

Mitigating a global expansion of toxic cyanobacterial blooms: confounding effects and challenges posed by climate change

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Abstract. Managing and mitigating the global expansion of toxic cyanobacterial harmful algal blooms (CyanoHABs) is a major challenge facing researchers and water resource managers. Various approaches, including nutrient load reduction, artificial mixing and flushing, omnivorous fish removal, algaecide applications and sediment dredging, have been used to reduce bloom occurrences. However, managers now face the additional challenge of having to address the effects of climate change on watershed hydrological and nutrient load dynamics, water temperature, mixing regime and internal nutrient cycling. Rising temperatures and increasing frequencies and magnitudes of extreme weather events, including tropical cyclones, extratropical storms, floods and droughts, all promote CyanoHABs and affect the efficacy of ecosystem remediation measures. These climatic changes will likely require setting stricter nutrient (including both nitrogen and phosphorus) reduction targets for bloom control in affected waters. In addition, the efficacy of currently used methods to reduce CyanoHABs will need to be re-evaluated in light of the synergistic effects of climate change with nutrient enrichment.

Additional keywords: cyanobacterial harmful algal bloom dynamics, CyanoHAB dynamics, mitigation and management strategies, nutrients.

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Introduction

The proliferation of toxic, food-web altering and hypoxia-generating cyanobacterial harmful algal blooms (CyanoHABs) is a global problem in lakes, rivers and estuaries (Chorus and Bartram 1999; Huisman *et al.* 2005). The proliferation of CyanoHABs is largely driven by overenrichment of those waters by nutrients from agriculture, septic systems, residential fertilisers and other human changes to the surrounding landscape (Fig. 1). CyanoHABs are expanding geographically and now threaten the ecological integrity and sustainability of some of the world's largest and most resourceful lakes (Huisman *et al.* 2018), with prominent examples including Lake Victoria in Africa (Ochumba and Kibaara 1989), Lake Erie (Bullerjahn *et al.* 2016) in the US and Canada, Lake Okeechobee in Florida (Havens *et al.* 2001; National Academy of Sciences, Engineering and Medicine 2016), Lake Taihu in China (Qin *et al.* 2010), Lake Kasimagaura in

Japan (Havens *et al.* 2001), the Baltic Sea in northern Europe (Conley *et al.* 2009a) and the Caspian Sea in West Asia (Paerl and Huisman 2008). Human and animal poisoning events from cyanotoxin exposures have been documented in the US (Backer *et al.* 2015) and elsewhere (Huisman *et al.* 2018), with those confirmed cases likely underrepresenting the true number due to gaps in surveillance and reporting systems. In addition to their negative ecological, biogeochemical and health effects, CyanoHABs have been implicated in serious economic losses to affected waters. In the US alone, losses to recreational (including residential areas) waters, drinking and agricultural water supplies amount to more than US\$2 billion annually (Dodds *et al.* 2009), and these losses continue to rise. The aesthetics of surface blooms and their associated odours may also have effects on the value of waterfront properties, although this has not been well studied. An economic analysis by the Florida Association of Realtors

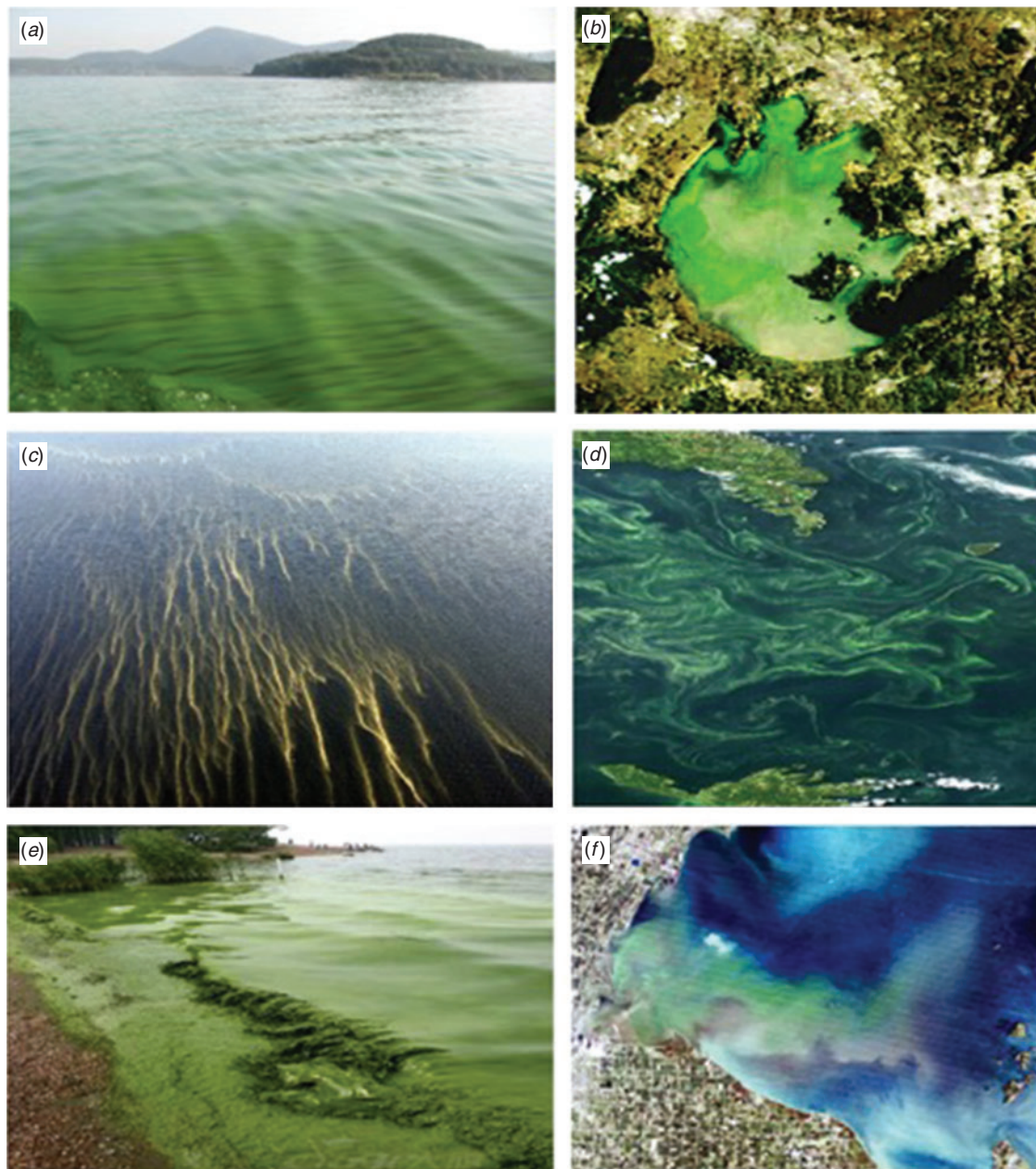


Fig. 1. Examples of large waterbodies that have experienced increases in frequency, magnitude and duration of cyanobacterial harmful algal blooms. (a, c, e) Photographs of the blooms and (b, d, f) remote sensing images of each system. (a) Lake Taihu, China (photograph by H. Paerl) and (b) moderate-resolution imaging spectroradiometer (MODIS) remote sensing image of the lake and nearby cities (Image courtesy of NASA). (c) Baltic Sea–Gulf of Finland (image courtesy of the Finnish Border Guard and Institute of Marine Research, Helsinki, Finland) and (d) Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) image of the same region in June 2005 (image courtesy of NASA). (e) Lake Erie, southern shore (photograph courtesy of the National Oceanic and Atmospheric Administration (NOAA)) and (f) Land Satellite (LANDSAT) image of a bloom in the western region of the lake, near Maumee Bay during summer 2003 (image courtesy of NASA).

(O’Conner *et al.* 2015) documented that a 35-cm reduction in Secchi disc transparency, caused primarily by *Microcystis* blooms that occurred in the 2010–16 time period, was associated with US\$428 million and US\$488 million declines in aggregate property values in just the two coastal counties adjacent to Florida estuaries. Identifying the suite of environmental factors driving

the rapid rise in CyanoHABs is paramount to developing management strategies for protecting a large fraction of the world’s fresh and brackish water resources.

With regard to devising CyanoHAB control and long-term management strategies, reducing nutrient inputs from human-dominated watersheds is a prime target (Schindler and

Vallentine 2008; Dodds and Smith 2016). However, there also is a strong synergy between human nutrient overenrichment with other modulating factors, including a warming climate and extreme weather, particularly a rise in the frequency and intensity of tropical cyclones, extratropical storms, record-breaking precipitation events, protracted droughts and hydrological manipulation (e.g. dams and weirs) of waterbodies. Understanding the interactive effects of anthropogenic and climatic drivers of CyanoHABs is a major challenge to predicting and managing proliferation dynamics, thus ensuring protection and sustainability of affected waters.

Here, we synthesise established and emerging information on environmental factors affecting CyanoHAB bloom potential using geographically diverse examples. The aim is to stimulate more integrative research, long-term assessment, modelling and management approaches instrumental to developing science-based, ecologically sound, long-term strategies needed for stemming CyanoHAB proliferation and increasing the efficacy of long-term control strategies in a world experiencing contemporaneous anthropogenic and climatically induced environmental change.

The 'players'

As a functional 'microalgal' group, cyanobacteria have benefited from over 2.5 billion years of evolutionary history that has served them well with numerous ecophysiological adaptations and mechanisms (Schopf 2000), allowing them to take advantage of environmental changes and extremes. Cyanobacteria possess high-affinity uptake and intracellular storage capabilities for nitrogen (N) and phosphorus (P) (Padisák 1997; Flores and Herrero 2005). This is ideal for exploiting periodic enrichment of these potentially limiting nutrients. Many genera are capable of rapid vertical migration by way of buoyancy regulation, enabling them to exploit radiant-rich surface waters and nutrient-rich bottom waters on diel and shorter time scales (Huisman *et al.* 2005, 2018). Some genera can convert atmospheric nitrogen (N_2) into ammonia, by N_2 fixation (Fogg 1969), ensuring access to biologically available N.

In addition, CyanoHABs produce secondary metabolites, some of which may promote mutually beneficial consortial interactions with other microbes (Paerl 1984; Paerl and Millie 1996), whereas others may be toxic to a range of organisms, including algae, zooplankton, fish and mammals (including humans) that use affected waters as habitat and for drinking and recreational purposes (Chorus and Bartram 1999; Carmichael 2001; Huisman *et al.* 2018; Fig. 2). Cyanotoxins are produced by large, modular enzyme complexes (non-ribosomal peptide synthetases (NRPS) and polyketide synthases (PKS)) at considerable metabolic expense to the cell (Briand *et al.* 2012). However, the physiological reason for cyanotoxin production remains unresolved, although there have been diverse studies investigating the role of cyanotoxins in nutrient acquisition, allelopathy, grazer defence, colony formation, redox balance etc. (Paerl and Otten 2013; Huisman *et al.* 2018). Furthermore, there have been numerous studies aimed at specifically elucidating which environmental factors promote the upregulation of toxin genes and select for toxigenic cyanobacterial strains over non-toxic ones (Neilan *et al.* 2013); however, these studies have

resulted in few concrete takeaways that apply to all genera able to produce a given toxin class. For example, non-diazotrophic cyanobacteria such as *Microcystis* and *Planktothrix* tend to produce more microcystin under N-replete conditions, whereas diazotrophs such as *Anabaena*, *Aphanizomenon* and *Nodularia* produce more toxin under N-depleted conditions (Kaebernick and Neilan 2001). A review of the literature suggests that toxin production, and the factors that stimulate toxin biosynthesis, may ultimately be group or strain specific (Paerl *et al.* 2016a). However, one important takeaway from many of these studies is that toxin concentrations tend to be most closely correlated with growth rate as well as abundance (Orr and Jones 1998; Oh *et al.* 2000; Wood *et al.* 2012), except when blooms are primarily composed of non-toxic genotypes (Bozarth *et al.* 2010). Because cyanotoxins are primarily stored intracellularly, and because cells tend to aggregate as dense scums near the surface (or as mats attached to the benthos), probably the most direct way to minimise cyanobacteria-related public health risks is to limit the ability for cyanobacteria to reach bloom magnitudes.

Nutrient controls: both N and P are important

It is well established that CyanoHABs are stimulated by excessive anthropogenic nutrient loading (Fogg 1969; Reynolds 1987; Paerl 1988; Fig. 3). In freshwater ecosystems, P availability has traditionally been viewed as a key factor limiting CyanoHAB proliferation (Schindler *et al.* 2008). Accordingly, controlling P inputs has been the primary mitigation target for resource managers. The emphasis on P reductions for CyanoHAB control is based on the knowledge that some CyanoHAB and eubacterial genera conduct N_2 fixation, helping satisfy cellular N requirements under N-limited ambient conditions (Fogg 1969). However, at the ecosystem level, usually far less than 50% of primary production demands are met by N_2 fixation, even when P supplies are sufficient (Howarth *et al.* 1988; Lewis and Wurtsbaugh 2008; Scott and McCarthy 2010; Paerl *et al.* 2016b). This indicates that N_2 fixation is controlled by factors in addition to P availability, including water column stability (turbulence), availability of micronutrients (especially iron), ambient dissolved oxygen concentrations, light intensity and organic matter availability (as an energy source) and selective grazing (Paerl 1990).

Nutrient loading dynamics have changed significantly over the past several decades. Although P reductions have been actively pursued, success has largely been with point sources, and waterbodies continue to be heavily affected by non-point source P pollution (Smith *et al.* 2014). Human population growth in watersheds has been paralleled by increased N loading (Peierls *et al.* 1991; Galloway *et al.* 2002), often at rates much higher than P (Rabalais 2002). Excessive N loads are now as large of a concern as P loads in mediating fresh water, estuarine and marine eutrophication and harmful algal blooms (including CyanoHABs; Havens *et al.* 2001; Conley *et al.* 2009b; Paerl *et al.* 2016b, 2016c).

In the Baltic Sea region, effective control of eutrophication and CyanoHAB outbreaks required reducing total amounts and ratios of N and P discharged to a nutrient-sensitive river–fjord–sea continuum (Elmgren and Larsson 2001). Similarly, single nutrient input reductions, including a P-detergent ban and

	
Unicellular (some N₂ fixing) Filamentous, non-heterocystous (some N₂ fixing) Filamentous heterocystous (N₂ fixing)	
Toxin	Produced by
Neurotoxins	
Anatoxin-a, (homo)anatoxin-a	<i>Anabaena</i> , <i>Aphanizomenon</i> , <i>Oscillatoria</i> (<i>Planktothrix</i>), <i>Phormidium</i>
Anatoxin-a(s)	<i>Anabaena</i> , <i>Oscillatoria</i> (<i>Planktothrix</i>)
Paralytic shellfish poisons (saxitoxins)	<i>Anabaena</i> , <i>Aphanizomenon</i> , <i>Cylindrospermopsis</i> , <i>Lyngbya</i>
Liver toxins	
Cylindrospermopsin	<i>Aphanizomenon</i> , <i>Cylindrospermopsis</i> , <i>Umezakia</i>
Microcystins	<i>Anabaena</i> , <i>Aphanocapsa</i> , <i>Hapalosiphon</i> , <i>Microcystis</i> , <i>Nostoc</i> , <i>Oscillatoria</i> (<i>Planktothrix</i>)
Nodularins	<i>Nodularia</i> (brackish to saline waters)
Contact irritant–dermal toxins	
Debromoaplysiatoxin	
Lyngbyatoxin	<i>Lyngbya</i> (marine)
Aplysiatoxin	<i>Schizothrix</i> (marine)

Fig. 2. Photomicrographs illustrating the diverse morphologies of cyanobacterial harmful algal bloom (CyanoHAB)-forming species (top) and a list of the major cyanotoxin classes produced by common CyanoHABs (bottom). Bold–italic, underlined–italic and italic-only species names in the list correspond to unicellular, filamentous non-heterocystous and filamentous heterocystous cyanobacteria respectively. Note that *Anabaena* has recently been changed to *Dolichospermum*.

improved wastewater treatment for P during the 1980s in North Carolina's (USA) Neuse River system helped solve one problem (arrest freshwater blooms), but exacerbated blooms in downstream N-sensitive estuarine waters (Paerl 2009). In both cases, parallel N and P input reductions were required to stem eutrophication along the fresh water–marine continuum (Paerl *et al.* 2016b, 2016c). In Florida freshwater lakes, which supply much of the state's irrigation water, excessive N loading in wastewater and agricultural discharges was identified (in addition to P) as a key driver of eutrophication and CyanoHAB expansion (Kratzer and Brezonik 1981; Havens *et al.* 2001). In some cases (e.g. Lake Okeechobee, FL, USA), dominance by N₂-fixing CyanoHABs (which were largely controlled by P input reductions) is now shared with non-N₂-fixing genera (e.g. *Microcystis*), as well as metabolically flexible CyanoHAB genera (e.g. *Cylindrospermopsis*) that effectively compete for reactive N when it is available but can also fix N₂ when N is depleted (Moisander *et al.* 2012). In these cases, both N and P reductions are needed to control CyanoHABs (Havens *et al.* 2001; Paerl

et al. 2016b). Similarly, in Erie, a lake thought to be 'recovered' from eutrophication in the 1970s–80s due to well-managed P (but not N) abatement programs, the current CyanoHAB problem is a resurgence of non-N₂-fixing *Microcystis*, *Lyngbya* and *Planktothrix* populations (Bullerjahn *et al.* 2016; Harke *et al.* 2016). Recent Lake Erie nutrient limitation studies indicate N and P colimitation commonly occurs (Davis *et al.* 2010, 2015; Chaffin *et al.* 2013), emphasising the need to consider dual nutrient input reductions to mitigate CyanoHABs.

By what means and mechanisms have CyanoHABs re-emerged, despite a focus on efforts to control P inputs? One reason is that in some cases, despite successful control of P sources, including agriculture, there remain large quantities of legacy P in wetlands, soils and bottoms of creeks, so that loads into lakes remain high. That is the case, for example, in Lake Okeechobee (FL, USA; National Academy of Sciences, Engineering and Medicine 2016). Large, shallow, eutrophic lakes like Okeechobee, Taihu (China) and Kasumigaura (Japan), and deeper systems like Lake Erie (USA), also tend to be colimited

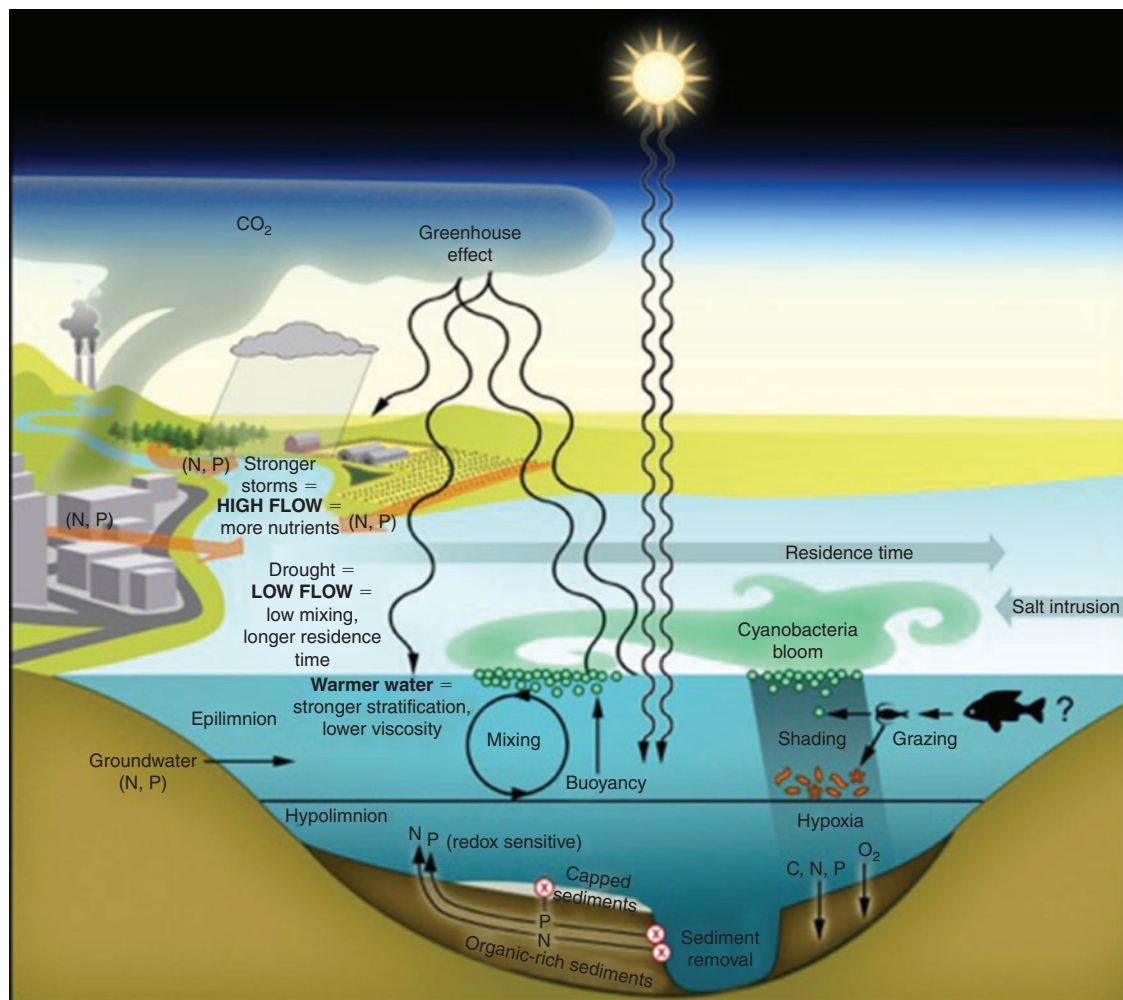


Fig. 3. Conceptual figure illustrating the environmental processes that control cyanobacterial blooms, including effects of climate change. Adapted from Paerl and Huisman (2009).

by N and P or mostly N limited (Havens *et al.* 2001; North *et al.* 2007; Davis *et al.* 2010, 2015; Xu *et al.* 2010; Chaffin *et al.* 2013; Steffen *et al.* 2014), largely because previously loaded 'legacy' P is effectively retained and recycled. Although some N can be removed by denitrification, this process does not appear to keep up with new N inputs, especially in systems heavily affected by N overenrichment (Seitzinger 1988; McCarthy *et al.* 2007). Overall, N and P colimitation, or limitation by only N, is common in eutrophic systems (Elser *et al.* 2007; Paerl *et al.* 2016b), which are also highly susceptible to CyanoHAB outbreaks (Huisman *et al.* 2005, 2018).

Hydrological manipulations

In addition to parallel reductions in N and P inputs, hydrological changes can suppress cyanobacterial blooms. Artificial mixing of lakes and ponds, by air bubbling or other mixing devices, is used to decrease water column stratification and enhance vertical mixing of the phytoplankton, thereby preventing the formation of surface blooms of buoyant cyanobacteria (Visser *et al.* 1996). Horizontal flushing, by increasing the water flow through

lakes or estuaries, reduces water residence time, thus providing less time for the development of cyanobacterial blooms (Mitrovic *et al.* 2003, 2011; Maier *et al.* 2004; Havens *et al.* 2016; Fig. 3). Although these tactics can yield positive results (i.e. decreased CyanoHAB intensity), in some systems they may actually exacerbate the problem by mixing nutrient-rich water from the hypolimnion into the photic zone of the epilimnion. In addition, hydrological modifications can be quite expensive, and as such, are generally restricted to small waterbodies. Therefore, for many medium-to-large lake systems, nutrient input restrictions are the only effective and economically feasible approach for dealing with CyanoHABs. Nevertheless, it is important to recognise that factors including depth and flushing can have major effects on the intensity of cyanobacterial blooms in certain shallow lakes, and that if the future has prolonged droughts and short intense rain events, those factors could lead to much more pronounced blooms (Havens *et al.* 2016; Paerl *et al.* 2016c; Havens and Ji 2018). This reinforces the need to control nutrient concentrations, the prime factor controlling bloom magnitude, before we enter a future where a combination

of warming, long droughts and continued high nutrient concentrations make it nearly impossible to attain that goal (Moss *et al.* 2011).

Altering sediment dynamics

Even when external nutrient inputs are reduced, the legacy of eutrophication in the form of P-enriched sediments can perpetuate high internal nutrient loads and reinitiate growth of vegetative cyanobacterial cells that fuel subsequent CyanoHAB events. Therefore, either removing sediments or capping them so that sediment–water column exchange of nutrients and algal cells is restricted has been proposed to help reduce CyanoHABs (Fig. 3).

Sediment removal usually involves expensive dredging and extensive disturbance of lake bottoms, which can lead to the release of ‘legacy’ stored nutrient (and potentially toxic substances) and destruction of bottom-dwelling plant and animal communities (Peterson 1982). There are few ‘success stories’ following such a radical approach, the most notable being Lake Trummen, in Sweden, a small (area $\sim 1 \text{ km}^2$, mean depth 1.6 m) lake that experienced CyanoHAB-related water quality degradation in response to domestic sewage and industrial nutrient inputs during the mid-1900s (Cronberg 1982). Suction dredging the upper half metre of sediments during 1970–71 resulted in a profound decrease in nutrient concentrations and CyanoHABs (Cronberg 1982). The uncommon success of these drastic measures was likely due to the small size of the lake and, equally, to reductions of external nutrient loads from its small (13 km^2) watershed (Cronberg 1982) following the dredging procedure (Peterson 1982). In very large lakes, the sheer volume of sediment material (e.g. $5 \times 10^6 \text{ m}^3$ in Lake Okeechobee) makes this approach unrealistic.

Less-radical and less-destructive approaches include using chemical treatments to precipitate P, keeping it bound in the sediments. One such treatment, Phoslock (CSIRO, Australia), uses a bentonite clay infused with the rare earth element lanthanum (Douglas *et al.* 1999). The lanthanum ions are electrostatically bound to the bentonite, while also strongly binding to phosphate anions. The bound phosphate then settles out of the water column and the thin layer (usually $< 1 \text{ cm}$) of Phoslock on the sediment surface forms an effective barrier to phosphate diffusing out of the sediments (Douglas *et al.* 1999). Phoslock has been shown to work well in small reservoirs, where it can lead to P-limited conditions that can control algal and CyanoHAB production (Robb *et al.* 2003; Haghseresht *et al.* 2009; Lürling and Faassen 2012). In addition, the thin Phoslock layer increases the critical erosional velocity of fine grained surficial sediments (Egemose *et al.* 2010), which should reduce the frequency of resuspension events and associated pulse nutrient loading. Sediment stabilisation and reduced phytoplankton biomass may aid with restoration of macrophyte communities in shallow, eutrophic systems where light limitation and low root anchoring capacity of fine-grained, organic-rich sediments often synergistically determine CyanoHAB dominance (Schutten *et al.* 2005; Egemose *et al.* 2010).

As with sediment removal, the efficacy of any chemical treatment is likely to be low unless external nutrient inputs are concurrently managed (Robb *et al.* 2003). Long-term effects from Phoslock applications have yet to be determined; however, such treatments can reduce oxygen concentrations in surface

sediments and the benthic boundary layer (Vopel *et al.* 2008), with unknown consequences for infauna and sediment carbon burial. In situations where allochthonous P remains high and unabated, repeated Phoslock applications are needed. The cost of multiple Phoslock treatments to immobilise continuing P inputs would rapidly accelerate. Even for a single application, Phoslock is prohibitively expensive for the treatment of large systems. For example, CyanoHAB-plagued Lake Taihu, in China, with a volume of $\sim 4 \times 10^{12} \text{ L}$ and a 0.15 mg L^{-1} stock of total P in the water column would require treatment with nearly $5 \times 10^6 \text{ kg}$ of Phoslock, at an approximate cost of US\$700 million for a single treatment (P. Hochman, unpubl. data).

Sediment removal and manipulation techniques are only a temporary fix of symptoms unless the cause of the problem is addressed in parallel (i.e. nutrient input reductions). The efficacy of chemical treatment is particularly poor in shallow lakes with a long wind fetch, because just one storm event that generates substantive waves and currents can move the chemicals off the treated location to areas such as the lake shoreline. This means that applications would need to be repeated (Cooke *et al.* 1993).

Integral role of climate change

In addition to evolving nutrient overenrichment issues, other environmental changes play integral roles in the recent upsurge of CyanoHABs. Climate change, specifically global warming, favours CyanoHABs in several ways. As a group, cyanobacteria exhibit optimal growth rates at high temperatures, usually in excess of 25°C (Paerl and Huisman 2008, 2009). At these elevated temperatures, CyanoHABs compete most effectively with eukaryotic algae. Intense light absorption by dense surface cyanobacterial blooms can locally increase water temperatures (Kahru *et al.* 1993; Ibelings *et al.* 2003; Paerl *et al.* 2016c; Fig. 3), thereby creating a positive feedback that perpetuates further CyanoHAB dominance (Hense 2007). Higher water temperatures will also extend the ice-free growing season at higher latitudes and high elevations, expanding the seasonal duration of CyanoHAB outbreaks (Foy *et al.* 1976).

A recent study that included over 70% of the world’s lakes in terms of water volume documented that there has been warming averaging 0.34°C per decade, with some locales having significantly higher rates (O’Reilly *et al.* 2015). Warming of surface waters could intensify vertical density stratification and lengthen the period of seasonal stratification, thus suppressing vertical mixing intensity and frequency. Under strong and persistently stratified conditions, positively buoyant cyanobacteria can form dense surface blooms (Reynolds 1987) that shade deeper non-buoyant eukaryotic phytoplankton, enhancing the competitive advantage of CyanoHABs (Huisman *et al.* 2004; Fig. 3). Increased water temperatures also decrease the viscosity of the water, and therefore the water’s resistance to vertical migration of phytoplankton, facilitating the aforementioned upward and downward migration by CyanoHABs, enhancing their competitive advantages in stratified waters (Fogg 1969; Reynolds 1987). Warmer, more-stratified waters can promote bottom water hypoxia. Internal nutrient loading from the sediments, particularly from redox-sensitive phosphorous pools, is often stimulated by hypoxia, further fuelling CyanoHABs (Paerl 1988; Paerl *et al.* 2016c).

Key drivers of global warming are the rising levels of the atmospheric greenhouse gases, including CO₂, CH₄ and N₂O. In nutrient-enriched waters, algal blooms exhibit high rates of photosynthesis and hence high demand for CO₂, which increases pH and restricts availability of free CO₂ in affected waters (Shapiro 1990; Ibelings and Maberly 1998). Under these conditions, buoyant CyanoHABs have a distinct advantage over subsurface phytoplankton populations. Because surface-dwelling taxa can directly intercept CO₂ from the atmosphere, they minimise the potential for dissolved inorganic carbon (DIC) limitation of photosynthetic growth (Paerl and Ustach 1982). The increasing atmospheric levels of CO₂ will provide surface-dwelling CyanoHABs an even greater advantage (Verspagen *et al.* 2014; Huisman *et al.* 2018).

Seasonal to multi-annual droughts in many parts of the world appear to be increasing in intensity and duration, possibly due to global warming (Trenberth 2008; Pachauri and Meyer 2014). Numerous studies have documented a link between droughts and the occurrence of intense CyanoHAB events, especially in shallow lakes (Bouvy *et al.* 1999, 2000; Nöges *et al.* 2003; Havens *et al.* 2016; Havens and Ji 2018). One consequence of droughts, and increased use of fresh water for municipal uses and irrigation, is rising salinity. Salinisation is a serious threat to supplies of fresh water and has major effects on freshwater plankton composition and possibly CyanoHAB potentials. One effect of salinisation is increased vertical density stratification, which would further benefit buoyant, scum-forming CyanoHABs (Fig. 3). Some freshwater CyanoHAB genera, such as *Anabaena*, *Microcystis* and *Nodularia*, can tolerate moderate salinities better than other non-bloom-forming phytoplankton (Moisander *et al.* 2002). This explains their occurrence at times in nutrient-enriched brackish waters, including the Baltic Sea, the Caspian Sea, Patos Lagoon Estuary in Brazil, the Swan River Estuary in Australia, the San Francisco Bay Delta in California and Lake Ponchartrain in Louisiana.

Global warming and associated changes in climatic oscillations affect the patterns, intensities and duration of precipitation and droughts, which may promote CyanoHAB dominance. For example, larger, more-intense precipitation events, including a rising frequency of tropical cyclones, extratropical storms (i.e. 'nor-easters') and more intense thunderstorms (Webster *et al.* 2005; Trenberth 2008; Seneviratne *et al.* 2012; Wuebbles *et al.* 2014), will increase enrichment of waterbodies with land-derived nutrients through enhanced erosion and liberation of legacy nutrients into surface run-off and groundwater discharge. In the short term, high rates of fresh water inflow and outflow may prevent blooms due to high flushing rates. However, as discharge subsides and water residence time increases, the associated increased nutrient inputs will be captured and cycled by receiving waterbodies, promoting CyanoHAB potential (Paerl *et al.* 2016c). This scenario can be observed in geographically diverse systems, including the Swan River in Australia, Hartbeespoort Dam in South Africa, the Neuse River Estuary in North Carolina (USA), the Potomac Estuary in Maryland (USA) and lakes in central Florida (USA). In addition, attempts to control fluctuations in the discharge of rivers and lakes by dams and sluices increase residence time, aggravating CyanoHAB problems (Burch *et al.* 1994).

Overall, it appears that the increased frequency of hydrological extremes (e.g. protracted droughts) positively benefit

CyanoHABs. If conditions get so extreme as to dry up lakes and reservoirs, most CyanoHAB species can survive such extremeness for long periods (up to many years) as dormant cysts in sediments, soils or desiccated mats (Potts 1994). Havens *et al.* (2016) hypothesised that in eutrophic shallow lakes with ample amounts of P and N to support blooms, the concentration of water into a reduced volume does two things: (1) it concentrates bioavailable nutrients; and (2) it allows for a greater effect of nutrient transport by benthivorous fishes from the sediments to the water column.

One of the factors that affects conditions in lakes worldwide is an oceanic climate cycle known as the El Niño Southern Oscillation (ENSO). This involves a cyclical (years) change in the temperature of surface waters off the coast of South America in the Pacific Ocean, in turn affecting the dynamics of atmospheric phenomena such as the jet streams. The phase of the ENSO (warm, El Niño; or cold, La Niña) affects lakes far removed from the Pacific. For example, Nöges *et al.* (2003) found that year-to-year changes in phytoplankton biomass in Lake Võrtsjarv, Estonia, are related to variations in rainfall that, in turn, are driven by the ENSO. In years of low rainfall, the phytoplankton switched from dominance by *Lyngbya* to dominance by the CyanoHAB *Anabaena*. Similarly, water column stability in Lake Victoria is affected by rainfall and the phase of the ENSO (Cózar *et al.* 2012), and a particular warm phase of the ENSO is thought to have caused a regime shift in Lake Superior that involved multiple years of reduced ice cover (Van Cleave *et al.* 2014) and changes in spring phytoplankton. Havens and Ji (2018) examined the effects of climate variability on water quality, including CyanoHABs in Lake Apopka, one of Florida's largest shallow lakes. They documented substantive effects of droughts. For the period from 1999 to 2016, monthly sampling revealed that total P, total N and chlorophyll-*a* increased significantly during periods of low water associated with rainfall deficit, and Secchi disc transparency increased (Havens and Ji 2018; Fig. 4). In each of three successive droughts, the lake rebounded and had improved water quality when the water level rose back to its historic level (i.e. at this time the lake is resilient to these perturbations, even when they occur at a high return frequency). The response in terms of CyanoHAB biomass followed what was seen for total P and chlorophyll-*a*.

Evidence is emerging (Cai *et al.* 2015) that the magnitude of variability in the ENSO will increase with global warming. This may lead to greater-intensity swings between wet and dry periods around the world, and thus contribute to huge variation in CyanoHAB intensity in nutrient-rich lakes. If future droughts are more severe, CyanoHAB events like those observed in Lake Apopka are likely to be more intense, and it is uncertain then if shallow lakes will exhibit the same resilience that was observed in the recent studies.

Some toxin-producing CyanoHABs appear to be particularly successful in exploiting climatic change. For example, the potentially toxic, low-light-adapted, N₂-fixer *Cylindrospermopsis raciborskii* was originally described as a tropical to subtropical species preferring water temperatures greater than 22°C (Padisák 1997). However, in recent years, the occurrence and dominance of *C. raciborskii* have expanded polewards into mid-latitudes of Europe, North America and South America, where it often

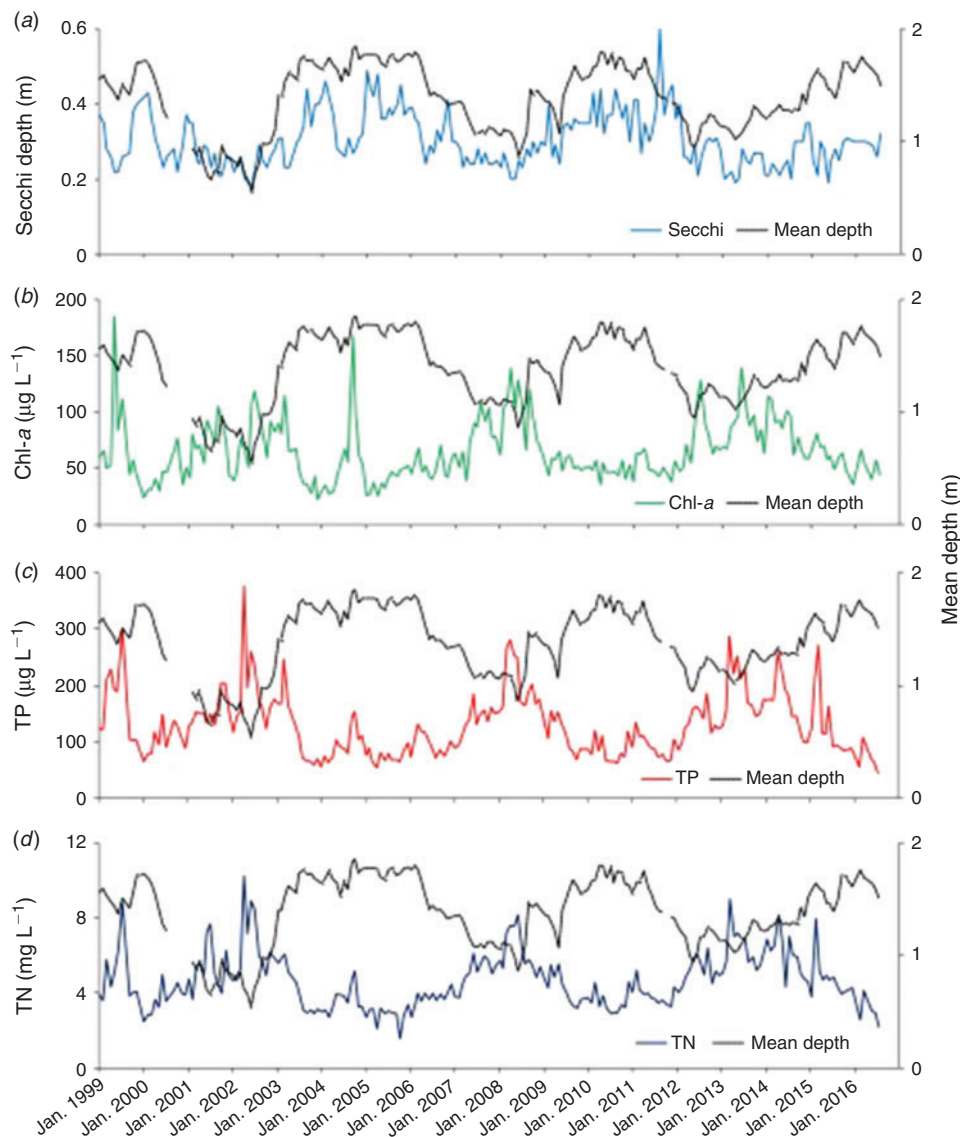


Fig. 4. Relationships between mean depth and (a) Secchi depth transparency, (b), chlorophyll (Chl)-a, (c) total phosphorus (TP) and (d) total nitrogen (TN) in Lake Apopka, Florida, from 1999 to 2016. The relationships with depth are significant at $P < 0.001$ based on non-parametric correlation analysis, with coefficients ranging from 0.56 to 0.74 (from Havens and Ji 2018).

proliferates in turbid, eutrophic lakes and reservoirs (Padišák 1997). Another example is the massive toxic *Microcystis* spp. blooms in Lake Taihu, China, that create severe drinking water supply crises for the surrounding municipalities (c.f. Qin *et al.* 2010). These blooms have increased in magnitude over the past few decades due to the combined effects of increased N and P loading and a multidecadal warming trend (Paerl and Huisman 2009; Kosten *et al.* 2012; Huisman *et al.* 2018).

Effects of tropical cyclones

Research conducted in the past decade indicates that, with a warming ocean, the intensity of land-falling tropical cyclones will increase (Webster *et al.* 2005; Holland and Webster 2007; Seneviratne *et al.* 2012; Wuebbles *et al.* 2014). We have

documented in earlier studies that cyclones and the associated increase in nutrient inputs and sometimes resuspension of benthic cyanobacteria can result in massive CyanoHABs (Havens *et al.* 2016).

Recent studies on China's third largest lake, Taihu, illustrate the effects of West Pacific typhoons (named hurricanes and cyclones in other world regions) that, during summer, frequently pass over the Shanghai to Nanjing corridor in which Taihu is located (Zhu *et al.* 2014). During this time of the year, toxic CyanoHABs, dominated by the non- N_2 -fixer *Microcystis* spp., prevail (Paerl *et al.* 2015; Xu *et al.* 2015). In years where typhoon passages took place, blooms were disrupted for a few days, after which the bloom intensity and duration increased to levels that were significantly higher than before typhoon

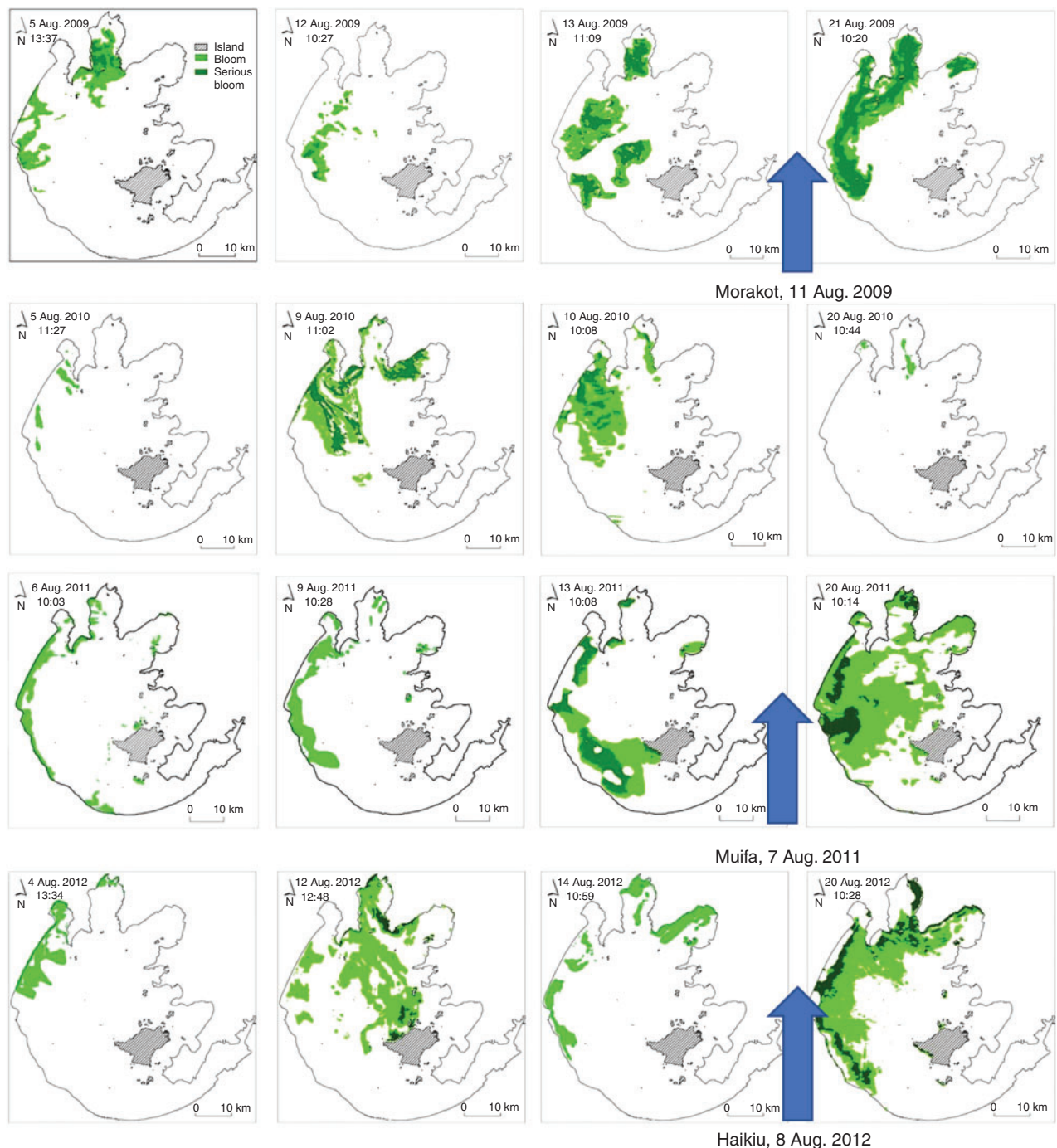


Fig. 5. Effects of tropical cyclones (typhoons) on cyanobacterial bloom biomass (as surface chlorophyll-*a* concentrations detected by NASA moderate-resolution imaging spectroradiometer (MODIS) satellite imagery) during summer bloom periods in Lake Taihu, China. In years where typhoons (tropical storm or higher wind categories) passed over Lake Taihu (arrows), cyanobacterial bloom biomass tended to be higher and more persistent than in a year devoid of typhoon activity. Figure adapted from [Zhu *et al.* \(2014\)](#).

passage ([Zhu *et al.* 2014](#)). In contrast, during typhoon-free years, the bloom tended to have lower biomass (as chlorophyll-*a*) and its duration was shorter than during typhoon years ([Fig. 5](#)). We attribute this to several factors associated with typhoon passages, including sediment resuspension and subsequent nutrient

release into the water column, and nutrient-rich run-off following heavy rainfall events accompanying typhoons. Interestingly, the typhoon-prone period is from July to September, which is also a period of strong nutrient limitation ([Paerl *et al.* 2015](#); [Zhu *et al.* 2014](#)). It appears that the typhoons, although disruptive in

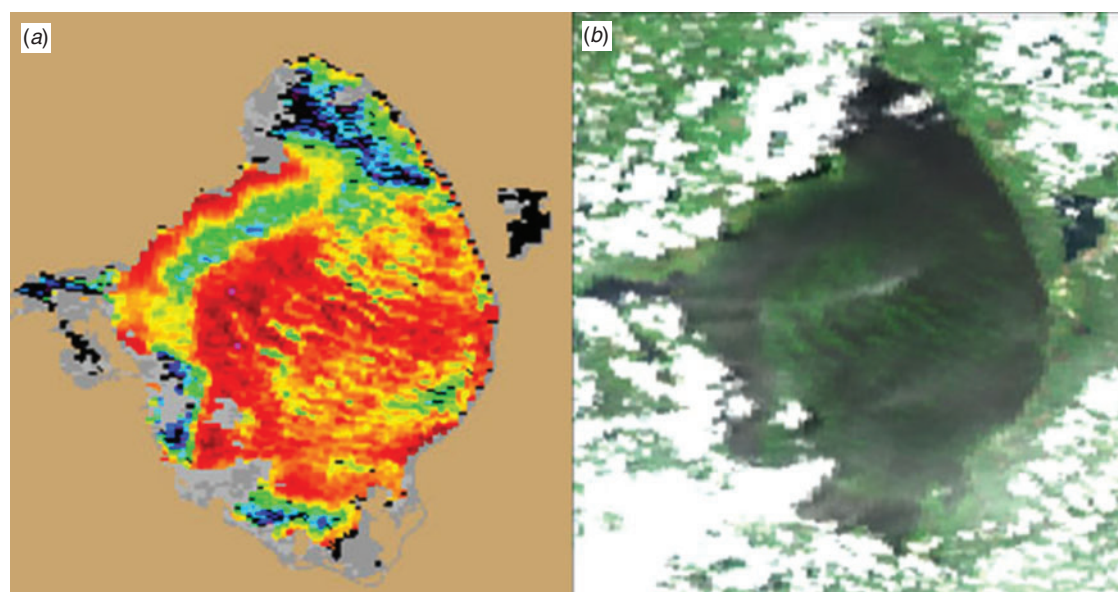


Fig. 6. (a) Image showing the intensity of cyanobacteria blooms (increasing in relative intensity from blue to red) in Lake Okeechobee, Florida, on 29 June 2018. Bloom intensity is inferred using an algorithm based on the spectral signature of the reflectance off the lake, ground-truthed by National Oceanic and Atmospheric Administration (NOAA) and the State of Florida over the prior summer. (b) Image showing the corresponding true-colour satellite image. Images provided by Richard Stumpf, NOAA National Ocean Service.

the short run, actually alleviate nutrient limitation at a time of the year when other growth-regulating factors, such as temperatures and irradiance, are maximal (Paerl *et al.* 2015).

In Lake Okeechobee, Florida, there have recently been widespread CyanoHABs, in 2005, 2016 and 2018, each time corresponding to an exceptional spring rainfall event or a hurricane. The longest-lasting bloom, in summer 2018, followed Hurricane Irma in September 2018, which delivered the second-highest load of P to the lake in 45 years and a comparably high load of N. Most of the loading happened during a period of 8 weeks after the storm, and in a month of intense spring rainfall. The hurricane also stirred up P-rich bottom sediments in the lake, as has happened with past storms (Havens *et al.* 2016). When water temperature increased and hot sunny days began in early June 2018, a bloom of *Microcystis* emerged in the south-west pelagic zone and, by early July, it covered nearly 100% of the pelagic surface area. The bloom subsided in mid-July and then reappeared, and included several N₂-fixing *Anabaena* spp., only to be replaced later by a near monoculture of *Microcystis*. Inferred bloom intensity from satellite imagery, provided by the National Oceanic and Atmospheric Administration (Fig. 6), allowed for estimates of the spatial extent of the bloom on an approximately twice-weekly basis through the summer, and ongoing until the event ended.

Changing CyanoHAB thresholds and tipping points

Developing nutrient CyanoHAB thresholds will be a challenge because climatic changes alter nutrient–growth relationships as well as overall growth potentials based on temperature, stratification potentials, flow and water residence time. The synergistic and antagonistic interactions of these regulatory variables will

lead to a range of CyanoHAB scenarios that include the initiation, magnitude and duration of blooms, as well as composition and successional patterns of the CyanoHAB community.

Furthermore, if there is increased frequency of severe events, ecosystems may not have sufficient time to recover, and this could possibly lead to regime shifts, as discussed in Havens *et al.* (2016). Likewise, systems that already have elevated levels of CyanoHABs because of increased water temperature and then experience severe events that are more extreme may be more readily pushed into a different regime, such as one where a lake contains shoreline plants and pelagic cyanobacteria to lake-wide CyanoHABs. There is a well-known example, namely that of Lake Apopka (FL, USA), where a build-up of nutrients from increased external inputs set up alternative stable states and then, in a single year, the lake changed from being macrophyte dominated and clear to cyanobacteria dominated and turbid. That regime change happened in 1947 after the lake was affected by a hurricane (Bachmann *et al.* 2005), and the lake continues to be turbid and phytoplankton dominated ≥ 70 years later (Havens and Ji 2018). Global climate models predict that tropical cyclones will become more severe as the Earth warms (Pachauri and Meyer 2014), and recent research suggests that the amplitude of the ENSO will increase (Cai *et al.* 2015) and so presumably will the intensity of droughts and periods of heavy rainfall. Modelling of these future scenarios is needed in the context of CyanoHAB formation and regime shifts in lakes in order to help better guide management actions that can be taken now to curtail such events from occurring in our lakes, rivers and estuaries in the future.

A starting point for management-oriented research may be to at least quantify how increased water temperature affects the

relationship between CyanoHAB blooms and concentrations of nutrients. That relationship has served as the foundation for setting nutrient loading targets in lakes around the world, and carefully designed experiments may elucidate to what extent temperature increase affects the threshold at which the frequency of occurrence of CyanoHABs quickly rises with increasing N and P.

Conclusions

Recent studies indicate that the synergistic combination of anthropogenic nutrient loading, rising temperatures, enhanced vertical stratification, increased residence time and more extreme climatic conditions overall will favour cyanobacterial dominance in a wide range of aquatic ecosystems. The expansion of CyanoHABs has serious consequences for human water supplies, fisheries and recreational resources. Ecosystem-scale physical–chemical–biotic mitigation strategies will have to incorporate nutrient (most often both N and P) input reductions. The magnitudes of these reductions will need to be system specific and will likely need to be adjusted with changing climatic conditions. Specifically, water quality managers will have to accommodate warming and greater hydrological variability and extremeness resulting from climate change in formulating their strategies. A key long-term control we can exert to reduce the rate and extent of global warming is curbing greenhouse gas emissions. Without this essential step, future warming trends, hydrological extremes (record rainfalls and droughts) and their effects on aquatic ecosystems will continue to promote opportunistic CyanoHABs.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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