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Review

Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change

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ABSTRACT

Harmful (toxic, food web altering, hypoxia generating) cyanobacterial algal blooms (CyanoHABs) are proliferating world-wide due to anthropogenic nutrient enrichment, and they represent a serious threat to the use and sustainability of our freshwater resources. Traditionally, phosphorus (P) input reductions have been prescribed to control CyanoHABs, because P limitation is widespread and some CyanoHABs can fix atmospheric nitrogen (N_2) to satisfy their nitrogen (N) requirements. However, eutrophying systems are increasingly plagued with non N_2 fixing CyanoHABs that are N and P co-limited or even N limited. In many of these systems N loads are increasing faster than P loads. Therefore N and P input constraints are likely needed for long-term CyanoHAB control in such systems. Climatic changes, specifically warming, increased vertical stratification, salinization, and intensification of storms and droughts play additional, interactive roles in modulating CyanoHAB frequency, intensity, geographic distribution and duration. In addition to having to consider reductions in N *and* P inputs, water quality managers are in dire need of effective tools to break the synergy between nutrient loading and hydrologic regimes made more favorable for CyanoHABs by climate change. The more promising of these tools make affected waters less hospitable for CyanoHABs by 1) altering the hydrology to enhance vertical mixing and/or flushing and 2) decreasing nutrient fluxes from organic rich sediments by physically removing the sediments or capping sediments with clay. Effective future CyanoHAB management approaches must incorporate both N and P loading dynamics within the context of altered thermal and hydrologic regimes associated with climate change.

Contents

1. Introduction

One of the most troublesome symptoms of nutrient over-enrichment is the proliferation of toxic, food-web altering and hypoxia-generating cyanobacterial harmful blooms, or CyanoHABs (Chorus and Bartram, 1999; Huisman et al., 2005) (Fig. 1). CyanoHABs are expanding geographically and now threaten the ecological integrity and sustainability of some of the world's largest and most resourceful water bodies, including Lakes Victoria, Africa; Erie, US–Canada; Okeechobee, Florida, USA (Havens et al., 2001); Taihu, China (Qin et al., 2010); Kasumigaura, Japan (Havens et al., 2001); the Baltic Sea in Northern Europe (Conley et al., 2009a); and the Caspian Sea in West Asia (Paerl and Huisman, 2008). In addition to their negative ecological, biogeochemical and health impacts, CyanoHABs cause serious economic losses to affected waters. In the USA alone, CyanoHABs result in losses of recreational, drinking, and agricultural water resources that are worth >\$2 billion annually (Dodds et al., 2009). Identifying environmental factors driving the rapid rise in CyanoHABs is paramount to developing management strategies

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Fig. 1. Examples of large water bodies that have experienced increases in frequencies, magnitudes, and duration of CyanoHABs. Shown (on the left) are photographs of the blooms and (on the right) remote sensing images of each system. Top: Lake Taihu, China (photograph by H. Paerl), and MODIS remote sensing image of the lake and nearby cities (May, 2007) (Courtesy NASA). Middle: Baltic Sea-Gulf of Finland (courtesy of Finnish Border Guard and Institute of Marine Research, Helsinki, Finland), and SeaWiFS image of the same region (June 2005) (Courtesy NASA). Bottom: Lake Erie, southern shore (photograph courtesy NOAA), and Modis satellite image of a bloom in the Western basin of the lake, near Maumee Bay during summer 2009 (Modis, NOAA Coastwatch-Great Lakes).

aimed at protecting a significant fraction of the world's fresh and brackish water resources.

When devising long-term CyanoHAB control strategies, ecologists and managers face two sets of covarying trends; 1) nutrient over-enrichment in human-dominated watersheds (Vitousek et al., 1997; Conley et al., 2009b), and 2) changing climatic conditions, including global warming and altered rainfall patterns with increased severity of droughts and floods (Paerl and Huisman, 2008). Understanding and, when possible, managing interactive impacts of anthropogenic and climatic drivers of CyanoHABs is a major challenge to ensuring protection and sustainability of affected waters. Here, we synthesize established and emerging information on environmental factors influencing CyanoHAB bloom potential and dynamics, in order to provide a perspective and integrative approach to their management in a world experiencing contemporaneous anthropogenic and climatically-induced environmental change.

2. CyanoHAB Characteristics

The 3.5+ billion year evolutionary history of cyanobacteria has provided them with numerous physiological adaptations and mechanisms, enabling them to take advantage of environmental changes and extremes. Many genera possess high affinity uptake and intracellular storage capabilities for nitrogen (N) and phosphorus (P) (Padisák, 1997; Flores and Herrero, 2005); ideal for exploiting periodic enrichment of these potentially-limiting nutrients. Some genera can convert "inert" atmospheric nitrogen (N_2) into ammonia, via nitrogen fixation (Fogg, 1969), ensuring access to biologically-available N. In addition, CyanoHABs produce secondary metabolites potentially toxic to higher-ranked consumer organisms, including zooplankton, fish, and mammals (including man) that use affected waters as a habitat, and for drinking and recreational purposes (Chorus and Bartram, 1999).

3. Nutrient Controls: Both N and P are Important

CyanoHABs are stimulated by excessive anthropogenic nutrient loading (Fogg, 1969; Reynolds, 1987; Paerl, 1988). In freshwater ecosystems, P availability is often the key factor limiting phytoplankton growth, including CyanoHAB species (Schindler et al., 2008). Accordingly, controlling P inputs has been the primary goal for resource managers. The emphasis on P reductions for CyanoHAB control is based on knowledge that some CyanoHAB genera can satisfy cellular N-requirements via N_2 fixation and thus are potentially less sensitive to decreases in N loading than to P loading (Fogg, 1969). However, at the ecosystem-level, only a fraction, usually far less than 50%, of primary production demands are met by N_2 fixation, even when P supplies are sufficient (Howarth et al., 1988; Lewis and Wurtsbaugh, 2008; Paerl and Scott, 2010; Scott and McCarthy, 2010). This indicates that N_2 fixation is controlled by factors in addition to P availability.

Nutrient loading dynamics have changed substantially over the past several decades. Practices such as bans on phosphate containing detergents, improved waste water treatment, and no till agriculture have been effective at reducing freshwater P loads but less so for N, which is more mobile throughout the environment (Galloway and Cowling, 2002; Howarth, 2008). As a result, human population growth in watersheds has been paralleled by increased N loading, often at rates much higher than P (Rabalais, 2002). Excessive N loads are now as large a concern as P loads in mediating freshwater, estuarine and marine eutrophication and HABs (including CyanoHABs) (Havens et al., 2001; Conley et al., 2009b; Howarth, 2008).

In the Baltic Sea region, effective control of eutrophication and HAB outbreaks required considering total amounts and ratios of N and P discharged to a nutrient-sensitive river–fjord–sea continuum (Elmgren and Larsson, 2001). Similarly, single nutrient input reductions, including a P-detergent ban and improved wastewater treatment for P during the 1980s in North Carolina's (USA) Neuse River System, helped solve one problem (arrest freshwater blooms), but exacerbated blooms in downstream N-sensitive estuarine waters (Paerl, 2009). In both cases, parallel N and P input reductions were required to stem eutrophication along the freshwater to marine continuum (Paerl, 2009).

In Florida's (USA) freshwater lakes, which provide drinking and irrigation water, excessive N loading, from expanding wastewater and agricultural discharges, was identified (in addition to P) as a key culprit in eutrophication and CyanoHAB expansion (Havens et al., 2001; Kratzer and Brezonik, 1981). In some cases (e.g. Lake Okeechobee), dominance by N_2 fixing CyanoHABs (which were largely controlled by P input reductions) is now shared with non-N_2 fixing genera (e.g. *Microcystis*), as well as 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 (Moisander et al., 2008). In these cases, both N and P reductions are needed to control CyanoHABs (Havens et al., 2001). Similarly, in Lake Erie, a lake in which eutrophication was effectively controlled from the 1970s until the turn of the century due to well-managed P (but not N) -abatement programs, the current CyanoHAB problem is a resurgence of non-N_2 fixing *Microcystis* populations.

By what means and mechanisms have CyanoHABs re-emerged, despite concerted efforts to control P? Large shallow lakes like Okeechobee, USA; Taihu, China, Kasumigaura, Japan; and the western basin of Lake Erie, USA tend to be co-limited by N and P (Havens et al., 2001; Guilford et al., 2005; North et al., 2007; Paerl et al., 2010; Xu et al., 2010); largely because previously-loaded P and N are effectively retained and recycled. While some N can be “lost” via denitrification, this process does not appear to keep up with “new” N inputs (Seitzinger, 1988). Overall, N and P co-limitation appears to be quite common in eutrophic systems (Elser et al., 2007) that are also most susceptible to CyanoHAB outbreaks (Huisman et al., 2005).

4. The Integral Role of Climate Change

In addition to nutrient over-enrichment issues, climate change, in particular global warming, is likely to favor CyanoHABs. As a group, cyanobacteria exhibit optimal growth rates at relatively high temperatures, usually in excess of 25 °C (Paerl and Huisman, 2008). At these elevated temperatures, CyanoHABs compete most effectively with eukaryotic algae (Fig. 2). Intense light absorption by dense surface cyanobacterial blooms can locally increase water temperatures (Kahru et al., 1993; Ibelings et al., 2003), thereby creating a positive feedback that perpetuates further CyanoHAB dominance (Hense, 2007). Higher water temperatures will also extend the ice-free growing season at higher latitudes and high elevations expanding the seasonal duration of CyanoHAB outbreaks (Peeters et al., 2007; Wiedner et al., 2007).

Warming of surface waters also intensifies vertical density stratification and lengthens the period of seasonal stratification, thus suppressing vertical mixing intensity and frequency. Some CyanoHABs form gas vesicles, which provide buoyancy (Reynolds, 1987). Under strong and persistently stratified conditions, buoyant cyanobacteria can form dense surface blooms which shade deeper non-buoyant eukaryotic phytoplankton, enhancing the CyanoHABs' competitive advantage (Huisman et al., 2004) (Fig. 3). Increased water temperature also decreases the viscosity of water. As viscosity decreases, the water's resistance to vertical migration also decreases; thus facilitating upward (optimizing photosynthetic production) and downward (optimizing nutrient acquisition) migration by highly motile CyanoHABs (Reynolds, 1987). Additionally, by enhancing heterotrophic bacterial activity and decreasing bottom water ventilation, warmer and more stratified waters can exacerbate the problem of bottom water hypoxia (Turner et al., 1987). Internal nutrient loading from the sediments, particularly from redox sensitive P pools, is often stimulated by hypoxia, further fueling CyanoHABs (Paerl, 1988).

A key driver of global warming is the rising level of the atmospheric greenhouse gases, most notably carbon dioxide (CO_2). In nutrient-enriched waters, algal blooms exhibit high rates of photosynthesis and, hence high demand for CO_2, which increases the pH of affected waters. At pH levels greater than 9, common within CyanoHAB blooms, free CO_2 represents less than 1% of total dissolved inorganic carbon (DIC) (Paerl and Ustach, 1982) and can become limiting for phytoplankton photosynthesis and growth (Shapiro, 1990; Ibelings and Maberly, 1998). Under these conditions, buoyant CyanoHABs have a distinct advantage over sub-surface phytoplankton populations. Surface-dwelling taxa can directly intercept CO_2 diffusing into the water from the atmosphere, thus minimizing DIC limitation of photosynthetic growth (Paerl and Ustach, 1982). A consequence of extremely low CO_2 concentrations within CyanoHAB scums is that the net flux of CO_2 and thus photosynthetic potential is largely determined by the atmospheric CO_2 concentration. Thus with increasing atmospheric CO_2 concentrations, increased intensity of CyanoHAB scums is likely. Below CyanoHAB surface scums, low light and DIC limitation act concertedly to the disadvantage of photosynthetic growth of eukaryotic algal populations, further ensuring CyanoHAB dominance (Huisman et al., 2004).

Changes in regional precipitation patterns will affect intensities and duration of floods and droughts (IPCC, 2007) which may promote CyanoHAB dominance. Summer droughts appear to be increasing in intensity and duration, possibly due to global warming (IPCC, 2007). This has serious implications for drinking water reservoirs, which are already stressed to provide enough water to sustain urban and agricultural needs. Increasingly, low-flow drought periods promote toxic CyanoHABs in these systems, and the extent to which this problem can be alleviated by increasing flushing rates and relocation of water intake structures is limited by dwindling upstream water supplies. This issue is creating an increasing focus on ecohydrology and spatiotemporal reservoir zone shifts and lacustrine responses

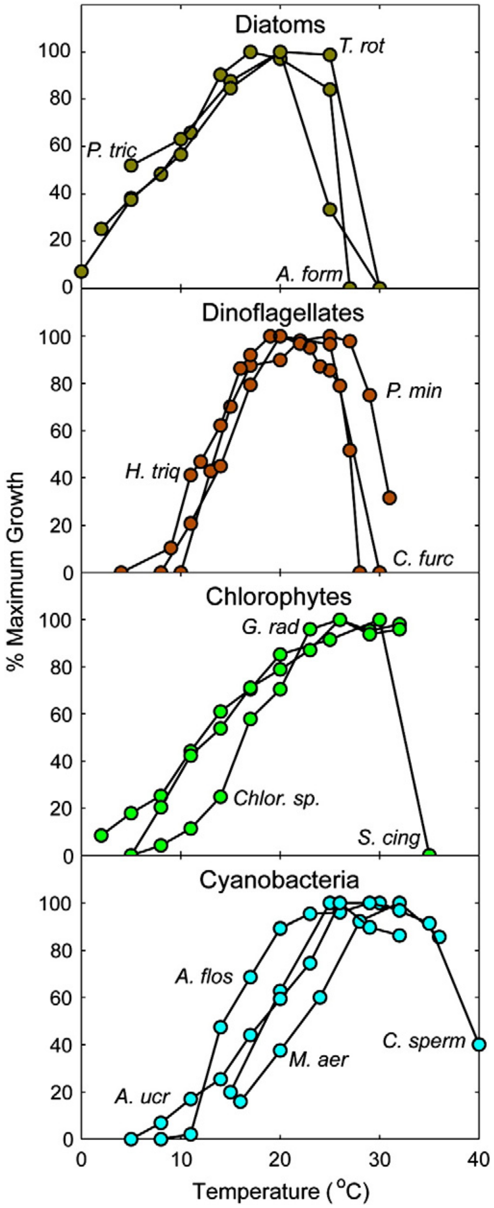

Fig. 2. Temperature dependence of the specific growth rates of representative species from three eukaryotic phytoplankton classes and of CyanoHAB species common in temperate freshwater and brackish environments. Growth data are from laboratory experiments under light and nutrient-saturated conditions and have been normalized by maximum observed growth rate. *A. form* = *Asterionella formosa* (Butterwick et al., 2005), *T. rot* = *Thalassiosira rotula* (Krawiec, 1982), *P. tric* = *Phaeodactylum tricornutum* (Kudo et al., 2000), *H. triq* = *Heterocapsa triquetra* (Litaker et al., 2002), *P. min* = *Prorocentrum minimum* (Grzebyk and Berland, 1996), *C. furc* = *Ceratium furcoides* (Butterwick et al., 2005), *G. rad* = *Golenkinia radiata* (Yamamoto and Nakahara, 2005), *Chlor. sp.* = *Chlorella sp.* (Yamamoto and Nakahara, 2005), *S. cing* = *Staurastrum cingulum* (Butterwick et al., 2005), *A. ucr* = *Anabaena ucrainica* (Tsujimura and Okubo, 2003), *M. aer* = *Microcystis aeruginosa* (Reynolds, 2006), *A. flos* = *Aphanizomenon flos-aquae* (Yamamoto and Nakahara, 2005), *C. sperm* = *Cylindrospermopsis raciborskii* (Briand et al., 2004).

such as pulsatory inflows to counter drought conditions, which are projected to increase over the next century in many world regions (e.g., Australia, southwestern US, Central Asia) (c.f. Vilhena et al., 2010).

This problem, combined with expanding use of freshwater for irrigation, has led to rising salinities of freshwater systems in many regions of 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 (Paerl and Fulton, 2006) (Fig. 3). In addition, some freshwater CyanoHAB genera, including *Anabaena*, *Microcystis* and *Nodularia*, can tolerate moderate salinities (Moisander et al., 2002). This allows for expansion of blooms into nutrient-enriched 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 Pontchartrain, Louisiana, USA (Paerl and Fulton, 2006).

More intense precipitation events will increase enrichment of water bodies with land-derived nutrients through enhanced erosion, surface runoff and groundwater discharge. Freshwater discharge would also increase, which in the short-term may prevent blooms by promoting flushing and mixing of the water column (Sherman et al., 1998; Mitrovic et al., 2003). However, as the discharge subsides and water residence time increases, its nutrient load can be captured and cycled by receiving water bodies, promoting bloom potentials. This scenario can be observed in geographically-distinct systems, including Lake Pontchartrain, LA, USA (Mize and Demcheck, 2009), Swan River, Australia (Atkins et al., 2001), Pamlico Sound, NC, USA (Peierls et al., 2003), and the Potomac Estuary, MD, USA (Sellner et al., 2003). In addition, attempts to control fluctuations in the discharge of rivers and lakes by dams and sluices increase residence time, further aggravating CyanoHAB problems (Burch et al., 1994).

Overall, it appears that increases in hydrologic variability and extreme conditions such as protracted droughts benefit CyanoHABs. If conditions get so extreme that lakes and reservoirs dry up, most CyanoHAB species can survive such severe environmental stress for long periods (up to many years) as dormant cysts in sediments, soils, or desiccated mats (Potts, 1994).

Some toxin-producing CyanoHABs appear to be particularly successful at exploiting climatic change. For example, the toxic, low light adapted, N_2 fixer *Cylindrospermopsis raciborskii* was originally described as a tropical to subtropical species preferring water temperatures greater than 22 °C (Padisák, 1997). However, in recent years, the occurrence and dominance of *C. raciborskii* have expanded polewards in mid-latitudes of Europe, North America and South America, where it often proliferates in turbid, eutrophic lakes and reservoirs (Padisák, 1997; Wiedner et al., 2007). Another example is the massive toxic *Microcystis* spp. blooms in Lake Taihu, China that have created severe drinking water supply problems for the surrounding municipalities (Qin et al., 2010). These blooms have increased in magnitude over the last few decades, due to the combined effects of increased N and P loading, and a multi-decadal warming trend (Qin et al., 2010).

In addition to parallel reductions in N and P inputs, water quality managers are in dire need of effective tools to break the synergy between nutrient loading and hydrologic regimes made more favorable for CyanoHABs by climate change. The more promising of these tools either alter the hydrodynamic or sediment processes within affected waters to make them less hospitable for CyanoHABs.

Artificial mixing of lakes and ponds, by air bubbling or other mixing devices, enhances vertical mixing of the phytoplankton, and counters formation of surface blooms of buoyant cyanobacteria (Huisman et al., 2005). Additionally, by oxygenating the hypolimnion, redox sensitive internal loading of P from the sediments is often reduced. Horizontal flushing, by increasing the water flow through lakes or estuaries, reduces water residence time, thus providing less time for the development of cyanobacterial blooms (Maier et al., 2004). In small reservoirs, turbulence generated by bed roughness also increases with higher flow velocities and the resultant natural vertical mixing can disrupt or prevent stratification and surface blooms of CyanoHABs (Mitrovic et al., 2003). While these hydrologic manipulation efforts can yield positive results (decreased CyanoHAB intensity), hydrologic changes can be quite expensive and restricted to relatively small water bodies, and freshwater supplies for flushing

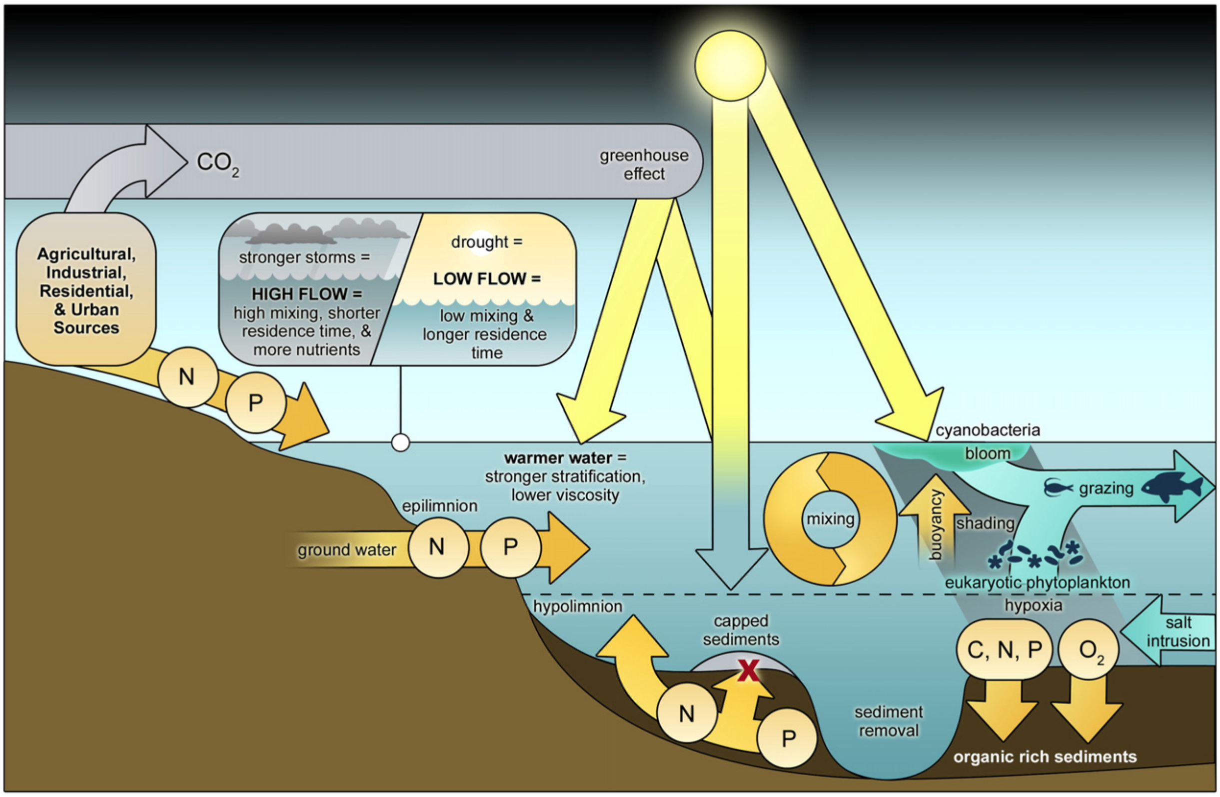

Fig. 3. Conceptual figure, illustrating the environmental processes that control cyanobacterial blooms, including man-made management actions and impacts of climate change.

may be limited. Therefore, for many medium to large lake systems, nutrient input restrictions are most attractive.

Even when external nutrient inputs are reduced, the legacy of eutrophication in the form of organic matter enriched sediments can perpetuate high internal nutrient loads and provide a steady inoculum of algal spores or cysts that can perpetuate 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 may help reduce CyanoHABs.

Sediment removal usually involves expensive dredging and extensive disturbance of lake bottoms, which can lead to additional nutrient (and potentially toxic substances) release and destruction of bottom-dwelling plant and animal communities (Petersen, 1982). There are few "success stories" following such a radical approach; the most notable being Lake Trummen, Sweden, a small (area ~1 km^2, 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 top half meter of sediments resulted in a profound decrease in nutrient concentrations and CyanoHABs (Cronberg, 1982). The uncommon success of these drastic measures was likely due to the small, easily manipulable size of the lake and, equally, to concurrent nutrient load reductions from its small (13 km^2) watershed (Petersen, 1982; Cronberg, 1982).

Alternative approaches include chemically-precipitating P from affected water bodies and keeping it "locked up" in the sediments. Common chemical treatments include alum or clays that tightly bind with phosphate anions. When applied at the surface, these treatments effectively precipitate P to concentrations that limit CyanoHAB growth (Robb et al., 2003). On the sediment surface, the thin layer of alum or clay can form an effective barrier to phosphate diffusing out of the sediments (Robb et al., 2003). Some of these treatments have been shown to work well in small water bodies, leading to P-limited conditions that can control algal and CyanoHAB production (Robb et al., 2003). However as with sediment removal, the efficacy of any chemical treatment is likely to be futile unless allochthonous nutrient inputs are concurrently managed (Haghseresht et al., 2009). Therefore, sediment manipulation techniques are only a temporary "fix" without parallel, long-term nutrient input reductions.

5. 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, warming, and the proliferation of cyanobacterial blooms (Fig. 3). This has ramifications for water management, since current controls of cyanobacterial blooms, which are largely based on the reduction of nutrient inputs, will also need to take thermal, hydrologic and physical–chemical (aside from nutrients) impacts of climate change into consideration. Effective long-term control will need to break the "synergy" between nutrient loading and:

1. Surface water warming (direct physiological and indirect physical—density stratification—effects).
2. Freshwater runoff, which controls nutrient delivery, salinity (in estuaries), water residence time and vertical density stratification.
3. Increased CO_2 limitation due to excessive nutrient loading (accelerated eutrophication) which will favor dominance by buoyant cyanobacteria.
4. Stratification, hypoxia, and redox sensitive internal P inputs from sediments.

Projected climate change scenarios alter each of these parameters, seemingly in favor of cyanobacteria. 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 to aquatic ecosystems. Therefore, *both* N and P input reductions are required 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 concurrent physical-hydrologic alterations resulting from warming and changes in precipitation patterns. This adds complexity to nutrient–eutrophication–bloom relationships, and calls for increased emphasis on space–time intensive monitoring able to capture both the event scale and longer-term trends. In addition, 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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