esa ECOSPHERE

SYNTHESIS & INTEGRATION

Cyanobacteria as biological drivers of lake nitrogen and phosphorus cycling

Kathryn L. Cottingham,[1,†] Holly A. Ewing,[2] Meredith L. Greer,[3] Cayelan C. Carey,[4] and Kathleen C. Weathers[5]

[1]*Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA*
[2]*Program in Environmental Studies, Bates College, Lewiston, Maine 04240 USA*
[3]*Department of Mathematics, Bates College, Lewiston, Maine 04240 USA*
[4]*Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia 24061 USA*
[5]*Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA*

Citation: Cottingham, K. L., H. A. Ewing, M. L. Greer, C. C. Carey, and K. C. Weathers. 2015. Cyanobacteria as biological drivers of lake nitrogen and phosphorus cycling. Ecosphere 6(1):1. http://dx.doi.org/10.1890/ES14-00174.1

Abstract. Here we draw attention to the potential for pelagic bloom-forming cyanobacteria to have substantial effects on nutrient cycling and ecosystem resilience across a wide range of lakes. Specifically, we hypothesize that cyanobacterial blooms can influence lake nutrient cycling, resilience, and regime shifts by tapping into pools of nitrogen (N) *and* phosphorus (P) not usually accessible to phytoplankton. The ability of many cyanobacterial taxa to fix dissolved N_2 gas is a well-known potential source of N, but some taxa can also access pools of P in sediments and bottom waters. Both of these nutrients can be released to the water column via leakage or mortality, thereby increasing nutrient availability for other phytoplankton and microbes. Moreover, cyanobacterial blooms are not restricted to high nutrient (eutrophic) lakes: blooms also occur in lakes with low nutrient concentrations, suggesting that changes in nutrient cycling and ecosystem resilience mediated by cyanobacteria could affect lakes across a gradient of nutrient concentrations. We used a simple model of coupled N and P cycles to explore the effects of cyanobacteria on nutrient dynamics and resilience. Consistent with our hypothesis, parameters reflecting cyanobacterial modification of N and P cycling alter the number, location, and/or stability of model equilibria. In particular, the model demonstrates that blooms of cyanobacteria in low-nutrient conditions can facilitate a shift to the high-nutrient state by reducing the resilience of the low-nutrient state. This suggests that cyanobacterial blooms warrant attention as potential drivers of the transition from a low-nutrient, clear-water regime to a high-nutrient, turbid-water regime, a prediction of particular concern given that such blooms are reported to be increasing in many regions of the world due in part to global climate change.

Key words: bloom; eutrophication; oligotrophic; phytoplankton; regime shift; resilience.

Received 4 June 2014; revised 6 September 2014; accepted 15 September 2014; final version received 24 October 2014; **published** 8 January 2015. Corresponding Editor: W. Cross.

Copyright: © 2015 Cottingham et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. http://creativecommons.org/licenses/by/3.0/

† **E-mail:** Kathryn.L.Cottingham@dartmouth.edu

Introduction

Lakes are a crucial and primary source of water for drinking, irrigation, cooling, recreation, food production, and dilution of wastes and pollutants (Wetzel 2001). At the same time, lakes are profoundly impacted by anthropogenic activities that modify both external (outside the

Box 1

Mechanisms by which cyanobacteria can alter lake N cycling

The ability of freshwater cyanobacteria to drive N cycling by bringing in "new" N (sensu (Dugdale and Goering 1967) is well-documented in the limnological literature (e.g., Howarth et al. 1988*a*, *b*). Cyanobacteria bring available N into the lake ecosystem by transforming dissolved, atmospherically-derived N_2 into biologically active forms that can partially alleviate N limitation and fuel phytoplankton population growth (Schindler 1977, Smith 1983, Howarth et al. 1988*b*, Wetzel 2001, Schindler et al. 2008, Schindler 2012, Beversdorf et al. 2013, Scott and Grantz 2013). For example, in Lake 227 at the Experimental Lakes Area, Canada, N-fixers helped to reduce N limitation and maintain relatively high primary productivity when P was added alone, or with N but at an N:P ratio well below phytoplankton demand (Schindler 1977, Schindler et al. 2008; but see Scott and McCarthy 2010). More generally, N-fixing cyanobacteria often dominate the phytoplankton community when there is excess P and insufficient N to support eukaryotic phytoplankton (Smith 1983, Paerl 1988, Reynolds 2006, Schindler 2012, Sommer et al. 2012).

The majority of cyanobacterial taxa that form blooms in freshwater lakes are capable of fixing N, including *Anabaena, Aphanizomenon, Cylindrospermopsis*, *Gloeotrichia*, and *Nostoc* (Paerl 1988), and some are capable of storing excess N intra-cellularly as cyanophycin (Allen et al. 1984). Interestingly, the few taxa that are not able to fix N (e.g., *Microcystis*) often dominate hyper-eutrophic lakes, where both N and P may be less limiting than in low-nutrient lakes due to high levels of anthropogenic enrichment from surrounding watersheds (Xu et al. 2010, Paerl and Otten 2013*b*).

boundaries of the lake itself) and internal (within-lake) drivers at a variety of spatial and temporal scales (Williamson et al. 2008). For example, a number of studies have linked recent increases in water column cyanobacterial blooms to warmer temperatures and stronger stratification already underway due to global climate change (Jöhnk et al. 2008, Wagner and Adrian 2011, Carey et al. 2012*b*, Posch et al. 2012) as well as ongoing nutrient loading from watersheds (Watson et al. 1992, Downing et al. 2001, Elmgren 2001, Conley et al. 2009, Smith and Schindler 2009, Brookes and Carey 2011, Paerl et al. 2011*a*). Because such blooms negatively impact property values (Wilson and Carpenter 1999) and can produce toxins that pose a health risk to both humans and livestock (Hudnell 2010), they garner substantial public attention.

Rising cyanobacterial abundance, especially in lower-nutrient lakes, may also be worth scientists' attention, as several interesting aspects of cyanobacterial ecophysiology and life history make it possible for cyanobacteria to alter lake nutrient cycling. Specifically, cyanobacteria can increase available pools of the limiting nutrients nitrogen (N) (Elser et al. 2007, Lewis and Wurtsbaugh 2008, Conley et al. 2009, Paerl et al. 2011*b*) and phosphorus (P) (Schindler 1977, Schindler and Hecky 2008, Schindler et al. 2008). As has been extensively noted in the literature (Howarth et al. 1988*a*, *b*, Wetzel 2001), many cyanobacteria—unlike eukaryotic phytoplankton—fix nitrogen (N) by accessing dissolved N_2 gas and can release the fixed N into the water column in biologically available forms, such as ammonium (see Box 1). Moreover, some cyanobacterial taxa are able to access pools of P in the sediments and bottom waters that are not generally available to other phytoplankton (see Box 2 and Fig. 1), similar to other mobile organisms that move nutrients from the sediments into the water column, such as benthic-feeding fish (Schindler et al. 1996, Vanni 1996), the large crustacean *Gammarus* (Wilhelm et al. 1999), and the phytoplankter *Gonyostomum* (Salonen and Rosenberg 2000). Cyanobacteria therefore have the potential to provide a subsidy of both N and P to the water column, nutrients that

Box 2

Mechanisms by which cyanobacteria can alter lake P cycling

Cyanobacteria may drive lake P cycling by accessing pools of P that are not generally available to eukaryotic phytoplankton (Fig. 1); these mechanisms are generally less widely appreciated than N fixation, especially outside of limnology. Many cyanobacterial taxa have ecophysiological traits that enable them to access the pool of sediment P, even in oxygenated conditions. These traits include a high-affinity phosphate uptake system activated at low P concentrations (Dignum et al. 2005), the production of extracellular polyphosphatase enzymes to access organic or sediment-bound P (Healey 1982), the capacity for luxury uptake (Healey 1982) and subsequent storage of P in excess of immediate demand (Whitton et al. 1991), and the ability to regulate buoyancy in the water column using gas vesicles (Perakis et al. 1996, Head et al. 1999*b*). These traits allow certain cyanobacterial taxa to access P stored in lake sediment (Xie 2006) or trapped in the hypolimnion of a stratified lake, sequester it in biological packets, and transport it to surface waters over daily to seasonal time scales (Fig. 1). This cyanobacterial translocation of P may be important in both stratified and well-mixed lakes, although the mechanisms may differ.

At a seasonal time scale, cyanobacteria in both stratified and well-mixed lakes can move P from the lake bottom into surface waters during recruitment from thick-walled dormant cells (akinetes) or from individuals that over-winter actively on or near the lake sediment (arrow 1 in Fig. 1). One example is *Gloeotrichia echinulata*, which overwinters as akinetes, germinates, and then spends 2–3 weeks in the sediment after germination, accessing sediment P via mechanisms that have not been well studied but are thought to include uptake of interstitial phosphate and excretion of extracellular enzymes to cleave phosphate from organic complexes (Whitton et al. 1991, Istvanovics et al. 1993, Pettersson et al. 1993). Because of its luxury uptake, each *G. echinulata* colony can contain as much as 81 pg P (Pettersson et al. 1993); this P is then moved into the water column during recruitment (Istvanovics et al. 1993, Pettersson et al. 1993, Tymowski and Duthie 2000). Less actively, entrainment may resuspend colonies, resulting in further upward transport (Mur et al. 1999).

Seasonal recruitment of cyanobacteria can be an important contribution to P cycles in stratified eutrophic lakes, above and beyond the contributions of redox-mediated recycling due to deep-water anoxia. For example, *G. echinulata* accounted for ~66% of the total internal P loading in Green Lake, Washington, USA (2.25 mg P m^{-2} d^{-1}; Barbiero and Welch 1992) and Lake Erken, Sweden (2.4 mg m^{-2} d^{-1}; Istvanovics et al. 1993). Moreover, water column particulate P in Antermony Loch, Scotland (Pitois et al. 1997) and total P in Lake Peipsi, Estonia (Noges et al. 2004) increased in association with *G. echinulata* blooms. Other cyanobacterial taxa implicated in P translocation through recruitment include *Cylindrospermopsis raciborskii* (Istvanovics et al. 2000, 2002), *Coelosphaerium naegelianum* (Perakis et al. 1996), and *Microcystis* (Johnston and Jacoby 2003).

At a daily time scale, vertical migration between the upper and lower parts of a stratified water column (arrow 2 in Fig. 1) has been observed for colonial cyanobacteria with strong buoyancy control, including *Anabaena* (Head et al. 1999*b*), *Aphanizomenon* (Trimbee and Harris 1984, Osgood 1988, Barbiero and Welch 1992, Barbiero and Kann 1994, Jacobsen 1994), and *Microcystis aeruginosa* (Head et al. 1999*b*). These taxa are able to descend from the warm, well-lit epilimnion to the colder, poorly lit hypolimnion that can contain large amounts of P, especially when bottom waters are anoxic. Once P-replete, colonies return to the well-lit, but nutrient-poor, surface waters using gas vesicles and other mechanisms (Paerl 1988). Because this P would otherwise be released into surface waters only via storm-induced entrainment or seasonal

Box 2. Continued.

mixing at lake turnover, diel vertical migration by cyanobacteria can provide a key source of P during periods of stable thermal stratification (Osgood 1988). For example, *Aphanizomenon flos-aquae* has been demonstrated to pump P into the water column during its diurnal migrations, increasing epilimnetic P concentrations when it is abundant (Trimbee and Harris 1984, Osgood 1988, Barbiero and Welch 1992, Barbiero and Kann 1994, Jacobsen 1994); estimated P loading rates for this species range from near those of *G. echinulata* (2.16–3.56 mg P m^{-2} d^{-1}; Barbiero and Kann 1994) to 10 times that much (33 mg P m^{-2} d^{-1}; Osgood 1988).

Finally, some cyanobacteria appear to be particularly effective at liberating bound P in sediments that can then be moved upward in biological packets or through physical processes such as entrainment (arrow 3 in Fig. 1). As with seasonal recruitment, this process can occur in both stratified and well-mixed lakes, and has been studied only in eutrophic systems. For example, *Microcystis* appears to facilitate the release of sediment-bound P, increasing soluble reactive P in and near the sediments (Brunberg and Bostrom 1992, Brunberg 1995) and in the water column during blooms (Xie et al. 2003, Shi et al. 2004), possibly due to productivity-induced increases in pH (Xie et al. 2003, Xie 2006). In fact, Xie et al. (2003) found that internal P loading by *Microcystis* during bloom formation could be two to four times as high as the average external loading in Lake Donghu, China (16.6–36.4 mg m^{-2} d^{-1} vs. 8.8 mg m^{-2} d^{-1}).

can then be liberated to the rest of the lake system through processes as diverse as cellular leakage or viral lysis (Healey 1982, Istvanovics et al. 2000), parasitism by bacteria or fungi (Paerl 1988), decomposition of detached filaments and dead colonies (Healey 1982), and grazing by herbivores (Fey et al. 2010). These subsidies may be particularly important in lakes that currently have relatively low nutrient concentrations, but which have recently begun to experience nuisance cyanobacterial blooms, possibly due to climate warming (Wiedner et al. 2007, Jöhnk et al. 2008, Kosten et al. 2012, Paerl and Otten 2013*b*).

The goals of this paper are to draw attention to the potential for cyanobacteria to have profound

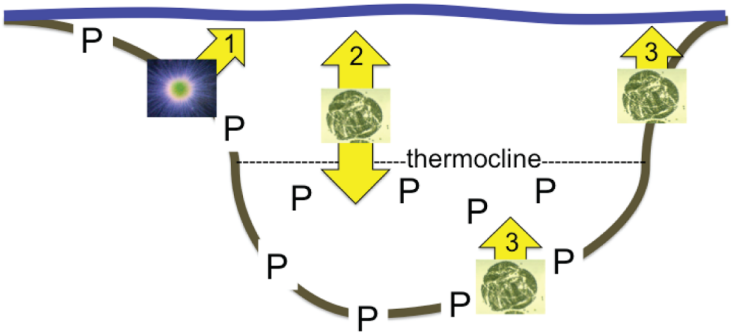

Fig. 1. The three primary mechanisms by which cyanobacteria can affect P recycling: (1) cyanobacteria that overwinter on or near lake sediments access sediment P and then transport it upward during seasonal recruitment; (2) in stratified lakes, cyanobacteria sink to the hypolimnion, acquire P, and then rise back to the surface during diel vertical migrations; and (3) benthic cyanobacteria enhance P release from sediments, increasing near-sediment P and also storing it in bodies. Each mechanism is explained in more detail in Box 1. Photographs used by permission: *Gloeotrichia echinulata* by Sam Fey (Dartmouth) and *Microcystis aeruginosa* by Sao Inouye (University of Tsukuba), Mark Schneegurt (Wichita State University), and Cyanosite (www-cyanosite.bio.purdue.edu).

effects on lake nutrient cycling and ecosystem resilience and begin to explore these effects using a simple model of coupled N and P cycling. We demonstrate how some cyanobacteria can influence nutrient transport, lake trophic state, and resilience via biological alterations of N and P cycles, potentially amplifying the effects of redox-mediated internal P loading, anthropogenic activities in watersheds, and climate warming. Moreover, because cyanobacteria can reach high densities even in lakes with relatively modest total P concentrations (Downing et al. 2001, Ernst et al. 2009, Winter et al. 2011, Carey et al. 2012*a*), they may drive nutrient dynamics and resilience in lakes across a range of trophic states and stratification regimes.

Cyanobacteria and Lake Regime Shifts

The idea that cyanobacteria have the potential to drive lake N and P cycling complements and extends current literature about resilience and regime shifts in lakes. Here, we define "resilience" as the ability of an ecosystem to maintain itself in the same general state despite perturbation (sensu Holling 1973) and a "regime shift" as a major reorganization in ecosystem structure and/or function (e.g., Scheffer et al. 2001) linked to changes in the dominant feedbacks controlling system functions (e.g., Scheffer et al. 2001, Carpenter 2003, Scheffer 2009). Changes associated with regime shifts can be summarized in three steps: first, stabilizing feedbacks that keep a system in its current state weaken; second, stabilizing feedbacks are replaced by switching feedbacks that drive the system to a new state; and third, stabilizing feedbacks for the new state are established, thereby inhibiting restoration to the original state.

For example, low-nutrient lakes remain clear in large part because there is strong nutrient limitation of phytoplankton growth (Wetzel 2001). However, hypolimnetic anoxia creates a difficult-to-reverse switching feedback during the transition to a turbid, eutrophic regime (Nurnberg 1984, Carpenter 2003): when bottom waters go anoxic, the large pool of stored sediment P is released from complexes with metals. This P mixes upward, decreasing P limitation and increasing phytoplankton productivity (blooms). Later, after phytoplankton blooms senesce, they sink to the bottom and decompose, reducing oxygen still further and releasing yet more P (e.g., Carpenter and Cottingham 1997, Cooke et al. 2005, Smith and Schindler 2009). Hypolimnetic anoxia can also become a stabilizing feedback maintaining the high-nutrient state (Carpenter 2003, Havens 2008), as can positive feedbacks resulting from the organic matter generated by cyanobacteria (e.g., Huisman et al. 2005, Paerl and Otten 2013*a*, *b*).

Building from this conceptual framework, we hypothesize that some cyanobacteria have the potential to serve as a switching feedback that decreases the resilience of low-nutrient lakes by tapping into pools of N and P that would not be otherwise available (Boxes 1 and 2). These "new" nutrients may alleviate some degree of nutrient limitation in the water column, thereby facilitating the growth of other phytoplankton whose later decomposition may promote hypolimnetic anoxia. For example, we know from eutrophic lakes that the large colonial cyanobacterium *Gloeotrichia echinulata* increases internal P loading (Barbiero and Welch 1992, Istvanovics et al. 1993, Pettersson et al. 1993) and can fix N (Stewart et al. 1967, Vuorio et al. 2006, 2009), suggesting that this species might stimulate phytoplankton by increasing nutrient availability. Consistent with this expectation, *G. echinulata* stimulates other phytoplankton in the laboratory (Carey and Rengefors 2010) and in nutrient-limited mesocosms (Carey et al. 2014*a*, *b*). Moreover, laboratory experiments suggest that large populations of *G. echinulata* may increase water column N and P (Carey et al. 2014*b*), as observed in more nutrient-rich lakes (Pitois et al. 1997, Noges et al. 2004). Further, paleoecological studies of Long Pond in Maine show increases in markers of eutrophication coincident with increases in *G. echinulata*, but without clearly corresponding increases in water column P (H. A. Ewing et al., *unpublished data*). Together, these lines of evidence suggest the potential for *G. echinulata* to initiate positive feedback loops that accelerate eutrophication.

Thus, a handful of studies provide evidence that at least one cyanobacterial taxon may contribute to positive feedbacks that enhance eutrophication, but we lack empirical studies quantifying the general role of many different

types of cyanobacteria in N and P cycling, especially in low-nutrient lakes. Are cyanobacteria important early in the process of eutrophication, in that they help drive a low-nutrient system to the eutrophic state? Does P translocation by cyanobacteria in mesotrophic lakes interfere with management strategies that attempt to limit P availability by keeping external loading low or by maintaining an oxic hypolimnion?

The ability of cyanobacteria to influence the availability of N and P is worth particular attention for several reasons. First, cyanobacterial dominance may be promoted by global climate change (Wiedner et al. 2007, Jöhnk et al. 2008, Kosten et al. 2012, Paerl and Otten 2013*b*), suggesting that these mechanisms may increase in importance in the future. Second, N and P can be co-limiting to phytoplankton growth (Elser et al. 2007, Lewis and Wurtsbaugh 2008) and the development of cyanobacterial blooms (Paerl et al. 2011*a*), suggesting that cyanobacteria that can tap into pools of both nutrients may have particularly strong effects on co-limited low-nutrient lakes and may also thwart attempts to manage symptoms of eutrophication in high-nutrient systems (Larsson et al. 2001, Lewis and Wurtsbaugh 2008, Conley et al. 2009, Lewis et al. 2011). Below, we explore the potential for cyanobacteria to contribute to switching feedbacks in oligotrophic systems using a simple differential equations model for coupled N and P cycling.

Switching Feedbacks: Explorations with a Simple Model

Model structure

Our model describes changes in the pools of N and P in the part of the water column occupied by phytoplankton and allows us to explore the factors that are likely to alter lake trophic state, resilience and regime shifts. Two state variables, N and P, represent the total pools of nitrogen and phosphorus, respectively, including all forms of the nutrients (e.g., available, dissolved organic, and particulate organic [stored in bodies]). Changes in N and P are a function of external inputs, internally mediated P recycling and N fixation, and a loss term (Fig. 2), with N fixation tied explicitly to P concentration (see Eq. 2).

We used the Carpenter et al. (1999) formulation for P:

$$\frac{dP}{dt} = I_P - sP + \frac{r\,P^q}{m^q + P^q} \tag{1}$$

where I_P is the external input of P (inflow + deposition in Fig. 2), s is the output rate (sP is outflow + sedimentation in Fig. 2), and the third term represents internally driven recycling of sediment P: r is the maximum P recycling rate, m indicates the P concentration at which P recycling reaches half the maximum rate (and at which it is increasing most rapidly), and q is a shape parameter that controls how quickly P recycling reaches its maximum ($q \geq 2$).

Using this framework, we considered two mechanisms by which cyanobacteria could affect the P cycle. First, we considered cyanobacteria that follow arrow 1 in Fig. 1 as increasing the inputs of P represented by the parameter I_P: their access to sediment P is generally independent of water column P concentrations and makes P available that would not normally be available in surface waters, especially in the well-oxygenated, low-nutrient systems in which redox-mediated recycling of sediment P occurs rarely, if at all. Alternatively, we considered cyanobacterial mobilization of P in arrows 2 and 3 in Fig. 1 as altering recycling rates depending on water column P concentration. In this case, cyanobacteria could increase r, the maximum P recycling rate, or decrease m, the P concentration at which P recycling reaches half of that maximum rate. We considered each of these possibilities in evaluating the potential effects of cyanobacteria on model behavior.

For N, we incorporated both stoichiometric constraints on N fixation and patterns in cyanobacterial abundance and N fixation across lakes (e.g., Smith 1983, Downing et al. 2001), such that

$$\frac{dN}{dt} = I_N - s\,N + f\,P\left[\frac{e^{-\alpha\left(\frac{N}{P}-k\right)}}{1 + e^{-\alpha\left(\frac{N}{P}-k\right)}}\right] \tag{2}$$

where I_N is the external input of N (inflow + deposition in Fig. 2); s is the output rate for losses due to outflow, sedimentation, and denitrification; f is the maximum N fixation rate; and k and α are shape parameters with the requirements that $k > 0$ and $\alpha > 0$. For this initial model, we assumed that cyanobacterial addition of "new" N via N fixation increases linearly with P

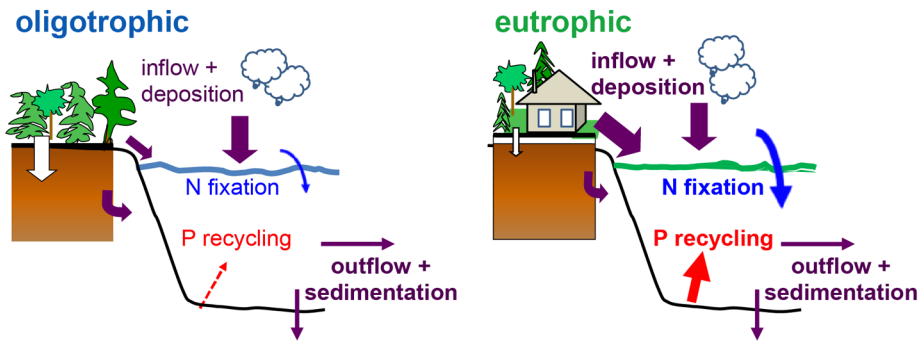

Fig. 2. Schematic of N and P fluxes in oligotrophic and eutrophic lakes examined in our model of coupled N and P cycling (see text). Our model assumes that external inputs (inflow + deposition), biologically mediated N fixation, and chemically and biologically mediated P recycling are higher in eutrophic conditions than in oligotrophic conditions. In each schematic, the size of an arrow represents its relative importance.

concentration, since P is needed to build the enzymes required in N fixation (Elser et al. 1996). This formulation is simpler than the asymptotic association reported by Jankowski et al. (2012) but provides a tractable starting point. We also assumed, based on cyanobacterial abundance patterns (Smith 1983, Gophen et al. 1999), that N fixation rates follow a logistic function of the N:P ratio (by mass) in which N fixation is highest at low N:P ratios, decreases as N:P ratios begin to increase, and declines to zero at high N:P ratios. As with the Carpenter et al. (1999) model of P dynamics, this equation is just a starting point: we recognize that N fixation is controlled by many different environmental conditions (e.g., Wetzel 2001, Forbes et al. 2008) and that this simple formulation ignores benthic N transformations, including N fixation (e.g., Reuter and Axler 1992) and denitrification (e.g., Seitzinger et al. 2006). We assume that denitrification losses are relatively small, and thus use the same output rate s for both P and N for the model runs presented here. This is likely reasonable for low-nutrient conditions, but an oversimplification for lakes with higher nutrient concentrations.

In parameterizing these equations, we assumed that only one cyanobacterial species is dominant or that the whole assemblage of cyanobacterial species responds similarly across a range of P and N:P ratios, even if the relative abundance of individual taxa within the assemblage changes. We first generated plausible ranges for each parameter based on the literature wherever possible, and in the absence of published studies for some parameters, used data from unpublished sources (Table 1).

Modeling results

Here, we describe the highlights of our model explorations as they relate to potential cyanobacterial effects on lakes, particularly the ability of cyanobacteria to facilitate a shift from a low-nutrient to a high-nutrient state. Most of our simulation studies began from the perspective of a lake with low-to-moderate nutrient conditions experiencing increased cyanobacterial abundance (the "default" values in Table 1), and we report findings primarily from ranges of parameters where small, realistic changes in the values—comparable to those that might be produced by changing cyanobacterial abundance—strongly influence equilibrial outcomes (Appendix). Although we focus on equilibrium dynamics, we recognize that both transient dynamics and stochasticity are likely to be important in lakes. Moreover, the relative importance of cyanobacteria-mediated nutrient cycling for any particular lake will depend on characteristics such as morphometry, stratification, and water residence time. Further refinement of the model would be needed to simulate conditions in any particular lake or to capture the entire array of possible processes.

Consistent with the empirical evidence that cyanobacteria can drive lake N and P cycling (Boxes 1 and 2), changes in several model parameters associated with cyanobacteria (e.g.,

Table 1. Model parameterization.

Parameter	Units	Low end	High end	Default	Justification
I_N	$\mu g\ N \cdot L^{-1} \cdot d^{-1}$	0.03	11.8	0.118	Default value estimated from estimated water flux for Lake Sunapee, NH (Schloss 1990) and measured expected in-lake N:P ratios and tributary N concentrations (Ewing et al., *unpublished data*) plus regional atmospheric deposition as measured by the National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu/data/) and Weathers et al. (2006); the range spans values collated by Wetzel (2001).
I_P	$\mu g\ P \cdot L^{-1} \cdot d^{-1}$	0.003	5	0.008	Default value estimated from tributary and atmospheric P loading to Lake Sunapee, NH (Schloss 1990); upper end of range exceeds high-end estimates from Carpenter (1992).
s	d^{-1}	0.001	0.3	0.01	Combines estimates of in-lake sedimentation rates with the inverse of the water residence time.
r	$\mu g\ P \cdot L^{-1} \cdot d^{-1}$	0.0001	6	0.15–0.35	Gonsiorczyk et al. (1997) reported maximum rates of 5.8 $mg \cdot m^{-2} \cdot d^{-1}$, which convert to ~6 $mg \cdot m^{-3} \cdot d^{-1}$ with a 10 m deep thermocline.
m	$\mu g\ P \cdot L^{-1}$	2	20	10	Tuned based on responses of internal loading to P dynamics (Carpenter et al. 1999, Cooke et al. 2005).
q	none	2	2	2	Based on value in Carpenter et al. (1999) for cold, deep lakes.
f	$\mu g\ N\ L^{-1} \cdot (\mu g\ P\ L^{-1})^{-1} \cdot d^{-1}$	0.0001	6	0.6	Developed from maximum N fixation rates reported in Wetzel (2001), together with expected P concentrations.
k	$\mu g\ N\ L^{-1} \cdot (\mu g\ P\ L^{-1})^{-1}$	0	50	30	Constraints from Wetzel (2001); default value chosen to be near the 29:1 N:P ratio reported in Smith (1983).
α	(none)	0	1	0.2	Constraints by mathematics; default value chosen so as to show some flexibility in response to N:P ratio.

I_P, r, m, and f) can alter the number, location, and stability of the equilibrium N and P concentrations. For example, the number and location(s) of stable equilibria depend strongly on the two parameters affecting P recycling, r (Figs. 3 and 4) and m (Fig. 4), consistent with Carpenter et al. (1999). As the maximum P recycling rate r increases (or the inflection point m decreases), the system moves from one stable low-nutrient equilibrium, to two stable equilibria separated by an unstable equilibrium, to one stable high-nutrient equilibrium (Fig. 3). In the region of parameter space where there are two stable equilibria, increases in the maximum P recycling rate r (and decreases in the inflection point m) decrease the resilience of the low-nutrient equilibrium (Fig. 4). Hence, to the extent that cyanobacteria have the ability to increase the maximum P recycling rate or decrease the lake P concentration at which recycling reaches half of its maximum value, they can erode the stability of the low-nutrient equilibrium and make it more likely that a lake might come to the point of substantial internal P loading.

If we focus on the role of cyanobacteria in increasing the P inputs to a lake (I_P), then equilibrium locations change within the constraints set by the recycling characteristics described by r and m: nutrient concentrations for both stable equilibria increase and the unstable equilibrium moves closer to the low-nutrient equilibrium (Fig. 3). Thus, even without extensive P recycling from the sediment, the resilience of the low-nutrient equilibrium can be eroded by cyanobacterial P loading. Increases in I_P also alter the critical values of the maximum P recycling rate r for which multiple equilibria occur (Fig. 3). As such, cyanobacteria that influence P inputs through diurnal migrations (arrow 2 in Fig. 1) or seasonal recruitment from dormant benthic stages to the water column (arrow 1 in Fig. 1) may increase the sensitivity of a low-nutrient system to a recycling-driven regime change, even before anoxia-driven internal P loading occurs.

In addition to enhancing switching feedbacks and so contributing to a shift to a more eutrophic regime by altering I_P, r, or m, cyanobacteria-mediated shifts in P cycling also increase the resilience of the eutrophic equilibrium, making a shift back to the low-nutrient equilibrium (i.e.,

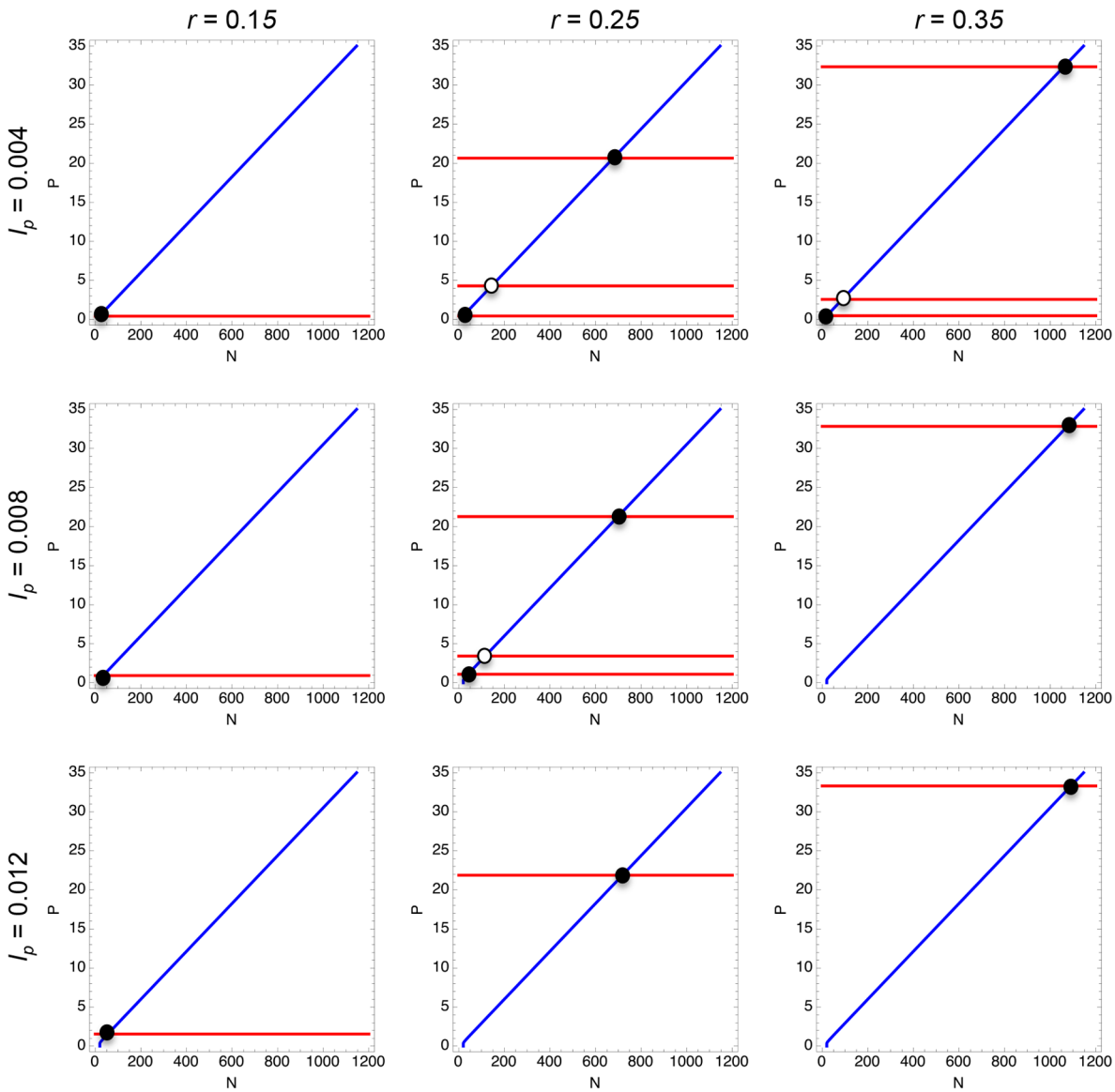

Fig. 3. Changes in system stability, visualized using isoclines (red for P and blue for N) indicating zero net change in nutrient concentration for selected values of the P recycling rate r (columns) and P input rate I_P (rows); other parameters are $I_N = 0.2$, $s = 0.01$, $f = 0.88$, $k = 30.0$, $m = 10.0$, $\alpha = 0.2$, and $q = 2.0$. Stable equilibria are denoted with filled circles and unstable equilibria with an open circle. In panels with multiple equilibria, the resilience of a stable equilibrium can be assessed using the distance from the stable equilibrium to the unstable point: the further the stable equilibrium is from the unstable point, the greater the ability of the system to stay in the basin of attraction for that equilibrium point (see Carpenter 2003). For example, when $r = 0.25$ and $I_P = 0.008$, the higher-nutrient equilibrium is more resilient than the lower-nutrient equilibrium. Note that increasing I_P tends to increase the stable equilibrium values for P and to move the unstable equilibrium point closer to the low-nutrient stable equilibrium in the region of parameter space where multiple equilibria are possible.

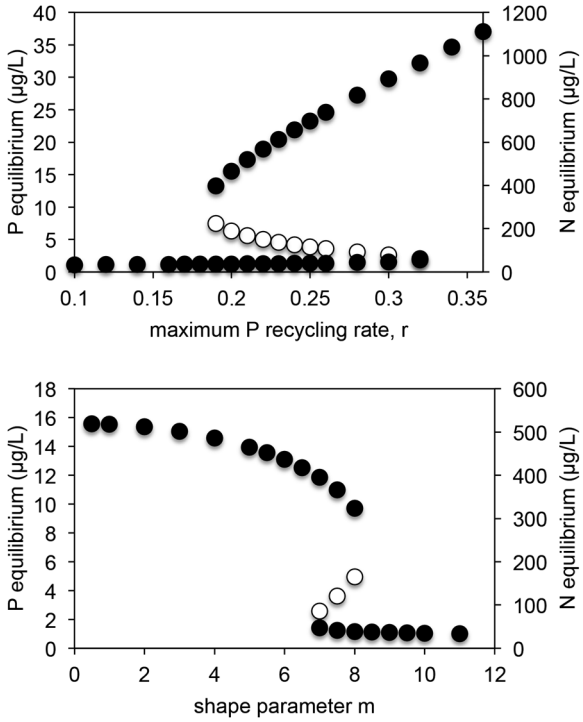

Fig. 4. Effect of parameters associated with P recycling (the maximum recycling rate, r [top, µg $P \cdot L^{-1} \cdot d^{-1}$] and the P concentration at which recycling reaches half of its maximum value, m [bottom, µg P L^{-1}]) on the number, stability, and resilience of model equilibria. Stable equilibria are denoted with filled circles and unstable equilibria with an open circle; for intermediate values of both r and m, there are low-nutrient and high-nutrient stable equilibria with an unstable equilibrium between them. The decreasing resilience of the low-nutrient equilibrium and increasing resilience of the high-nutrient equilibrium are indicated by the movement of the unstable equilibrium toward the low-nutrient equilibrium as r increases and m decreases. Effects of r are evaluated at $m = 10$ and effects of m are evaluated at $r = 0.15$. Equilibria are estimated at $I_N = 0.2$, $I_P = 0.008$, $s = 0.01$, $f = 0.88$, $k = 30.0$, $\alpha = 0.2$, and $q = 2.0$.

lake restoration) more difficult (Fig. 4). At the high-nutrient equilibrium, reversal to the low-nutrient state requires parameter changes that can be difficult to effect in nature without substantial cost and effort, similar to management activities to remove nutrients by increasing sedimentation or outflow (s) (e.g., alum or flocculation treatment; Cooke et al. 2005), decreasing external inputs of N and P (I_N and I_P), or decreasing internal loading (e.g., by removing cyanobacteria or oxygenating bottom water to prevent anoxia-driven P release). This model finding is consistent with empirical studies demonstrating that cyanobacteria can enhance the resilience of the eutrophic regime by creating stabilizing feedbacks that can maintain internal nutrient loading, even if external nutrient loading is curtailed by management activities (e.g., Fogg 1969, Reynolds and Walsby 1975, Huisman et al. 2005, Reynolds 2006). In fact, numerous authors have noted that a better understanding of the effects of cyanobacteria on nutrient feedbacks is essential for the development of more effective strategies for lake restoration (e.g., Scheffer et al. 1993, Jeppesen et al. 1998, Xie et al. 2003, Havens 2008).

In considering the effects of cyanobacteria on N cycling, we found that adjusting parameters associated with N fixation does not change the number of equilibria, although these parameters do change the equilibrium concentrations of N (e.g., Appendix) and the resilience of the stable equilibria in the regions of parameter space where multiple equilibria are possible (Fig. 5). For example, increases in the maximum N fixation rate f decrease the slope of the N isocline, tilting the diagonal line in Fig. 3 ever further to the right, towards horizontal. A more horizontal N isocline increases the N concentration at equilibrium but leaves the location of the P equilibrium unchanged. In the region of parameter space where multiple equilibria are possible (based on the P recycling parameters r or m as described above), the resilience of both stable equilibria increases with the maximum N fixation rate f, although the resilience of the high-nutrient equilibrium is much higher and increases to a greater degree than that of the low-nutrient equilibrium (Fig. 5). Therefore, as with P recycling, N fixation resulting from cyanobacteria in lakes that are N-limited may make restoration of high-nutrient lakes more difficult. More work is needed, however, to capture other complexities in the N cycle, including how benthic N fixation or denitrification might alter the locations and stability of the high-nutrient equilibrium.

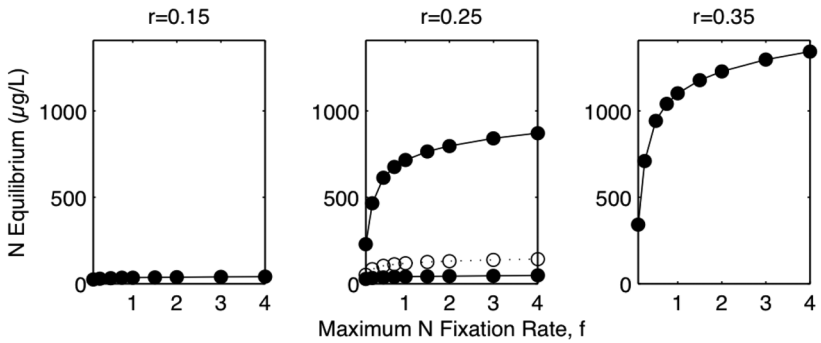

Fig. 5. Effects of maximum N fixation rate f [μg N L^{-1}·(μg P L^{-1})$^{-1}$·d^{-1}] on the location and resilience of the N equilibrium, depending on the value for maximum P recycling rate r (panels from left to right). The P equilibrium does not change with f (see text). Stable equilibria are denoted with filled circles and unstable equilibria with an open circle. At intermediate r, the increasing resilience of both stable equilibria with increased f is indicated by the increasing distance from the unstable equilibrium. Equilibria are estimated at $I_N = 0.2$, $I_P = 0.008$, $s = 0.01$, $m = 10.0$, $k = 30$, $\alpha = 0.2$, and $q = 2.0$.

Synthesis and Testable Hypotheses

This simple model suggests that the ability of cyanobacteria to alter N and P cycling could influence not only lake N and P concentrations, but also the range of trophic states likely to occur, the proximity of a system to a threshold that leads to a regime shift, and the tendency of a lake to remain in either a high- or low-nutrient condition. As such, it draws our attention to several testable hypotheses about the influence of cyanobacteria on lake nutrient cycling and resilience, especially in the lower-nutrient lakes for which the model was parameterized.

(1) Cyanobacteria-mediated modification of N and P cycling can facilitate a shift from a low-nutrient to a high-nutrient state, depending on the species present and the interaction between the characteristics of those taxa and other lake characteristics. We hypothesize that cyanobacterial taxa that can both fix N and acquire P are particularly likely to have strong effects on trophic state and resilience. In addition to *Gloeotrichia echinulata*, at least three other colonial taxa in the Nostocales are known to have life histories that may allow them to initiate or sustain positive feedback loops that lead to eutrophication by bringing both N and P into the water column: *Anabaena* (Thompson et al. 1994), *Aphanizomenon* (Barbiero and Welch 1992, Barbiero and Kann 1994, Jacobsen 1994), and *Cylindrospermopsis* (Istvanovics et al. 2002). Like *G. echinulata*, their germination from sediment resting stages is dependent upon the high light conditions most commonly found in low-nutrient systems (Barbiero and Kann 1994, Karlsson-Elfgren et al. 2003, Carey et al. 2008), suggesting that these taxa may have similar effects to *G. echinulata* in increasing nutrients and phytoplankton in the water column in low-nutrient lakes. However, other taxa may exert a stronger effect on either N or P. For example, *Microcystis* has been strongly implicated in increasing P concentrations in the water column in shallow eutrophic lakes (Xie et al. 2003, Xie 2006), but does not fix N. It seems likely, therefore, that the effects of cyanobacteria on N and P cycling in a particular lake ecosystem will depend on such factors as the degree of limitation by N versus P and the cyanobacterial taxa present.

(2) Systems with long residence times or slower sedimentation rates (i.e., smaller output rates, s) are more susceptible to cyanobacteria-mediated increases in the maximum P recycling rate, r (Fig. 6). When the output rate s is low, there is a narrow range of maximum P recycling rates associated with the low-nutrient

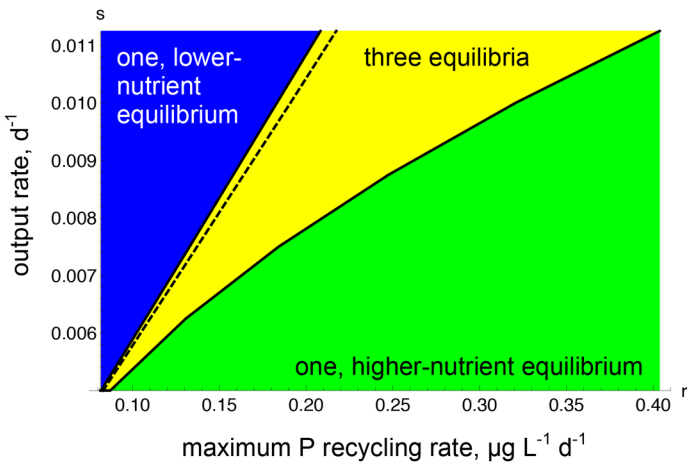

Fig. 6. Relative effects of the P recycling parameter r (horizontal axis) and the output rate s (vertical axis) on the numbers and types of equilibria. In the blue region, lower r (less P recycling) and higher s (shorter water residence times and higher sedimentation rates) produce a model with a single, low-nutrient equilibrium value of P for any particular combination of r and s. In the green region, combinations of higher r and lower s produce a higher-nutrient equilibrium value of P. In the yellow region, there are three equilibrium values of P: stable lower-nutrient and higher-nutrient attracting points, along with an in-between unstable value. This middle region represents the situation in which switching feedbacks may, with minimal change in s or r, move a lower-nutrient system toward a significantly higher nutrient level. The dashed line indicates the parameter values for which the unstable equilibrium value of P lies halfway between the two stable values; the proximity of that line to the blue region indicates that the lower-nutrient equilibria will be less resilient than their higher-nutrient counterparts for the vast majority of parameter combinations associated with multiple equilibria. In this graph, $I_P = 0.008$, $m = 10.0$, and $q = 2.0$.

equilibrium (the blue area in Fig. 6). Further, if the maximum P recycling rate increases through the cyanobacterial activities described in Box 2 without a substantial increase in output rate (s), the model suggests that a lake is far more likely to end up at the high-nutrient equilibrium. Although the sedimentation rate might be expected to increase to some degree with higher productivity, the output rate s is also constrained by lake water residence time, suggesting that lakes with longer residence times are more susceptible to regime shifts facilitated by cyanobacteria that can increase the maximum P recycling rate (Fig. 6). This hypothesis could be tested through comparative studies across lakes that differ in their residence times but have similar nutrient conditions and cyanobacterial populations.

Since this model, as with all other models, is an abstraction that does not represent the full complexity of lake ecosystems, it is illustrative of processes and interactions. Nevertheless, more work can be done to establish the generality of these findings and the conditions under which we expect cyanobacteria to be important in nature. For example, applications to real-world systems that may never come to equilibrium and exploration of alternative, more complex models—for example, those that provide a more detailed description of the N cycle or incorporate hydrodynamics—are logical next steps.

One particularly fruitful area for further inquiry may be linking an open-source hydrodynamic model (e.g., the General Lake Model, Hipsey et al. 2013) to a simple N and P model such as ours. With a model that couples hydrodynamics, N, and P, we could begin to explore hypotheses about the particular conditions that may affect the relative importance of cyanobacteria-mediated changes in nutrient cycling for any particular lake. For example, our

literature review (Box 2) suggests that the relative importance of P translocation by cyanobacteria depends on lake stratification and morphometry. Stratified oligotrophic lakes in which water column productivity is strongly nutrient-limited and the hypolimnion is well-oxygenated are likely to be more susceptible to changes in cyanobacteria-driven internal P loading than lakes with anoxic hypolimnia, as suggested by the strong sensitivity of trophic state to small changes in P recycling rates (Fig. 3). Moreover, cyanobacterial transport of nutrients via diel vertical migration (arrow 2 in Fig. 1) may be most important during periods of stable thermal stratification, whereas benthic species that mobilize sediment P (arrow 3 in Fig. 1) may be most important in well-mixed lakes. Finally, P translocation by seasonal recruitment from sediment resting stages to the water column (arrow 1 in Fig. 1) seems most likely in lakes with an ample area of shallow, relatively warm, well-lit sediments (Head et al. 1999*a*), even if the maximum depth is quite deep. These hypotheses can be tested in models and with rigorous, cross-lake comparisons.

Additional Research Opportunities and Practical Challenges

Although the model shows that our hypotheses about cyanobacteria and regime shifts are plausible and empirical data strongly support the role of cyanobacteria in affecting lake N cycles, quantitative empirical evidence in support of cyanobacteria as drivers of lake P cycling is currently available only for a subset of taxa and lakes (Trimbee and Harris 1984, Osgood 1988, Barbiero and Welch 1992, Istvanovics et al. 1993, Pettersson et al. 1993, Barbiero and Kann 1994, Jacobsen 1994, Perakis et al. 1996, Head et al. 1999*b*, Istvanovics et al. 2000, Tymowski and Duthie 2000, Istvanovics et al. 2002, Xie et al. 2003, Xie 2006). Nevertheless, we find those examples and our model sufficiently compelling to believe that it is essential to further evaluate changes in P cycling due to cyanobacteria and the potential for cyanobacteria to influence lake resilience and regime shifts. For maximum effectiveness, this work should proceed using a variety of tools, including more detailed coupled biogeochemical models, small-scale experiments, paleoecological reconstructions across multiple systems, and perhaps even whole-lake experiments that manipulate cyanobacterial presence and biomass in the absence of hypolimnetic anoxia.

More broadly, the interaction between internal and external drivers of lake regime shifts poses some of the most pressing and challenging questions at the intersection of limnology and lake ecosystem management. Management, remediation, and policy actions must be tailored to address both external and internal drivers of ecosystem change and the interactions among drivers that may act across spatial and temporal scales. For example, catchment P loading is a local-to-regional external driver that can be controlled through local regulations (Brookes and Carey 2011), while atmospheric deposition of N and other pollutants is a regional problem whose sources can be many kilometers away (Weathers et al. 2006, Holtgrieve et al. 2011) and hence may require national or international regulation. Given that external P loading can, in theory, be controlled on a catchment basis, reductions in P loading are relatively easy targets for controlling cyanobacterial biomass (Brookes and Carey 2011) and thus cyanobacteria-driven eutrophication. However, the reality of drivers beyond the catchment—such as global climate change—and the importance of within-lake loading due to both hypolimnetic anoxia and cyanobacteria pose complex challenges for management that necessitate multi-faceted monitoring of both in-lake and external contributors to nutrient loading. Given the potential for cyanobacteria to erode the resilience of the low-nutrient state, increases in their biomass should be a warning sign that lake managers monitor closely.

Acknowledgments

We thank Nina Caraco, Jon Cole, Sam Fey, Laurie Griesinger, Cristina Herren, Elizabeth Traver, Nelson Hairston Jr., Alex Flecker, Emil Rydin, Jessica Trout-Haney, Peter Leavitt, Mike Vanni, Lars-Anders Hansson, and Sabrina Hepburn for helpful discussions; Amanda Lindsey for data support; and Chris Klausmeier for Mathematica tips. Tony Ives, Mireia Bartrons, Sam Fey, and four anonymous reviewers provided comments on earlier drafts. We appreciate financial support from the U.S. National Science Foundation, including DEB-0749022 to K. L. Cotting-

ham., K. C. Weathers, and H. A. Ewing; EF-0842267 to K. L. Cottingham; EF-0842112 to H. A. Ewing; EF-0842125 to K. C. Weathers; DEB-1010862 to C. C. Carey and Nelson G. Hairston, Jr.; and a Graduate Research Fellowship to C. C. Carey. Our work has also been supported by Dartmouth, Bates, and the American-Scandinavian Foundation.

Literature Cited

Allen, M. M., R. Morris, and W. Zimmerman. 1984. Cyanophycin granule polypeptide protease in a unicellular cyanobacterium. Archives of Microbiology 138:119–123.

Barbiero, R. P., and J. Kann. 1994. The importance of benthic recruitment to the population development of *Aphanizomenon flos-aquae* and internal loading in a shallow lake. Journal of Plankton Research 16:1581–1588.

Barbiero, R. P., and E. B. Welch. 1992. Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. Freshwater Biology 27:249–260.

Beversdorf, L. J., T. R. Miller, and K. D. McMahon. 2013. The role of nitrogen fixation in cyanobacterial bloom toxicity in a temperate, eutrophic lake. PLoS ONE 8(2):e56103.

Brookes, J. D., and C. C. Carey. 2011. Resilience to blooms. Science 333:46–47.

Brunberg, A. K. 1995. Microbial activity and phosphorus dynamics in eutrophic lake-sediments enriched with *Microcystis* colonies. Freshwater Biology 33:541–555.

Brunberg, A. K., and B. Bostrom. 1992. Coupling between benthic biomass of *Microcystis* and phosphorus release from the sediments of a highly eutrophic lake. Hydrobiologia 235:375–385.

Carey, C. C., K. L. Cottingham, N. G. Hairston, and K. C. Weathers. 2014*a*. Trophic state mediates the effect of a large colonial cyanobacterium on phytoplankton dynamics. Fundamental and Applied Limnology 14:247–260.

Carey, C. C., K. L. Cottingham, K. C. Weathers, J. A. Brentrup, N. M. Ruppertsberger, H. A. Ewing, and N. G. Hairston, Jr. 2014*b*. Experimental blooms of the cyanobacterium *Gloeotrichia echinulata* increase phytoplankton biomass, richness, and diversity in an oligotrophic lake. Journal of Plankton Research 36:364–377.

Carey, C. C., H. A. Ewing, K. L. Cottingham, K. C. Weathers, R. Q. Thomas, and J. F. Haney. 2012*a*. Occurrence and toxicity of the cyanobacterium *Gloeotrichia echinulata* in low-nutrient lakes in the northeastern United States. Aquatic Ecology 46:395–409.

Carey, C. C., B. W. Ibelings, E. P. Hoffmann, D. P. Hamilton, and J. D. Brookes. 2012*b*. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. Water Research 46:1394–1407.

Carey, C. C., and K. Rengefors. 2010. The cyanobacterium *Gloeotrichia echinulata* stimulates the growth of other phytoplankton. Journal of Plankton Research 32:1349–1354.

Carey, C. C., K. C. Weathers, and K. L. Cottingham. 2008. *Gloeotrichia echinulata* blooms in an oligotrophic lake: helpful insights from eutrophic lakes. Journal of Plankton Research 30:893–904.

Carpenter, S. R. 1992. Destabilization of planktonic ecosystems and blooms of blue-green algae. Pages 461–481 *in* J. F. Kitchell, editor. Food web management: a case study of Lake Mendota. Springer-Verlag, New York, New York, USA.

Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. International Ecology Institute, Luhe, Germany.

Carpenter, S. R., and K. L. Cottingham. 1997. Breakdown and restoration of resilience in lakes. Conservation Ecology 1(1):2. http://www.consecol.org/vol1/iss1/art2

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications 9:751–771.

Conley, D. J., H. W. Paerl, R. W. Howarth, D. F. Boesch, S. P. Seitzinger, K. E. Havens, C. Lancelot, and G. E. Likens. 2009. Controlling eutrophication: nitrogen and phosphorus. Science 323:1014–1015.

Cooke, G. D., E. B. Welch, S. Peterson, and S. A. Nichols. 2005. Restoration and management of lakes and reservoirs. CRC Press, Boca Raton, Florida, USA.

Dignum, M., H. C. P. Matthijs, P. E. L. Roel, H. J. Laanbroek, and L. R. Mur. 2005. Nutrient limitation of freshwater cyanobacteria. Pages 65–86 *in* J. Huisman, H. C. P. Matthijs, and P. M. Visser, editors. Harmful cyanobacteria. Springer, New York, New York, USA.

Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting cyanobacteria dominance in lakes. Canadian Journal of Fisheries and Aquatic Sciences 58:1905–1908.

Dugdale, R. C., and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography 12:196–206.

Elmgren, R. 2001. Understanding human impact on the Baltic ecosystem: Changing views in recent decades. Ambio 30:222–231.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and

terrestrial ecosystems. Ecology Letters 10:1135–1142.

Elser, J. J., D. R. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry. BioScience 46:674–684.

Ernst, B., S. J. Hoeger, E. O'Brien, and D. R. Dietrich. 2009. Abundance and toxicity of *Planktothrix rubescens* in the pre-alpine Lake Ammersee, Germany. Harmful Algae 8:329–342.

Fey, S. B., Z. A. Mayer, S. C. Davis, and K. L. Cottingham. 2010. Zooplankton grazing of *Gloeotrichia echinulata* and associated life history consequences. Journal of Plankton Research 32:1337–1347.

Fogg, G. E. 1969. Leeuwenhoek Lecture, 1968: Physiology of an algal nuisance. Proceedings of the Royal Society B 173:175–189.

Forbes, M. G., R. D. Doyle, J. T. Scott, J. K. Stanley, H. Huang, and B. W. Brooks. 2008. Physical factors control phytoplankton production and nitrogen fixation in eight Texas reservoirs. Ecosystems 11:1181–1197.

Gonsiorczyk, T., P. Casper, and R. Koschel. 1997. Variations of phosphorus release from sediments in stratified lakes. Water, Air, & Soil Pollution 99:427–434.

Gophen, M., V. H. Smith, A. Nishri, and S. T. Threlkeld. 1999. Nitrogen deficiency, phosphorus sufficiency, and the invasion of Lake Kinneret, Israel, by the N-2-fixing cyanobacterium *Aphanizomenon ovalisporum*. Aquatic Sciences 61:293–306.

Havens, K. E. 2008. Cyanobacteria blooms: effects on aquatic ecosystems. Pages 733–747 *in* H. K. Hudnell, editor. Cyanobacterial harmful algal blooms: state of the science and research needs. Springer, New York, New York, USA.

Head, R. M., R. I. Jones, and A. E. Bailey-Watts. 1999*a*. An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake. Freshwater Biology 41:759–769.

Head, R. M., R. I. Jones, and A. E. Bailey-Watts. 1999*b*. Vertical movements by planktonic cyanobacteria and the translocation of phosphorus: implications for lake restoration. Aquatic Conservation—Marine and Freshwater Ecosystems 9:111–120.

Healey, F. P. 1982. Phosphate. Pages 105–124 *in* N. G. Carr and B. A. Whitton, editors. The biology of cyanobacteria. University of California Press, Berkeley, California, USA.

Hipsey, M. R., L. C. Bruce, and D. P. Hamilton. 2013. GLM: general lake model. Model overview and user information. Version 1.3.2. http://aed.see.uwa.edu.au/research/models/GLM/Download/AED_GLM_v1.3.2_20131031.pdf

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holtgrieve, G. W., et al. 2011. A Coherent signature of anthropogenic nitrogen deposition to remote watersheds of the Northern Hemisphere. Science 334:1545–1548.

Howarth, R. W., R. Marino, and J. J. Cole. 1988*a*. Nitrogen fixation in fresh-water, estuarine, and marine ecosystems 2: Biogeochemical controls. Limnology and Oceanography 33:688–701.

Howarth, R. W., R. Marino, J. Lane, and J. J. Cole. 1988*b*. Nitrogen fixation in fresh-water, estuarine, and marine ecosystems 1: Rates and importance. Limnology and Oceanography 33:669–687.

Hudnell, H. K. 2010. The state of US freshwater harmful algal blooms assessments, policy and legislation. Toxicon 55:1024–1034.

Huisman, J., H. C. P. Matthijs, and P. M. Visser. 2005. Harmful cyanobacteria. Springer, Dordrecht, The Netherlands.

Istvanovics, V., K. Pettersson, M. A. Rodrigo, D. Pierson, J. Padisak, and W. Colom. 1993. *Gloeotrichia echinulata*, a colonial cyanobacterium with a unique phosphorus uptake and life strategy. Journal of Plankton Research 15:531–552.

Istvanovics, V., H. M. Shafik, M. Presing, and S. Juhos. 2000. Growth and phosphate uptake kinetics of the cyanobacterium, *Cylindrospermopsis raciborskii* (Cyanophyceae) in throughflow cultures. Freshwater Biology 43:257–275.

Istvanovics, V., L. Somlyody, and A. Clement. 2002. Cyanobacteria-mediated internal eutrophication in shallow Lake Balaton after load reduction. Water Research 36:3314–3322.

Jacobsen, B. A. 1994. Bloom formation of *Gloeotrichia echinulata* and *Aphanizomenon flos-aquae* in a shallow, eutrophic, Danish lake. Hydrobiologia 289:193–197.

Jankowski, K., D. E. Schindler, and G. W. Holtgrieve. 2012. Assessing nonpoint-source nitrogen loading and nitrogen fixation in lakes using delta N-15 and nutrient stoichiometry. Limnology and Oceanography 57:671–683.

Jeppesen, E., M. Sondergaard, J. P. Jensen, E. Mortensen, A. M. Hansen, and T. Jorgensen. 1998. Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: An 18-year study of a shallow hypertrophic lake. Ecosystems 1:250–267.

Jöhnk, K. D., J. Huisman, J. Sharples, B. Sommeijer, P. M. Visser, and J. M. Stroom. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. Global Change Biology 14:495–512.

Johnston, B. R., and J. M. Jacoby. 2003. Cyanobacterial toxicity and migration in a mesotrophic lake in western Washington, USA. Hydrobiologia 495:79–91.

Karlsson-Elfgren, I., E. Rydin, P. Hyenstrand, and K.

Pettersson. 2003. Recruitment and pelagic growth of *Gloeotrichia echinulata* (Cyanophyceae) in Lake Erken. Journal of Phycology 39:1050–1056.

Kosten, S., V. L. M. Huszar, E. Becares, L. S. Costa, E. van Donk, L. A. Hansson, E. Jeppesenk, C. Kruk, G. Lacerot, N. Mazzeo, L. De Meester, B. Moss, M. Lurling, T. Noges, S. Romo, and M. Scheffer. 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. Global Change Biology 18:118–126.

Larsson, U., S. Hajdu, J. Walve, and R. Elmgren. 2001. Baltic Sea nitrogen fixation estimated from the summer increase in upper mixed layer total nitrogen. Limnology and Oceanography 46:811–820.

Lewis, W. M., and W. A. Wurtsbaugh. 2008. Control of lacustrine phytoplankton by nutrients: erosion of the phosphorus paradigm. International Review of Hydrobiology 93:446–465.

Lewis, W. M., W. A. Wurtsbaugh, and H. W. Paerl. 2011. Rationale for control of anthropogenic nitrogen and phosphorus to reduce eutrophication of inland waters. Environmental Science & Technology 45:10300–10305.

Mur, L. R., O. M. Skulberg, and H. Utkilen. 1999. Cyanobacteria in the environment. Pages 15–40 *in* I. Chorus and J. Bartram, editors. Toxic cyanobacteria in water: a guide to the public health consequences, monitoring, and management. World Health Organization, London, UK.

Noges, T., I. Tonno, R. Laugaste, E. Loigu, and B. Skakalski. 2004. The impact of changes in nutrient loading on cyanobacterial dominance in Lake Peipsi (Estonia/Russia). Archiv für Hydrobiologie 160:261–279.

Nurnberg, G. K. 1984. The prediction of internal phosphorus load in lakes with anoxic hypolimnia. Limnology and Oceanography 29:111–124.

Osgood, R. A. 1988. A hypothesis on the role of *Aphanizomenon* in translocating phosphorus. Hydrobiologia 169:69–76.

Paerl, H. W. 1988. Growth and reproductive strategies of freshwater blue-green algae (cyanobacteria). Pages 261–315 *in* C. D. Sandgren, editor. Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, New York, New York, USA.

Paerl, H. W., N. S. Hall, and E. S. Calandrino. 2011*a*. Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. Science of the Total Environment 409:1739–1745.

Paerl, H. W., and T. G. Otten. 2013*a*. Blooms bite the hand that feeds them. Science 342:433–434.

Paerl, H. W., and T. G. Otten. 2013*b*. Harmful cyanobacterial blooms: causes, consequences and controls. Microbial Ecology 65:995–1010.

Paerl, H. W., H. Xu, M. J. McCarthy, G. W. Zhu, B. Q. Qin, Y. P. Li, and W. S. Gardner. 2011*b*. Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): The need for a dual nutrient (N & P) management strategy. Water Research 45:1973–1983.

Perakis, S. S., E. B. Welch, and J. M. Jacoby. 1996. Sediment-to-water blue-green algal recruitment in response to alum and environmental factors. Hydrobiologia 318:165–177.

Pettersson, K., E. Herlitz, and V. Istvanovics. 1993. The role of *Gloeotrichia echinulata* in the transfer of phosphorus from sediments to water in Lake Erken. Hydrobiologia 253:123–129.

Pitois, S. G., M. H. Jackson, and B. J. B. Wood. 1997. Summer bloom of *Gloeotrichia echinulata* and *Aphanizomenon flos-aquae* and phosphorus levels in Antermony Loch, central Scotland. International Journal of Environmental Health Research 7:131–140.

Posch, T., O. Koster, M. M. Salcher, and J. Pernthaler. 2012. Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. Nature Climate Change 2:809–813.

Reuter, J. E., and R. P. Axler. 1992. Physiological characteristics of inorganic nitrogen uptake by spatially separate algal communities in a nitrogen-deficient lake. Freshwater Biology 27:227–236.

Reynolds, C. S. 2006. The ecology of phytoplankton. Cambridge University Press, Cambridge, UK.

Reynolds, C. S., and A. E. Walsby. 1975. Water blooms. Biological Reviews of the Cambridge Philosophical Society 50:437–481.

Salonen, K., and M. Rosenberg. 2000. Advantages from diel vertical migration can explain the dominance of *Gonyostomum semen* (Raphidophyceae) in a small, steeply-stratified humic lake. Journal of Plankton Research 22:1841–1853.

Scheffer, M. 2009. Critical transitions in nature and society. Princeton University Press, Princeton, New Jersey, USA.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8:275–279.

Schindler, D. E., S. R. Carpenter, K. L. Cottingham, X. He, J. G. Hodgson, J. F. Kitchell, and P. A. Soranno. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. Pages 96–105 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman Hall, New York, New York, USA.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science 195:260–262.

Schindler, D. W. 2012. The dilemma of controlling

cultural eutrophication of lakes. Proceedings of the Royal Society B 279:4322–4333.

Schindler, D. W., and R. E. Hecky. 2008. Reply to Howarth and Paerl: Is control of both nitrogen and phosphorus necessary? Proceedings of the National Academy of Sciences USA 105:E104–E104.

Schindler, D. W., R. E. Hecky, D. L. Findlay, M. P. Stainton, B. R. Parker, M. J. Paterson, K. G. Beaty, M. Lyng, and S. E. M. Kasian. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. Proceedings of the National Academy of Sciences USA 105:11254–11258.

Schloss, J. 1990. Lake Sunapee nutrient budget study. University of New Hampshire, Durham, New Hampshire, USA.

Scott, J. T., and E. M. Grantz. 2013. N-2 fixation exceeds internal nitrogen loading as a phytoplankton nutrient source in perpetually nitrogen-limited reservoirs. Freshwater Science 32:849–861.

Scott, J. T., and M. J. McCarthy. 2010. Nitrogen fixation may not balance the nitrogen pool in lakes over timescales relevant to eutrophication management. Limnology and Oceanography 55:1265–1270.

Seitzinger, S., J. A. Harrison, J. K. Bohlke, A. F. Bouwman, R. Lowrance, B. Peterson, C. Tobias, and G. Van Drecht. 2006. Denitrification across landscapes and waterscapes: A synthesis. Ecological Applications 16:2064–2090.

Shi, X. L., L. Y. Yang, F. P. Wang, L. Xiao, L. J. Jiang, Z. M. Kong, G. Gao, and B. Q. Qin. 2004. Growth and phosphate uptake kinetics of *Microcystis aeruginosa* under various environmental conditions. Journal of Environmental Sciences-China 16:288–292.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221:669–671.

Smith, V. H., and D. W. Schindler. 2009. Eutrophication science: where do we go from here? Trends In Ecology & Evolution 24:201–207.

Sommer, U., R. Adrian, L. De Senerpont Domis, J. J. Elser, U. Gaedke, B. W. Ibelings, E. Jeppesen, M. Lurling, J. C. Molinero, and W. M. Mooij. 2012. Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. Annual Review of Ecology and Systematics 43:429–448.

Stewart, W. D. P., G. P. Fitzgerald, and R. H. Burris. 1967. In situ studies on N_2 fixation using the acetylene reduction technique. Proceedings of the National Academy of Sciences 58:2071–2078.

Thompson, P. A., H. M. Oh, and G. Y. Rhee. 1994. Storage of phosphorus in nitrogen-fixing *Anabaena flos-aquae* (Cyanophyceae). Journal of Phycology 30:267–273.

Trimbee, A. M., and G. P. Harris. 1984. Phytoplankton population dynamics of a small reservoir: use of sedimentation traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green algae. Journal of Plankton Research 6:897–918.

Tymowski, R. G., and H. C. Duthie. 2000. Life strategy and phosphorus relations of the cyanobacterium *Gloeotrichia echinulata* in an oligotrophic Precambrian Shield lake. Archiv für Hydrobiologie 148:321–332.

Vanni, M. J. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. Pages 81–95 *in* G. A. Polis and K. O. Winemilller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Vuorio, K., M. Meili, and J. Sarvala. 2006. Taxon-specific variation in the stable isotopic signatures (delta C-13 and delta N-15) of lake phytoplankton. Freshwater Biology 51:807–822.

Vuorio, K., M. Meili, and J. Sarvala. 2009. Natural isotopic composition of carbon (delta(13)C) correlates with colony size in the planktonic cyanobacterium *Gloeotrichia echinulata*. Limnology and Oceanography 54:925–929.

Wagner, C., and R. Adrian. 2011. Consequences of changes in thermal regime for plankton diversity and trait composition in a polymictic lake: a matter of temporal scale. Freshwater Biology 56:1949–1961.

Watson, S., E. McCauley, and J. A. Downing. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. Canadian Journal of Fisheries and Aquatic Sciences 49:2605–2610.

Weathers, K. C., S. M. Simkin, G. M. Lovett, and S. E. Lindberg. 2006. Empirical modeling of atmospheric deposition in mountainous landscapes. Ecological Applications 16:1590–1607.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. Academic Press, San Diego, California, USA.

Whitton, B. A., S. L. J. Grainger, G. R. W. Hawley, and J. W. Simon. 1991. Cell-bound and extracellular phosphatase activities of cyanobacterial isolates. Microbial Ecology 21:85–98.

Wiedner, C., J. Rucker, R. Bruggemann, and B. Nixdorf. 2007. Climate change affects timing and size of populations of an invasive cyanobacterium in temperate regions. Oecologia 152:473–484.

Wilhelm, F. M., J. J. Hudson, and D. W. Schindler. 1999. Contribution of *Gammarus lacustris* to phosphorus recycling in a fishless alpine lake. Canadian Journal of Fisheries and Aquatic Sciences 56:1679–1686.

Williamson, C. E., W. Dodds, T. K. Kratz, and M. A. Palmer. 2008. Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Frontiers in Ecology and the Environ-

ment 6:247–254.

Wilson, M. A., and S. R. Carpenter. 1999. Economic valuation of freshwater ecosystem services in the United States: 1971–1997. Ecological Applications 9:772–783.

Winter, J. G., A. M. DeSellas, R. Fletcher, L. Heintsch, A. Morley, L. Nakamoto, and K. Utsumi. 2011. Algal blooms in Ontario, Canada: Increases in reports since 1994. Lake and Reservoir Management 27:107–114.

Xie, L. Q., P. Xie, and H. J. Tang. 2003. Enhancement of dissolved phosphorus release from sediment to lake water by *Microcystis* blooms: an enclosure experiment in a hyper-eutrophic, subtropical Chinese lake. Environmental Pollution 122:391–399.

Xie, P. 2006. Biological mechanisms driving the seasonal changes in the internal loading of phosphorus in shallow lakes. Science in China Series D, Earth Sciences 49:14–27.

Xu, H., H. W. Paerl, B. Q. Qin, G. W. Zhu, and G. Gao. 2010. Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. Limnology and Oceanography 55:420–432.

Supplemental Material

Appendix

Analytical evaluations of the model and simulation studies

The form of the equations for phosphorus (P) and nitrogen (N) cycling given in the text are as follows:

$$\frac{dP}{dt} = I_p - sP + \frac{r\,P^q}{m^q + P^q} \tag{A.1}$$

$$\frac{dN}{dt} = I_N - s\,N + f\,P\left[\frac{e^{-\alpha\left(\frac{N}{P}-k\right)}}{1+e^{-\alpha\left(\frac{N}{P}-k\right)}}\right] \tag{A.2}$$

where I_P and I_N are the external input of P and N, respectively (inflow + deposition in Fig. 2); s is the output rate (outflow + sedimentation in Fig. 2); r is the maximum P recycling rate; f is the maximum N fixation rate; and m, q, k and α are shape parameters with the requirements that $m > 0$, $q \geq 2$, $k > 0$ and $\alpha > 0$.

The non-linearities in the equations for both P and N make it difficult to solve for equilibrium nutrient concentrations analytically. However, we can put bounds on both equilibria. In the equation for dP/dt, the term $rP^q(m^q + P^q)^{-1}$ cannot become greater than r, and therefore any equilibrium value of P must be less than $(I_P + r)/s$. Within the N equation, the logistic function for N fixation means that dN/dt is bounded between $I_N - sN$ (when there is no N fixation due to a high N:P ratio) and $I_N - sN + fP$ (when N fixation is at the maximum rate). This means that the equilibrium concentration for N will be between I_N/s and $(I_N + fP)/s$; given the restriction on P—that it must be less than $(I_P + r)/s$—we can show that N cannot exceed $[I_N + (f/s)(I_P + r)]/s$. These expressions make it clear that external loading directly, and linearly, increases the bounds on the equilibrium values. Higher levels of N fixation and P recycling also increase equilibrium value bounds linearly, and higher levels of outputs decrease equilibrium value bounds.

For the figures shown in the main text, we used Wolfram *Mathematica* v8 to visualize potential equilibria and their stability using ContourPlot and to estimate equilibrium locations using the Solve function. Isoclines for Fig. 3 in the main text were generated with code in the Mathematica notebook "Figure 3.nb". Equilibria in Figs. 4 and 5 were generated with code structured as in "Demo code for Figures 4 and 5.nb", but modified for the particular parameter values of interest. Isoclines for Fig. 6 were generated using "Figure 6.nb". All three Mathematica notebooks are available as a Supplement.

To complement these analytical explorations, we visualized model dynamics through time for a wide range of parameter values and initial conditions using simulations in MATLAB 7.10.0.499 (R2010a) with an adaptive step-size algorithm

(ode45) and a variety of initial conditions. These studies were not used to generate figures for this paper, but were essential to exploring model behavior. Code for these simulations was built using the core program "runmodel.m", calling the subprogram "derivsub_ratio.m", with different versions again tuned to the parameters of interest; both programs are included in the Supplement. Programs were typically run for at least four different initial conditions to confirm convergence of outcomes.

Supplement

Mathematica notebooks and Matlab programs used to analyze our coupled model of nitrogen and phosphorus cycling, as explained in the Appendix (*Ecological Archives*, http://dx.doi.org/10.1890/ES14-00174.1.sm).