCE 0726989, 0812913, 0825466, and CBET 0825819), the U.S. Dept. of Agriculture NRI Project 00-35101-9981, U.S. EPA-STAR project R82867701, NOAA/EPA-ECOHAB Project NA05NOG471194, and North Carolina Sea Grant Program R/MER-47. This is contribution #853 of the Smithsonian Marine Station at Fort Pierce.

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