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It Takes Two to Tango: When and Where Dual Nutrient (N & P) Reductions Are Needed to Protect Lakes and Downstream Ecosystems

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It Takes Two to Tango: When and Where Dual Nutrient (N & P) Reductions Are Needed to Protect Lakes and Downstream Ecosystems

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ABSTRACT: Preventing harmful algal blooms (HABs) is needed to protect lakes and downstream ecosystems. Traditionally, reducing phosphorus (P) inputs was the prescribed solution for lakes, based on the assumption that P universally limits HAB formation. Reduction of P inputs has decreased HABs in many lakes, but was not successful in others. Thus, the "P-only" paradigm is overgeneralized. Whole-lake experiments indicate that HABs are often stimulated more by combined P and nitrogen (N) enrichment rather than N or P alone, indicating that the dynamics of both nutrients are important for HAB control. The changing paradigm from P-only to consideration of dual nutrient control is supported by studies indicating that (1) biological N fixation cannot always meet lake ecosystem N needs, and (2) that anthropogenic N and P loading has increased dramatically in recent decades. Sediment P accumulation supports long-term internal loading, while N may escape via denitrification, leading to perpetual N deficits. Hence, controlling both N and P inputs will help control HABs in some lakes and also reduce N export to downstream N-sensitive ecosystems. Managers should consider whether balanced control of N and P will most effectively reduce HABs along the freshwater-marine continuum.
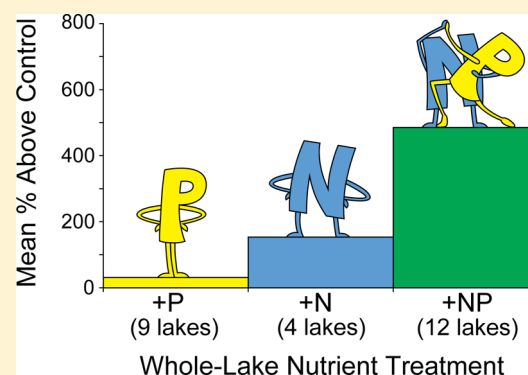
INTRODUCTION

The need to reduce nutrient inputs to the world's surface waters is intensifying as water quality deteriorates and clean water demands increase along the freshwater to marine continuum (Figure 1). In lakes, the problem is often addressed by reducing phosphorus (P) inputs based on the premise that P universally limits primary productivity, algal biomass, and harmful algal bloom (HAB) formation.[1] This practice was successful in some but not all lakes.[2,3] Therefore, we argue that generalizing the "P-only" paradigm is not appropriate, nor is it responsible to shift the eutrophication burden to vulnerable ecosystems downstream (e.g., the Gulf of Mexico, Baltic Sea) by only controlling P upstream. HAB-impacted lakes and reservoirs include some of the world's largest and culturally most important waterbodies (e.g., Lakes Erie and Okeechobee, North America; Lake Victoria, Africa; Lakes Taihu and Dianchi, China; Lakes Balaton and Maggiore, Europe; Lakes Rotorua

and Rotoiti, New Zealand). These lakes exhibit varying nutrient loading and cycling patterns, including periods of P or nitrogen (N) limitation, as well as periods of balanced growth, where N and P act in concert to stimulate biomass production.[2,4−7] Based on geographically diverse evidence presented below, scientists and resource managers should take a more holistic view regarding P-only vs N and P control of HABs for both lakes and coastal ecosystems.
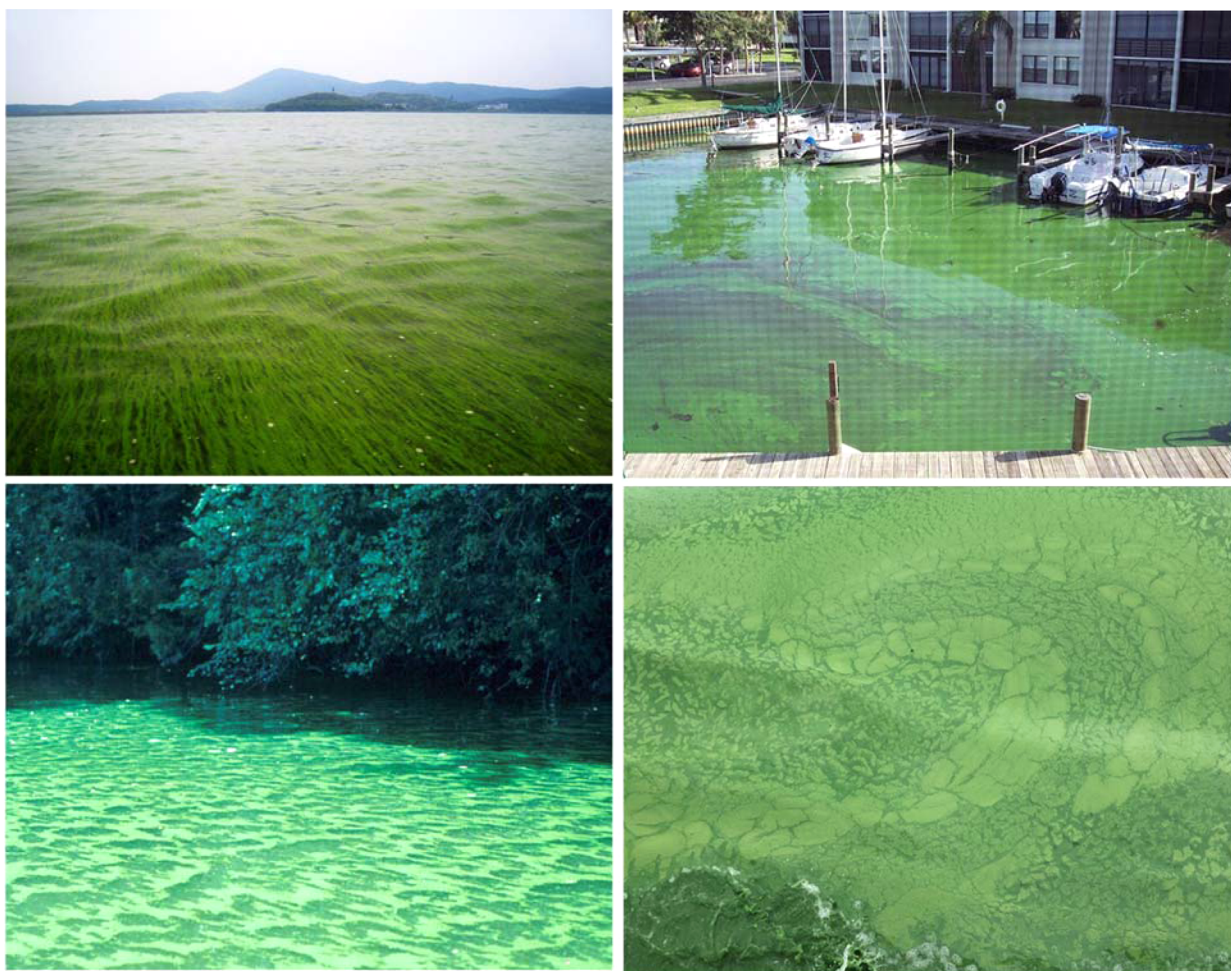
The increasing uses of anthropogenic and bioavailable N and P with increasing population size, intensifying agricultural land use, and associated applications of chemical fertilizers are stressing aquatic resources. This trend has led to increased

Figure 1. Examples of freshwater and estuarine ecosystems with accelerated anthropogenic nitrogen and phosphorus loading, resulting in hyper-eutrophication and harmful algal blooms. Upper left: Toxic cyanobacterial (*Microcystis* spp.) bloom near drinking water intake in Lake Taihu, China. Photo, Hans Paerl. Lower left: Toxic cyanobacterial (*Microcystis aeruginosa*) bloom in the lower Neuse River, NC. Photo, Hans Paerl. Upper right: Mixed species cyanobacterial bloom in a marina on the St. Lucie Estuary, Florida. Photo, Edward Phlips. Lower right: Toxic cyanobacterial (*Microcystis aeruginosa*) bloom in the western basin of Lake Erie, August 2015. Photo, Daniel Hoffman.

nutrient-rich wastewater discharge and intensified nutrient runoff from landscapes.[8−13] Fertilizer use is increasing, and the chemical composition of the fertilizers being applied is changing. For example, in the United States, nearly 90% of the N fertilizer now being applied is urea (Figure 2), a moiety that is rarely even measured in water quality analyses but is known to stimulate HABs and toxin production.[14] Other agricultural practices contributing to nonpoint source nutrient loads include the massive expansion of field tile drainage systems, which remove excess surface water but act as a direct conduit for dissolved nutrients into freshwaters.[15,16] The combined effect of N and P enrichment has accelerated eutrophication and proliferation of HABs on a global scale.[9,10,12,15] These increasing nutrient loads have also promoted eutrophication of nutrient-sensitive, downstream rivers,[17] wetlands,[18] estuaries, and coastal marine ecosystems (e.g., Chesapeake Bay, Albemarle-Pamlico Sound, NC; northern Gulf of Mexico; San Francisco Bay delta; Po River Delta-northern Adriatic Sea).[10,19]

New policies directing managers to control both N and P are needed to protect these aquatic resources. For example, the US Environmental Protection Agency (EPA) has identified the need for water quality standards for both N and P,[20] but the
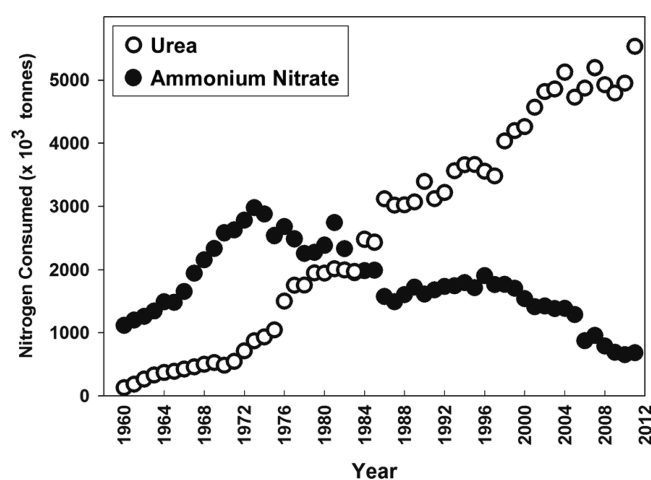

Figure 2. Use of nitrogenous fertilizers in the United States (1960−2011). The data show a definitive shift from ammonium nitrate to urea as the predominant N-fertilizer (data replotted from USDA-ARS).

present approach to remediating HAB-impacted lakes is to only mandate total maximum daily loads (TMDLs) for P. The TMDL process needs to be broadened to include N in

Table 1. Selected Examples of Successful N + P Loading Reductions in Aquatic Systems[a]

location	nutrient reductions	system response
Wuli Lake, China[23]	lake restoration via dredging (removed 41 tons TN, 90 tons TP) and external load reduction	significant decrease in annual TP (33%), TN (54%), Chl *a* (69%) phytoplankton biomass decreased by 91% rapid response to change in TN loading
Tampa Bay, FL[24,25]	60% N load reduction from wastewater treatment, fertilizer reductions, stormwater diversion	reduced algal blooms and hypoxia seagrass coverage highest since 1950 secchi depth more than doubled
Lake Tohopekaliga, FL[26]	66% TP and 60% TN reduction from wastewater treatment and fertilizer reductions, stormwater diversion, and dredging	in-lake TP reduced by 56% in-lake TN reduced by 29% 50% significant long-term decrease in Chl *a* after wastewater diversion
Lake Albufera, Spain[27]	77% P, 24% N loading reduction from sewage diversion	in-lake P reduced by 30% chlorophyll reduced by 50% phytoplankton community shift
Scheldt estuary, Belgium[28,29]	reduction in P and N from industry and P from municipal sources	decreased DIN and DIP, improved O_2 conditions estuary evolved from net DIP sink to net source, net DIN source to sink riverine chlorophyll decreased to <10% of prereduction level

[a]Relevant references are cited below each location.
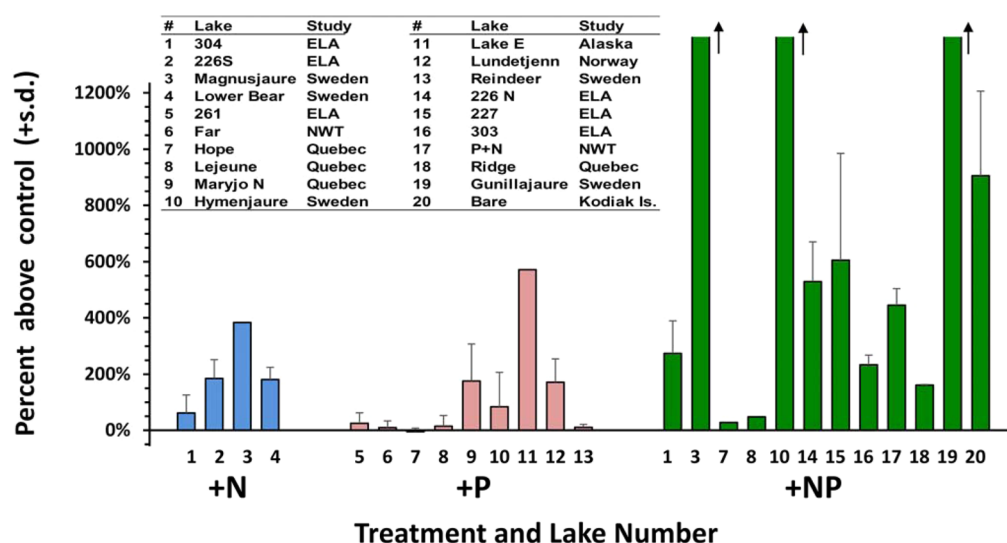
Figure 3. Mean response of phytoplankton to nitrogen (+N), phosphorus (+P), or N+P additions in 20 whole-lake experiments. Responses of chlorophyll, algal biomass, or primary production are expressed relative to controls (either pretreatment sampling or nearby control lakes). Geometric mean responses and standard deviations for the three treatments were +N — 169% ± 100%; +P —34% ± 397%; +NP — 425% ± 419%. Each lake is indicated by a different number. Some lakes received different nutrient additions in subsequent years. Studies were done in the Experimental Lakes Area in Ontario, Canada (ELA;[33,81,82]), northern Sweden,[83,84] Northwest Territories of Canada (NWT;[85]), Norway,[86] Quebec,[87,88] Kodiak Island and Lake E, Alaska.[89] Note that levels of nutrients added to each lake varied between studies, and thus are not directly comparable. The SD when present on a histogram, indicates annual variability of a lake that was treated for more than one year. Note that all of these lakes were oligotrophic and located in north-temperate or arctic zones, and thus are not necessarily representative of lakes in more southern latitudes.

situations where analyses indicate that HABs and detrimental effects in downstream systems are caused or exacerbated by both nutrients. For example, a recent modeling study suggests that nutrients (N and P) must be reduced by 69% to achieve targets for the summer hypoxic zone in the Gulf of Mexico,[21] which supports a $30 billion seafood and recreational fishing industry.[22] Accomplishing loading reductions of this magnitude for a system the size of the Mississippi River watershed would require broad-scale reductions in loading from all sources and all areas of the watershed. Advocating for loading reductions of just one nutrient from individual systems within larger watersheds[1] inhibits progress on achieving these goals, threatens valuable resources throughout the watershed and coastal receiving waters, and is irresponsible on many socioeconomic levels.

Which Nutrients (e.g., P vs N) Control Eutrophication and HABs? Phosphorus removal has improved water quality in many lakes,[1] but improvements from P-only removal are often temporary (e.g., Lake Erie), and many case studies show successful eutrophication control from combined N and P reductions or N alone (Table 1). It is important to note that nutrient management efforts focused on a single nutrient are likely to result in reductions in both nutrients, even if unintended and/or unquantified. Thus, it is often not possible to credit subsequent ecosystem improvements to control of a single nutrient.[30]

A global analysis of nutrient limitation experiments ranging from 1-L microcosms to >10 000-L mesocosms incubated over periods from less than a day to several months also indicated that costimulation by N and P is the rule, rather than the

exception, in eutrophic ecosystems, and strictly N-limited growth occurs with equal magnitude to P-limited growth.[2,31] These containerized experiments were criticized as not being applicable to whole-lake conditions,[1] but multiscale analyses of fertilization experiments showed that phytoplankton responded similarly from bottles to small pond mesocosms.[18,32] Perhaps more importantly, a review of whole-lake fertilization experiments indicates similar patterns (c.f., 33) (Figure 3). In those ecosystem-scale experiments, N and P additions alone often stimulated some algal growth, but much higher growth occurred when both nutrients were added together.

The nutrient that limits phytoplankton growth can vary temporally and geographically (even on microscales at the cellular level), with P limitation in spring often changing to N limitation in summer and fall when temperature and meteorological conditions are conducive to HABs.[4,7,15,34] Impaired ecosystems often receive simultaneously high N and P inputs. If only N or only P is reduced from external inputs, then excess biomass may still occur and perpetuate the problem due to legacy loading, particularly of P, which does not have a gaseous form. A singular focus also threatens downstream ecosystems, such as the northern Gulf of Mexico, which experiences annual bottom-water hypoxia related to excessive N and P inputs (e.g., refs 21 and 22). Internal loading of legacy nutrients illustrates the importance of nutrient recycling dynamics in regulating and exacerbating eutrophication[34] and is particularly high where sulfate concentrations are high. Reduced sulfide binds iron in the sediments, ultimately allowing phosphate to be released (e.g., ref 35). Consequently, in many situations, reducing both N and P from external inputs provides the best opportunity to reduce phytoplankton biomass and prevent shifting nutrient problems to downstream systems. Increasing nutrient inputs worldwide coincide with an unprecedented increase in HABs, especially toxic, non-N-fixing cyanobacterial blooms. These HABs have impeded human water uses (e.g., drinking water, recreational, and commercial fishing) and threaten the long-term sustainability of impacted waters.[15,36] Thus, we can no longer afford to ask whether we have an N or a P problem—we have a nutrient problem that should be addressed at whole-watershed scales.

The fact that many lakes are impacted by both P and N is due in part to the traditional focus on controlling only P inputs, which has resulted in a lack of control of N inputs from watersheds, including N in urban runoff and increased use of fertilizers in agriculture.[15] Other agricultural practices contributing to nonpoint source nutrient loads include the massive expansion of field tile drainage systems, which remove excess surface water but act as a direct conduit for dissolved nutrients into freshwaters.[15,16]

These changes are occurring worldwide and coincide with an unprecedented increase in HABs, especially toxic, non-N-fixing cyanobacterial blooms, which have impeded human uses (e.g., drinking water, recreational, and fishing) and threaten the long-term sustainability of impacted waters.[15,36] For example, estimated costs for the 2011 and 2014 *Microcystis* blooms in Lake Erie (U.S.-Canada) were $71 and $65 million, respectively, for ecosystem service interruptions, such as reduced property values, tourism, recreation, and increased water treatment.[37] It is important to note, however, that the costs of the drinking water shutdown in August 2014 for the City of Toledo are not included in the estimate; therefore, the $65 million figure is likely a large underestimate.[37] However, the cost of not reducing watershed nutrients, and thus having to

respond to and mitigate bloom events, is potentially much greater. Responsibility for dealing with nutrient pollution, like climate change, is a national, and in many instances (Europe, Asia, North America), an international issue.

Cyanobacterial HAB Taxa of Concern with Regard to Nutrient Overenrichment. A prominent example of a cyanobacterial bloom requiring N control occurs in Lake Erie, on the U.S.-Canada border. Severe blooms of toxic, non-N_2 fixing cyanobacteria (e.g., *Microcystis*) have emerged in Lake Erie and other nutrient-enriched systems worldwide (Figure 1), despite previous and ongoing P-focused control.[1,4,5,11] Because these taxa cannot fix atmospheric N, they require combined N sources, such as nitrate (NO_3), ammonium (NH_4), and dissolved organic N (e.g., urea) to support growth, toxin, and bloom formation. Other explanations, which focused on P, have been offered for the emergence of non-N-fixing cyanobacteria (*Microcystis*) and eukaryotic *Cladophora*[38] in Lake Erie, including the increase of spring soluble reactive P loading in recent decades.[39,40] However, these explanations do not consider the fact that these organisms also require combined N for growth and toxin production, and they also fail to resolve temporal discrepancies in the loading of bioavailable P and bloom timing. Cyanobacteria capable of N_2 fixation occur in Lake Erie and other systems, but they often proliferate using combined N from the environment.[15,34,36,41] Recent laboratory evidence has identified at least one of these possible diazotrophs (*Cylindrospermopsis*) as a "reluctant" N_2-fixer, since the process provides only enough cellular N to support very low growth rates.[42] The recent dominance and persistence of non-N_2 fixing taxa, some producing N-rich toxins enhanced by N loading,[43] sends a strong signal that management should focus on reducing N as well as P inputs in this system and others with *Microcystis* or other non-N-fixing taxa (e.g., Lake Okeechobee in Florida, and Lake Taihu in China).[44,45]

While the influence of climate change cannot be ignored,[46,47] additional factors, such as changing land use and related increases in N and P pollution, dominate the persistent eutrophication of Lake Erie and other cyanobacteria-impacted systems.[9,11,12] In February 2016, the governments of Canada and the U.S. signed an agreement to reduce P loads to Lake Erie by an additional 40% by February 2018.[48] While reducing the loading of any nutrient is a positive step, no agreements have mandated N reductions. However, the U.S. EPA recently published a policy brief recommending a dual nutrient management approach.[20] Reducing N loading is challenging, in part because of its diffuse nonpoint source origin, significant release from point sources, and complex biogeochemical transformations that can occur before and after it is delivered to the receiving water body.[13,49,50] Control of nonpoint N sources has attracted limited attention in the freshwater eutrophication literature or from water quality managers,[1−9,11,13,31] but simple, educational approaches targeting agricultural P fertilizer management could easily be expanded, at minimal or no cost, to include N reductions within existing and planned P management approaches. Additionally, new mitigation measures are being developed for agricultural landscapes that would reduce N export.[51] Newer point-source treatments, such as advanced biological nutrient removal and wastewater reuse, reduce both N and P simultaneously and negate the need to choose between one nutrient or the other.[52]

What Are the Sources, Forms, And Fate of the Nutrients Causing Cyanobacterial Blooms? In addition to its sources, the chemical form of N and turnover rates can
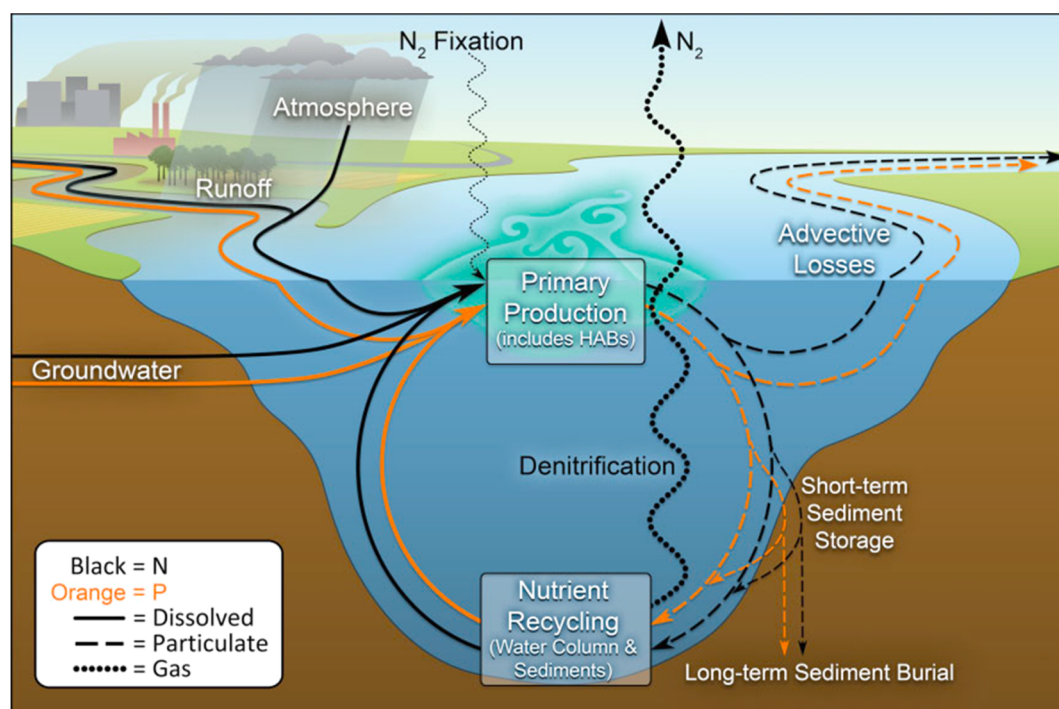
Figure 4. Conceptual diagram, illustrating nitrogen (N) and phosphorus (P) inputs, outputs, and storage in freshwater ecosystems. Note that only N has gaseous forms (stippled lines) that can exchange with the atmosphere (Adapted from[49]).

also affect dominant bloom-formers. For example, in Lake Okeechobee, FL, the cyanobacteria proportion increased, and diatom proportion decreased, as the ratio of NH_4^+:NO_x increased.[53] Additionally, reduced forms of N promote toxin production, high NH_4^+ concentrations are required for expression of toxin production genes,[54] and urea uptake may lead to both increased *Microcystis* biomass and toxin production.[55] Recent cyanobacterial blooms in Lake Okeechobee are dominated by non N_2-fixing *Microcystis*, whereas in the late 1980s, extensive pelagic blooms were caused primarily by the N_2-fixing *Anabaena circinalis*.[56] Decades of excessive P inputs have often resulted in N limitation with surplus soluble reactive P.[57] A strict P standard for Okeechobee and a P-TMDL was set by the U.S. EPA, but no such limit or standard has been established for N. The underlying, unsupported premise of lake managers is that if N were controlled more effectively than P, and the lake's N:P ratio decreased, then it would lead to increased prevalence of N_2-fixing cyanobacteria.[1] Rather than advocating for stricter N control, some constituents in the region have suggested that the regulatory agencies allow pumping of N-rich water from south of the lake back into the ecosystem, as it did in the past, to elevate the N:P ratio. Other recent studies have also proposed N additions to decrease cyanobacteria blooms and toxins in lakes (e.g., ref 58). However, total N is often the best predictor of toxin concentrations in lakes,[59] and there are numerous studies showing that toxin production is associated with N supply (e.g., ref 43). Therefore, adding N to mitigate cyanobacterial blooms is not likely to be a suitable or responsible management approach.

One concern is that HABs may be exacerbated by the changing chemical nature of N and P being applied to agricultural landscapes (Figure 2;[2,9,60]). Experimental and modeling studies have now linked these changes in both P (as SRP;[15,40]) and N (as urea) to increased biomass and

changes in community structure toward HABs.[60−64] Indeed, in the last 50 years there has been a tremendous shift in the chemistry of nitrogenous-fertilizers used in agriculture: while ammonium nitrate had been historically preferred, urea (due to concerns that range from yield relative to cost and even safety) has markedly increased as the N-source of choice (Figure 2). And while the chemistry of different N-sources does not appear in at least a few cases to be shaping total plankton biomass,[14] ammonium and urea are also linked to up-regulation of microcystin production, and urease activity has been correlated with increased microcystin concentrations.[14] Given the need for specific enzymes for cells to directly utilize urea as a nitrogenous source, it is expected that such a shift in nitrogen chemistry may alter microbial (including plankton) community structure.

How Much Improvement Can Be Attained by Reducing N in Addition to P? The primary argument against combined N and P control of eutrophication is that N_2 fixation can make up ecosystem-scale N deficits, making N control irrelevant to eutrophication management.[1,65] However, N_2 fixation is controlled by the organism's needs and capabilities relative to environmental and/or biogeochemical factors (i.e., denitrification, grazing, nutrient regeneration[66]) and are constrained by factors other than nutrient availability.[67−70] For example, N_2 fixation is typically not detectable in phytoplankton when measurable NO_3 and NH_4 exists in the water column.[69,70] This pattern results from different energetic costs associated with N utilization by phytoplankton, with NH_4 being the most energetically favorable, and N_2 the least favorable.[71] The N cycle also has natural removal mechanisms at whole-lake scales, such as denitrification (the conversion of NO_3 to relatively inert N_2), which can counteract N inputs from N_2 fixation. Denitrification increases with increased P-driven eutrophication[72] because of increased organic matter availability and hypoxic and anoxic zones conducive to

Figure 5. Conceptual model showing that the interaction between external N and P inputs and the net flux of N_2 gas into and out of the reactive N pool of lakes determines whether N or P are in shortest supply relative to phytoplankton demand and indicates a possible mechanism for explaining the preponderance of N Figure + P colimited conditions in lakes throughout the world. The stoichiometric thresholds identified in the external inputs is derived from global patterns of phytoplankton stoichiometry and strict P limitation (N:P ≥ 23 by mass), strict N limitation (N:P ≤ 9 by mass), or N+P colimitation (23 > N:P > 9) as described by Guildford and Hecky.[75] See text for explanation.

denitrification.[73] Because N occurs in gaseous forms, while P has no gaseous form, P inputs are often retained at higher proportions than N inputs (Figure 4). The relative magnitude of N loss through denitrification and N gain through N_2 fixation is an important barometer for the importance of combined N pollution in aquatic ecosystems.

Data on the balance between denitrification and N_2 fixation is limited, especially in lakes,[74] but groupings of theoretical lake conditions can demonstrate the importance of N transformations on whole lake nutrient status. Figure 5 shows categories of lakes based on their N:P ratio from external inputs and the balance between N_2 fixation and denitrification. Strict P limitation occurs when the N:P ratio of external inputs is greater than 23 (by mass),[75] and N_2 fixation is either greater than or equal to annual denitrification rates (panels 4 and 7, Figure 5). Phytoplankton would be strictly N-limited where the N:P of external inputs is less than 9, and denitrification exceeds N_2 fixation (panel 3, Figure 5). Where loading N:P is less than 9, and annual N_2 fixation and denitrification are approximately equal, phytoplankton growth is either N-limited or exhibits balanced growth, depending on the short-term efficiency of N_2 fixation. When the rate of external N inputs exceeds rates of N_2 fixation or denitrification,[66,69,76−78] lakes will usually exhibit balanced growth (i.e., N+P costimulation) when the N:P ratio of external inputs is between 9 and 23 (panels 2, 5, 8 in Figure 5). Lakes will also exhibit balanced growth when the N:P ratio of external inputs is greater than 23, and the annual denitrification rate exceeds N_2 fixation (panel 1, Figure 5), or when the N:P ratio of external inputs is less than 9, and the annual denitrification rate is less than N_2 fixation (panel 9, Figure 5). Thus, in five of the nine scenarios shown in Figure 5,

lakes will exhibit balanced growth via N+P costimulation. These results are supported by findings from small-scale bioassays,[2,7,32,34] larger scale incubations,[32,34] and whole-lake fertilization experiments (Figure 3). As such, arguments against N control based on apparent short-term bottle effects[1] do not hold up under greater scrutiny of results. When properly interpreted, even results from whole-lake experiments continually support the need for dual nutrient control (e.g., refs 33,79 Figure 3).

■ CONCLUSIONS

Given that lakes sometimes respond to P-only control, but in other instances to a balanced control of N and P, and given that downstream ecosystems are sensitive to excess N loading, a new paradigm is needed. Resource managers need to (1) holistically consider lakes and downstream rivers, estuaries, and other coastal systems in developing nutrient control strategies; (2) move away from presuming that P-only control is the only solution to eutrophication issues; and (3) determine whether a source control program targeted at both N and P will provide greater ecosystem benefits.

Many of the approaches already being implemented to target P loading reductions will undoubtedly also influence N loads, but recognizing the importance of N in promoting HABs should also stimulate innovation for reducing N loads. Control of both nutrients will require substantial financial investment but will be cost-effective over the long-term relative to the high costs associated with responding to HAB issues (e.g., Toledo). Initial efforts should include implementation of N control based on stoichiometric needs relative to allowed P regulations. Incorporating emerging science into water quality policies is

critical to successful rehabilitation of inland and coastal aquatic resources. For example, P control is improved by differentiating dissolved reactive P from total P (e.g., ref 11), but such management actions ignore internal P loading and will have little effect on HABs that rely on combined N for growth and toxin production. Similarly, differentiating reduced N loads from total N loads is critical for creating management guidelines. Conceptual models of N and P dynamics in ecosystems susceptible to HABs should be developed, refined, and incorporated into quantitative models based on experimental studies of N and P transformations in the water and sediments of these ecosystems. Management guidelines should be revisited regularly based on subsequent improvements in our understanding of the interactive effects of these two critical nutrients. These policy changes are urgent because warming caused by climate change is expected to make HAB control even more difficult[80] in the future if external nutrient loads are not reduced. Ref 64.

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Notes

The authors declare no competing financial interest.

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