Mitigating harmful cyanobacterial blooms: strategies for control of nitrogen and phosphorus loads

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Abstract Harmful blooms of cyanobacteria (CyanoHABs) have increased globally and cyanotoxins associated with some CyanoHAB species pose serious health risks for animals and humans. CyanoHABs are sensitive to supply rates of both nitrogen and phosphorus, but sensitivity may vary among species (e.g., between diazotrophic and non-diazotrophic species) and a range of physiographic and environmental factors. A sustainable approach to manage CyanoHABs is therefore to limit the supply of nitrogen and phosphorus from catchments to receiving waters. Alternative approaches of within-lake treatment have increased risks and large capital and operational expenditure. The need to manage catchment nutrient loads will intensify with climate change, due to expected increases in nutrient remineralization rates, alteration in hydrological regimes, and increases in lake water temperature and density stratification. Many CyanoHAB species have physiological features that enable them to benefit from the effects of climate change, including positive buoyancy or buoyancy control, high replication rates at elevated water temperature, and nutrient uptake strategies adapted for the intermittency of nutrient supply with greater hydrological variability expected in the future. Greater attention needs to be focused on nonpoint sources of nutrients, including source control, particularly maintaining nitrogen and phosphorus in agricultural soils at or below agronomic optimum levels, and enhancing natural attenuation processes in water and solute transport pathways. Efforts to achieve effective catchment management and avert the dire ecological, human health and economic consequences of CyanoHABs must be intensified in an era of anthropogenically driven environmental change arising from increasing human population, climate change and agricultural intensification.

Keywords CyanoHABs · Nitrogen · Phosphorus · Lakes · Climate change · Land use change · Cyanotoxins

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Introduction

One of the most concerning trends in freshwater systems globally is an unprecedented increase in harmful (and often toxic) cyanobacterial blooms (CyanoHABs) (Harke et al. 2016; Paerl et al. 2016). Accumulation of these prokaryotic organisms to levels that constitute massive surface blooms can have direct economic impacts as well as affecting ecosystem services derived from lakes (Hamilton et al. 2014). Moreover, toxin production by some species or strains, which is often closely linked to cell accumulations in blooms (Wood et al. 2015), has serious health effects on humans and animals, and can even result in death (Codd et al. 2005). Occurrences of CyanoHABs in lakes are often linked to excessive phosphorus (P) and nitrogen (N) inputs as a consequence of human activities; the literature and experiences regarding this topic are vast (e.g., Table 1; McComas 2003; Finger et al. 2013). However, a more complex picture is the emergence of how environmental change may favor dominance of cyanobacteria in the 'era of the Anthropocene' (Carey et al. 2012), re-emphasizing the importance of control strategies. Here, we explore environmental change in more detail in the context of the global expansion of CyanoHABs, particularly the roles of land use change and climate change, as well as the changing paradigms of nutrient limitation.

At the catchment scale, the problem of CyanoHABs was addressed historically by reducing P inputs, based on the premise that P limits freshwater primary production, algal biomass, and CyanoHAB formation (Schindler et al. 2008). This practice has been successful (see examples in Table 1), and there is little doubt that phosphorus removal has been instrumental in improving water quality (Schindler et al. 2008), but recent enclosure and whole lake experiments in eutrophic systems demonstrate that strictly P-limited growth may be the exception, rather than the rule (Conley et al. 2009). Instead, many such systems exhibit maximum rates of algal growth in response to combined N and P additions, or even at times only N addition (Elser et al. 2009; Lewis et al. 2011). Focus on P reduction may therefore no longer be adequate for many eutrophic lakes, including some of the world's largest and highly culturally important lakes (e.g., Erie, Winnipeg, and Okeechobee, North America; Victoria, Africa; Taihu and Dianchi, China; Leven, Scotland; Albufera, Spain) (Table 1). A broader integrated approach is required based on effectiveness of dual nutrient (N and P) control, learnings from failed restoration attempts, and mitigation actions linked to future environmental change.

In ecosystems globally, there is an ever-increasing supply of reactive N from anthropogenic sources (Galloway et al. 2002). Much of this N arises from rapidly increasing and poorly controlled inputs related to urbanization and the desire to maximize agricultural production. For example, between 1900 and 1950 surpluses of N and P in agricultural soils increased by nearly two- and eight-fold, respectively, by around four-fold for both nutrients between 1950 and 2000, and are projected to increase further to 2050 despite greater efficiency of nutrient recovery (Bouwman et al. 2013). The outcome is increasing nitrogen inputs to aquatic systems, leading to water quality degradation and acceleration of eutrophication, even in systems already classified as eutrophic (US Environmental Protection Agency 2007; Elser et al. 2009; Lewis et al. 2011; Paerl and Otten 2016). Estuarine and coastal marine systems have long been known to be sensitive to these nitrogen additions (US Environmental Protection Agency 2007; Conley et al. 2009), but attention must also now be directed to eutrophic freshwater ecosystems in view of what is known about the status of N inputs and sensitivity of CyanoHABs to these inputs (Elser et al. 2009). Therefore, while historically the focus has been on the impact of P on the trophic status and phytoplankton structure in inland waters (e.g., Schindler 2006), the role of N in the control of both diazotrophic and non-diazotrophic CyanoHABs has recently been widely reconsidered and necessitates greater focus on N control strategies based on numerous monitoring and experimental observations (Paerl and Otten 2016).

Shifts in the freshwater nutrient limitation paradigm have important implications for catchment nutrient control strategies, as these strategies must address inputs of both nitrogen and phosphorus through land use change and/or management. Our focus in this paper includes identification of nutrient sources and extends to general principles for catchment nutrient management actions to reduce the frequency, magnitude and severity of occurrences of CyanoHABs and the risks of cyanotoxin production. Management of catchment nutrient sources ultimately represents the most efficient and effective mechanism for sustainable control of CyanoHABs. Direct or

Table 1 Selection of case studies demonstrating the effects due to the adoption of management strategies aimed at the reduction in P and/or N originating from point (PSP) and nonpoint (NPSP) pollution sources

Waterbody	Area z_{max}	Main pollution source	Main restoration strategies	Other measures	TP (µg L^{-1}) N (mg L^{-1})	Decrease in cyanobacteria YES, NO	Reference
Lake Garda (Italy)	368 km^2 350 m	PSP (and NPSP)	Ring trunk sewer; STW (central and southern basin)	–	12[a] 0.2[a] (DIN)	YES *Planktothrix rubescens*	Boscaini (2009); Salmaso and Cerasino (2012)
Lake Müggelsee (Berlin, Germany)	7.4 km^2 8 m	PSP, NPSP	Improvement in wastewater treatment in the catchment area	Land use (decline in industrial and agricultural production); lignite mining ceased	128 1.25 (TN)	YES *Limnothrix redekei* and *Planktothrix agardhii*; no decrease in N-fixers	Kohler et al. (2005)
Loch Leven (Scotland, UK)	13.3 km^2 25.5 m	PSP, NPSP	Elimination of P usage at a major industrial source, upgrades of STWs.	Channeling of effluent from a small works out of the catchment	31 0.63 (NO_3-N)	NO Diazotrophic (*Anabaena* sp.) increasing under limiting N-conditions	Bailey-Watts and Kirika (1999); Elliott and May (2007); Dudley et al. (2012)
Lake Mjøsa (Norway)	362 km^2 453 m	PSP, NPSP	Sewage pipe lines and municipal treatment plants	Restrictions in order to reduce discharges from agriculture and industries	5 0.16 (TN)	YES Near absence of cyanobacteria	Løvik and Kjellberg (2003)
Lake Albufera (Valencia, Spain)	23.2 km^2 1.5 m	PSP, NPSP	Removal of urban and industrial sewage, but TP still high and no removal N-rich runoff from rice fields		340 0.97 (NO_3-N)	NO *Planktothrix agardhii* replaced by smaller Chroococcales	Romo et al. (2005)
Lake Bourget (France)	44.5 km^2 145 m	PSP (and NPSP)	Development and/or improvement of SWT; diversion of treated sewage from the two main cities	Control of the combined sewer overflows	8[a] ~0.67[a] (TN)	YES Disappearance of *Planktothrix rubescens* blooms	Jacquet et al. (2005, 2014)
Lake Rotorua (New Zealand)	80 km^2 21 m[b]	PSP and NPSP	Removal from lake of treated sewage discharge to forest in catchment	Land use rules for agriculture (no net increase allowed) Alum treatment of inflows to address diffuse P sources	35 0.33 (TN)	YES Large reduction in *Anabaena, Microcystis*	Burger et al. (2007); Smith et al. (2016)
Lake Washington (Oregon, USA)	87.6 km^2 65.2 m	PSP and NPSP	Treated sewage discharge diverted to Puget Sound	Washington has various land use nutrient management programs including the Total Maximum Daily Load	20 0.5 (TN)	YES Disappearance of *Planktothrix rubescens* blooms	Edmondson (1961); Edmondson (1970); Edmondson and Lehman (1991)
Esthwaite Waters (UK)	1.1 km^2 6.4 m	PSP	Removal of treated sewage from lake reduced P load by $>\sim 50$ %, large internal P load remained	Sewage removal may have been partially negated by fish farm, farmed trout introductions to lake	25 ~250 (NO_3-N)[c]	NO Appearance of *Aphanizomenon flos-aquae* and *Anabaena* sp.	Heaney et al. (1986); Drake and Heaney (1987)

Table 1 continued

Waterbody	Area z_{max}	Main pollution source	Main restoration strategies	Other measures	TP ($\mu g\ L^{-1}$) N ($mg\ L^{-1}$)	Decrease in cyanobacteria YES, NO	Reference
Lake Constance (Germany)	571 km^2 90 m	PSP and NPSP	Treated wastewater discharge mostly responsible for ~10-fold decrease in TP from early 1980s	Protection agreements as part of European Water Framework Directive and Rhine international management plan	8 N/A	NO Picocyanobacteria dominate cyanobacteria; may be inhibited by nutrient additions (*Synechococcus* sp.)	Prasuhn and Sieber (2005); Lang et al. (2010)

STW sewage treatment works; *S* lake surface (km^2); z_{max} maximum depth (m). *TP* total phosphorus; *TN* total nitrogen; *DIN* dissolved inorganic nitrogen

[a] Epilimnetic

[b] Excludes localized deep hole ($z = 45$ m) outside of main basin

[c] High seasonal variability

indirect in-lake methods of CyanoHAB control (e.g., hydrogen peroxide treatment (Matthijs et al. 2012) or geoengineering (Spears et al. 2014) represent a final fallback position, sometimes necessary to avert the dire ecological and human health consequences of severe CyanoHABs but mostly failing to address the root cause of over-supply of nutrients. These in-lake approaches generally have high costs and, in the case of geoengineering, have risks of being largely ineffective, producing unforeseen outcomes and causing ecotoxicological effects from the geoengineering material itself (Mackay et al. 2014). Artificial destratification and hypolimnetic oxygenation may similarly be effective in directly (i.e., by mixing) and indirectly (i.e., by reducing bottom-sediment nutrient releases) controlling CyanoHABs but have high capital and operating costs, and are not always effective, sometimes leading to abandonment of these operations and raising questions about their long-term sustainability (Hamilton et al. 2014).

Point source pollution (PSP): a problem solved?

Some four or five decades ago, increasing and uncontrolled release of untreated or partially treated sewage into natural lakes and rivers was leading to general impairment of water quality across the world. Investigations carried out in the 1960s demonstrated the key role played by phosphorus in the eutrophication of temperate lakes (Cullen and Forsberg 1988), and much of this literature also related higher rates of nutrient supply to the development of CyanoHABs (e.g., Edmondson 1970; see Table 1). The early studies were instrumental in the development of models relating macronutrient (usually P) loads and concentrations to the increase in algal biomass (OECD 1982). The negative effect on water quality and human use of water resources, together with output from the models, fostered several actions aimed at decreasing P and N loads (Ryding and Rast 1989), including removal of P from detergents and wastewater treatment. Yet surprisingly there is no universality in the removal of P in detergents, and there are many cases where P from detergents continues to be an important component of P in surface waters as well as imposing a major burden on treatment processes at wastewater plants (Van Drecht et al. 2009).

In addressing the need for macronutrient control, great progress has been made in removing nutrient and organic pollutant inputs to inland waters. Reduction in PSP generally involves diversion of sewage from waterbodies and reduction in P and N concentrations in the wastewater discharge (Sedlak 1991). Not all treatments are similarly effective or remove N and P in similar proportions, however, and treatment plants can be of varying complexities, equipped with different physical, chemical and biological treatments. The degree of dilution of the treated wastewater, when discharged directly to receiving waters, also remains critical in assessing the environmental impact and potential to lead to CyanoHABs. The benefits of removal of PSP are widely evident in the documented history of improvements in water quality of many lakes around the world (see Table 1), including reductions in CyanoHABs. Point source pollution continues to remain a major problem in many developing countries, however, where there can be issues with funding or prioritizing the capital investment required to support wastewater treatment infrastructure for large populations (Baum et al. 2013). In summary, the technology for wastewater treatment is now well established and the impediments to addressing PSP are primarily related to lack of funding or political will.

Below we provide a brief description of nutrient removal processes in wastewater treatment to outline the potential for plant operators and policy makers to intentionally or unintentionally alter total and relative loads of N and P, and fractions of both particulate/dissolved and labile/refractory forms of both macronutrients. For example, treatment focused on N removal (e.g., through engineered nitrification–denitrification processes) without due consideration of P may be adequate to protect many estuarine and coastal marine systems, but high P concentrations in wastewater discharges from plants using conventional carbon and nitrogen removal processes could, if not diluted adequately, fuel proliferations of diazotrophic cyanobacteria in particular. Removal of nutrients by wastewater treatment tends to be costly in terms of mass of N or P removed relative to many land management options (Abell et al. 2011), especially for plants required to produce high-quality discharge, but it may also be less contentious than targeting diffuse sources (e.g., from agriculture) and its impact can be more immediate (cf., land use change) and quantifiable. It also has primary benefits for human health by reducing pathogens and removing the majority of persistent organic pollutants.

Nitrogen removal from wastewater generally makes use of coupled nitrification–denitrification processes using a carbon source from the wastewater itself or complemented with external carbon additions (e.g., using methanol) (US Environmental Protection Agency 2007). Design of wastewater treatment plants to facilitate nitrification–denitrification became commonplace through the 1960s and 1970s, using technologies such as Bardenpho or Biodenipho (Oldham and Stevens 1984). More recent innovations have included partial nitrification (to nitrite only) or use of ANAMMOX to attempt to reduce energy costs, external carbon additions and the volume of sludge production (Kartal et al. 2010). Phosphorus removal is achieved by physical, biological and chemical means, using sedimentation, microbial uptake to incorporate P into biomass, and chemical precipitation methods, respectively. Enhanced biological phosphorus removal is generally achieved in treatment plants engineered to select for polyphosphate-accumulating microbes which are subsequently removed in the sludge (Mino 2000). While it may be a cheaper alternative to chemical treatment, biological phosphorus removal is not as reliable and it can be difficult to reduce total P to $<\sim 0.3$ mg L^{-1}. Where a lower concentration of P is required, chemical treatment is almost always used, either in conjunction with enhanced biological P removal or as the primary removal process (Takacs et al. 2006). Chemical treatment involves addition of a chemical compound containing a reactive metal cation, commonly as aluminum III (Al^{3+}) or iron III (Fe^{3+}), which is used to precipitate P-containing solids and to remove the precipitate through a subsequent sedimentation and/or filtration step.

Drivers of nonpoint source pollution (NPSP) and interactions with point source pollution (PSP)

Compared with PSP, the issue of NPSP is more complex and not confined specifically to the economic status of a country; NPSP may be even more problematic for First World countries because its relative contribution to nutrient loads of inland waters has progressively increased with advanced treatment of PSP. Moreover, most countries have strong political imperatives to increase food production to meet demands of growing human populations and changing food consumption patterns. This challenge is generally met with intensification of agricultural production, which can also be linked to an increase in NPSP. The control of nutrients originating from NPSP is demanding due to the diffuse nature of the sources (Paerl et al. 2016), the complex delineation of property rights and authorities, and economic and social issues.

A selection of case studies demonstrating the outcomes from the adoption of management strategies aimed at the reduction in P and N is shown in Table 1. Additional recent case studies of restoration of eight lakes by avoiding or treating inflows (mostly point sources) with high P load have been discussed by Fastner et al. (2015; this issue). In general, a decrease in nutrient loads after the control of both PSP and NPSP has resulted in a general decline in cyanobacteria biomass. The two cases presented in Table 1 where cyanobacteria have continued to maintain high biomass are for two lakes where the decrease in nutrient loads was insufficient and not coupled with removal of point source loads. Lake Albufera has high loads of N from rice fields (Romo et al. 2005) and Loch Leven shows increases of diazotrophic species (pelagic *Anabaena* sp.) during summer depletion of nitrogen to limiting concentrations (Dudley et al. 2012). In a number of other cases, low concentrations of N have been instrumental in the development of diazotrophic species. Kosten et al. (2009) found N-fixing cyanobacteria exclusively in waterbodies with dissolved inorganic nitrogen (DIN) concentrations $<100\ \mu g\ N\ L^{-1}$. Conversely, N-fixers were also often absent in lakes with low DIN concentrations (Dudley et al. 2012). Cyanobacteria were also absent or at low levels in lakes where there was strong re-oligotrophication and recovery of the lake ecosystem (e.g., Lake Mjøsa; Løvik and Kjellberg 2003).

Land use effects on CyanoHABs

Contrary to the high number of studies relating water quality characteristics and land use types, the number of investigations relating phytoplankton species composition and land use is quite limited (Salmaso et al. 2012). Katsiapi et al. (2012) analyzed the watershed land use types and freshwater phytoplankton structure of 18 lakes and reservoirs in Greece. They found a significant association between cyanobacteria and modified and agricultural land use types, and between euglenophytes and industrial, commercial, and transport areas. Conversely, chrysophytes (a well-known oligotrophic group; Salmaso et al. 2015) were closely associated with forested areas. These results were consistent with those found in a study carried out in 11 lakes in the Rotorua region, New Zealand, by Paul et al. (2012). The trophic state in that group of lakes was correlated positively with the area of pasture and urban cover, and negatively with area of native forest cover. Cyanobacteria cell densities were correlated positively with pasture and trophic state, and negatively with native forest. In general, lakes with higher nutrient loads were dominated by cyanobacteria. These results are relevant to landscape planning for mitigating the future impact of climate change on the drainage network, surface runoff, nutrient loads and, ultimately, on the development of toxigenic cyanobacteria (see section on climate change below). Paleolimnological studies using pigments or diatom indicators provide an opportunity to complement information from the limited number of contemporary studies of relationships of land use and phytoplankton species composition (Pienitz et al. 2006; Kpodonu et al. 2016). These studies generally rely on transfer functions to relate historical changes in phosphorus loading to dominance by diatom communities in sediment cores and assume that pigments specific to different phytoplankton taxa are similarly preserved through time in the bottom sediments.

Land use change and management practices to mitigate CyanoHABs

Addressing the occurrence of CyanoHABs through improved catchment management practices usually targets reductions in nutrient loads to meet defined targets, rather than making direct use of statistical relationships between cyanobacteria and land use, which are catchment-specific (see above) and would pertain specifically to considerations of land use change. It is generally well known that different types of land use vary in their areal rates of nutrient loss (Quinn and Stroud 2002; Park et al. 2011) and there is an abundant literature on impacts of agriculture on nutrient yields (e.g., Garcia et al. 2016). Agricultural and urban land uses, as major contributors to nutrient losses, are the obvious targets for implementation of remediation actions. At the same time, however, urban populations have increased around fivefold since 1950 and are expected to increase by a further 60 % by 2050 (United Nations 2014). Close relationships between urban and industrial land use and water quality have been highlighted by Arienzo et al. (2001) and Wang et al. (2001), and these areas affect nitrogen and phosphorus at regional and global scales (Morée et al. 2013). Despite the significance of urban areas as a source of nutrients for receiving waterbodies, surprisingly little is known about the source and fate of nutrients from these areas (Carey et al. 2013). They generally have multiple artificial drainage networks that hasten transit times of water from the landscape to often sensitive downstream ecosystems, greatly curtailing natural attenuation processes. 'Revitalization' and renewal of these processes, including redesign of stormwater systems, water conservation, 'softening' of hard surfaces to increase infiltration, and creation of ecotones bridging artificial and natural systems, are required to counter the effects of growing urban populations and the pressure on existing urban infrastructure (White 2010).

In the literature, it has been documented that intensive agricultural systems (e.g., dairy farming, market gardening) may have areal yields up to two orders of magnitude or more higher than those of undisturbed forest systems (Drewry et al. 2006). Thus, land use change, usually focused on reducing areal nutrient losses through conversion of intensive agricultural systems to low-yield land uses, can be an important part of the repertoire of management to mitigate the occurrence of CyanoHABs. Land use change is not considered further here, however, except to note that it may be required where the combination of point source treatment and changes in management practices across existing land uses may not meet nutrient load targets. Land use change inevitably invokes questions about the achievable and sustainable balance of economic and environmental values (Correll 1996), and interdisciplinary studies that integrate economic, social and environmental contexts will increasingly be used in future to support planning and policy frameworks for land and water management (Arheimer et al. 2005).

Use of ecosystem models as integrative tools for considerations of CyanoHAB control

An integrated approach based on a combination of different actions is almost always required to meet catchment nutrient load reduction targets (e.g., Cherry et al. 2008). Quantifying the individual and combined effects of remediation actions is complicated, however, as there is substantial variability in lithology, hydrology and biogeochemical transformations within and between catchments (McDowell et al. 2014). Catchment models are therefore a critical component of the remediation and target-setting strategy and can help to integrate and prioritize actions that are cost-effective, including relevant timescales (Drewry et al. 2006). These models also help to better understand connectivity at different scales within a catchment. They vary in complexity and utility depending on their level of process representation and time- and space scales. For example, the Surface Water Assessment Tool (SWAT) dynamically simulates nutrient losses to streams and may delineate hundreds of hydrological units within a catchment or subcatchment, operating at daily or even sub-daily time steps (Her et al. 2016). By contrast, the SPAtially Referenced Regression On Watershed attributes (SPARROW) model provides predictions (e.g., responses to land use change) of long-term average stream discharge and nutrient concentrations from empirical fit of these variables to a series of explanatory physical and environmental predictors (Alexander et al. 2008). This diversity of models can add value; for example, SWAT may be used to better understand the relationships between variations in nutrient delivery (e.g., from stormflows) and occurrence of CyanoHABs, while SPARROW could provide a long-term perspective on lake eutrophication based on land use in a catchment. Both models can add value in generating scenarios, e.g., ranging from 'business as usual' without climate or land use change, to hypothetical cases where, for example, a heavily developed catchment undergoes complete afforestation to offset projected impacts from climate change. An example is the approach used to model impacts of future global climate and land use change on water quality of Liu et al. (2000) in the Ohio River basin. The aim of this research was to evaluate how change in land use could be used as a mitigation strategy to reduce the impact of climate change on water runoff. The model simulations showed that the surface runoff volume decreased after a change from agricultural land use to low-density residential land use. The highest discharge was generated by expanding high-density residential and commercial land use types. This 'visioning' element of scenario generation in models can provide a valuable mechanism for engagement among scientists, politicians, land owners, environmental managers, policy makers and conservationists but requires regular and sustained dialogue, as well as education to define the limits of model applicability and error bounds.

Coupled lake catchment models can be used to help define targets for catchment nutrient loads to meet trophic state outcomes for lakes (e.g., Trolle et al. 2008; Jeppesen et al. 2009; Pierson et al. 2013; Molina-Navarro et al. 2014). The models often have relevance to water policy frameworks such as the European Union Water Framework Directive (Trolle et al. 2008) or the United States Total Maximum Daily Load (Borok 1984). These models are also relevant to water supplies; New York City Department of Environmental Protection uses a variety of coupled climate, catchment and lake simulation models as part of a forecasting strategy aimed mostly at management responses to floods and high-turbidity events (Department of Environmental Protection 2014), and Sydney Catchment Authority uses short-term model forecasts as part of its management strategy for water supply to Sydney (Kristiana et al. 2011). Currently, however, few lake-scale models, particularly those coupled with catchment models, explicitly output cyanobacteria biomass, have adequate validation data, or possess adequate process representation or parameterization to capture the dynamics of CyanoHABs (Shimoda and Arhonditsis 2016). This area of development and application of ecosystem-level modeling requires a sustained research effort to address some of the questions being asked of how catchment nutrient control strategies affect the occurrence of CyanoHABs, particularly in association with climate change.

Remediation measures for nonpoint source pollution

Remediation actions in catchments for nutrient control may be described in terms of their mode of action, applicability, effectiveness, time frame and environmental side effects (Schoumansa et al. 2014). The side effects relate to actions that leave large pools (legacies) of nutrients on the landscape which may subsequently be mobilized (Jarvie et al. 2013). Actions should be aligned firstly to source control, i.e., where the nutrient is initially mobilized, and secondly to enhancement of natural processes occurring along hydrological pathways where the nutrient may be intercepted and potentially immobilized or removed (McDowell et al. 2014). In agricultural systems, maintaining phosphorus and nitrogen in soils at levels close to or below agronomic optima is critical and represents one of the simplest and cost-effective methods to reduce eutrophication and potential for CyanoHABs in receiving waters, with significant agronomic benefits (Drewry et al. 2006; Rasouli et al. 2014). Many agricultural soils worldwide now have a legacy of over-enrichment of nutrients from past practices of excessive fertilization and improper management of manure, and historical livestock management practices (Sharpley et al. 1994; Cherry et al. 2008). Over-enrichment of soil P has been implicated in recent CyanoHABs in Lake Erie (Michalak et al. 2013) and, counterintuitively, the use of best management practices, including conservation crop rotations, cover crops and no-till, may potentially play a role by increasing losses of dissolved P (through restricting runoff of sediment that could bind P) even though these measures are highly effective in attenuating sediment losses (Her et al. 2016). With conservation cropping and no-till practices becoming more widespread, it is likely that CyanoHABs may become more frequent in Lake Erie and other lakes where there is intensive agriculture within their catchments, until P stores in highly enriched soils run down through time.

Hydrological pathways for delivery of N and P to receiving waters tend to be quite different, and this has implications for control strategies and the duration on which these strategies become effective. Nitrogen losses occur most commonly as nitrate, an anion not generally sorbed by soil constituents. Thus, once below the root zone, nitrate is transported passively with the flow through the vadose zone and into groundwater. This pathway of nitrate loss emphasizes the importance of farm plans, soil testing and knowledge of agronomic optimum N levels in order to minimize leaching of N to groundwater (Rasouli et al. 2014). The use of innovative technologies can play an important role in determining the timing and amount of N-fertilizer required (Ahrens et al. 2008; Muñoz-Huerta et al. 2013). Grazing regimes connected with pasture moisture levels are also important as large domesticated animals may cause the majority of N loss in pastoral grazing systems through concentrated leaching areas arising from urine ‘patches’ (Haynes and Williams 1993). The fate of the nitrate, once leached to groundwater, will depend on the oxidation state of the aquifer system and the interface where the water re-emerges as surface discharge (e.g., to a wetland, stream or lake). The period until re-emergence can potentially be decades or centuries, depending on the catchment size and volume of aquifer. Denitrification is overwhelmingly the dominant nitrate loss mechanism, and this process may be capable of being enhanced in the interfacial zone where groundwater re-emerges. For example, enhancing or engineering saturated areas associated with wetlands, bogs and riparian areas can stimulate denitrification, particularly where there is natural peat or detritus accumulation from vegetation to act as a carbon source (Tiemeyer and Kahle 2014).

Transport of P is complicated by the different forms in which it may be delivered and transformations between these (i.e., sorbed particulate and dissolved species), as well as by the heterogeneity of flow paths. The majority of P is delivered in surface runoff and interflow, with the latter greatly enhanced by the presence of macropores or preferential flow paths (McDowell and Houlbrooke 2009). Aside from source control, maintaining adequate vegetation cover and implementing conservation tillage to reduce erosion under intense rainfall events, this diversity of flow paths also provides multiple mitigation opportunities; for example, use of sedimentation basins, wetlands and infiltration zones can slow the flow and remove particulate P by sedimentation. Re-engineering of artificial drainage networks and creation of vegetated buffer strips can also be highly effective, particularly where these can be connected to runoff from critical source areas (e.g., stock paths, vulnerable soils and steep slopes) (Drewry et al. 2006).

Nutrient load targets potentially provide opportunities to achieve N and P concentrations that conform not only to a given lake trophic status but may also influence the phytoplankton composition, including the biomass of diazotrophic and non-diazotrophic species of cyanobacteria. The focus for highly eutrophic shallow lakes where there are prolific non-diazotrophic CyanoHABs (e.g., Taihu and Dianchi, China) may be to reduce N inputs to levels that lead to co-limitation with P, as internal sediment P stores in these lakes will provide a legacy of supply which is regularly activated through, for example, resuspension of bottom sediments (e.g., especially during typhoons; Zhu et al. 2014). In other lakes with diazotrophic CyanoHABs (e.g., Loch Leven, Scotland—see Table 1), the focus of catchment remediation measures may be on P source control and surface hydrological pathways associated with phosphorus delivery, e.g., sedimentation basins, reconfiguration of artificial drainage networks, and preservation and restoration of riparian ecotones between agricultural lands and receiving waters. It is important to emphasize that many of the strategies for N and P control are not mutually exclusive and should be assessed for effects on both of these macronutrients.

Climate change effects on catchment runoff and nutrient sources

At the catchment level, climate change can seriously affect the effectiveness of ‘best management practices’ (e.g., Kleinman et al. 2011) for nutrient load reductions from agricultural, natural and urban areas (see Table 1). Under the RCP (Representative Concentration Pathways) 8.5 scenario (Intergovernmental Panel on Climate Change 2015), in which emissions will continue to rise throughout the present century, the high northern latitudes, many mid-latitude wet regions, and the equatorial Pacific regions will likely experience an increase in annual mean precipitation. Conversely, under the same scenario, mean precipitation will likely decrease in many mid-latitude and subtropical dry regions. In parallel, over most mid-latitude regions and over wet tropical areas, extreme precipitation events will become more intense and more frequent as global mean surface temperature increases (Intergovernmental Panel on Climate Change 2015). These projections are consistent with present observed trends, which show a decrease in streamflow in the south and east of Europe, and an increase in northern latitudes in particular (Wilson et al. 2010; Jiménez Cisneros et al. 2014). Current trends and future projections suggest specificity by region of impacts of global warming on the hydrological regime and nutrient loads, with a requirement to adopt different types of actions to counterbalance water scarcity or flooding, and assuring, at the same time, that macronutrient loads to groundwaters, rivers and lakes can be tightly controlled.

A better knowledge of the relationships between land use type and discharge is essential to foresee the effects of climate change on drainage basins and therefore to evaluate potential triggers of CyanoHABs. In regions where there is increased storm runoff, the outcome will be shorter hydraulic retention times and higher loads of nutrients, salts, fecal coliforms, pathogens and heavy metals (Jiménez Cisneros et al. 2014). Higher temperatures in combination with greater runoff will increase soil contaminant losses and associated loads to receiving waters (Boxall et al. 2009; Benítez-Gilabert et al. 2010; Gascuel-Odoux et al. 2010; Jeppesen et al. 2010). Changes in nutrient loads may be able to be offset by modifications in agricultural practices, including those discussed above (e.g., fertilization regimes, conservation or no tillage), as well as careful choice of crops and their rotation, planting and harvesting times (Olesen 2005; Olesen et al. 2007). Regions in northern latitudes of the northern hemisphere could be advantaged by the introduction of new crop species and higher crop production rates (e.g., grapes, maize, sunflower) which may be associated with expansion of crop cultivation areas in these regions (Elsgaard et al. 2012). In cropping systems, higher temperatures may lead to earlier harvest, followed by later planting of winter crops, prolonging the period of bare soil in autumn and increasing the risk of P loss, especially in association with more intense precipitation in temperate regions (Olesen et al. 2004; Jeppesen et al. 2010). Moreover, higher temperature and rainfall may increase N leaching from crops (Olesen et al. 2004). The impact of climate change should be evaluated taking into account the specificity of the affected systems as well as the potential for synergistic or antagonistic effects in receiving waters. For example, Paerl and Huisman (2009) showed that in the Neuse River (North Carolina) hurricanes and intense storms washed out nutrients from the estuary, resulting in a decrease in trophic state and reduced risk of CyanoHABs. On the other hand, increased temperature may prolong the duration of stratification in temperate lakes, resulting in greater potential for anoxia and sediment nutrient releases into stratified bottom waters, as well as favoring buoyant CyanoHABs with stronger and more prolonged water column stratification (Trolle et al. 2011).

Contrary to the northern regions of the northern hemisphere, in southern regions the effects of global warming are likely to cause water shortages and extreme weather events. This outcome is not dissimilar to those regions of the southern hemisphere experiencing a Mediterranean-like climate. In agriculture, effects will include a decrease in harvestable yields, higher yield variability and a reduction in areas suitable for traditional crops. The limited number of available studies (e.g., Stern 2006) predicts that water runoff in already-dry areas such as the Mediterranean basin and several areas in southern Africa and South America would decrease by 30 % for a 2 °C warming, and by 40–50 % for a 4 °C increase (Cline 2007). These projections are not dissimilar to what has already occurred in the south-west region of Western Australia where streamflows have decreased rapidly in the past 2–3 decades in response to regionally intense warming (Kingwell 2006). In general, decreased runoff, while potentially reducing transport of nutrients, will increase retention time of lentic systems. Under these conditions, the occurrence and proliferation of CyanoHABs will be a balance between the magnitude and timing of delivery of water and nutrients, the lake thermal regime, and internal recycling of nutrients.

Climate change effects on lakes and implications for proliferation of CyanoHABs

A climate-driven change in water temperature can modify phytoplankton communities by (1) favoring cyanobacteria, which have a competitive advantage by being able to sustain higher replication rates at elevated water temperatures, (2) increasing extremes (favoring fast-growing taxa generally but also some cyanobacterial bloom species), especially during heat waves and prolonged droughts (Havens and Paerl 2015; Paerl et al. 2016) and (3) increasing physical stability of the water column and the duration of thermal stratification, which may be particularly favorable for the massive development of gas-vacuolated colonial or filamentous cyanobacteria able to regulate their buoyancy and gain access to the nutrient pool in subsurface and hypolimnetic waters (O'Neil et al. 2012). Several studies have indicated that the recent global expansion in CyanoHABS may be linked to such effects induced by global warming (Paerl and Huisman 2008, 2009; Moss et al. 2011; Harke et al. 2016) and notably to physiological aspects of cyanobacteria that may be advantageous in the presence of warming (Paerl and Huisman 2009; Sukenik et al. 2012; O'Neil et al. 2012; Carey et al. 2012). One of these may be to directly increase rates of cyanotoxin production and produce shifts toward toxigenic strains of cyanobacteria (Dziallas and Grossart 2011; Wood et al. 2015). Links of CyanoHABs and cyanotoxin production to warming has found additional support from studies that have confirmed widespread increases in surface water temperatures in lakes across the globe, at rates comparable to, or higher than, increases in air temperature (e.g., Dokulil et al. 2006; Schneider and Hook 2010; O'Reilly et al. 2015).

Shallow, eutrophic polymictic lakes may be particularly vulnerable to climate change. Periods of stratification and deoxygenation will be extended, and increased water temperature will increase nutrient mineralization rates and releases from sediments to the overlying water column (Jensen and Andersen 1992). This means that for the many lakes and estuaries in agricultural watersheds, with legacy P and N in their catchment soils and bottom sediments, conditions could become much worse, increasing the urgency for remedial catchment actions as well as for in-lake actions such as geoengineering to bind excess and 'legacy' nutrients (Spears et al. 2014). A well-studied example is Lake Okeechobee, Florida, USA, where the catchment has been subject to decades of intensive agricultural activity and now has residual stores in its agricultural soils and wetlands that could maintain P loads to the lake of around 500 t yr^{-1} for the next 20–50 years (Reddy et al. 2011).

The adaptation strategies to reduce the impact of climate change and land use (e.g., agricultural practices) on freshwater ecosystems primarily include a further tightening in the control of P and N loads (Table 1). Nutrients can be trapped by the restoration and enhancement of riparian habitats along river corridors. Woody-vegetation riparian buffers and constructed wetlands have been shown to remove from 50 % to >65 % of TP and TN, respectively, from agricultural watersheds (Paerl et al. 2016). Increased wetland areas in river catchments may serve to preserve base flows and thus ecosystem functioning during the dry season (Jeppesen et al. 2010). A disadvantage of wetlands is that they are difficult to manage and control, especially under varying climatic conditions. Additionally, wetlands require considerable space, and conflicts could arise between the services provided and undesirable increases in mosquito production (Knight et al. 2003; Trájer et al. 2015), including those species, such as the Asian tiger mosquito (*Aedes albopictus*), which are able to transmit pathogens that cause chikungunya, dengue fever, yellow fever and various encephalitides (Proestos et al. 2015). The construction of higher storage capacity basins may counteract the effects of increased flooding and stormwaters, helping to preserve water resources, especially in warmer and drier regions. However, in turn, the flow-attenuation reservoirs might be susceptible to CyanoHABs (Paerl et al. 2016).

Climate change will strongly increase the difficulty to control CyanoHABs (Paerl and Otten 2016; Paerl et al. 2016). The longer the period of procrastination to take actions to control blooms, and the more time that climate change has to exert synergistic effects with nutrients (Moss et al. 2011), the less likely it becomes that an acceptable level of control can be attained. Furthermore, increasing frequencies, intensities and durations of storms and droughts may magnify the impacts of anthropogenic increases in nutrients on cyanobacterial blooms. Hence, climate change poses an additional challenge to formulating nutrient-based CyanoHAB thresholds as part of a strategy for controlling blooms. With warmer water, achieving a desired low level of occurrence of CyanoHABs in the future will require greater reductions in the inputs of N and P to lakes than is needed under the current climate conditions (Paerl and Huisman 2009). With odd exceptions based mostly on model output (e.g., Trolle et al. 2011), climate change has not been widely factored into mitigation strategies for CyanoHABs.

Conclusion

Great advances have been made in recognizing the importance of point sources of pollutants in eutrophication of surface waters, including loads contributed from P-based detergents. Many point sources have been dealt with through technological advances in wastewater treatment, but actions and policies have not necessarily been universally applied and implemented. For some lake catchments, especially those in developing countries, further efforts in dealing with point source discharges will be critical to combat future effects of climate change, land use intensification and invasive species. The direction of change in lakes in response to these pressures is mostly known and has been demonstrated through increased duration of stratification, greater anoxia of bottom waters, higher rates of primary production, simplified food webs and increased frequency of CyanoHABs. Our ability to more accurately predict and quantify these responses needs to build in nonlinear trajectories indicated by observations in lakes of ecological thresholds, tipping points, and abrupt and potentially irreversible change. Further work is also required to better understand how socioeconomic and political drivers change distributions of human populations and land use patterns and intensity, which in turn lead to changes in the delivery of water and nutrients to lakes, and will alter the extent of climate warming at longer (decadal) timescales. The convergence of adverse impacts from land use change ('cultural eutrophication') and climate change ('climatic eutrophication') represents a potentially dangerous situation because it is likely to reinforce current trends of increasing occurrence of CyanoHABs, including more toxin-producing species and strains, and severely compromise ecosystem services and direct economic benefits derived from lakes. Mitigation actions to avert this situation are essential, but in-lake actions are generally expensive, symptom-focused, and unlikely to be propagated more widely than a few key lakes. By contrast, management of point and diffuse sources of nutrients can be extended to landscape scale and provides a sustainable approach to avoid legacies (e.g., of sediments, nutrients) or ecological tipping points that severely compromise lake ecosystems. Addressing critical source areas of nutrient generation within the landscape can help to prioritize restoration actions and increase their efficiency. More work is required to understand how changes in the timing and magnitude of delivery of water and nutrients affect CyanoHABs, including the balance of toxic versus non-toxic species and diazotrophic versus non-diazotrophic species. This work needs to be linked with the balance of particulate and dissolved, as well as organic and inorganic nutrient loads, and how management actions (e.g., focused on erosion and sediment control) could potentially alter the balance of prokaryotic and eukaryotic phytoplankton, diazotrophic and non-diazotrophic and toxin-producing species and strains of cyanobacteria.

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