Global expansion of harmful cyanobacterial blooms in water supplies due to human development and climate change.

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Abstract

Blue-green algae, or cyanobacteria, can form massive surface growths or "blooms" that produce toxins, taste and odor compounds that threaten drinking water supplies, and negatively impact fishing and recreational use of lakes, reservoirs, and rivers. Many of these harmful cyanobacteria (CyanoHABs) take advantage of rapidly-expanding human activities, including nutrient over-enrichment and resultant eutrophication, and hydrologic modifications, including water withdrawal for irrigation and industrial use, and reservoir construction. Current strategies aimed at protecting drinking waters from toxic CyanoHAB outbreaks are focused on reducing nutrient inputs. In addition, however, recent studies reveal that regional and global climatic change, specifically increases in water temperature and vertical stratification, will also benefit CyanoHABs by increasing their growth rates, dominance, persistence and geographic distributions. Furthermore, increases in climatic extremes, pulsed nutrient loads associated with storms, increases in water residence times due to summer droughts, and salination of freshwaters all tend to favor the competitive dominance of cyanobacteria over other planktonic species. Cyanobacteria are ancient photosynthetic microorganisms, and they have had major impacts on shaping the Earth's atmosphere and biosphere. Their long evolutionary history has enabled them to develop survival strategies and persist as important primary producers in response to extreme environmental conditions and major geochemical changes that have taken place on Earth during the past 3.5 billion years. Today, CyanoHABs appear capable of taking advantage of unprecedented levels of nutrient enrichment *and* regional and global climatic change, especially warming. This adds yet one more reason for reducing greenhouse gas emissions and to invest in strategies that will help reduce global warming.

Introduction

Nutrient over-enrichment from urbanization, agricultural and industrial expansion is a serious threat to the ecological integrity, sustainability and safe use (drinking water, recreational purposes, fishing) of aquatic ecosystems. One of the most troublesome symptoms of nutrient-over-enrichment is the proliferation of blue-green algal, or cyanobacterial, blooms as unsightly, odoriferous, green-yellow paint-like scums (Fig. 1). These blooms are problematic from ecological, economic and health perspectives; hence the designation "harmful" (Chorus and Bartram 1999; Huisman et al. 2005; Paerl and Fulton 2006) (Fig. 1). Toxic, food-web altering, hypoxia-generating harmful cyanobacterial blooms, or CyanoHABs, are geographically expanding and proliferating in large lakes, reservoirs and river systems at alarming rates. In the US, recurring CyanoHABs in 3 of the 5 Great Lakes, other large lake systems (L. Okeechobee, L. Ponchartrain, Great Salt Lake), reservoirs, wetlands and estuaries all point to the potential problems resource managers will face in coming decades (Hudnell 2008). Identifying environmental factors driving the rapid rise in CyanoHABs is paramount to developing management strategies aimed at protecting and ensuring sustainability of impacted lakes and reservoirs, which contain a bulk of the world's drinking and irrigation water supply.

Figure 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, NC, USA; Lake Volkerak, the Netherlands (courtesy of J. Huisman); Lake Taihu, China; St. Johns River, FL, USA (courtesy of J. Burns); Lake Ponchartrain, LA, USA (courtesy of J. Burns); Baltic Sea-Gulf of Finland (courtesy of Finnish Border Guard and Institute of Marine Research, Helsinki, Finland).

While nutrient over-enrichment plays a central role in CyanoHAB proliferation, the amounts and proportions of the nutrients nitrogen (N) and phosphorus (P) controlling algal production and composition are changing in human-dominated watersheds. This has major ramifications for eutrophication and bloom dynamics. Other environmental changes may also affect these dynamics; particularly global warming, which alters physical-chemical conditions and may enhance cyanobacterial growth (Paerl and Huisman 2008). Here, we discuss the interactive effects and management implications of these changing anthropogenic and climatic "drivers" of CyanoHABs.

The Players

Cyanobacteria are the oldest known oxygen-evolving photosynthetic organisms on Earth; they have been present since the Precambrian period, some 3 billion years ago. Their proliferation during this period is largely responsible for the formation of an oxygen-rich atmosphere, paving the way for the evolution of higher plant and animal life (Schopf and Walter 1982). Today, the cyanobacteria remain a remarkable evolutionary success story. They exploit anthropogenic nutrient enrichment, and some genera can convert "inert" atmospheric nitrogen (N_2) into biologically-usable ammonia, by utilizing nitrogen fixation (Fogg 1969; Paerl 1990); thus providing their own nitrogen source when necessary. The CyanoHABs exist in 3 major morphologically distinct groups (Fig. 2): 1) coccoid cells, often aggregated in colonies. Most of these genera do not fix nitrogen (e.g. *Microcystis*). 2) filaments of largely undifferentiated cells, This group is mostly comprised of non-N_2 fixing genera (e.g. *Oscillatoria*, *Planktothrix*); however, a few N_2 fixers capable of toxin production exist (e.g. *Lyngbya*). 3) filamentous cyanobacteria with differentiated, biochemically-specialized, cells called heterocysts. There are numerous CyanoHAB genera in this

- **Unicellular, (non-N₂ fixing)**
  Microcystis*, Gomphosphaeria

- **Filamentous, non-heterocystous (mostly non-N₂ fixing)**
  Lyngbya*, Oscillatoria*,

- **Filamentous, heterocystous (N₂ fixing)**
  Anabaena*, Aphanizomenon*, Cylindrospermopsis*, Nodularia*
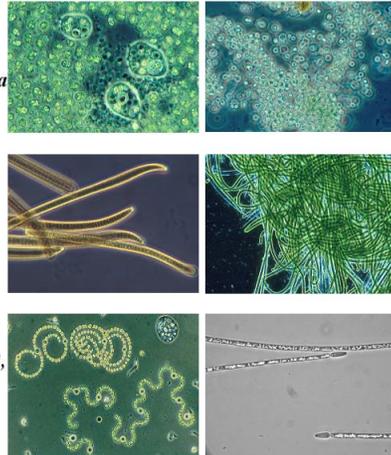
  * Contains toxic strains

Figure 2. Photomicrographs of genera representing the three major CyanoHAB morphological groups, including coccoid, filamentous non-heterocystous, and filamentous heterocystous types.

third group (e.g., *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis, Nodularia*). In addition to planktonic species floating in the open water, this group also includes benthic filamentous species (*Calothrix*, *Rivularia*, *Scytonema*, *Lyngbya*, *Oscillatoria*) that can undergo explosive growths as epiphytes, mats and biofilms. Each group contains non-toxic as well as toxic species (Carmichael 1997; Chorus and Bertram 1999; Huisman et al. 2005). The toxic species produce a variety of different toxins, including liver toxins (e.g., microcystins, nodularins), neurotoxins (e.g., anatoxins, saxitoxins), and dermatotoxins (e.g., lyngbyatoxins).

The Nutrient Connection

CyanoHABs are stimulated by excessive anthropogenic nutrient loading (Paerl 1988). In freshwater ecosystems, the causative agent of advanced eutrophication and CyanoHABs has traditionally been identified as phosphorus (c.f., Likens 1972). Accordingly, control of this element has been the "holy grail" for resource managers; indeed, phosphorus control has been successful in several well-described cases: for example, the enactment of the North American Water Quality Agreement led to a drop in bloom-forming cyanobacteria in many small lake and reservoir systems. The early emphasis on P reductions for CyanoHAB control is based on the observation that phosphorus is an important limiting element for algal growth in many lakes (Sas

1989), and the fact that some CyanoHAB genera are capable of N_2 fixation, which is P-limited in many aquatic ecosystems (Paerl and Fulton 2006). Indeed, studies pursuing controls on CyanoHABs in the 1960's and 70's showed that reducing P inputs and maintaining relatively high N:P input ratios were effective in controlling CyanoHABs in lakes where such inputs could be manipulated (Sas 1989; Smith 1990).

Nutrient loading-wise, however, things have changed a great deal since the 1960s. While P reductions have been actively pursued, unabated human population growth in watersheds has been paralleled by increased anthropogenic generation and release of nitrogen. This has led to a dramatic increase in reactive N in the biosphere, with significant consequences for N-sensitive waters.

Excessive N loads are now as large a concern as P loads as stimulants of freshwater, estuarine and marine eutrophication and harmful algal (including CyanoHAB) blooms (Paerl and Fulton 2006). Recent studies in diverse systems are showing that controls on *both* N and P input will be needed for effective, long term control of eutrophication, associated CyanoHAB outbreaks and their ecological, biogeochemical and human health impacts. One example is the Baltic Sea region, where Elmgren and Larsson (in Paerl and Fulton 2006) showed that effective control of eutrophication and HAB outbreaks required considering total amounts *and* ratios of N and P discharged to nutrient-sensitive river-fjord-sea continuum. Similarly, Paerl et al. (2004) pointed out that single nutrient input reductions, including a P-detergent ban and improved wastewater treatment for P during the 1980's in North Carolina's Neuse River System, helped solve one problem (freshwater CyanoHABs), but exacerbated blooms in downstream N-sensitive waters. In this case, parallel N input reductions were required in addition to P reductions to stem eutrophication and HAB potentials along the *entire* freshwater to marine continuum.

In Florida's inland waters, some of which are used for drinking water purposes, excessive N loading, much of it from expanding wastewater and agricultural discharges has been identified (in addition to P) as a key culprit in eutrophication and CyanoHAB expansion (Kratzer et al. 1981). In some of these waters, dominance by N_2 fixing CyanoHABs (which were largely controlled by P input reductions) has been replaced by co-dominance with non N_2 fixing genera (e.g. *Microcystis*), as well as "switch hitter" CyanoHAB genera (e.g. *Cylindrospermopsis*, *Lyngbya*) that effectively compete for reactive N when it is available and then fix N_2 when N is depleted. In these cases, *both* N and P reductions are needed to reduce and control CyanoHAB bloom potentials.

In the Great Lakes, the CyanoHAB problem has manifested itself as the resurgence of non-N_2 fixing *Microcystis* populations during the last decade. Since 1995, blooms of *Microcystis* have annually reoccurred throughout Lake Erie, a lake thought "recovered" from eutrophication due to well-managed P-abatement programs. However, N inputs, dominated by non-point source agricultural runoff and atmospheric deposition, have remained unchecked and increased dramatically.

By what means and mechanisms have CyanoHABs re-emerged, despite concerted efforts to control P? Large systems, especially shallow eutrophic lakes like Taihu, in China, the Florida large lakes (e.g. Lakes Okeechobee and George), and Lake Erie tend to be co-limited by N and P

because a bulk of previously-loaded P is effectively retained, recycled, hence optimizing internal P availability. Thus, when N enrichment occurs it can stimulate primary production and algal biomass formation. The resultant increase in organic matter stimulates decomposition and nutrient regeneration (i.e. internal recycling), thereby enhancing P (and N) availability. It is therefore concluded that a key to controlling and ultimately managing enhanced internal nutrient recycling is controlling *both* N and P inputs.

In addition to parallel reductions in N and P inputs, studies have shown that hydrologic changes can be highly successful in suppressing cyanobacterial blooms. Two approaches can be discerned. Artificial mixing of lakes, by air bubbling or other mixing devices, is often aimed at decreasing water column stratification and enhancing vertical mixing of the phytoplankton, thereby preventing the formation of surface blooms of buoyant cyanobacteria (Visser et al. 1996; Huisman et al. 2004). Horizontal flushing, by increasing the water flow through lakes or estuaries, aims at the reduction of the water residence time, thus providing less time for the development of cyanobacterial blooms (Mitrovic et al. 2003; Maier et al. 2004; Verspagen et al. 2006). While these studies can yield positive results (i.e. decreased CyanoHAB intensity), hydrologic changes can be quite expensive (Burch et al. 1994) and are therefore neither practical nor feasible in many water bodies experiencing frequent blooms. Accordingly, nutrient reductions remain the all-around most applied tool in controlling CyanoHABs.
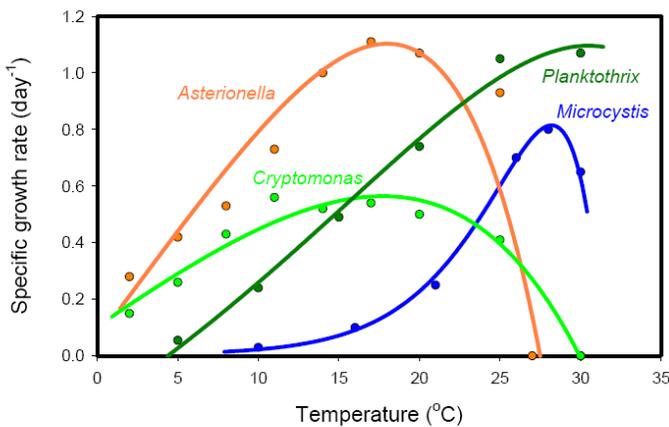
The Role of Climate Change

Figure 3: Temperature dependence of the specific growth rates of the cyanobacteria *Microcystis aeruginosa* 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 Jöhnk et al. (2008).

In addition to nutrient over-enrichment, other environmental changes may play critical roles in a recent upsurge of CyanoHABs. Climate change, specifically global warming, is one such factor. Rising temperatures favor CyanoHABs in several ways. As a group, cyanobacteria exhibit optimal growth rates at relatively high temperatures, usually in excess of 25° C. At these elevated temperatures, CyanoHABs compete very effectively with eukaryotic algae. Thus, as the growth rates of these eukaryotic taxa decline, cyanobacterial growth rates reach their optima (Fig. 3).

Warming of surface waters also intensifies vertical density stratification and thus suppresses vertical mixing. Furthermore, warming lengthens the period of stratification. Some CyanoHABs form gas vesicles, which provide buoyancy. Under strong and persistent vertically stratified conditions, buoyant cyanobacteria can float upwards to form dense surface blooms which shade

deeper non-buoyant eukaryotic phytoplankton, enhancing the CyanoHABs' competitive advantage (Huisman et al. 2004; Jöhnk et al. 2008). Increased water temperatures also decrease the viscosity of water. Therefore, rising temperatures will decrease the water's resistance to vertical migration of phytoplankton. This will facilitate upward (optimizing photosynthetic production) and downward (optimizing nutrient acquisition) migration by CyanoHAB species, further enhancing their competitive advantages in stratified waters.

Dense surface blooms of cyanobacteria may locally increase water temperatures, through the intense absorption of light by their photosynthetic and photoprotective pigments. In the Baltic Sea and in Lake IJsselmeer (Netherlands), for example, surface blooms tend to be warmer than ambient waters (Kahru et al. 1993; Ibelings et al. 2003). This represents a potential positive feedback mechanism, whereby CyanoHABs favor their own competitive dominance over eukaryotic phytoplankton (Hense et al. 2007).

A key driver of global warming is the rising level of the atmospheric greenhouse gas carbon dioxide (CO_2), emitted from rising rates of fossil fuel combustion and biomass burning. In nutrient-enriched waters, 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 control the rate of algal biomass production (Shapiro 1990). High rates of photosynthesis and hence high demand for CO_2 will also increase the pH of affected waters, thereby restricting availability of free CO_2 (Ibelings and Maberly 1998). If and when this occurs, buoyant CyanoHABs have a distinct advantage over sub-surface phytoplankton populations, since surface-dwelling taxa can directly intercept CO_2 from the atmosphere, thus minimizing dissolved inorganic carbon (DIC) limitation of photosynthetic growth (Paerl and Ustach 1982). Under conditions of DIC limitation, subsurface eukaryotic algal populations would be highly dependent on relatively slow diffusional processes to supply new CO_2; hence they are at a disadvantage.

Summer droughts appear to be increasing in intensity and duration, possibly another symptom of global warming. This, combined with increased use of freshwater for irrigation has led to rising salinities around the world. Increased salination is a serious threat to freshwater supplies; it also has major impacts on freshwater plankton composition and possibly CyanoHAB potentials. One impact of salination is increased vertical density stratification, which would benefit buoyant, scum-forming CyanoHABs. In addition, some species of common CyanoHAB genera such as *Anabaena*, *Microcystis* and *Nodularia* are more salt tolerant than their eukaryotic freshwater algal counterparts. For example, 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}, which is 30% of the salinity of seawater (Tonk et al. 2006). Temporary salinity fluctuations of up to 15-20 g L^{-1} may still allow survival of *Microcystis* populations, but causes salt stress leading to leakage of cells and excretion of intracellular microcystin. Likewise, *Anabaena aphanizominoides* can withstand salt levels up to 15 g L^{-1}, while *Anabaenopsis* and toxic *Nodularia spumigena* tolerate salinities ranging from 0 g L^{-1} to more than 20 g L^{-1} (Moisander et al. 2002; Mazur-Marzec et al. 2005). Laboratory experiments indicate that the nodularin (toxin) content of *Nodularia* correlates positively with salinity. The high salt tolerance of these CyanoHABs is reflected by expanding blooms in brackish waters, including the Baltic Sea, the Caspian Sea, Patos Lagoon Estuary, Brazil, the Swan River Estuary, Australia, San Francisco Bay Delta, California and Lake Ponchartrain, Louisiana (Paerl and Huisman 2008).

Global warming and associated changes in climatic oscillations affect patterns, intensities and duration of precipitation and droughts. These hydrologic changes may enhance CyanoHAB dominance. For example, larger and more intense precipitation events will increase enrichment of water bodies with land-derived nutrients through enhanced surface runoff and groundwater discharge. Freshwater discharge to downstream waters would also increase, which in the short-term may prevent blooms by promoting flushing. However, as the discharge subsides and water residence time increases, its nutrient load will be captured and cycled by receiving water bodies, promoting bloom potentials. This scenario appears to be unfolding in geographically-distinct places including the Swan River, Australia, Hartbeespoortdam, South Africa, the Neuse River Estuary, North Carolina, USA, and the Potomac Estuary, Maryland, USA. In addition, attempts to control fluctuations in the discharge of rivers and lakes by dams and sluices may increase the residence time, thereby further aggravating CyanoHAB problems.

Overall, it appears that increases in hydrologic variability and "extremeness" such as protracted droughts benefit CyanoHABs. If conditions get so extreme as to dry up lakes reservoirs, most CyanoHAB species can survive such extremeness for long periods (up to many years) as dormant cysts in sediments, soils, or desiccated mats.

Some toxin-producing CyanoHABs appear to be particularly successful in exploiting climatic change. The planktonic, toxin-producing, N_2 fixer *Cylindrospermopsis raciborskii* and the benthic filamentous N_2 fixing genus *Lyngbya* have shown remarkable expansion of their geographical ranges, and this expansion may be linked to warming and associated hydrodynamic changes. *Cylindrospermopsis* was originally described as a tropical and subtropical species. However, *C. raciborskii* appeared in southern Europe during the 1930s, and has shown a progressive increase in colonization from Greece and Hungary up to the Netherlands and northern Germany near the end of the 20th century (Padisák 1997; Wiedner et al. 2007). *C. raciborskii* was first identified in the United States in Midwest lakes in the 1950s. *C. raciborskii* has probably existed in Florida inland waters for many years, but it wasn't until the 1980s that it began to aggressively proliferate and bloom in lake and river systems throughout central Florida (Chapman and Schelske 1997). More recently, this CyanoHAB has spread throughout US Southeast and Midwest reservoirs and lakes, especially those undergoing eutrophication accompanied by a loss of water clarity. The mechanisms of invasion and proliferation have been elusive. However, it is known that *C. raciborskii* is typically dispersed throughout the water column, is adapted to low light conditions encountered in many turbid eutrophic waters, and prefers water temperature conditions in excess of 17°C (Wiedner et al. 2007).

The filamentous toxin-producing CyanoHAB genus *Lyngbya* has likewise exhibited remarkable abilities to proliferate 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, though some species, such as *L. birgei*, are planktonic. *L. majuscula* produces a large suite of bioactive compounds, including the dermatoxic aplysiatoxins and lyngbyatoxin A, as well as the potent neurotoxins kalkitoxin and antillatoxin. In freshwater environments, *L. wollei* has been associated with the production of paralytic shellfish poisoning (PSP) toxins (Carmichael 1997).

There is little doubt that *Lyngbya* blooms are occurring at increasing frequencies in nutrient-enriched waters. In these eutrophying waters, both *L. majuscula* (marine) and *L. wollei* (freshwater) have proven to be opportunistic invaders and bloom-formers when environmental conditions permit. Following large climatic and hydrologic perturbations such as hurricanes, *L. wollei* is an aggressive initial colonizer of flushed systems. *Lyngbya* blooms can proliferate as dense floating mats that shade other algae, thus promoting their ability to compete for light. This CyanoHAB appears to be able to take advantage of *both* human and climatically-induced environmental change.

Conclusions

In addition to the well-documented promotion of CyanoHABs by anthropogenic nutrient enrichment, there is an increasingly important connection between rising levels of atmospheric CO_2, climate change, and the intensification of cyanobacterial blooms (Paerl and Huisman 2008). The various mechanisms involved are conceptualized in Figure 4. Expansion of cyanobacterial blooms has serious consequences for human drinking water supplies, fisheries and recreational resources. This has ramifications for water management, since current controls of cyanobacterial blooms, which are largely based on the reduction of nutrient inputs, will also be affected by climatic change. In particular, in addition to nutrient reduction, water authorities fighting harmful algal blooms will have to accommodate the hydrological and physical-chemical effects of climatic change in their management strategies, with particular focus on surface water heating, density stratification, freshwater runoff, residence time, and even the rising atmospheric CO_2 content.
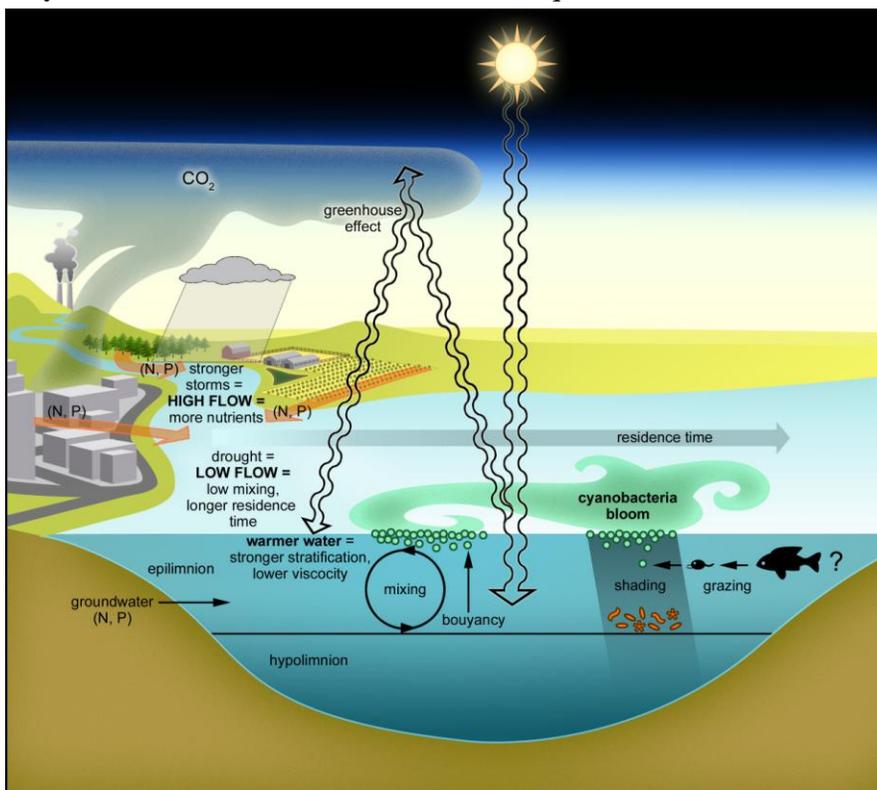

Figure 4. Conceptual figure, illustrating the environmental processes that control cyanobacterial blooms, and the impacts of climate change on these processes and on bloom potentials.

We suspect that these climate change scenarios will play into the hands of CyanoHAB species. These species are able to capitalize on ecosystem-level biogeochemical responses (increased rates of primary production, enhanced internal nutrient cycling) to accelerating loads of N and P in increasing numbers of riverine, lacustrine, estuarine and coastal ecosystems. Therefore, *both* N and P

inputs are likely to require reductions for effective long-term control of CyanoHABs. Traditionally, water quality managers have addressed eutrophication and HAB problems by developing nutrient-bloom threshold relationships that set targets for nutrient load reductions. However, these relationships are confounded by coinciding physical-hydrologic changes resulting from climatic change, including warming and changes in precipitation patterns. This introduces a great deal of additional complexity into simplified nutrient-eutrophication-bloom relationships, which calls for increased emphasis on space-time intensive monitoring able to capture both the event scale and longer-term trends. In this regard, water quality models designed to improve CyanoHAB predictability will need to incorporate both nutrient and climatic drivers so that they can serve managers in meaningful and practical ways.

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