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RESTORATION OF EUTROPHIC LAKES

Opinion Paper

Mitigating eutrophication and toxic cyanobacterial blooms in large lakes: The evolution of a dual nutrient (N and P) reduction paradigm

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Abstract Cyanobacterial harmful algal blooms (CyanoHABs) are an increasingly common feature of large, eutrophic lakes. Non-N_2-fixing CyanoHABs (e.g., *Microcystis*) appear to be proliferating relative to N_2-fixing CyanoHABs in systems receiving increasing nutrient loads. This shift reflects increasing external nitrogen (N) inputs, and a > 50-year legacy of excessive phosphorus (P) and N loading. Phosphorus is effectively retained in legacy-impacted systems, while N may be retained or lost to the atmosphere in gaseous forms (e.g., N_2, NH_3, N_2O). Biological control on N inputs versus outputs, or the balance between N_2 fixation versus denitrification, favors the latter, especially in lakes undergoing accelerating eutrophication, although denitrification removal efficiency is inhibited by increasing external N loads. Phytoplankton in eutrophic lakes have become more responsive to N inputs relative to P, despite sustained increases in N loading. From a nutrient management perspective, this suggests a need to change the freshwater nutrient limitation and input reduction paradigms; a shift from an exclusive focus on P limitation to a dual N and P co-limitation and management strategy. The recent

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proliferation of toxic non-N_2-fixing CyanoHABs, and ever-increasing N and P legacy stores, argues for such a strategy if we are to mitigate eutrophication and CyanoHAB expansion globally.

Keywords Harmful algal blooms · Toxins · Management · Pollution

Introduction

Nutrient-driven eutrophication, accompanied by the proliferation of harmful cyanobacterial blooms (CyanoHABs), continues to be a principal threat to the integrity and sustainability of large lake ecosystems (Paerl & Otten, 2013a). Although there are some examples of improved water quality following several decades of efforts to reverse this growing threat (Jeppesen et al., 2005), there are few examples of improvement for large lake ecosystems.

The link between nutrient over-enrichment and accelerating eutrophication has been recognized for well over a century (Forel, 1901; Birge & Juday, 1911; Wetzel, 2001). Early studies concluded that primary production in large lakes was largely limited by the supply of phosphorus (P) (c.f. Vollenweider, 1968; Schindler & Fee, 1974), which led to a management focus on reducing anthropogenically derived, point source P inputs (Likens, 1972). There were some early success stories in response to P input reductions, including Lake Washington (USA; Edmondson & Lehman, 1981) and Lake Erie (Canada/USA; Scavia et al., 2014) in North America, Lake Constance (Germany–Switzerland; Schindler, 2012), and Lake Balaton (Hungary; Istvánovics et al., 2007). In the watersheds of these lakes, wastewater point source diversions and steps to reduce non-point sources (best land management practices, construction of bordering riparian buffers and wetlands) resulted in reduced P inputs and led to significant, albeit temporary in some cases (e.g., Lake Erie), declines in phytoplankton biomass and increased water clarity. Nitrogen (N) inputs were also likely reduced (c.f., Hamilton et al., 2016), but not quantified, as a result of these efforts. Reductions of point and non-point source nutrient inputs have achieved similar benefits in smaller lakes and reservoirs (e.g., Lake Trummen, Sweden; Cronberg, 1982; Little Mere and Rosthern Mere, England; Jeppesen et al., 2005).

Research and management efforts on CyanoHABs in the lakes mentioned above were mostly aimed at reducing blooms of nitrogen (N_2)-fixing genera, including *Anabaena* (recently renamed *Dolichospermum*), *Aphanizomenon*, *Cylindrospermopsis,* and *Nodularia*, because they presumably could supplement their N needs by N_2 fixation (Fogg, 1969; Table 1) and bring ecosystem-scale balance between N and P (Schindler 1977). The conventional wisdom was that reducing N inputs would have no effect on reducing their growth, which led to a strong and largely exclusive focus on P controls (c.f., Likens, 1972; Schindler & Fee, 1974; Smith et al., 1984). In recent decades, and despite previous improvements, lakes Erie and Balaton, and many other systems worldwide, have experienced resurgent blooms of toxic, non-N_2-fixing CyanoHABs that have vastly exceeded historical CyanoHABs in terms of bloom severity and

Table 1 Commonly observed cyanobacteria in large lake ecosystems and the toxins they may produce (Adapted from Paerl, 2018)

Genus	Potential toxin(s)	Characteristic
Anabaena	ATX, CYN, MC, STX	B,P,D,F
Anabaenopsis	MC	P,D,F
Aphanizomenon	ATX, CYN, STX	P,D,F
Cylindrospermopsis	ATX, CYN, STX	P,D,F
Cylindrospermum	ATX, MC	B,D,F
Dolichospermum	ATX, CYN, MC, STX	P,D,F
Fischerella	MC	B,D,F
Haplosiphon	MC	B,D,F
Lyngbya	CYN, LYN, STX	B,F
Microcystis	MC	P,C
Nostoc	ATX, MC	B,D,F
Oscillatoria	ATX, CYN, MC, STX	B/P,D,F
Phormidium	ATX, MC	B,D, F
Planktothrix	ATX, MC	P, D, F
Raphidiopsis	ATX, CYN, MC	P,F
Scytonema	MC, STX	B,D,F
Umezakia	CYN, MC	P,D,F

Toxin abbreviations: *ATX* Anatoxin-a, *CYN* Cylindrospermopsin, *LYN* Lyngbyatoxin, *MC* Microcystin, *NOD* Nodularin, *STX* Saxitoxin

Characteristics abbreviations: *B* Benthic, *C* Coccoid, *D* Diazotrophic, *F* Filamentous, *P* Planktonic

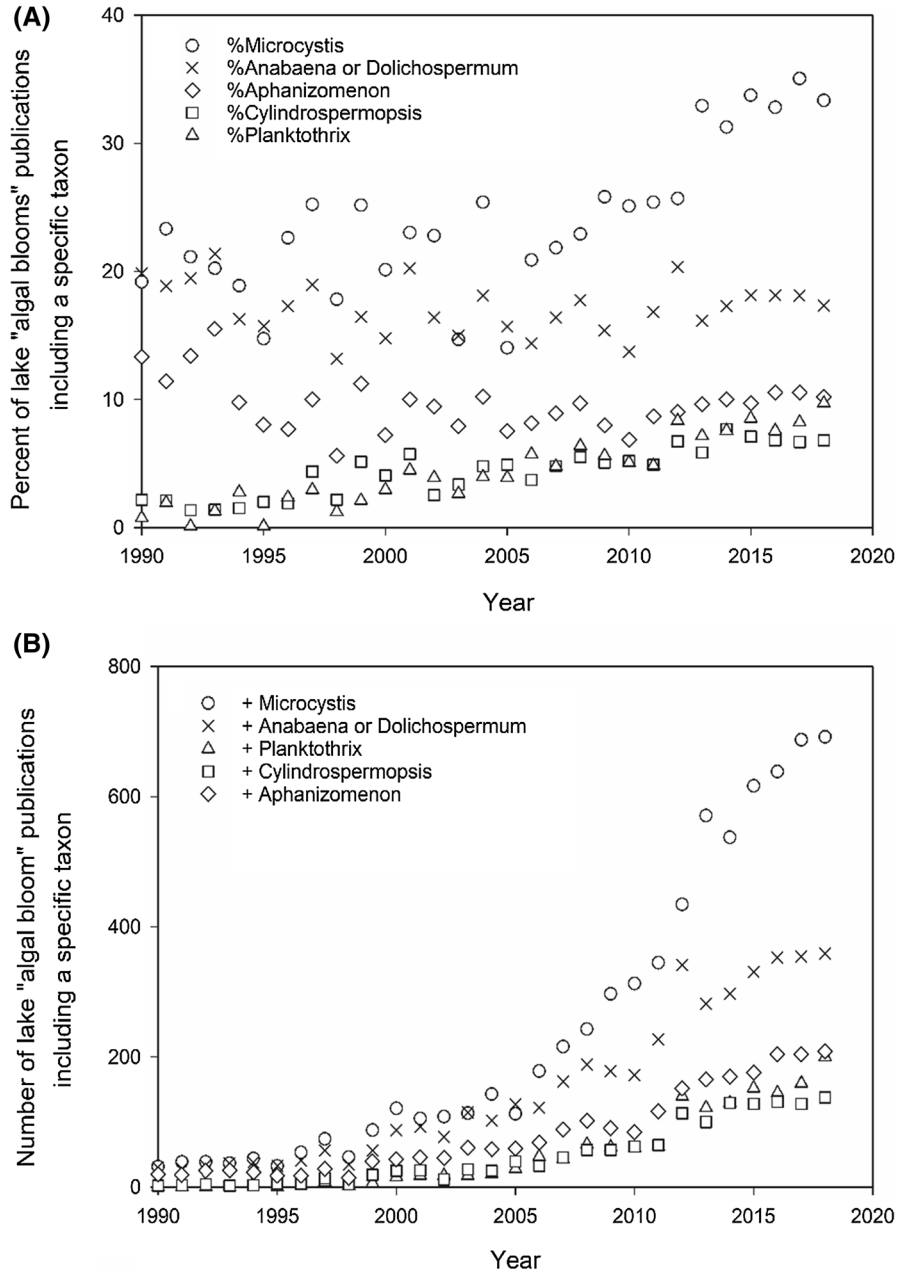


Fig. 1 Number of publications from 1990 to 2018 resulting from a series of Google Scholar searches for "lake" + "algal bloom" or "lake" + "algal bloom" + specific taxa (*Aphanizomenon*, *Cylindrospermopsis*, *Planktothrix*, *Microcystis*, *Anabaena*, or *Dolichospermum*). Results for each taxa are shown as (**A**) a percentage of the total number of results with no taxa specified to correct for an increase in publications overall and (**B**) the total number of publications for each search result.

societal impacts (e.g., Steffen et al., 2014; Gobler et al., 2016).

In particular, blooms of toxic *Microcystis* and *Planktothrix*, and other non-N_2-fixing genera (Bullerjahn et al., 2016; Harke et al., 2016), have become increasingly common and dominant in large lakes that provide multiple ecosystem services (drinking and irrigation water, fisheries, recreational use, and esthetics; Otten & Paerl, 2015; Table 1). This trend is reflected in the recent literature on freshwater CyanoHABs (Fig. 1). Dominance by these taxa in contemporary blooms signals a need for stricter

control of N inputs, in addition to P (Lewis & Wurtsbaugh, 2008; Lewis et al., 2011; Paerl et al., 2016a). Here, we examine the evolution of a new paradigm, namely the need for dual nutrient (N & P) controls to mitigate CyanoHABs in large lakes, based on data from several large lakes experiencing dominance and persistence of toxic, non-N_2-fixing taxa.

This paradigm shift is based on the biological mechanism that productive lakes become increasingly N-limited because N is lost through denitrification (Scott et al., 2019), and the empirical evidence that decades-long efforts to reverse eutrophication solely by reducing P loading have not always produced positive improvements (Paerl et al., 2016a). For example, the phytoplankton community of Lake Erie has been dominated by potentially toxic cyanobacteria—especially *Anabaena*, *Aphanizomenon,* and, more recently, *Microcystis*—in the central and western basins since the 1960s (Davis, 1964; Rosa & Burns, 1987; Makarewicz, 1993; Allinger & Reavie, 2013; Steffen et al., 2014). Initially, the intensity and frequency of cyanobacterial blooms waned during the 1970s and 1980s with the implementation of P load reductions (Nichols & Hopkins, 1993; Fahnenstiel et al., 1989); however, by the mid-1990s, CyanoHABs dominated by the non-N_2-fixers *Microcystis* and *Planktothrix* returned to Lake Erie (Brittain et al., 2000; Scavia et al., 2014; Newell et al., 2019).

Similarly, in Lake Okeechobee (Florida, USA), pelagic blooms were once dominated by N_2-fixing *Anabaena* (now termed *Dolichospermum*) (Jones, 1987), and the eutrophication management program was focused on reducing P inputs to meet legally mandated minimal loading requirements (Havens & Walker, 2002). However, there have been recurrent lake-wide blooms of *Microcystis* in 2005, 2010, 2016, and most recently, in 2018, and those blooms have seeded intense blooms in the downstream rivers and estuaries (Kramer et al., 2018). These cases highlight the urgent need to revisit nutrient reduction strategies and to consider the inputs of N, which is required in large amounts to support both biomass and toxin production in non-N-fixing taxa (van de Waal et al., 2014, Davis et al., 2015; Gobler et al., 2016). Microcystin-LR ($C_{49}H_{74}N_{10}O_{12}$), a common variant of the most common cyanotoxin, contains ten atoms of N per molecule—but no P. Interestingly, while microcystin production tends to increase in response to a variety of N forms (NH_4^+, NO_3^-, urea) in non-N_2-fixers, such as *Microcystis* (Harke & Gobler, 2015) and *Planktothrix* (Chaffin et al., 2018), the eco-physiological reason for microcystin production remains a subject of considerable speculation and research (c.f., Paerl & Otten, 2013b; Huisman et al., 2018).

We are left with persistent questions: Why has there been such limited success in combating eutrophication and CyanoHABs—and especially non-N_2-fixing genera? What are the underlying factors that are hindering eutrophication mitigation and preventing large lake restoration? Lastly, what can be done to accelerate CyanoHAB abatement? In this contribution, we delve into several case studies to better understand why P-only reduction strategies have sometimes been ineffective (e.g., lakes Erie and Okeechobee). We also review and evaluate biogeochemical and ecological mechanisms that provide the rationale for the increasingly common utilization of dual (N and P) nutrient reduction strategies for combating the global expansion of CyanoHABs. We also offer several broadly applicable strategies aimed at mitigating this expansion.

The phosphorus and nitrogen "legacy" problem

One of the major factors impeding the long-term cessation of CyanoHABs in eutrophic lakes is the presence of legacy nutrients in their sediments and watersheds (Jarvie et al., 2013; Sharpley et al., 2013). Once added to a landscape or water body, phosphorus is lost very slowly because it is highly particle-reactive and is only lost via physical export since it lacks a gaseous phase. For example, the Lake Okeechobee (Florida, USA) watershed contains an immense supply of legacy P that provides inputs to the lake after major rain events, and it is estimated to be so large that it could maintain currently high P inputs for over 50 years—even if contemporary sources are reduced to zero (Reddy et al., 2011). The lake itself has sufficient P in surficial sediments such that recycling into the water column and desorption of phosphate from sediment particles is sufficient to prevent a decline in P concentration in the water column for up to 75 years (James & Pollman, 2011). Lakes that are rich in P and located in temperate to tropical regions are ideal for the formation of *Microcystis* blooms and other non-N_2-fixing CyanoHABs, as long as there is an

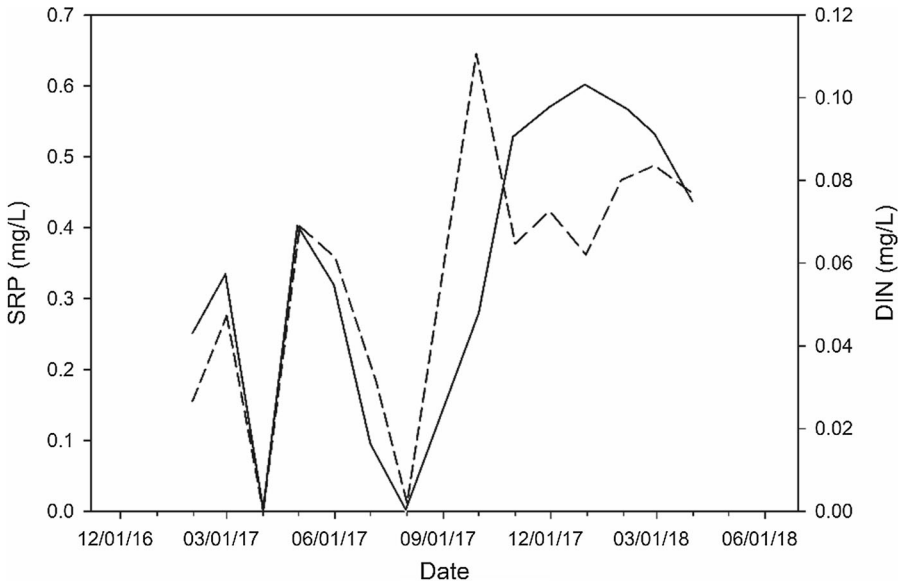


Fig. 2 Dissolved inorganic N (DIN) (dashed line) and soluble reactive P (SRP) (solid line) concentrations in lake water at the northern end of Lake Okeechobee, near the main river inflow. Heavy rainfall and runoff happened for weeks after Hurricane Irma passed to the west of the lake on September 15, 2017.

adequate supply of dissolved organic or inorganic N. Nitrogen inputs often come from agricultural, industrial, or domestic runoff, as well as from biomass decomposition and subsequent release of NH_4^+ from vegetation and sediment organic material, or from displaced legacy N mobilized by large storm events in the watershed (Boyer et al., 2002; van Egmond et al., 2002; Van Meter et al., 2016).

Because of the traditional emphasis on P control in lakes, there has also been a focus on identifying P sources in polluted watersheds, especially those subject to intensive agricultural nutrient loading from fertilizer and animal waste (Sharpley & Menzel, 1987; Sharpley et al., 2006). However, recent work showed that watersheds with intensive agriculture also contain large stores of legacy N in their soils and that this N can be mobilized and carried downstream to lakes, rivers, and estuaries following large precipitation and snowmelt events (Van Meter et al., 2016) and may also chronically pollute groundwater (Sanford & Pope, 2013). Legacy N in the Mississippi River Basin (USA) contributes a substantial amount of the total N load to the Gulf of Mexico (Alexander et al., 2008), and the 142 Tg of N that has accumulated in the basin over the last 30 years as soil organic N could continue to load the river with N for 35 years, even with complete cessation of agricultural activities (Van Meter et al., 2016). Watersheds dominated by animal agriculture can retain significant legacy N that is exemplified by high nitrate concentrations during river base flow conditions (Grantz et al., 2014; Stelzer & Scott, 2018).

Legacy N has not been quantified in the watershed of Lake Okeechobee, where toxic *Microcystis* blooms have occurred, often after hurricane-related, historic rain events in 2005, 2010, 2016, and 2018. The phytoplankton of many lakes can become severely N-limited in summer (Scott et al., 2008, 2009; Kramer et al., 2018), and intense rainfall and runoff events, combined with internal recycling of previous N loading, deliver the necessary dissolved N to fuel or sustain blooms in those ecosystems. This scenario could explain recent conditions in Lake Okeechobee, where intense rainfall and runoff after Hurricane Irma in 2017 led to large increases in dissolved inorganic N and soluble reactive P (Fig. 2).

Research is needed to determine whether or not watershed best management practices (BMPs), occurring at the parcel and sub-basin scale and designed to control P, can also be effective at reducing N inputs (Hamilton et al., 2016). Further, research needs to determine whether agricultural, residential, and urban BMPs that help reduce N efflux from anthropogenic sources are overwhelmed and rendered ineffective after intense rain events. This inefficiency could be the result of a dependence on long residence times to allow for denitrification, or that the capacity of the system is exceeded, thereby allowing untreated runoff to enter surface waters.

Recognizing and addressing the role of N in modulating freshwater eutrophication

Some lakes are typically dominated by potential N_2-fixers (Paerl, 1990; Scott & Marcarelli, 2012), which tend to grow and fix N_2 in summer, when waters are warm and water column inorganic N has been sequestered into phytoplankton biomass or sediments (Scott et al., 2009). Nitrogen-fixing cyanobacteria can increase reactive N concentrations in lakes; however, they can also alter the resilience of low-nutrient ecosystems by facilitating a shift to a higher-nutrient, turbid water state (Cottingham et al., 2015). Thus, N_2-fixing cyanobacteria may couple the biogeochemical cycles of N and P and modify nutrient availability. However, this idea is not supported by the results of a long-term, whole-lake experiment in which Lake 227 of the Experimental Lakes Area in Canada was initially fertilized with N and P, then only P for the last 29 years, resulting in consistent and recurring summer blooms dominated by N_2-fixing cyanobacteria (Schindler et al., 2008). The total N pool of Lake 227 decreased in parallel during this time (Scott & McCarthy, 2010; Paterson et al., 2011), even though N_2 fixation rates increased (Paterson et al., 2011; Higgins et al., 2018). If N_2 fixation adds reactive N to an ecosystem proportionally to P availability, as indicated by Schindler et al., (2008) and the Cottingham et al., (2015) model, then the N pool in Lake 227 should have maintained an equilibrium with fertilizer P inputs (Scott & McCarthy, 2010, 2011). The long-term and consistent decrease in the N pool in Lake 227 indicates the following: (1) N_2 fixation in natural systems is controlled by numerous factors beyond P availability, including light, turbulence and vertical mixing, dissolved oxygen, organic matter, trace metals, and selective grazing (Paerl et al., 2016a, b; Wurtsbaugh et al., 2019); and (2) denitrification rates can exceed N_2 fixation rates on seasonal and annual scales (Paerl et al., 2016a, b; Scott et al., 2019).

The temporal and spatial scaling of N_2 fixation efficiency as an ecosystem process may also help explain the inability of N fixation to completely compensate for reduced external N loads (Levin, 1992; Currie, 2011; Scott et al., 2019). As only a very limited number of organisms can carry out N_2 fixation, its immediate effect is at the organismal scale, but may ultimately have influence at the community scale. Individual cyanobacterial cells uptake atmospheric N_2 and CO_2 simultaneously, and cyanobacterial N_2-fixers require substantial energy derived from photosynthesis (Oliver et al., 2012). The capacity to fix N_2 gives these cyanobacteria a competitive advantage over other phytoplankton when N concentrations are low (Smith, 1983). However, N_2-fixers preferentially utilize reactive inorganic N when it is available due to the high energetic costs of N_2 fixation (Flores & Herrero, 2005; Moisander et al., 2012). Interestingly, N_2-fixers can also leak substantial amounts of N from their cells, which can fuel photosynthesis by other non-N_2-fixing phytoplankton (Mulholland et al., 2006). However, fixed N is eventually exported from the photic zone of lakes and must be recycled to efficiently fuel subsequent primary production.

Recycling of recently fixed N can happen effectively within a single growing season in the water column and sediments of shallow lakes (Paerl et al., 2011; McCarthy et al., 2013, 2016; Hampel et al., 2018, 2019) (Fig. 3). Recent work by Hampel et al., (2019) in Sandusky Bay/Lake Erie highlighted the importance of internal NH_4^+ recycling in fueling cyanobacterial blooms during N-deplete periods. Over three summer months, the internal water column NH_4^+ recycling was equivalent to $\sim$ 77% of the annual, external total N (TN) load. The importance of internal NH_4^+ turnover increased throughout the bloom season, with NH_4^+ regeneration rates 2–5 times higher than the Sandusky River TN load in June, increasing up to $>$ 1000 times greater than the river TN load by the end of August (Fig. 3). While the TN load decreased in summer, the proportion of chemically reduced N (both organic N and NH_4^+) to TN in Sandusky River loading increased from 13.2% at the beginning of June to 91.9% by the end of August, corresponding with the increased importance of internal NH_4^+ dynamics and highlighting the importance of considering N forms and potential bioavailability in external loading. A similar pattern was observed for western Lake Erie, with the proportion of TN loading comprised of chemically reduced N significantly associated with CyanoHAB biomass and toxicity (Chaffin et al., 2019; Newell et al., 2019).

Winter sampling (e.g., Nov–April) is one of the largest data gaps in limnology (Hampton et al., 2017). Historically, field sampling in temperate lakes has focused on the 'growing season' from May through October, given the emphasis on summer CyanoHABs and the many logistical issues that inhibit sample

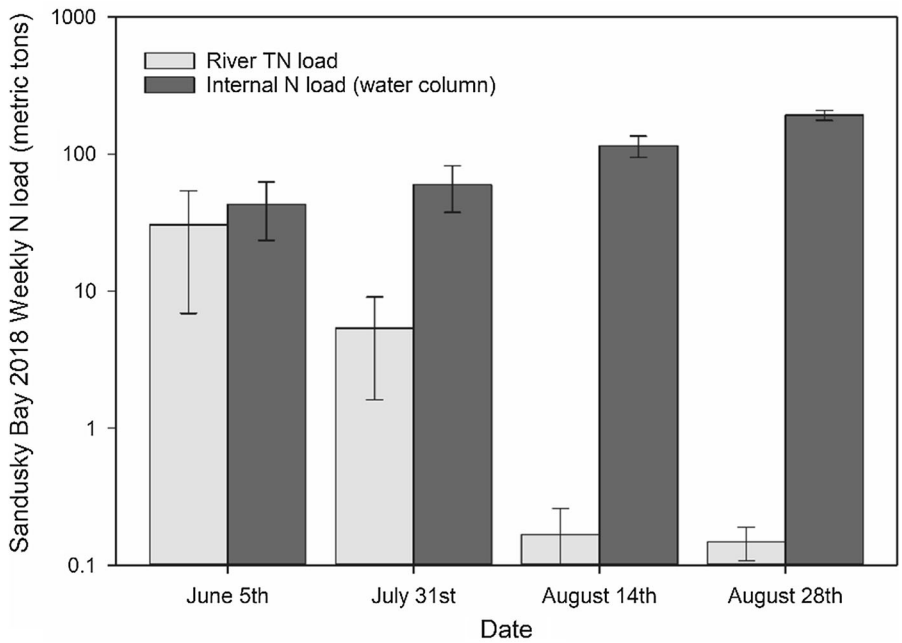


Fig. 3 External N loading from the Sandusky River (grey) compared to internal water column NH_4^+ regeneration (black) in summer 2017. (Data from Hampel et al., 2018)

collection in winter and transitional seasons (spring and fall). However, winter N cycling (e.g., under-ice NO_3^- production and loss) is likely linked to spring and summer blooms (Twiss et al., 2012; Wilhelm et al., 2014). NO_3^- accumulation via nitrification occurs during the winter under-ice period (Powers et al., 2017a, b), and winter nitrification and N turnover may drive NO_3^- accumulation and higher N:P ratios (Hampton et al., 2017; Powers et al., 2017b). A low NH_4^+:NO_3^- in spring promotes diatom growth (Glibert et al., 2016; McCarthy et al., 2009) and N removal from the system via denitrification. However, global climate change is leading to shorter winters with less ice cover and less NO_3^- accumulation (Powers et al., 2017a; Reavie et al., 2016). More NH_4^+ and urea (rather than NO_3^-) favors cyanobacteria over diatoms (Glibert et al., 2016; McCarthy et al., 2009), and high DIN concentrations promote highly toxic cyanobacteria (Gobler et al., 2016; Scott et al., 2013). New research constraining the effects of winter and under-ice N cycling, and the effects of climate change on this cycling, is needed to construct annual N budgets and accurately develop and validate ecosystem models used for informing policy decisions.

Grazers and heterotrophic bacteria further influence the rate and stoichiometry of nutrient recycling (Cherif & Loreau, 2009). Thermal stratification in lakes may slow the sinking of organic matter sufficiently enough to accelerate fixed N recycling in the upper mixed layer (Scott & Grantz, 2013), and many cyanobacteria can control their own buoyancy (Paerl, 2012), which can help minimize N losses from the euphotic zone. A community shift from diatoms to cyanobacteria also promotes recycling in the water column and may disrupt benthic–pelagic coupling in lakes (Gardner and Lee 1995). These recycling processes decrease the demand for continued N_2 fixation, while maintaining recently fixed N as a primary resource fueling primary production. Presumably, fixed N recycling could continue across years if fixed N effectively accumulated in lake sediments and was periodically resuspended into the water column as internal N load (Schindler, 2012). Given sufficient time (tens to hundreds years), fixed N could alleviate any long-lasting N limitations to primary production at the ecosystem scale if N_2 fixation exceeded denitrification and other N loss mechanisms (Vitousek et al., 2010). However, a recent continental-scale analysis of US lakes indicated that ecosystem-scale denitrification exceeds ecosystem-scale N_2 fixation on an annual basis in most lakes (Scott et al., 2019). This finding indicates that N loss to denitrification may represent a positive feedback to initiate and maintain N-depletion

in eutrophic lakes. Indeed, this large-scale biological mechanism explains why N fixation has not balanced the N supply in long-term experiments like Lake 227 (Scott & McCarthy, 2010; Higgins et al., 2017).

Quantifying the long-term balance between N_2 fixation and denitrification has meaningful implications for environmental science and policy regarding eutrophication management and water quality. If fixed N effectively accumulates in lake ecosystems, then managing anthropogenic N inputs to control eutrophication is meaningless, as argued by Schindler et al., (2008), because reactive N should always be present in sufficient quantities relative to P. However, if multiple limitations or constraints on N_2 fixation lead to perpetual N limitation of primary production in some lakes over seasonal to decadal scales, then controlling anthropogenic N inputs would be a useful tool to supplement the traditional P control measures (Lewis & Wurtsbaugh, 2008; Conley et al., 2009). For example, despite a 79% reduction in external P loading, P concentrations remained high for about 20 years in Lake Müggelsee (Germany), likely due to the "legacy" effect. However, parallel N reductions (by 69%) led to a rapid decrease in N concentrations and improvement in water quality, without N_2-fixing cyanobacteria compensating for the N requirements of primary production in the lake (Shatwell & Köhler, 2019).

Changes in rainfall and runoff driven by climate change will increase riverine N loading by an estimated 19% in the USA (Ballard et al., 2019), with similar impacts expected for freshwaters in India, China, and Southeast Asia (Sinha et al., 2017). This situation presents a major concern for lake ecosystem services because species that require dissolved inorganic N (non-N-fixers) now are predominant, and they will likely be further fueled by greater N inputs in upcoming decades. Increased N loading also inhibits the ability of aquatic systems to efficiently remove N via denitrification (Mulholland et al., 2008; Gardner & McCarthy, 2009), further exacerbating internal N recycling and availability to CyanoHABs. A global N pollution crisis in the twenty-first century is evident and will require comprehensive management approaches to mitigate its effects (Galloway et al., 2002; Erisman et al., 2015). From a scientific standpoint, this paradigm shift is challenging, because eutrophication management is deeply rooted in the presumption that P control is the solution to eutrophication and CyanoHABs (Lewis & Wurtsbaugh, 2008; Sterner, 2008). However, this paradigm is the result of past conditions and, perhaps, misinterpretation of data (e.g., see Scott & McCarthy, 2010, 2011; Paerl et al., 2016a, b) and cannot be applied without consideration of loading sources and individual lake characteristics.

Need to effectively reduce non-point source nutrient inputs

Rapidly expanding urban, agricultural, and industrial development in large lake watersheds has greatly accelerated the production and delivery of nutrients to nutrient-sensitive waters. In most watersheds, the bulk of anthropogenic and natural sources of N and P are delivered by (1) surface water discharge from creeks and rivers, (2) subsurface discharge from groundwater, and (3) atmospheric deposition. The proportions of these nutrient sources vary geographically and demographically. In rural, agriculturally- dominated regions, approximately 50 to 75% of N and P input originates from diffuse, non-point sources (NPS) such as surface runoff, rainfall, atmospheric deposition, and groundwater (Paerl, 1997; U.S. EPA, 2011; Hamilton et al., 2016). Point sources (PS), including wastewater, industrial, and municipal discharges, account for the rest. In contrast, N and P loading in urban watersheds are dominated ($> 50\%$) by PS, while watersheds encompassing both urban centers and intensive agriculture exhibit a more even distribution of these nutrient sources (Castro et al., 2003).

In recognition of a growing eutrophication problem for many large lakes, aggressive reductions in PS nutrient inputs have been undertaken, primarily in developed regions. The focus on PS is based on the fact that these sources are identifiable, accessible, and technologically feasible to reduce. However, as noted above, NPS often dominate and are logistically, economically, and politically more challenging to address (Smith, 2003; Sharpley et al., 2006). NPS are also the most rapidly increasing nutrient sources, especially in watersheds experiencing agricultural expansion (both row crops and animal-based operations). The use of chemical fertilizers, including various forms of N (nitrate, ammonium, urea) and P (largely as phosphate) has grown exponentially (Sharpley et al., 2006; Glibert & Burford, 2017). In

urban and agricultural regions, air pollution is a significant additional NPS, accounting for as much as 30% of external N inputs alone (Paerl et al., 2002; Castro et al., 2003; US EPA, 2011; Erisman et al., 2013; 2015). In the USA, reductions in atmospheric N emissions from fossil fuel combustion through the US EPA Clean Air Act (US EPA, 2011) led to significant reductions in N deposition (Eshleman et al., 2013); although, in agricultural regions, NH_4^+ emissions have continued to rise (Aneja et al., 2007). Realistically, without aggressive NPS reductions, large lake eutrophication will continue unabated in many regions. While it is beyond the scope of this study to formulate and recommend specific and effective NPS reduction strategies, these have been articulated in numerous publications relative to lake ecosystems (Lowrance et al., 1984; Swackhamer et al., 2004; Simpson et al., 2008; Hamilton et al., 2016).

Addressing dual nutrient input reductions in rapidly developing regions: The Lake Taihu, China, experience

Lake Taihu is the third largest freshwater lake in China. About 40 million people live in cities and towns within the Taihu watershed. With recent economic growth, urbanization, and continuing population increases, nutrient loadings and eutrophication of Taihu have rapidly accelerated (Guo, 2007; Qin et al., 2007). Since the mid-1980s, blooms of toxin-producing *Microcystis* spp. have occurred annually (Qin et al., 2007), leading to two highly publicized disruptions in domestic and industrial water usage in 1990 and 2007 (Shen, 1992; Qin et al., 2010).

Results from mesocosm and microcosm bioassays (Xu et al., 2010; Paerl et al., 2011) indicated that phytoplankton production was controlled mainly by P availability in winter–spring, while N availability became a more important controlling factor from summer through fall, when CyanoHABs are most severe (Xu et al., 2010; Paerl et al., 2011) (Fig. 4). Highest biomass yields and greatest potential for bloom formation occurred when both N and P were added, indicating that this hypertrophic lake, like many others (c.f., Elser et al., 2007; Paerl et al., 2016a, b), exhibits varying responses to N and P depending on season and other factors (Paerl et al., 2011; 2014a, b; 2015).

Nutrient dilution and enrichment bioassays indicated that DIN and SRP concentration threshold targets should be set below 0.40 mg N l^{-1} and 0.03 mg P l^{-1}, respectively, to limit intrinsic growth rates of *Microcystis* dominated blooms (Fig. 5). In 1960, Taihu was categorized as oligotrophic because total inorganic N (TIN) in the lake was only 0.05 mg N l^{-1}, and SRP was 0.02 mg P l^{-1}. By 1981, TIN had increased to 0.89 mg N l^{-1}, and SRP remained stable (Sun & Huang, 1993). In 1988, TIN and TN concentrations were 1.12 and 1.84 mg N l^{-1}, respectively, and TP was 0.032 mg P l^{-1} (Sun & Huang, 1993). By 1998, TIN and TN concentrations had increased to 1.58 and 2.34 mg N l^{-1}, respectively, whereas TP was 0.085 mg P l^{-1} (Qin et al., 2007). The 0.89 mg l^{-1} TIN in 1981 can be regarded as a threshold, above which large-scale cyanobacterial blooms regularly occur. During the summer and fall in Taihu, available N levels are below the threshold N concentration, suggesting that further increases in available N load would enhance CyanoHABs in Taihu. CyanoHABs are now even common in Taihu during the winter and spring (Ma et al., 2014). Since *Microcystis* spp. are non-N_2-fixers, controlling N inputs should be effective in reducing the bloom potential for this organism. Although P load reductions remain important, N load reduction is also critical for controlling the severity, spatial extent, and duration of Taihu's cyanobacterial blooms.

Accounting and compensating for climatic change

Recent studies (Paerl & Scott, 2010; Paerl et al., 2011; Havens & Paerl, 2015; Burford et al., 2019; Shi et al., 2019) have pointed to the need to recognize and accommodate climatic changes taking place when developing and modifying watershed nutrient and sediment management strategies aimed at controlling eutrophication and CyanoHABs. Specific symptoms of climatic changes taking place include warming—especially at higher latitudes; increased precipitation, as well as more protracted droughts in various regions of the globe; and increased frequency and intensity of major storm events, including tropical and extra-tropical cyclones, thunderstorms, and other major frontal passages (Trenberth, 2005; Seneviratne et al., 2012;

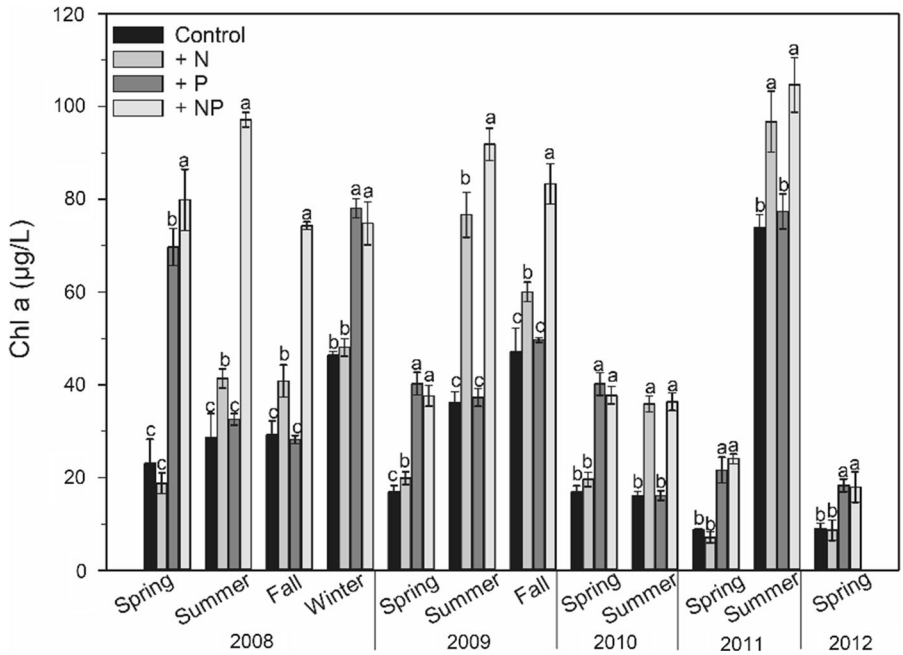


Fig. 4 Phytoplankton biomass (chlorophyll *a*) responses in Lake Taihu, China, bioassays conducted in spring (May–June), summer (July–August), fall (September–October), and winter (December) between 2008 and 2012). Water used in these bioassays was obtained from Meiliang Bay. Initial chlorophyll *a* concentrations are shown. Responses are shown for 3-day incubations in spring, summer, and fall in 2018, with 6-day incubations in winter 2008, and 2-day incubations in spring, summer, and fall 2009–2012. Error bars represent ± 1SD of triplicate samples. Differences between treatments are shown based on ANOVA post hoc tests (a > b > c; $P < 0.05$)

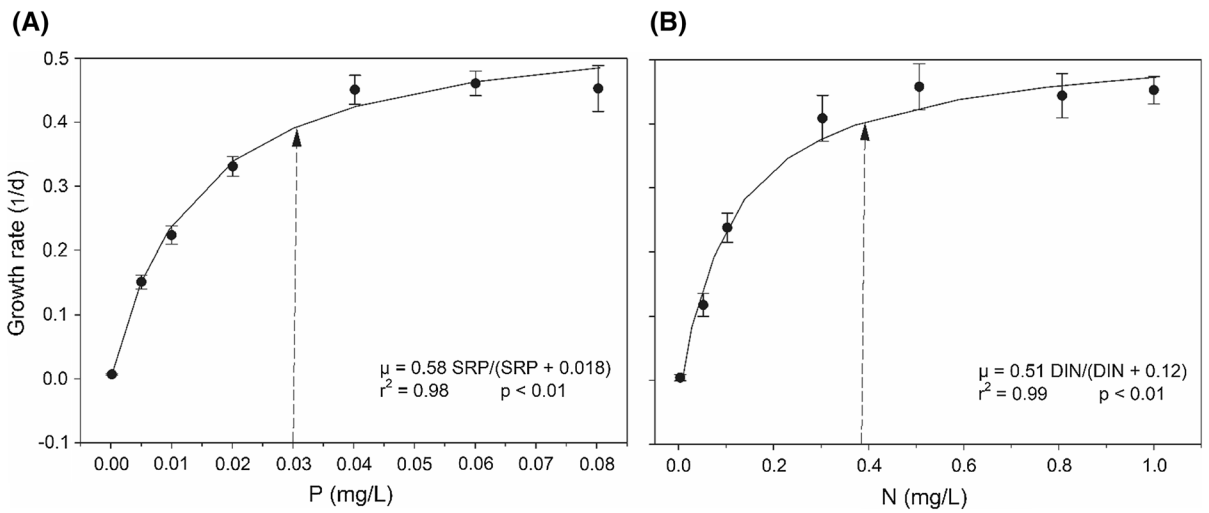


Fig. 5 Growth kinetics of Lake Taihu natural phytoplankton assemblages in response to a range of (A) daily supplied P concentrations and (B) daily supplied N concentrations during summer 2013. Curves were fitted by nonlinear regression. Water for bioassays was collected from the surface of highly eutrophic Meiliang Bay, on the northern side of the lake (Xu et al., 2010). Error bars represent ± 1SD of triplicate samples.

Wuebbles et al., 2014). More severe storms and droughts have led to increased nutrient-laden freshwater discharges to receiving waters (e.g., Ballard et al., 2019), as well as major hydrologic perturbations and shifts. These shifts include changes in water flow and residence time, which, alone or in

combination, affect the initiation, magnitude, toxicity, and duration of bloom events (Zhu et al., 2014; Paerl et al., 2016a, b; Havens et al., 2016).

In addition to more severe storms, climate change influences the El Niño Southern Oscillation (ENSO), which impacts large lakes around the world. For example, a major reduction in ice cover on Lake Superior during a warm El Niño winter in 1997–1998 led to a 'regime shift,' with greater summer evaporation and water temperature and less ice in subsequent winters (Van Cleave et al., 2014). In Lake Kivu (Africa), phytoplankton biomass is highly correlated with the condition of the ENSO (Darchambeau et al., 2013).

Watershed nutrient and sediment management efforts must adapt and adjust to climate change. These climate change events increase hydrologic variability, such as more extreme wet and dry periods leading to more episodic discharges, capture and transport of nutrients, and rapid pulses of elevated nutrient enrichment. Excessive rainfall and runoff, followed by lengthy droughts with increasing hydraulic residence times, provide a perfect growth scenario for CyanoHABs. If these conditions are accompanied by warming (i.e., spring to summer transition), CyanoHABs can continue to proliferate, since they exhibit maximum growth rates at high temperatures (Butterwick et al., 2005; Paerl & Paul, 2012; Guo et al., 2018). Our ability to manage eutrophication and CyanoHABs will depend in part on our capacity to forecast future weather conditions (Hall, 2014). These conditions in turn will affect stratification patterns, dissolved oxygen levels, and nutrient inputs and dynamics, such as internal nutrient recycling and N removal via denitrification (Grantz et al., 2012, 2014; Bruesewitz et al., 2013), all of which may lead to altered food web dynamics.

These physical and biogeochemical changes present a challenge to resource managers aiming to control eutrophication and CyanoHABs in a future favoring their occurrence. A research program that focuses on how extant strategies will be influenced by global warming is needed to support effective large lake CyanoHAB control programs. Specific areas of priority research identified in this study include the following:

(1) Determine how changes in precipitation (intensity and temporal dynamics) resulting from climate change will affect atmospheric N deposition onto inland and coastal waters and watersheds.
(2) Develop new approaches to incorporate this information into ecosystem models and nutrient control strategies that suppress CyanoHABs.
(3) Evaluate effectiveness of existing physical, chemical, and biological control measures with continued changes in hydrology, stratification, and nutrient dynamics caused by climate change.
(4) Evaluate the importance of internal N loading, including legacy N, in fueling CyanoHAB biomass and toxicity, as well as the capacity of denitrification to mitigate excess N loading.
(5) Continue efforts to understand the opposing roles of N_2 fixation and denitrification on annual N budgets and the form and amount of bioavailable N.
(6) Constrain winter N and P dynamics influencing phytoplankton community composition and CyanoHAB biomass and toxicity.
(7) Determine the extent to which existing P loading reduction measures also reduce external N loading and any effects on the N form within those loads.

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