

Mitigating the global expansion of harmful cyanobacterial blooms: Moving targets in a human- and climatically-altered world

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ABSTRACT

Cyanobacterial harmful algal blooms (CyanoHABs) are a major threat to human and environmental health. As global proliferation of CyanoHABs continues to increase in prevalence, intensity, and toxicity, it is important to identify and integrate the underlying causes and controls of blooms in order to develop effective short- and long-term mitigation strategies. Clearly, nutrient input reductions should receive high priority. Legacy effects of multi-decadal anthropogenic eutrophication have altered limnetic systems such that there has been a shift from exclusive phosphorus (P) limitation to nitrogen (N) limitation and N and P co-limitation. Additionally, climate change is driving CyanoHAB proliferation through increasing global temperatures and altered precipitation patterns, including more extreme rainfall events and protracted droughts. These scenarios have led to the “perfect storm scenario”; increases in pulsed nutrient loading events, followed by persistent low-flow, long water residence times, favoring bloom formation and proliferation. To meet the CyanoHAB mitigation challenge, we must: (1) Formulate watershed and airshed-specific N and P input reductions on a sliding scale to meet anthropogenic and climatic forcings. (2) Develop CyanoHAB management strategies that incorporate current and anticipated climatic changes and extremes. (3) Make nutrient management strategies compatible with other physical-chemical-biological mitigation approaches, such as altering freshwater flow and flushing, dredging, chemical applications, introduction of selective grazers, etc. (4) Target CyanoHAB toxin production and developing management approaches to reduce toxin production. (5) Develop broadly applicable long-term strategies that incorporate the above recommendations.

1. Introduction

Global expansion of harmful cyanobacterial blooms (CyanoHABs), is a major threat to safety and sustainability of water supplies for human consumption, agriculture (irrigation), inland fisheries resources, as well as recreational and aesthetic values of impacted waters (Burford et al., 2020; Paerl et al., 2019a, b). Nutrient over-enrichment has been strongly linked to CyanoHAB expansion in aquatic ecosystems (Paerl, 1988). This link has a long history; going back at least to eutrophication that spawned massive blooms during the Roman Empire (Haas et al., 2019). Historically, P over-enrichment associated with agricultural, urban and industrial development has been identified as a key factor promoting this expansion (Elser and Bennett, 2011; Likens, 1972; Motew et al., 2017; Schindler, 2012; Smith, 2003). As such, reduction of P inputs to CyanoHAB-impacted waters has generally been prescribed as a key bloom mitigation step (Schindler, 2012). Because there are no gaseous forms of P that can potentially escape aquatic ecosystems, P accumulates in both the water column and

sediments, leading to a “P legacy”, supporting persistent internal loading which can sustain eutrophication and blooms (Lewis et al., 2011; Reddy et al., 2011). Lake and reservoir systems can have lengthy water residence (or water age) times, often on the order of months to multiple years. Therefore, even if P inputs are reduced, it will take appreciable time to naturally “wean” these systems of internal P supplies (Havens, 1997; Paerl et al., 2016a, b).

The other major nutrient element controlling eutrophication, nitrogen (N), while also undergoing excessive anthropogenic enrichment, has gaseous forms (e.g. N₂, N₂O, NO, NH₃), that can readily exchange with the atmosphere. Thus, even though anthropogenic N loading has increased at alarming rates (Erisman et al., 2013; Galloway et al., 2002) and has been shown to be directly implicated in both marine and freshwater eutrophication (Boesch et al., 2001; Conley et al., 2009; Elser et al., 2007; Lewis et al., 2011; Nixon, 1995; Ryther and Dunstan, 1971; Wurtsbaugh et al., 2019), there is an “escape route” via gaseous transformation processes. Furthermore, natural inputs of “new” N via N₂ fixation are generally exceeded by losses due to in-system

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denitrification, especially in bloom-prone eutrophic systems (Paerl et al., 2016b; Scott et al., 2019). As a result, chronic N limitation is perpetuated, and external N inputs play a key role in maintaining eutrophic, bloom-prone conditions (Paerl et al., 2016b). Furthermore, recent studies have stressed the need to reduce N inputs into CyanoHAB-plagued systems due to the ties between N inputs, CyanoHAB growth and toxicity (Gobler et al., 2016; Harke et al., 2016; Shatwell and Köhler, 2019). Clearly, there is good reason to constrain external loads of both N and P, and impose more nutrient-limited conditions in order to help mitigate the CyanoHAB problem (Chaffin and Bridgeman, 2014; Müller and Mitrovic, 2015; Zohary et al., 2005).

Therefore, while P input reductions should be part of any long-term eutrophication and CyanoHAB control strategy, in order to speed up the “de-eutrophication” or “oligotrophication” process, parallel N input reductions are urgently needed, especially in light of global agricultural, urban and industrial expansion (Paerl et al., 2019a).

2. Legacy effects of nutrients in freshwater ecosystems

The term legacy effect entered the scientific literature in the late 1980s and early 1990s (Corbet, 1985; Molina and Amaranthus, 1991). Legacy effects are defined as the impacts that one generation leaves on the environment for future generations to inherit (Button et al., 1999). In ecological terms, legacy effects can be considered to be ecological inheritance (Cuddington, 2011). In freshwater ecosystems, nutrient legacy effects add to the issues related to anthropogenic eutrophication (Duff et al., 2009). A large portion of the nutrient legacy is driven by land use and land cover changes, which have led to nutrient-enriched urban and agricultural runoff (Bain et al., 2012; Martin et al., 2011).

Since the rapid increases in chemical fertilizer use after WWII, nutrient loading has accelerated dramatically (Haygarth et al., 2014). As mentioned earlier, P can mainly leave aquatic systems by flushing or ending up in the sediments. Approximately 20–30% of P applied to agricultural land is exported directly out of the watershed as crop and animal production. The remaining 70–80% of the applied P ends up as stores in soils, river sediments, groundwater, wetlands, riparian floodplains, lakes, and estuaries (Jarvie et al., 2013; Sharpley et al., 2013). Even though N can leave the aquatic systems as gases, some N also end up leaving a legacy on water bodies. Anthropogenic loading of N into agricultural soils can leach into groundwater, leading to an N legacy in aquifers (Puckett et al., 2011). A substantial fraction of accumulated CyanoHAB biomass is decomposed in the water column and surface sediments, fueling hypoxia ($< 2.0 \text{ mg O}_2 \text{ L}^{-1}$) and anoxia ($< 0.5 \text{ mg O}_2 \text{ L}^{-1}$) (Buzzelli et al., 2002; Paerl, 2014). The biomass fraction that is not immediately decomposed ends up in the sediments as legacy organic carbon, organic N, and organic P. Legacy nutrients provide for a positive feedback loop supporting CyanoHAB growth (Fig. 1), and it is a key reason why reversing the harmful effects of eutrophication can take a substantial amount of time, especially in large, long water residence time aquatic ecosystems (Paerl et al., 2019b).

3. Climate change effects on nutrient loading in freshwater ecosystems

While nutrient input reductions represent the “bottom line” in mitigating eutrophication and CyanoHAB expansion, there are additional, interacting drivers modulating this process, the most prominent and challenging being climate change (Paerl and Paul, 2012). Global warming, changes in precipitation patterns and amounts and altered wind speeds are strong modulators of eutrophication and CyanoHAB expansion (Deng et al., 2018; Paerl et al., 2016a; Paerl and Huisman, 2009, 2008; Weber et al., 2020). Both of these symptoms of climate change are increasing in frequency and geographic distribution (Burford et al., 2020; Sinha et al., 2017; Trenberth, 2008;

Wuebbles et al., 2013). Increasing temperatures, stronger vertical stratification, and salinization are also associated with climate change and linked to CyanoHAB magnitudes, frequency, distribution and duration (Chapra et al., 2017; Moore et al., 2008; Paerl, 2017; Paerl et al., 2011; Paerl and Huisman, 2009, 2008). As pointed out in Paerl et al. (2016a), the “perfect storm” scenario for CyanoHAB development and proliferation is excessive episodic rainfall events, followed by droughts, which can promote large nutrient input pulses followed by lengthy residence times, enabling blooms to develop and proliferate. Increased temperatures and nutrient loading can also enhance CyanoHAB toxicity (Botana, 2016; Gehringer and Wannicke, 2014; Lehman et al., 2013; Moe et al., 2013). Furthermore, it is likely that these nutrient reduction thresholds will change with changing climatic conditions, human watershed and airshed activities, as populations continue to expand (Erisman et al., 2013; Galloway et al., 2002; Moss et al., 2008; Peierls et al., 1991). Wildfires brought on by climate change can also lead to nutrient loading due to increased mobility of sediments (Emelko et al., 2016), especially when followed by extensive rainfall and flooding as has been the case in California and most recently in Eastern and Southern Australia (Malsheimer et al., 2008; Sharples et al., 2016). In addition to enhancing P inputs associated with sediment mobilization, deforestation also leads to N loading, as seen in N cycle shifts the Laurentian Great Lakes (Guiry et al., 2020). Therefore, changes in these climatic drivers will need to be incorporated into the development of nutrient input reductions that will effectively maintain bloom potentials below specific nutrient loading thresholds for individual water bodies. Warming, nutrient loading and temperature synergistically increase the intensity and recurrence of CyanoHABs, which amplify the feedback loop promoting CyanoHAB growth (Fig. 1).

Anthropogenic influences on the atmosphere are also modulating CyanoHABs. Increasing atmospheric pCO_2 can enhance phytoplankton blooms, including CyanoHABs (Verspagen et al., 2014). The augmented pCO_2 will also favor CyanoHAB growth due to rapid adaptation to higher pCO_2 environments as seen in microcosm and chemostat experiments (Sandrini et al., 2016; Shi et al., 2017; Ji et al., 2020). While the effects of increased pCO_2 appear to promote CyanoHABs, much less is known about the *in situ* mechanisms compared to the effects of temperature (Verspagen et al., 2014; Ji et al., 2020). In addition to atmospheric carbon emissions, N and P emissions also impact CyanoHAB proliferation. Atmospheric deposition has been shown to be significant source of both N and P into aquatic systems. For example, Paerl et al. (2002) estimated that from 20 to $>35\%$ of N inputs to N-limited US Atlantic estuarine and coastal waters was attributed to atmospheric N deposition, while 63% of total N and 42% of total P loading in Cultus Lake near Vancouver, BC, Canada, come from atmospheric deposition (Putt et al., 2019). Atmospheric deposition also indirectly impacts coastal systems, as an average of 64% of riverine N export to coastal ocean systems is derived from NO_x and NH_x deposition (Church and Sickle, 1999; Jaworski et al., 1997). Groundwater inputs of N and P, much of it due to human pollution, provide an additional source of nutrients promoting eutrophication along the freshwater to marine continuum (Paerl, 1997). The combined effect of increased anthropogenic surface, subsurface and atmospheric nutrient loading, in addition to promoting eutrophication, has driven receiving waters into N and P co-limitation and N-limitation (Chaffin et al., 2014; Dodds and Smith, 2016; Elser et al., 2007).

4. Management recommendations

When reducing external N&P loading, both point-source and non-point-source nutrient inputs need to be addressed. Point source pollution is the easiest target for N and P reduction, as this source can be reduced by targeting readily identified and well-defined origins, such as effluents from wastewater treatment plants and industrial discharge points (Hamilton et al., 2016; Wu et al., 2006). Reduction in point

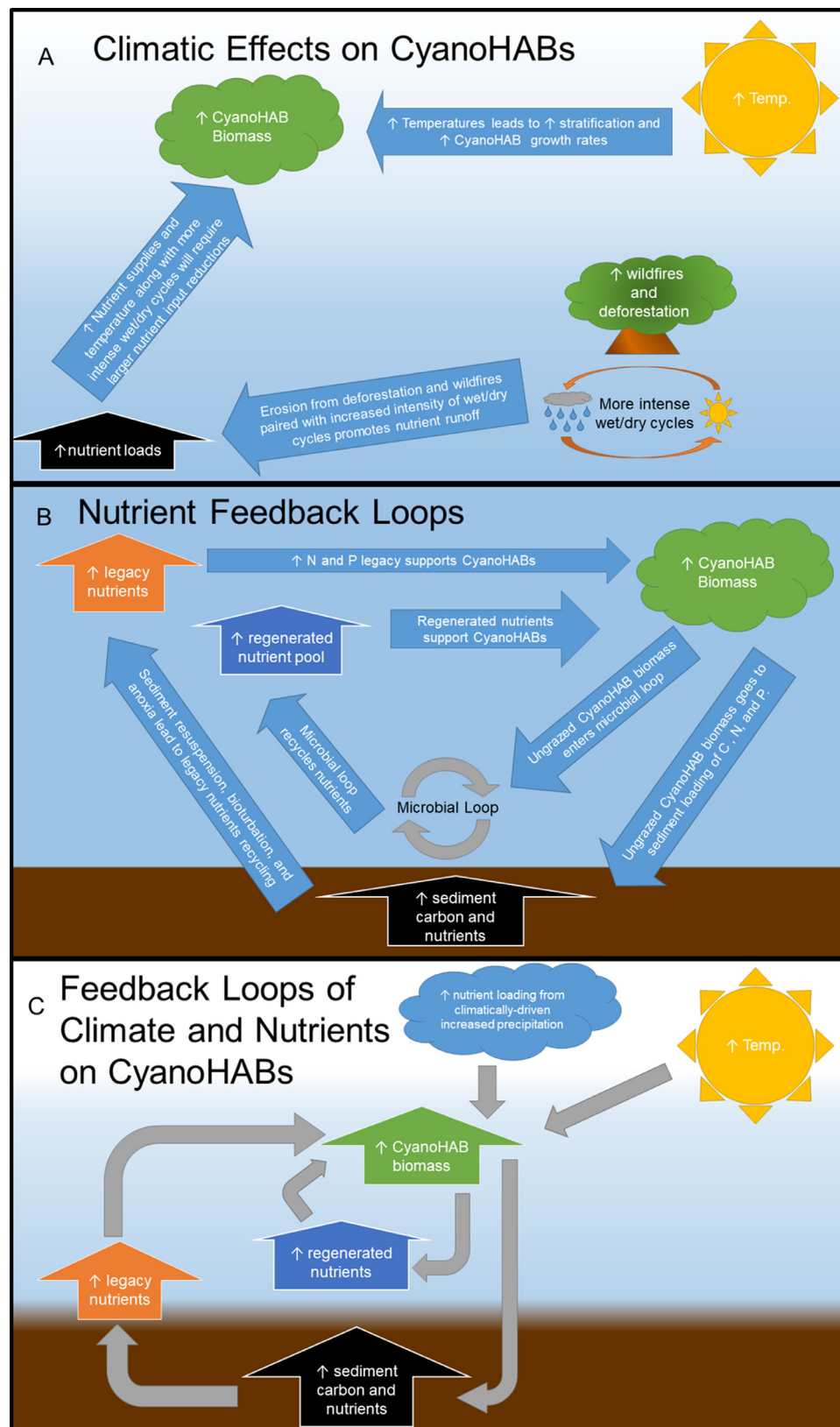


Fig. 1. Conceptual diagram, showing the feedback loops of climatic effects and nutrients on CyanoHAB biomass. (a) Climate change is causing more intense wet/dry cycles, widespread wildfires, and warming, leading to an increase in CyanoHAB biomass. (b) Increased CyanoHAB biomass is involved in a positive feedback loop with legacy nutrients and regenerated nutrients derived from the microbial loop. (c) These feedback loops combined with climatic effects constitute a key challenge to mitigating CyanoHABs.

source pollution generally involves diversion of sewage from waterbodies and reduction in P and N concentrations in the wastewater discharge (Sedlak, 1991). N removal from wastewater generally makes use of coupled nitrification–denitrification (US EPA, 2013). P removal occurs either through burial or flushing of P bound in biomass out of the system (Downing, 1997). Buried P can be removed by dredging (Reddy et al., 2007), although a short term P spike often results from dredging (Smith et al., 2006). While P-based detergent bans have been successful at reducing blooms (Dolan and McGunagle, 2005), there are cases where P from detergents continues to be an important component of P in surface waters while also imposing a major burden on wastewater treatment processes (Hamilton et al., 2016; Van Drecht et al., 2009). Greater attention needs to be focused on nonpoint sources of nutrients, which in many watersheds is the largest source of nutrient loading and is often dominated by agriculture (Hamilton et al., 2016). Furthermore, nonpoint-source pollution continues to increase as a relative proportion of total loading as more advanced treatment of point source pollution is implemented (Hamilton et al., 2016). Removing N and P from stormwater runoff can be achieved by using combined wetlands and infiltration ponds to naturally filter N and P (Marsalek and Schreier, 2009; Zheng et al., 2006). Retaining fertilizer-based N and P in agricultural soils should receive high priority (Hamilton et al., 2016). Maintaining N and P in soils at levels close to or below agronomic optima is critical and represents one of the simplest and most cost-effective methods to reduce eutrophication in receiving waters (Drewry et al., 2006; Rasouli et al., 2014). Where feasible, fertilizer should be directly injected into the soil to minimize nutrient-rich surface runoff (Seo et al., 2005).

Another method of removing nutrients from non-point sources is through *in situ* biological filtration, using non-harmful algal “scrubber” and “raceway” devices (Adey et al., 2013; Barnard et al., 2017; Mulbry et al., 2010, 2008). Adding denitrifying bacteria can greatly speed up N removal (Chen et al., 2017). Vegetated buffers are also a useful tool for remediating nonpoint source pollution; trees, shrubs and grasses in the vegetated buffer have been shown to remove more than 85% of pollutants (Zhang et al., 2010), including 85% of N and 84% of P (Polyakov et al., 2005). However, the biomass from buffers needs to be periodically harvested and exported in order to have net nutrient removal effect, unless processes such as denitrification are additionally enhanced by this approach (Hoffmann et al., 2009). Additionally, natural and constructed wetlands are very effective, low cost solutions for removal of nonpoint source nutrients from aquatic systems (O’Geen et al., 2010; Ribaud et al., 2001), with removal of over 80% of N loading and over 50% of P loading (Braskerud, 2002a, 2002b; Kao and Wu, 2001).

There is a significant association between cyanobacterial blooms and land use types (i.e., industrial, commercial, and transport areas) (Arthington, 1996; Soranno et al., 1996). These results are relevant to landscape planning for mitigating future impacts of climate change on the drainage network, surface runoff, nutrient loads and, ultimately, on the development of toxigenic cyanobacteria (Hamilton et al., 2016). 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 (Jimenez Cisneros et al., 2014).

Higher amounts of freshwater runoff can enhance vertical density stratification (reduced vertical mixing) in waters having appreciable salinity, including estuarine and coastal waters as well as saline lakes and rivers; by allowing relatively light freshwater lenses to establish themselves on top of heavier (denser) saltwater. The resultant enhanced vertical stratification will favor CyanoHABs capable of rapid vertical migration to position themselves at physically-chemically favorable depths in both freshwater and marine systems (Paerl, 2014; Paerl and Huisman, 2009) by rapidly altering their buoyancy in response to varying light, temperature and nutrient regimes (Walsby et al., 1997).

The large biomass and long survival time of CyanoHABs in

sediments can help explain the delayed recovery of affected lakes after reduction of external nutrient loads (Brunberg and Boström, 1992; Paerl et al., 2016a). 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 (~1 km², 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). Lake Trummen's rapid CyanoHAB eradication is attributed to its small size and the ability to simultaneously reduce external nutrient loads effectively from its small watershed (13 km²) (Cronberg, 1982; Peterson, 1982). Dredging is not a feasible solution for reducing internal P loading in large lakes, where P-rich sediments are distributed over hundreds or thousands of square kilometers and are highly mobile (James and Pollman, 2011).

CyanoHABs can be treated with chemical and/or biological agents to limnetic systems. Chemical treatments, including precipitation and immobilization of phosphorus in bottom sediments (Phoslock, alum, etc.), application of algacides (Cu compounds, hydrogen peroxide, permanganate, etc.), as well as biological controls, such as the introduction of invertebrate and fish grazers, lytic bacteria, and viruses, may temporarily halt the advance of CyanoHABs (Matthijs et al., 2012; Paerl et al., 2015; Pan et al., 2006; Robb et al., 2003). However, there are unintended negative impacts on flora and fauna of the limnetic systems that make these chemical treatments potentially detrimental to these systems (Bishop et al., 2018; Escobar-Lux et al., 2019; Paerl et al., 2015). Addition of selective grazers is another option, but successful control of CyanoHABs by grazers is unlikely except in specific cases (Paerl et al., 2001). This is due to cyanobacteria being generally considered to be relatively low preference foods for marine and freshwater herbivores because of chemical and structural defenses and poor nutritional quality (Cruz-Rivera and Villareal, 2006; DeMott and Moxter, 1991; Paerl et al., 2001; Paerl and Paul, 2012). The addition of the grazers can also have negative effects on the food webs through trophic cascades (Jeppesen et al., 2007; Wright and Shapiro, 1984). Given the lack of feasibility, unpredictable and unintended effects of chemical and biological additions, the most prudent and defensible approach is to prioritize nutrient input reductions; however, if nutrient reduction is not enough to reduce the impacts of the blooms, then re-assessment of nutrient reduction thresholds as well as the use of any of the above mitigation methods should be considered to manage the CyanoHABs.

Remote sensing technology can be useful for tracking and evaluating management of blooms as a means of linking nutrient sources to bloom dynamics over varying temporal and spatial scales (Dorigo et al., 2007; Field et al., 1995; Mishra et al., 2019). Using remote sensor networks, satellite imagery, and machine learning, the extent and drivers of CyanoHABs can be remotely sensed and analyzed (Davis et al., 2019; Mishra et al., 2018, 2019; Zhang et al., 2016). Satellite-based imagery paired with Raspberry-Pi-based remote sensors (CyanoSense), cellular-phone-based application CyanoTracker, and social networking services such as Twitter can document the progression and proliferation of blooms (Boddula et al., 2017; Mishra et al., 2018, 2019, 2020; Page et al., 2018; Scott et al., 2016; Stumpf et al., 2016). While satellite imagery can measure biomass in CyanoHABs using the different spectral properties of chlorophyll and phycocyanin (Binding et al., 2019), it cannot accurately measure cyanotoxin production as CyanoHAB cellular toxin content can vary even on short time scales and can persist extracellularly after bloom biomass is dissipated (Davis et al., 2019). Therefore, remote sensing should be paired with long-term monitoring. On-lake long-term monitoring of water quality parameters is also critical for protecting human exposure to cyanotoxins during blooms

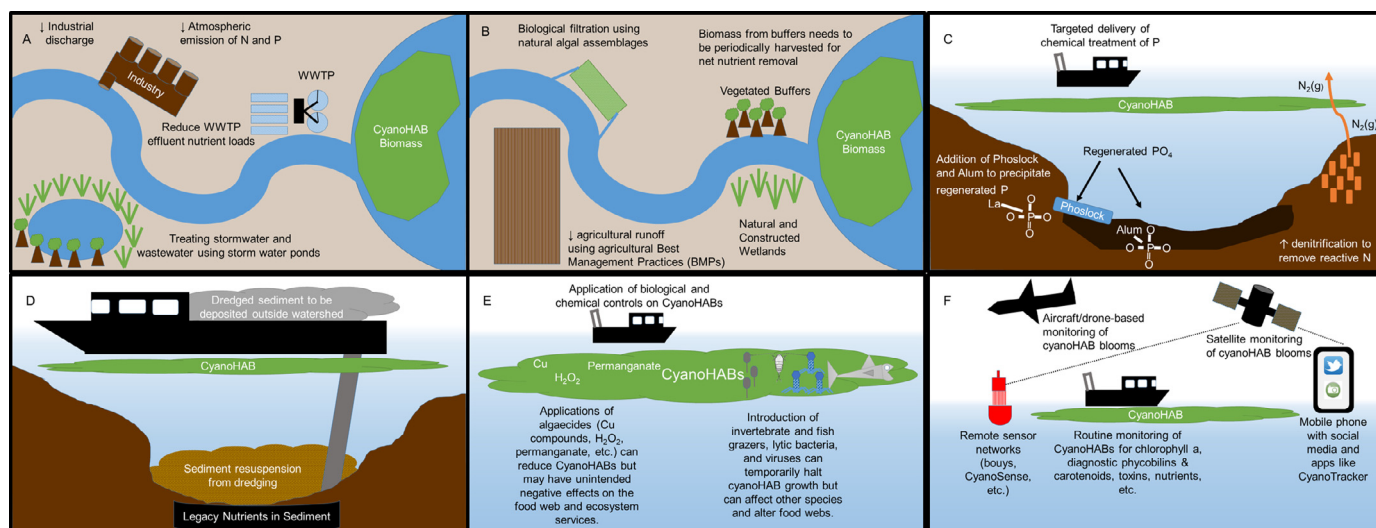


Fig. 2. Conceptual diagram, illustrating multiple, interacting controls in CyanoHAB management. Climatic influences have led to the need to reduce nutrient loading below previous reduction standards, putting additional pressure on reducing nutrient inputs from (a) point source pollution and (b) non-point source pollution, (c) regenerated nutrients, and (d) legacy nutrients through various mechanical, chemical, and biological means. (e) Short-term (several months) treatment, chemical and biological approaches used. (f) Appropriate monitoring is essential for assessing the CyanoHAB scales and the efficacy of management approaches.

(Davis et al., 2019). Management recommendations are outlined in Fig. 2.

Anthropogenic forcing continues to alter natural systems and the climate, with major ramifications for nutrient loading, hydrologic changes (e.g., more intense and larger rainfall and flooding events), warming and changes in wind speed - all of which will alter the rates of eutrophication and nutrient-bloom threshold relationships. This calls for the formulation of adaptive nutrient management strategies aimed at maintaining bloom potentials and proliferation below critical nutrient-bloom thresholds. Given the current trajectory of climate change (warming, more extreme wet/dry cycles, reduced wind speed in many locations), it is likely that nutrient loading threshold levels above which blooms will occur, will be lowered, because CyanoHABs will grow more efficiently at elevated temperatures and persist longer under extreme wet/dry cycles (Paerl et al., 2016a). Furthermore, with more extensive wet/dry cycles, both external and internal nutrient cycling will be altered, and this will likely benefit CyanoHABs, which can affect internal cycling by lasting longer during the growth season and can promote positive feedbacks on sediment-water column nutrient cycling to maintain blooms (Fig. 1). This is especially true if CyanoHABs are not effectively consumed by grazers and ultimately finfish or shellfish, which can be exported from the system. More likely, CyanoHAB biomass will enter the detrital-microbial loop component of nutrient cycling, enhancing microbial decomposition and recycling of nutrients more effectively during a single growth season. Overall, this means that current nutrient loading targets aimed at controlling CyanoHABs will need to be set at lower levels than currently prescribed for many regions. With legacy nutrients and climate change leading to positive feedback loops of CyanoHAB proliferation, we need to focus on watershed and airshed nutrient reductions that can help reduce and ultimately break the loops. Lastly, we can complement these efforts with (where feasible and effective) biological and chemical treatments, remote sensing technology, and routine monitoring to help manage CyanoHABs into the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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