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Review

Mitigating cyanobacterial harmful algal blooms in aquatic ecosystems impacted by climate change and anthropogenic nutrients



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ABSTRACT

Mitigating the global expansion of cyanobacterial harmful blooms (CyanoHABs) is a major challenge facing researchers and resource managers. A variety of traditional (e.g., nutrient load reduction) and experimental (e.g., artificial mixing and flushing, omnivorous fish removal) approaches have been used to reduce bloom occurrences. Managers now face the additional effects of climate change on watershed hydrologic and nutrient loading dynamics, lake and estuary temperature, mixing regime, internal nutrient dynamics, and other factors. Those changes favor CyanoHABs over other phytoplankton and could influence the efficacy of control measures. Virtually all mitigation strategies are influenced by climate changes, which may require setting new nutrient input reduction targets and establishing nutrient-bloom thresholds for impacted waters. Physical-forcing mitigation techniques, such as flushing and artificial mixing, will need adjustments to deal with the ramifications of climate change. Here, we examine the suite of current mitigation strategies and the potential options for adapting and optimizing them in a world facing increasing human population pressure and climate change.

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1. Introduction

The global expansion of cyanobacterial harmful algal blooms (CyanoHABs) is a serious threat to the ecological integrity,

ecosystem services, safe use, and sustainability of inland and coastal waters (Carmichael, 2001; Huisman et al., 2005; Paerl and Fulton, 2006; Paul, 2008; Paerl et al., 2011; Paerl and Otten, 2013; O'Neil et al., 2012). CyanoHABs often are toxic, disrupt food webs, can lead to hypoxia, and result from high anthropogenic nutrient inputs to impacted ecosystems (Fogg, 1969; Reynolds and Walsby, 1975; Paerl, 1988). Some ecosystems are more susceptible to CyanoHABs than others due to varying morphometry, hydrology,

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geography, and the relative size and influence of watersheds (Fee, 1978; Wetzel, 2001; Huisman et al., 2005; Paerl and Otten, 2013). Differences in human activities in water- and airsheds influence the hydrology, qualitative and quantitative loads of nutrients, sediments, and other pollutants, which lead to differential responses by cyanobacteria vs. eukaryotic algae (Smith, 1983, 1990; Paerl and Otten, 2013).

Climate change, including global warming, is causing changes to regional rainfall and hydrology, which will have cumulative effects with nutrient-over-enrichment in modulating CyanoHABs (Paerl and Scott, 2010; Moss et al., 2011). Regional and global warming enhances the initiation, magnitude, duration, and distribution of CyanoHABs (Peeters et al., 2007; Jöhnk et al., 2008; Paul, 2008; Paerl and Huisman, 2008; Paerl et al., 2011; Kosten et al., 2012). Furthermore, increasing variability in rainfall patterns impacts nutrient and sediment delivery, sediment-water exchange and metabolism, flushing and water residence time, and vertical stratification, which, in turn, may affect CyanoHAB dominance and persistence (Mitrovic et al., 2003; Scott et al., 2008; Paerl and Huisman, 2008; Elliott, 2010; Paerl, 2014; Zhu et al., 2014). For example, changes in rainfall patterns, including more intense rainfall events followed by extensive summer droughts, result in episodic nutrient inputs, followed by strengthened and prolonged stratification, favoring CyanoHAB development and persistence (Paerl and Huisman, 2008, 2009; Winston et al., 2014). Forecasting these events is preempted by the inability to downscale climate predictions, both temporally and spatially (Hall, 2014).

Controlling CyanoHABs may be more challenging in the future than now due to warming effects. Examination of 143 lakes along a climate gradient in Europe and South America (Kosten et al., 2012) indicated that increased water temperature led to a gradual rise in the frequency of occurrence of cyanobacteria, up to a maximum of 60% at a total nitrogen (TN) concentration of 2 mg $\rm L^{-1}$. However, cyanobacterial dominance increased stepwise along the temperature gradient when TN concentrations were increased to 4 mg $\rm L^{-1}$, and the frequency of occurrence of cyanobacteria reached 80% at the highest temperatures (near 30 °C). Non-linear state changes in

lake ecosystems are difficult to predict and extremely difficult to reverse after they occur (Scheffer et al., 2001). If the same kind of response trajectories occur for harmful cyanobacterial blooms, nutrient controls become much more crucial as increasing atmospheric temperatures approach these critical thresholds.

While forecasting the effects of climate change is a challenge, especially on local and regional scales, the high probability that future climatic conditions will favor bloom formation poses an added challenge to developing effective mitigation strategies that consider both nutrient and climate drivers (Figs. 1 and 2). Interactions between warming, changing hydrology, agricultural and industrial expansion, and nutrient delivery to aquatic ecosystems will require new approaches to managing CyanoHABs. Nutrient-growth threshold responses for CyanoHAB taxa likely will be altered as physical (e.g., temperature) and geochemical (e.g., nutrient fluxes) controls on these thresholds also change, resulting in moving targets in our quest for long-term CyanoHAB control.

In this contribution, we consider the impacts of current and anticipated climate changes, specifically warming and increased hydrologic variability and extremes, on CyanoHAB mitigation strategies. We evaluate these strategies for a range of impacted aquatic ecosystems and identify research priorities when there is insufficient information to reach conclusions about how climate change will influence the efficacy of a particular treatment.

2. Influence of climate change and human activities on CyanoHAB mitigation strategies

CyanoHAB mitigation strategies can be categorized as: (1) within water- and airsheds and (2) within waterbodies.

2.1. Watersheds and Airsheds

Extensive literature links macronutrient supply rates with the distribution and abundance of cyanobacteria (c.f., Likens, 1972; Vincent, 1987; Potts and Whitton, 2000; Huisman et al., 2005; Paerl and Fulton, 2006). Therefore, control of anthropogenic

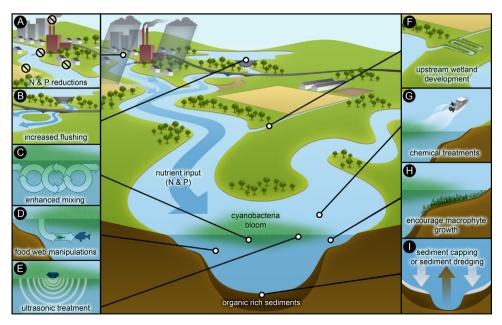


Fig. 1. Conceptual illustration of various approaches currently in use to control CyanoHABs, including control measures in the watershed and within the ecosystem. A. Point and non-point source nutrient (in most cases, both N and P) input reductions. B. Increasing flushing rates (decreasing water residence times). C. Mechanically-enhanced vertical mixing. D. Manipulating food webs to encourage filtering and consumption of CyanoHABs. E. Utilizing ultrasound waves to control algal growth. F. Nutrient attenuation/removal through upstream wetland development. G. Application of algaecides, including copper salts, hydrogen peroxide. H. Encourage growth of submersed and emergent aquatic vegetation for nutrient attenuation and removal. I. Dredging and capping of bottom sediments to reduce sediment-water column nutrient regeneration.

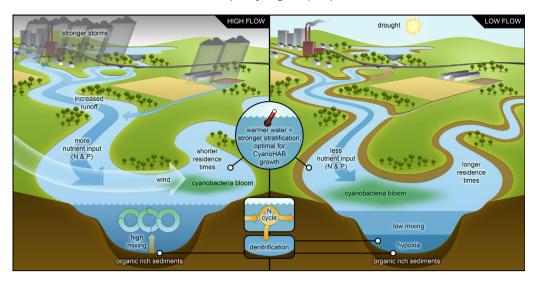


Fig. 2. Impacts of warming, increasing hydrologic variability, and extremeness on physical-chemical and biotic conditions that modulate CyanoHABs in shallow water ecosystems. Under high freshwater discharge conditions (left hand side) an increase in nutrient loading will occur, mixing depth will increase, with enhanced nutrient cycling and regeneration in the water column. Even though external nutrient loads will increase, higher rates of flushing (shorter water residence times) will tend to offset algal growth rates and biomass accumulation. Under low freshwater discharge conditions (right hand side), external nutrient loads will decrease, but reduced flushing will lead to longer residence times, which will optimize algal nutrient removal and biomass accumulation. In addition, relatively low vertical mixing rates will lead to more sustained periods of vertical stratification, which will allow buoyant CyanoHABs to dominate. Stronger dissolved oxygen gradients associated with enhanced vertical stratification will enhance internal nutrient cycling and denitrification as an N loss mechanism.

nutrients must be the primary focus when addressing CyanoHABs (Table 1). Historically, the reduction of phosphorus (P) inputs was the strategy applied to counter CyanoHABs in freshwater systems (Likens, 1972; Smith and Schindler, 2009). Now, increasing evidence suggests that effective nutrient control strategies must consider and address both nitrogen (N) and P (Elser et al., 2009a; Sterner, 2008; Conley et al., 2009; Lewis et al., 2011). Furthermore, controlling only P inputs in freshwater systems can exacerbate downstream eutrophication in N sensitive estuarine and coastal waters (Elmgren and Larrson, 2001; Paerl, 2009; Finlay et al., 2013). In the USA, the costs for reactive N discharges to the environment, from anthropogenic activities in the early 2000s, were estimated at US\$210 billion in health and environmental damages (Sobota et al., 2014).

A key management priority for impacted watersheds is to establish Total Maximum Daily Loads (TMDLs) for nutrients, below which CyanoHABs may be controlled (Paerl, 2013; Xu et al., 2015). Although TMDLs have been useful in identifying nutrient sources in watersheds, they have rarely been successful at mitigating nutrient inputs, in part because compliances with non-point source (NPS) load thresholds are voluntary (General Accountability Office, 2013). Point sources are associated with municipal and industrial wastes permitted through the National Pollution Discharge Elimination System (NPDES; http://water.epa.gov/ polwaste/npdes/). Targeting point sources is attractive, because nutrient load reductions identified by TMDLs can be implemented by modifying the permitted discharge limits of point-source dischargers. Many permitted dischargers have reduced nutrients in effluents in recent years (Scott et al., 2011), but these reduced concentrations often still exceed nutrient concentration thresholds that cause eutrophication and promote CyanoHABs. The uncertainty in forecasting local and regional effects of climate change (e.g., temperature and hydrology) further hamper the effectiveness of this approach. Existing TMDLs likely will need to be adjusted as our understanding of CyanoHAB ecology and regional climate forecasts improve.

NPS inputs are challenging to control due to the diffuse nature of the nutrient sources (Sharpley et al., 2010; US EPA, 2011; Smith et al., 2014). Agricultural best management practices (BMPs), and

other measures at the nutrient source (e.g., pastures, row crops, confined animal feeding operations, etc.) may require a regional focus, because legacy nutrients have been sequestered in soils. wetlands, and tributaries (Dunne et al., 2011; Jarvie et al., 2013a,b). Increased fertilizer use, discharge of animal waste, soil disturbance and erosion, atmospheric fossil fuel and agricultural emissions, and septic systems accompanying human population growth are increasing non-point N and P loadings (Galloway et al., 2002, 2004; Sharpley et al., 2010; US EPA, 2011; Townsend and Howarth, 2010). The complexity of agricultural NPS nutrient loads requires different mitigation strategies, because animal agriculture (relatively high P) and row crop agriculture (relatively high N) differ in their relative influences on N and P loads (Alexander et al., 2008). Climate change, especially an increase in "flashiness" of storm and runoff events, is likely to make control more challenging.

Human population growth demands high-yield agriculture, and agronomists generally recognize the need to balance yields with protection of receiving waters. However, recent analysis of global fertilization practices shows that increased fertilizer application has resulted in decreased nutrient use efficiency (Lassaletta et al., 2014). Modern agricultural science has proposed several new approaches to optimize nutrient use efficiency (e.g., Bodirsky and Muller, 2014), and many of these techniques are being implemented or tested for efficacy. For example, soil fertilization indices, such as the Nitrogen Soil Test for Rice (N-STaR), help maximize N use efficiency and minimize losses (Roberts et al., 2013). Similarly, farmers in Yaqui Valley, Mexico use handheld N sensors (Greenseekers) to determine the timing and amount of N fertilizer additions. Validation trials saved an average of 69 kg N ha⁻¹ and US\$62 ha⁻¹, while maintaining crop yields and quality (Ahrens et al., 2008).

Fertilizer applications in the United States would be reduced greatly if such approaches were applied more broadly. Theoretically, the same level of nutrient reductions from the Yaqui Valley, applied to the 20 million ha of Mississippi River watershed cropland (Goolsby et al., 1999), would virtually eliminate the excess anthropogenic N load to the Gulf of Mexico (i.e., a 69 kg N ha⁻¹ reduction would equal 1.4 million metric tons

Table 1 Major CyanoHAB genera, their ability to fix N₂, harmful characteristics and toxins produced, and the range of potential mitigation strategies.

CyanoHAB genus	N2 fixation			HAB characteristics											
		Yes	N	O	Surfac		Throughout water column		In metal layers	limnetic	Odors and tast	e	Hypoxia generating		Food web disrupting
Anabaenopsis		Х			Х						Х		X		
Aphanizomenon		X			X						X		X		X
Cylindrospermopsis		X					X				X				X
Dolichospermum		X			X						X		X		X
Gloeotrichia		X					X				X				
Lyngbya		S	M	1	X						X		X		
Microcystis			X		X						X		X		X
Nodularia		X			X						X		X		Χ
Nostoc		X					X				X				X
Phormidium			X				X				X				X
Planktothrix			X				X		X		X		X		X
Raphidiopsis			X		X		X		Λ		X		Λ		X
Synechococcus			M.		Λ		X				X				Λ
•	T		IV.	ı			X				X				
	Toxins prod														
	Aeruginosin	Anatoxin-a	Anatoxir a(S)	1- Aplysiatoxin	s Beta alan	a-methylamino-L- nine	Cyanopeptolii	i Cylindro	ospermopsin	Homoanatox	n-a Jamaicamid	es Lyngbyatoxii	n Microcystin	Noduların	Saxitoxin
Anabaenopsis													X		
Aphanizomenon		X						X					X		X
Cylindrospermopsis		X			X			X		X			X		X
Dolichospermum		X	X		Х		X	X		X			X		X
Gloeotrichia															
Lyngbya		X		X							X	X			X
Microcystis		X	X		Х		X	X					X	X	
Nodularia		**			X		••	••					••	X	
Nostoc					X								X		
Phormidium		X			X					X			X		
	X	X			X					X		X	7.	X	
Raphidiopsis	Λ	Λ			Λ		X	X		Λ		Λ		Λ	
Synechococcus					Х		Χ	Λ					X		
	Mi	tigation optio	ons (numb	ered in order of	priorit	ty)									
	Nι	trient input		Encourage		Manipulate	Lake dept	h	Upstream		nhanced	Enhanced	Sedimer	nt	Dredging
	ree	ductions		macrophyte growth		turbidity	and photi zone	C	wetland de	ev. fl	ushing ^a	mixing ^a	capping	a,b	
Anabaenopsis	1			2		3	4		5	6		7	8		9
Aphanizomenon	1			2		3	4		5	6		7	8		9
Cylindrospermopsis	1			2					3	4			5		6
Dolichospermum	1			2		3	4		5	6		7	8		9
Gloeotrichia	1								2	3					
Lyngbya	1			3					4	2			5		6
Microcystis	1			2		4	5		3	6		7	8		9
Nodularia	1								2	3		4	5		6
Nostoc	1								2				3		
Phormidium	1								2	3			4		5
	•											4	_		7
Planktothrix	1						2		3	ל		4	n		
Planktothrix Raphidiopsis	1						2		3 2	5 4		4 3	6 5		6

S, some species; M, most species.

a Only feasible in relatively small system.
 b Only in systems that exhibit vertically-stratified conditions during bloom periods.
 c Following environmental assessment and only if dredge spoils can be deposited outside the watershed.

annually, close to the current annual N load; Aulenbach et al., 2007).

Preserving and restoring riparian habitat between agricultural lands and receiving waters can trap nutrients moving across the surface or subsurface (Fig. 4). A 12 m woody-vegetation riparian buffer reduced a 40 mg L $^{-1}$ TN concentration by $>\!50\%$ and a 34 µg L $^{-1}$ TP concentration by $>\!66\%$ (Aguiar et al., 2015). Similarly, constructed wetlands removed $\sim\!50\%$ of TN and TP from an agricultural watershed across varying construction methods (Vymazal, 2007), even in winter (Gao et al., 2014). The effectiveness of constructed wetlands will be improved by strategically placing and managing them in high-intensity agricultural landscapes (Kröger et al., 2014) (Fig. 3). Climate change will likely affect the efficacy and capacity of these nutrient attenuation and removal processes and approaches, but in a yet to be determined manner.

Clearly, climate change poses a significant challenge to reducing NPS nutrient inputs. Traditional BMPs for agricultural lands may not accommodate current and future climate scenarios that include regionally intense periods of rain and prolonged droughts (Trenberth, 2005; IPCC, 2012). Nutrients from wetlands and soils may be mobilized if additional warming occurs, especially if prolonged droughts are followed by high rainfall and runoff. Future construction and operation of basin-scale water treatment systems, considering climate change, may require increased capacity to store large amounts of water over short times. However, these flow-attenuation reservoirs will themselves be susceptible to CyanoHAB blooms.

Innovative watershed remediation techniques, such as N-STaR, the Yaqui Valley trials, and constructed wetlands examples above, may represent viable mechanisms for long-term nutrient load

reductions from agricultural and urban land uses. As growing seasons become longer in some regions due to climate change, hydrological cycles become more episodic, and population growth drives more intensive agriculture and urbanization, these strategies will become more important to prevent eutrophication and CyanoHABs. The scale of future wetland and riparian zone restoration projects may be increased to attenuate the anticipated larger volumes of runoff from extreme precipitation events. Temperature and hydrology changes also may influence the selection and viability of target plant species for these restoration projects. In some cases, sea-level rise and extended drought could cause salinity to become a new factor. Relative to external nutrient reductions and the susceptibility of water bodies to CyanoHABs, critical research needs include understanding how climate change will affect: (1) the efficacy of existing agricultural BMPs; (2) the mobilization of nutrients from soils, wetlands, and tributary sediments; and (3) construction and operation of basin-scale treatment facilities, including constructed wetlands, reservoirs, and flow-attenuation basins.

Atmospheric N input, which is often overlooked, can also be an important N source to surface waters and watersheds (Paerl et al., 2002; Elser et al., 2009b; US EPA, 2011) and may account for >30% of estimated "new" N inputs to N-sensitive waters (Paerl et al., 2002). Atmospheric nutrient inputs are affected by both wet and dry deposition quantities and patterns. For example, wet deposition of ammonium has increased in the US, especially in the heavily agricultural Midwest (Du et al., 2014), where non-N-fixing CyanoHABs have disrupted drinking water supplies in recent years (e.g., Scavia et al., 2014). Hence, current and future estimates of atmospheric deposition should rely on projected (modeled)



Fig. 3. (Clockwise from top left) Floating booms at Hartbeespoort Dam, located in the North West Province of South Africa, are used to concentrate cyanobacteria so they can be pumped out and composted (photo credit: Dept. of Water and Sanitation, Republic of South Africa); a constructed wetland at Open Grounds Farm, near Beaufort, NC, designed to reduce the amount of nutrients and sediments entering the headwaters of the South River, a tributary of the Neuse River (credit: Google Earth); a pumping barge is used to remove harmful cyanobacteria from Dianchi Lake, China (photo credit: J. Carl Ganter/Circle of Blue); aluminum sulfate and sodium aluminate are pumped into Ticklenaked Pond in Ryegate, VT, to combat phosphorus loading and harmful cyanobacterial blooms (photo credit: Vermont Dept. of Env. Conservation, Watershed Management Div.); a dredging operation in Lake Roaming Rock, Ohio, to remove nutrient-rich sediments (photo credit: RomeRock Association); a riparian buffer along Bear Creek in Story County, Iowa, designed to filter runoff of nutrients and sediments from adjacent farmland (photo credit: USDA); a LG Sonic, MPC-Buoy uses ultrasound waves to control algae (photo credit: LG Sonic); a SolarBee solar water circulator, used to reduce surface algae blooms in Santuit Pond in Mashpee, Massachusetts (photo credit: Friends of Santuit Pond); Phoslock is applied to Laguna Niguel Lake, CA, to bind and remove phosphorus from the water column (photo credit: Aquatechnex).

estimates of wet and dry deposition rates and trajectories to distribute loads along the freshwater to marine continuum (Paerl, 2009). These estimates should be coupled to watershed surface and subsurface nutrient loading dynamics. Critical research needs include understanding how changes in precipitation (intensity and temporal dynamics) resulting from climate change will affect the deposition of N onto inland and coastal waters and watersheds. New approaches that incorporate this information into nutrient control strategies are needed to ensure that they will suppress CyanoHABs.

2.2. Within waterbody CyanoHAB controls

A plethora of physical, chemical, and biotic approaches to CyanoHAB control have been proposed, implemented, and evaluated (Figs. 1 and 3; Table 1). Physical manipulations include: (1) removal of buoyant surface blooms by skimming, collecting, and concentrating, with subsequent use of bloom material (after toxins have been removed or converted to non-toxic substances) as mulch, soil additives, and land fill (Fig. 3); (2) deployment of vertical mixing and ultrasonic emission devices aimed at disrupting surface blooms, promoting competition from subsurface eukaryotic phytoplankton, and oxygenating the hypolimnion and surface sediments (Visser et al., 1996; Huisman et al., 2004; Molot et al., 2014) (Fig. 3); (3) enhancing flushing (reducing water residence time) by diverting upstream riverine waters and canals through the impacted reservoir or lake (Mitrovic et al., 2003; Maier et al., 2004); and (4) manipulating (lowering) lake and reservoir levels to encourage the growth and competitive abilities of rooted macrophytes.

These approaches have been successful in small (<50 ha) ecosystems, but not in larger lakes and reservoirs (Moss et al., 1996; Scheffer, 1998; Paerl and Paul, 2012). Artificial mixing depressed CyanoHAB dominance in some shallow eutrophic lakes (Huisman et al., 2004), but was not effective in other lakes (Burford and O'Donohue, 2006). External nutrient inputs must be reduced in parallel with internal measures (Moss et al., 1996; Jeppesen et al., 2007a,b). In some lakes exhibiting shallow, near-surface stratification in response to artificial mixing, upwelling of P from hypolimnetic waters may counteract the beneficial effects of mixing (Haynes, 1973).

The efficacy and applicability of these physical approaches depend in part on climate conditions and changes. Changes in freshwater discharge, while modulating nutrient delivery, also impact flushing rates and water residence times, which in turn affect competition between CyanoHABs and eukaryotic taxa. In freshwater ecosystems, increased runoff and shorter residence times weaken stratification and may inhibit both surface dwelling (e.g., Anabaena - recently renamed Dolichospermum, Aphanizomenon, Microcystis, Nodularia) and metalimnetic (Planktothrix) CyanoHAB taxa. In estuarine ecosystems, vertical density stratification is often strengthened by increased freshwater input, especially during moderate to low wind stress periods. This stratification extends the downstream distribution of CyanoHABs, especially under eutrophic conditions (Piehler et al., 2004) (Fig. 2). On its own, warming of lakes will enhance the strength of thermal stratification and favor bloom formation (Paerl and Huisman, 2008, 2009). Bloom characteristics vary by CyanoHAB taxa and present a specific set of challenges (surface scum, toxin production, etc.; see Table 1).

Variability in precipitation amounts and patterns, including tropical cyclones, extra-tropical storms, and thunderstorms (now year-round in many regions), is becoming more extreme (Trenberth, 2005; Webster et al., 2005; Holland and Webster, 2007; Allan and Soden, 2008; Bender et al., 2010; IPCC, 2012) and may magnify CyanoHABs (Paerl and Huisman, 2008, 2009).

Droughts are becoming more severe and geographically extensive (Trenberth, 2005) and are predicted to increase in occurrence and duration (IPCC, 2012). These events increase hydrologic variability; i.e., wetter wet and drier dry periods, leading to more episodic discharges, capture and transport of nutrients, and rapid and high nutrient enrichment. Excessive rainfall and runoff, often followed by lengthy droughts with increasing residence times, provides a "perfect storm" scenario for CyanoHAB formation. If this scenario is accompanied by warming (i.e., spring to summer transition), CyanoHABs can proliferate, since they exhibit maximum growth rates at relatively high temperatures (Butterwick et al., 2005; Paul, 2008; Paerl and Paul, 2012) (Fig. 4). Our ability to manage CyanoHABs resulting from extremes in rainfall and drought conditions will depend in part on our capacity to forecast future weather conditions (Hall, 2014). These conditions, in turn, will affect stratification patterns, oxygen levels, and nutrient inputs and dynamics, such as internal nutrient recycling and N removal via denitrification (Grantz et al., 2012, 2014; Scott and Grantz, 2013; Bruesewitz et al., 2015).

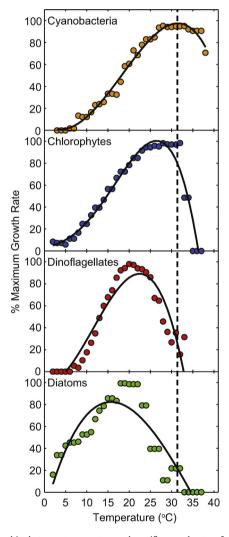


Fig. 4. Relationships between temperature and specific growth rates of cyanobacterial species and eukaryotic phytoplankton in three different taxonomic groups (chlorophytes, dinoflagellates, and diatoms). The dashed line is for comparison of optimal cyanobacterial growth temperature with temperature—growth relationships in other groups. Data points are 5 °C running bin averages of percent maximum growth rates from 3 to 4 species within each group. Fitted lines are third order polynomials and are included to emphasize the shape of the growth versus temperature relationship. Figure from Paerl (2014). Data sources and percent maximum growth rates of individual species are provided in Paerl (2014).

Extensive droughts, rising sea levels, and increased irrigation demand can lead to salinization, and increasing demand for potable water exacerbates these issues. Some CyanoHABs are salttolerant, despite being common in freshwater ecosystems. These species include the N2 fixers, Anabaenopsis, Dolichospermum, Nodularia, and some species of Lyngbya and Oscillatoria, and the non-N2 fixers Microcystis, Oscillatoria, Phormidium, and picoplanktonic Synechococcus and Chroococcus (Table 1). Some strains of Microcystis aeruginosa remain unaffected by salinities up to 10 (Tonk et al., 2007). For example, this species thrived under "mixohaline" conditions in Patos Lagoon, Brazil. Some Dolichospermum and Anabaenopsis withstand salinities up to 15 (Montagnolli et al., 2004), while the common Baltic Sea bloom-former Nodularia spumigena, tolerates salinities exceeding 20 (Mazur-Marzec et al., 2005; Moisander et al., 2002). These CyanoHABs are promoted by the combined effects of nutrients and salinization (Paerl and Paul, 2012) (Table 1).

Warmer temperatures favor CyanoHABs over eukaryotic algae (Weyhenmeyer, 2001; Elliot, 2010) because maximal growth rates of most CyanoHABs occur at temperatures >25 °C (Foy et al., 1976; Robarts and Zohary, 1987; Butterwick et al., 2005). Eukaryotic growth rates decline in response to warming, when cyanobacteria growth is most rapid (Fig. 4). Warming of surface waters also enhances vertical stratification, which favors buoyant CyanoHAB genera (e.g., Aphanizomenon, Dolichospermum, Microcystis, Nodularia; Table 1) (Reynolds and Walsby 1975; Havens et al., 1998; Paerl and Huisman, 2009). The strength of stratification depends on density differences between warmer surface water and colder water beneath. As mean temperatures rise, water stratifies earlier in the spring and persists longer into the fall (Stüken et al., 2006: Peeters et al., 2007; Suikkanen et al., 2007; Wiedner et al., 2007; Wagner and Adrian, 2009) (c.f., Figs. 1 and 2). High latitude ecosystems exhibit earlier "ice out", later "ice on", and stronger stratification, which extend the periodicity and range of Cyano-HABs. In polar regions, small temperature increases can have significant impacts on CyanoHAB activities, biogeochemistry, and trophodynamics. Along the margins of Antarctica, CyanoHABs (e.g., Nostoc, Oscillatoria, Lyngbya, Synechococcus) occur in exposed soils, glaciers, ice shelves, frozen lakes, and stream beds (Vincent, 1988). These communities occur mostly as desiccated, frozen mats, but surface temperatures are high enough to melt the ice briefly during Austral summer. Virtually all primary production, nutrient cycling, and trophic transfers are confined to this ice-free period (Vincent, 1988; Priscu, 1998). Climate change will extend this temporal window (Vincent and Quesada, 2012) and affect nutrient cycling in the aquatic and terrestrial ecosystems.

Various chemical treatments, including algaecides, are directed toward controlling CyanoHAB blooms. Copper sulfate is an effective algaecide but is toxic to a wide variety of plants and animals, and its residue in sediments is problematic as a legacy pollutant. Hydrogen peroxide (H₂O₂) is selective for cyanobacteria (vs. eukaryotic algae and higher plants) and poses no serious longterm effects on the system (Matthijs et al., 2012). Both of these treatments are restricted to fairly small impoundments, and H₂O₂ treatment must be repeated throughout the bloom period because it is degraded rapidly through physical-chemical and biotic processes. The multiple treatments that are needed to remain effective make the approach very costly. Also, caution must be practiced with these algaecides for toxin-producing CyanoHABs (see Table 1), because the endotoxins can be released into the bulk water phase upon death of the organisms and contaminate drinking water and irrigation supplies. H₂O₂ treatment is more desirable than copper sulfate from this standpoint, because oxidation by peroxide is stimulated by light and breaks down microcystins into peptide residues (Matthijs et al., 2012). This approach could therefore help detoxify waters impacted by microcystin-producing blooms. However, it is unknown how these chemical treatments affect other microbes mediating nutrient and carbon cycling (e.g., decomposition, sulfate reduction, nitrification, denitrification) and how they will be affected by temperature and hydrologic changes accompanying climate change.

Chemical precipitation has been used to immobilize P in sediments (US EPA, 1981). Commonly used precipitants include lime (Ca(OH)₂), which reacts with the natural in waters acidity to produce calcium carbonate. Hydrated aluminum sulfate (alum), ferric chloride or sulfate, and ferrous sulfate are all used widely for P removal in wastewater treatment plants and in small ponds and impoundments (US EPA, 1981). These treatments often need to be repeated, are expensive, and may not be effective in some systems. Hence, they do not solve P over-enrichment problems, and their effects on internal N cycling are unknown. It is also unknown whether climate change and the associated changes in P input and internal P cycling will influence the efficacy of immobilization methods

Another commonly used treatment, "Phoslock", uses a bentonite clay infused with lanthanum (Robb et al., 2003). Lanthanum ions are electrostatically bound to bentonite, and also bind phosphate. The bound phosphate settles out of the water column, and the thin layer (\sim 1 mm) of Phoslock on the sediment surface forms a diffusion barrier. Phoslock has been applied to small lakes and reservoirs, where it can lead to P-limited conditions (Robb et al., 2003; Egemose et al., 2010). The Phoslock layer also increases the critical erosional velocity of fine-grained surficial sediments, which may reduce sediment resuspension and associated internal loading. However, sediment resuspension and P recycling into the photic zone are very difficult to control in shallow (<10 m), poorly stratified, periodically wind-exposed ecosystems. Overall, the use of these chemical precipitants is expensive in large water bodies and does not prevent external P loading. Their efficacy in a future with changes in lake physics and chemistry induced by climate change will need to be determined.

All bioavailable N forms are soluble in natural waters, so there are no chemical precipitation techniques available to immobilize this nutrient. Managers therefore rely on biological removal by denitrification as the only effective in situ mitigation approach. However, care should be taken not to negate the positive effects of denitrification with other CyanoHAB management strategies that may be used simultaneously. For example, reducing vertical stratification by artificial mixing could affect denitrification potential of the system in question by oxygenating the entire water column and surface sediments. On the positive side, however, enhanced nitrification (via mixing and surface sediment aeration) could stimulate coupled nitrification-denitrification, especially if NO₃ availability is limiting denitrification rates.

Legacy nutrients in sediments can persist for many years, perpetuating high internal nutrient loads that fuel algal blooms (Barbiero and Kann, 1994; Head et al., 1999). The large biomass and long survival time of *Microcystis* in sediments can help explain the common delayed recovery of affected lakes after reduction of external nutrient loads (Brunberg and Boström, 1992). Sediment removal involves expensive dredging and disturbance of lake bottoms, which can release additional nutrients (and potentially toxic substances) and adversely affect benthic flora and fauna. However, CyanoHABs were eradicated successfully with this approach in Lake Trummen, Sweden ($\sim 1 \text{ km}^2$, mean depth 1.6 m), which experienced CyanoHABs and water quality degradation from domestic sewage and industrial nutrient inputs during the mid-1900s (Cronberg, 1982; Peterson, 1982). Suction dredging the upper half-meter of sediments over two years led to significant decreases in nutrient concentrations and CyanoHABs (Cronberg, 1982; Peterson, 1982). The Lake Trummen success can be attributed to its small size and the ability to target reductions of external nutrient loads effectively from its small (13 km²) watershed following dredging. Dredging is not a feasible solution for reducing internal P loading in large lakes, where P-rich sediments are spread over hundreds or thousands of square kilometers and are highly mobile (James and Pollman, 2011).

Added clays and other sorbent minerals can flocculate algal cells, filaments, and aggregates (including CyanoHABs), thereby accelerating their sedimentation and removal from the water column (Sengco and Anderson, 2004; Pan et al., 2006). While these techniques can provide an effective short-term treatment for blooms in small ecosystems, repeated treatments are required to suppress blooms, and the basic problem of excessive nutrient loading is not solved. Further, clay-enhanced sedimentation of blooms can increase benthic organic matter accumulation, increasing the potential for hypoxia, internal nutrient releases, and benthic habitat degradation. Effects of thermal and hydrodynamic changes associated with climate change on the efficacy of these techniques need to be determined.

Biological controls include approaches to change the aquatic food web to increase grazing pressure on cyanobacteria and/or reduce nutrient recycling. Protecting herbivorous zooplankton by reducing populations of zooplanktivorous or piscivorous fish grazers is one approach to mitigating CyanoHABS (Shapiro and Wright, 1984; Jeppesen et al., 2007a,b). Benthic fish can stimulate CyanoHABs via N and P releases by grazing on particulate material and then excreting dissolved nutrients (Schaus and Vanni, 2000); however, removal of benthic fish has produced mixed results. Removal of 5.4 million kg of gizzard shad from Lake Apopka, Florida, resulted in estimated annual reductions in sediment release of 45,800 kg N and 7700 kg P (Schaus et al., 2010). Yet, investigations of the effects on chlorophyll a concentrations and Secchi transparency in a similar study of nearby lakes suggested 'little short-term benefit' (Catalano et al., 2010). In a future with different rates of nutrient input and cycling caused by climate change, larger removal rates may be needed.

Table 1 summarizes the most common CyanoHAB taxa, their habitat preferences (e.g. surface vs. subsurface bloom forming), their toxic properties and nitrogen fixing capabilities, which in addition to negative esthetic, trophic and habitat altering (e.g., turbidity and hypoxia generating) properties, should be taken into consideration when weighing and prioritizing potential control measures.

In general, there is no clear information about how climate change will influence the efficacy of all the within waterbody control measures. Critical research needs include understanding how these physical, chemical, and biological control measures will work in the future with changes in hydrology, stratification, and nutrient dynamics caused by climate change. How will climate change affect stratification and the efficacy of devices that aim to de-stratify the water column? How will climate change influence the choice and frequency of chemical treatments and physical removal of sediments to maintain reduced internal loading? How will climate change (e.g., warmer water and altered metabolic rates of both CyanoHABs and their grazers) affect the outcome of biological controls? Based on our current understanding of how CyanoHABs respond to changes in their physical, chemical, and biological environments, there is reason to believe that climate change will influence control outcomes profoundly. However, without targeted research, we will not know the extent of influence, or the manner in which to modify, those control measures to be effective in response to future climatic changes.

3. Concluding remarks and recommendations

We understand many of the factors that facilitate CyanoHABs in inland and coastal waters, and the wide range of measures employed to control (sometimes with limited success) their frequency of occurrence, intensity, and impacts. Climate change alters local hydrologic and biogeochemical processes, including rainfall and runoff (amount and temporal dynamics), nutrient export from watersheds, mixing regimes, internal nutrient cycling, and food web dynamics. These changes present a significant challenge to resource managers aiming to control CyanoHABs in a future favoring bloom occurrence. A research program that focuses on how extant strategies will be influenced by climate change is needed to support effective CyanoHAB control programs. Specific areas of priority research identified in this paper include:

- 1. Determine how changes in precipitation (intensity and temporal dynamics) resulting from climate change will affect rates of P and N input to inland and coastal waters and watersheds.
- 2. Determine changes in temperature and wind fields seasonally and over longer periods due to climate change, specifically thermal changes in various water systems, and link these to changes in phytoplankton community structure and function, including CyanoHAB occurrences and intensities.
- 3. Develop new approaches to incorporate this information into nutrient control strategies and watershed loading targets to suppress CyanoHABs.
- Evaluate the effectiveness of existing physical, chemical, and biological control measures with continued changes in hydrology, stratification, and nutrient dynamics caused by climate change.

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