

Early warning signals precede cyanobacterial blooms in multiple whole-lake experiments

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Abstract. Ecosystem regime shifts are abrupt changes from one dynamical state to another, such as the shift from a clear-water state to an algal bloom state in lakes. These transitions are hard to forecast but theory suggests that early warning indicators can predict impending regime shifts that may allow for management intervention to prevent or mitigate an unwanted change. The efficacy of early warning indicators has been demonstrated in modeling and laboratory experiments, but rarely in the field, where environmental drivers are numerous and interacting. It is unclear if early warning indicators are observable or timely enough to allow for intervention under these conditions. We performed six whole-lake experimental nutrient additions to test the utility of early warning indicators for predicting the regime shift from a clear-water state to a cyanobacteria-dominated state. The lakes were monitored for increases in resilience indicators including rises in standard deviation and autocorrelation of algal pigments and dissolved oxygen saturation. A statistical method, quickest detection, determined when resilience indicators in manipulated lakes deviated substantially from those in a reference ecosystem. Blooms occurred in five of the six lake-years. Although there was substantial variability in bloom size and timing, at least one indicator foreshadowed the peak chlorophyll *a* concentration in all instances. Early warnings occurred 1–57 d prior to a bloom, which in some instances, may allow managers to notify the public or intervene to prevent blooms. The resilience indicators generally identified changes in resilience over time within a lake and also ranked large differences in resilience among lakes. Our findings suggest that resilience indicators can be useful for classifying ecosystems on a landscape and across time with respect to proximity to a critical threshold.

Key words: bloom; cyanobacteria; early warnings; lake; phosphorus; regime shift.

INTRODUCTION

Ecosystems can undergo abrupt changes called regime shifts. Regime shifts are transitions from one dynamical state to an alternative state driven either by large external shocks or by crossing a critical threshold (Carpenter 2003, Scheffer et al. 2009b). Regime shifts have been documented in many ecosystems including coral reefs (Hughes 1994), shallow coastal ecosystems (van der Heide et al. 2007, McGlathery et al. 2013), marine fisheries (Hutchings and Reynolds 2004, Rocha et al. 2015), rangelands (Janssen et al. 2004), and lakes (Scheffer and Jeppesen 2007, Carpenter et al. 2011, Wang et al. 2012). These shifts are often accompanied by a loss in ecosystem services and potentially have negative impacts on human well-being (Crépin et al. 2012, Rocha et al. 2015). Feedbacks and hysteresis can help maintain the

new state after a regime shift making it difficult and often expensive to reverse (Nyström et al. 2012). As such, it would be beneficial to predict when a regime shift is going to occur in order to intervene and prevent the shift or mitigate the loss of ecosystem services.

Some types of ecological regime shifts are preceded by changes in generic resilience indicators (Scheffer 2009a, Scheffer et al. 2015). As an ecosystem approaches a threshold, its rate of recovery from environmental perturbations, such as weather fluctuations, slows down. As a result, the variance and autocorrelation of ecosystem time series increase (Carpenter and Brock 2006, van Nes and Scheffer 2007). These changes in time-series statistics are discernible in rolling window analyses of time series measurements of appropriate variables, such as biomass or production of key ecosystem components (Dakos et al. 2012). Other rolling window, time-series-based, resilience indicators have also been identified, such as skewness (Guttal and Jayaprakash 2008), kurtosis, changes in power spectra (Biggs et al. 2009), and conditional heteroscedasticity (Seekell et al. 2011).

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Additionally, changes in spatial structure such as increases in spatial variance and autocorrelation serve as resilience indicators (Kéfi et al. 2014, Butitta et al. 2017).

There are many reasons why resilience indicators may not be detectable or timely in practice, and therefore experimental tests are needed to evaluate them (Boettiger et al. 2013, Dakos et al. 2015). Rises in resilience indicators in ecosystems approaching a regime shift have been observed in controlled laboratory experiments (Drake and Griffen 2010, Dai et al. 2012, Veraart et al. 2012), a field experiment (Carpenter et al. 2011), and post hoc analyses of observational time series data (Dakos et al. 2008, Lenton et al. 2008, Gsell et al. 2016). In modeling and laboratory experiments, the degree of environmental variability can be controlled by the investigator. However, in field studies, variability in drivers that decrease resilience could potentially mask early warning signals and impede timely intervention. It is unclear if early warning indicators are always observable under varying environmental conditions, especially when drivers that decrease resilience are numerous and interacting (Brock and Carpenter 2010, Perretti and Munch 2012). Additionally, it is uncertain if the early warnings are sufficiently timely and reliable to allow for intervention or mitigation before the regime shifts occurs (Biggs et al. 2009, Contamin and Ellison 2009).

In this study, we tested the robustness of early warning indicators of an impending regime shift under varying environmental conditions. We performed daily nutrient additions to two lakes over three years to induce algal blooms. While nutrient availability is the main driver of the regime shift from a clear-water to an algae-dominated state, other environmental variables can regulate algal growth and impede early warning detection. For example, high concentrations of colored dissolved organic matter decrease light availability, inhibiting algal growth (Ask et al. 2009) and controlling recruitment of phytoplankton resting stages from the sediment bank (Rengefors et al. 2004). Large grazers such as *Daphnia* spp. can also suppress algal biomass. Temperature effects algal growth by regulating enzymatic activity at the cellular level and contributes to recruitment of phytoplankton resting stages. Given the numerous interacting drivers, it is likely that variation in environmental conditions could hamper the detection of early warning signals of an impending algal bloom.

The regime shift from a stable clear-water state to the algal-dominated state in lakes can involve shifts among several dynamical regimes (Scheffer et al. 2000). In models, these regime shifts cause increases in standard deviation (SD) and autocorrelation (AC) preceding the onset of an algal bloom (Batt et al. 2013a, Kéfi et al. 2013). Algal blooms, particularly those dominated by toxin-producing cyanobacteria, disrupt ecosystem services such as providing safe water for consumption, irrigation, industry, recreation, and fisheries

(Falconer 1999, Carmichael and Boyer 2016). There is evidence that these blooms are becoming more frequent in surface waters and will continue to be more frequent as agriculture and climate change intensify (Kudela et al. 2015, Michalak 2016). Given the consequences and increasing potential for this regime shift to occur in a given aquatic ecosystem, the ability to reliably predict an impending algal bloom in a timely manner may help protect natural resources and human well being.

In this study, we added nutrients to lakes and monitored for increases in SD and AC as early warning indicators of an impending shift while slowly approaching a state of cycling algal blooms. We used the quickest detection method (Carpenter et al. 2014) to identify when the manipulated lakes deviated significantly from a reference lake, triggering an early warning “alarm.” Specifically, we tested

1. Efficacy. Are early warning alarms generated before algal blooms?
2. Timeliness. How early are alarms detected before the onset of a bloom and evidence of a critical transition?
3. Reliability. Do alarms occur in multiple resilience indicators preceding blooms, increasing confidence in the early warning?

The nutrient additions were repeated on two lakes over the course of three years from 2013 to 2015 while observing a reference system in each of the three years, for nine total lake-years of experimentation. The environmental conditions varied between lakes and among years as did the nutrient loading rate (the main driver of the regime shift) allowing us to examine the efficacy, reliability, and timeliness of early warning indicators under variable conditions. In doing so, we tested the potential utility of early warning indicators as a tool for predicting forthcoming large changes in ecosystems under a range of conditions.

METHODS

Study sites

The nutrient manipulations were carried out on Peter and Tuesday Lakes located in Gogebic County, Michigan, USA (46°25' N, 89°50' W). Before the nutrient manipulations, Peter Lake was oligotrophic and Tuesday Lake was oligo-mesotrophic (Carlson 1977). Tuesday Lake is a brown water lake (Table 1) with a food web dominated by planktivorous fish. Peter Lake is a clearer lake dominated by largemouth bass (*Micropterus salmoides*). Nearby Paul Lake, also a clearer, bass-dominated lake, served as an unmanipulated reference ecosystem during the experiments. The lakes are all small (<3 ha), softwater, seepage lakes located within 1 km of each other in forested, undisturbed watersheds.

TABLE 1. Lake physical, chemical, and biological variables for all three years in the two manipulated lakes (Peter and Tuesday) and the reference lake (Paul).

Variable	Unit	Paul (reference)			Peter			Tuesday		
		2013	2014	2015	2013	2014	2015	2013	2014	2015
Color	m ⁻¹	1.5 (0.2)	1.3 (0.2)	1.2 (0.1)	2.4 (0.5)	2.2 (0.3)	1.6 (0.2)	6.0 (0.9)	5.3 (1.0)	4.4 (0.3)
DOC	mg/L	4.5 (1.0)	4.3 (0.4)	3.9 (0.1)	5.9 (0.4)	5.9 (0.5)	5.8 (0.7)	12.8 (3.4)	12.3 (4.7)	10.3 (1.0)
pH	n.a.	6.4 (0.3)	6.4 (0.1)	6.5 (0.3)	6.7 (0.2)	6.6 (0.2)	7.2 (0.9)	5.9 (0.3)	5.8 (0.2)	6.0 (0.2)
DIC	μmol/L	124.3 (13.4)	153.1 (165.1)	124.1 (8.6)	116.2 (11.4)	90.5 (28.2)	86.9 (28.4)	56.9 (21.8)	46.6 (12.7)	47.0 (14.9)
k _D	m ⁻¹	0.8 (0.1)	0.8 (0.1)	0.7 (0.04)	0.9 (0.1)	1.0 (0.07)	0.9 (0.1)	1.8 (0.3)	1.7 (0.1)	1.7 (0.1)
TN†	μmol/L	20.2 (2.8)	18.1 (2.4)	16.7 (1.8)	27.7 (4.9)	28.7 (5.2)	31.0 (11.7)	36.3 (6.5)	38.6 (4.5)	36.6 (7.3)
TP†	μmol/L	0.1 (0.3)	0.3 (0.2)	0.4 (0.1)	0.4 (0.3)	0.6 (0.2)	0.5 (0.3)	0.7 (0.3)	1.2 (0.3)	1.0 (0.3)

Notes: Values are means with SD in parentheses. Mean values are from weekly samples ($n = 14-16$ per year) unless otherwise noted. DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; k_D, light extinction coefficient; TN, total nitrogen; TP, total phosphorus.

†Daily surface samples were taken in 2013 and 2014 and weekly samples were taken in 2015.

Nutrient additions

Nutrients were added to the epilimnia of Peter and Tuesday Lakes from 2013 to 2015 during the period of summer stratification. Ammonium nitrate (NH₄NO₃) and phosphoric acid (H₃PO₄) were dissolved in ~20 L of lake water and distributed in the epilimnion of each lake in the propeller wash of an underway electric motor. Nutrient additions occurred between 11:00 and 13:00 daily.

The aerial loading rate of both P and N (mg·m⁻²·d⁻¹) was equal for the two lakes within a given year, but varied in duration and among years (Table 2). In 2013, the daily nutrient loading rate increased weekly in order to slowly approach the regime shift threshold. In 2014 and 2015, the daily nutrient loading rate was held constant (Figs. 1 and 2). In Peter Lake, 2015 nutrient additions were halted on day of year (DOY) 180 in order to test if the early warning statistics could be used in real time to intervene and prevent the transition to the algae-dominated state (Pace et al. 2017).

State variable monitoring

Chlorophyll *a* and phycocyanin relative fluorescence (RF) were measured every 5 min in all three lakes using Hydrolab DS5X sensors (OTT Hydromet, Loveland, Colorado, USA) deployed at 0.75 m. Phycocyanin RF has a monotonic relationship to manual measurements of phycocyanin concentration performed in the laboratory (Pace et al. 2017). Simultaneous measurements of the same variables, as well as dissolved oxygen saturation, were taken at the same frequency with a YSI 6600V2-4 multiparameter sonde (YSI, Yellow Springs, Ohio, USA). Brief gaps in the data record due to calibration or sensor malfunction were interpolated using a bivariate autoregressive state-space model fitted using the MARSS package (MARSS package version 3.9; Holmes et al. 2015) in R (version 3.1.30; R Core Development Team 2015) to time series from both Hydrolab and YSI sensors. The MARSS interpolation of the high frequency time series created a continuous daily data record for over 100 d in each lake and each year (Table 2). The 2015 high frequency time series from Paul and Peter Lakes are also presented in Pace et al. (2017).

Water samples from a depth of 0.5 m were collected over the deepest point in the lake each day before nutrient additions. The water was filtered through Whatman 47 mm GF/F filters and extracts from the filters were analyzed fluorometrically for chlorophyll *a* concentration (Holm-Hansen 1978). In 2013 and 2014, daily water samples from the same depth were preserved using 1 mL of 0.5 mol/L per 100 mL of water and analyzed for total nitrogen (TN) and total phosphorus (TP) concentration. In 2015, TN and TP were sampled weekly.

Other limnological variables were determined weekly in the epilimnion, including water color, light extinction (k_D), zooplankton biomass, pH, dissolved organic

TABLE 2. Summary of nutrient manipulations in Peter and Tuesday Lakes.

Year	Lake	N:P of nutrient addition	Aerial P loading rate	Nutrient addition days	High frequency sampling days
2013	Peter and Tuesday	5:1, increased to 10:1 on DOY 203	0.5 mg P·m ⁻² ·d ⁻¹ increasing weekly by 0.3125 mg P·m ⁻² ·d ⁻¹ until DOY 203, after which the weekly increase was 0.625 mg P·m ⁻² ·d ⁻¹	154–238	137–249
2014	Peter and Tuesday	15:1	3 mg P·m ⁻² ·d ⁻¹	153–241	136–250
2015	Peter	15:1	3 mg P·m ⁻² ·d ⁻¹	152–180	129–247
	Tuesday	15:1	3 mg P·m ⁻² ·d ⁻¹	152–240	

Note: The N:P ratio is molar and days refers to day of year (DOY).

carbon (DOC), dissolved inorganic carbon (DIC), and soluble nutrients. Water color of filtered samples (Whatman GF/F filters) was measured spectrophotometrically as the absorbance at 440 nm (Cuthbert and del Giorgio 1992). The light extinction coefficient was calculated from weekly light profiles using a LiCor LI-1000 light meter with a spherical light sensor. The slow equilibration technique of Stauffer (1990) was used to measure pH. Filtered water for dissolved organic carbon (DOC) was preserved with 200 μ L of 1 mol/L per 20 mL of sample and analyzed with a Shimadzu 5050 TOC analyzer (Shimadzu, Kyoto, Japan). Dissolved inorganic carbon (DIC) was measured by equilibrating 20 mL of He headspace with 10 mL of sample water acidified with 200 μ L of 2N H₂SO₄. Then 10 mL of headspace was flushed through the 0.5-mL sample loop, which was automatically injected into a Shimadzu GC-8A gas chromatograph with a 2-m column, packed with Porapak-Q, and connected to a thermal conductivity detector.

Zooplankton biomass was estimated by enumerating and measuring the length of individuals collected from daytime verticals tows through the upper two-thirds of the water column at the deepest point using an 80- μ m mesh conical net. Samples for algae identification and enumeration (Phycotech, St. Joseph, Michigan, USA) were preserved with 2 mL of 25% aqueous glutaraldehyde (C₅H₈O₂) per 200 mL of sample.

Resilience indicators and alarms

Standard deviation (SD) and lag-1 autocorrelation (AC) of the daily mean of chlorophyll *a* concentration, phycocyanin RF, and dissolved oxygen (DO) saturation (DO_{%sat}) were calculated as resilience indicators. The resilience indicators were monitored for increasing SD in the manipulated system (Carpenter and Brock 2006) as well as AC increasing toward one (Dakos et al. 2012a). The backward-looking rolling window length was set to 21 d for analyses reported here. The differences between the resilience indicators calculated with a 21-d vs. 28-d rolling window were minor (Appendix S1). The algal pigments (chlorophyll *a* and phycocyanin) were log-

transformed before calculating rolling window SDs and ACs. Linear regression within the rolling window length was also used to detrend the state variable time series for a comparative analysis (presented in Appendix S1).

The quickest detection method was used to evaluate shifts in the SD and AC time series. The method, also called the Shiryayev-Roberts (S-R) statistic, determines if the resilience indicator in a manipulated lake deviates substantially from the reference lake at each time step (Carpenter et al. 2014). With each new data point (time step), the quickest detection method evaluates the ratio of the likelihood that an early warning has arrived to the likelihood that the lake is in the baseline state. The S-R statistic minimizes the time to detection of an early warning if the expected time to a false alarm is greater than a user-defined threshold (Polunchenko and Tartakovsky 2012). Once an alarm is triggered at a time step, the statistic resets for the subsequent time step. The threshold for the likelihood ratio was selected using numerical experiments that identified a range in which the time to first alarm was not sensitive to the selected threshold (Carpenter et al. 2014). The S-R statistic compares two $N(\mu, \sigma)$ probability densities: one for the baseline state and the other for an alarm state in which resilience indicators are elevated. For evaluating resilience using AC, μ and σ in the baseline state were set to the observed values in Paul Lake. In the alarm state, $\mu = 1$ and σ was the observed value in each manipulated lake. For evaluating resilience using SD in the baseline ecosystem state, μ is the value observed in Paul Lake and σ is the pooled value observed in Paul and each manipulated lake, σ_{pool} . In the alarm state, μ is the observed value for Paul Lake plus $2\sigma_{\text{pool}}$, and $\sigma = \sigma_{\text{pool}}$. Additional details on the QD calculations are available in the Appendix S1.

The timing and number of AC and SD alarms calculated using the S-R statistic (quickest detection alarms) were used to assess the efficacy, reliability, and timeliness of early warning indicators to predict algal blooms. Efficacy was evaluated as whether or not quickest detection alarms for any resilience indicator (SD or AC of chlorophyll *a*, phycocyanin, and DO_{%sat}) triggered before the

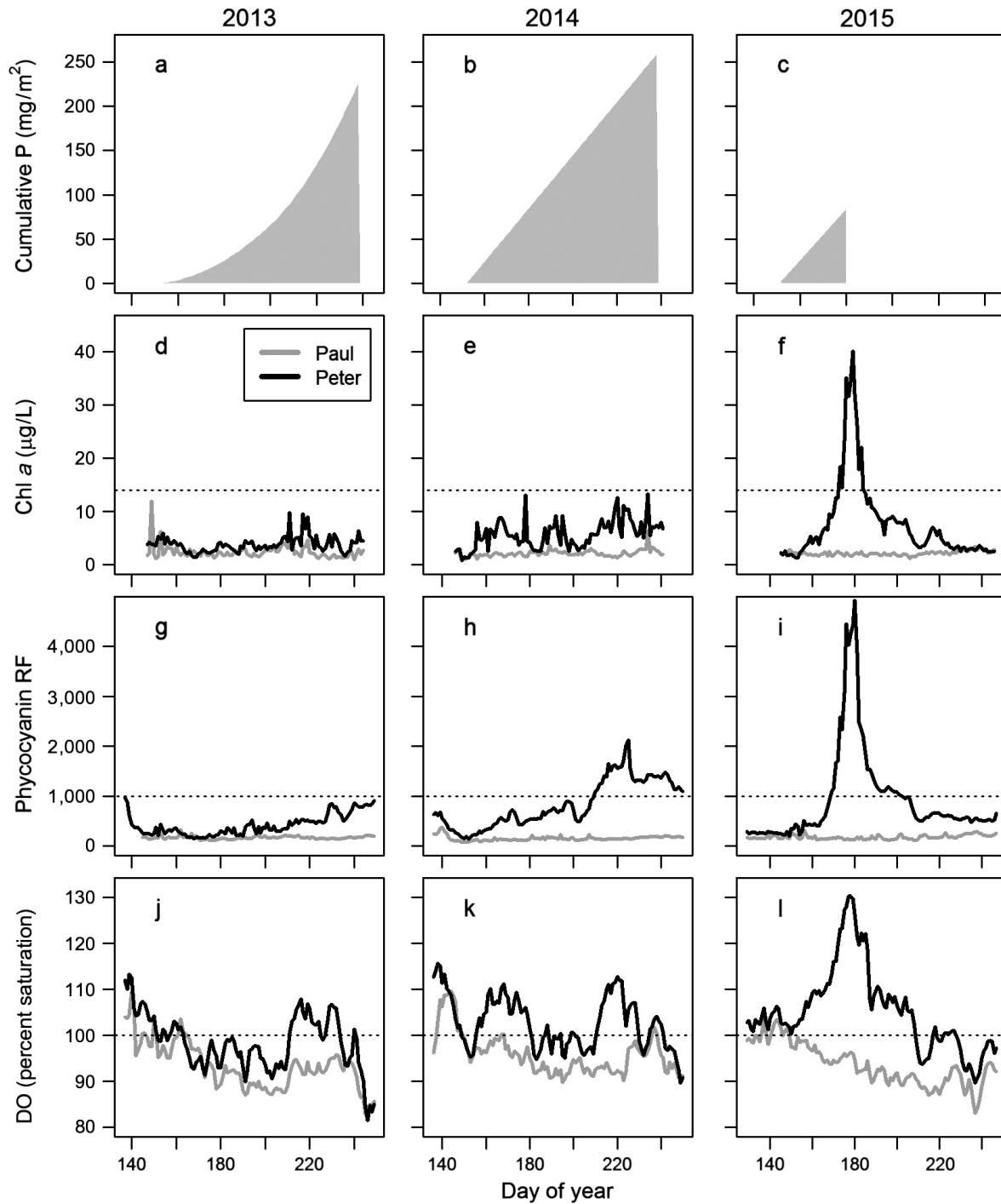


FIG. 1. Time series of the (a–c) cumulative P loading, (d–f) manual chlorophyll *a* concentration, (g–i) phycocyanin concentration (relative fluorescence, RF), and (j–l) dissolved oxygen percent saturation for Peter Lake and the reference system, Paul Lake from 2013 to 2015. The dashed line in panels d–i is lake-specific bloom definition for the manipulated lake. The dashed line in panels j–l denotes 100% DO saturation.

onset of a bloom. Reliability was evaluated as the number of variables with alarms preceding the onset or peak of the bloom (considered the maximum chlorophyll *a* concentration). Timeliness was evaluated as the number

of days between an early warning alarm and the onset of an algal bloom in the lake.

There is not a commonly accepted definition of an algal bloom, in part because bloom characteristics differ

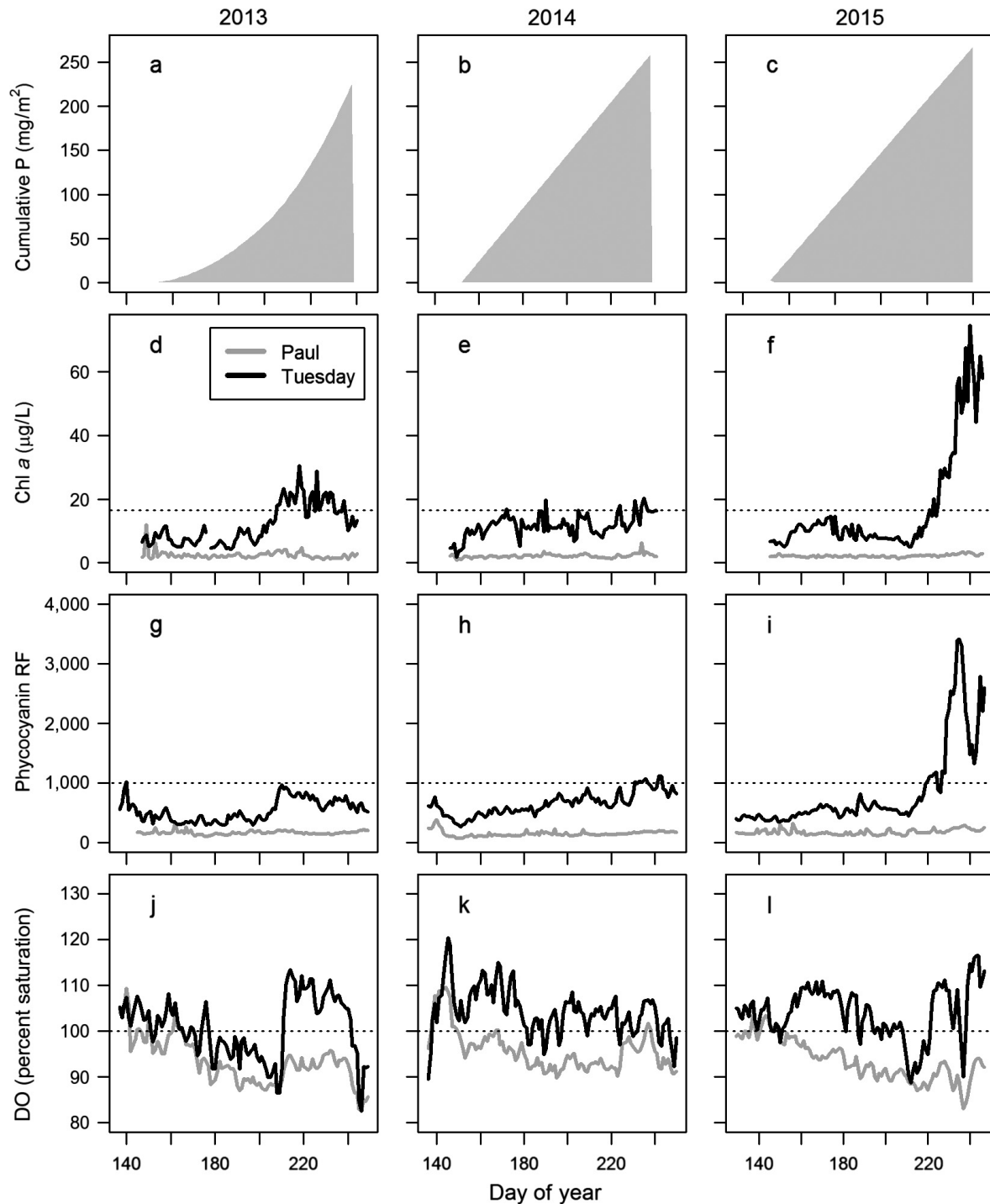


FIG. 2. Time series of the (a–c) cumulative P loading, (d–f) manual chlorophyll *a* concentration, (g–i) phycocyanin concentration, and (j–l) dissolved oxygen percent saturation for Tuesday Lake and the reference system, Paul Lake from 2013 to 2015. The dashed line in panels d–i is lake-specific bloom definition for the manipulated lake. The dashed line in panels j–l denotes 100% DO saturation.

among lakes. For example, in brown-water Tuesday Lake, the long-term (1984–2007) summer average of chlorophyll *a* concentration is 6.10 µg/L, which is higher

than both Peter (4.10 µg/L) and Paul Lakes (3.96 µg/L) for the same time period. In order to evaluate whether the early warning alarms arrived before the onset of a

bloom, we operationally defined the beginning of a bloom based on the historical chlorophyll *a* data for each lake. The bloom threshold was defined as the chlorophyll *a* concentration at which there is <5% probability that, at most, one out of every 100 daily chlorophyll *a* samples would exceed the threshold in non-nutrient enrichment years. This resulted in a bloom threshold of 14.0 µg/L for Peter Lake, 16.6 µg/L for Tuesday Lake, and 11.2 µg/L for Paul Lake. The operational definition of a phycocyanin bloom was set at 1,000 RF for all lakes. We do not have historical phycocyanin data, so we were unable to use the same approach for estimating a bloom threshold. Quickest detection alarms for each lake year were then tallied as either occurring before the onset of the bloom (defined as surpassing either the chlorophyll *a* or phycocyanin bloom threshold) or before the maximum chlorophyll *a* concentration was reached, signifying the peak of the bloom. The alarm tallies were used to evaluate the efficacy, reliability, and timeliness of the resilience indicators providing early warning of impending algal blooms.

Retrospective analysis

In addition to the quickest detection analyses for early warnings, we estimated the eigenvalues of the time series of all state variables. If the time series approach a critical transition, the eigenvalues should cross above one from below (Carpenter and Brock 2006). We estimated the eigenvalues by fitting an autoregressive (AR) model with time-varying coefficients to each time series (Ives and Dakos 2012). Eigenvalues that approach and exceed one are consistent with a loss of resilience and a critical transition in the lake. Conversely, eigenvalues that do not approach one indicate stable time series and do not suggest evidence of a critical transition. Time varying AR (p) models were fit to each time series by the method of Pole et al. (1994) using a discount factor of 0.9 and optimal order was chosen by AIC. Optimal order was $P = 1$ for all time series presented here. Eigenvalues were computed according to Box and Jenkins (1976).

RESULTS

Bloom dynamics

Fluctuations in the ecosystem time series in the reference lake, Paul, were minimal compared to the manipulated lakes. Paul chlorophyll *a* concentrations were less than the bloom threshold in all years (Fig. 1d–f) except for one day in early 2013, and were generally lower than the chlorophyll concentrations in the manipulated lakes (Figs. 1d–f, 2d–f). Paul Lake also had low concentrations of phycocyanin (Fig. 1g–i) consistent with the low occurrence of cyanobacteria in the lake (Figs. 3 and 4). The DO concentration in Paul Lake was supersaturated each year before DOY 150 and then decreased below

atmospheric concentrations and remained undersaturated for the duration of the sampling period (Fig. 1j–l).

There was not a bloom in Peter Lake in 2013 as chlorophyll *a* did not surpass the 14.0 µg/L threshold (Fig. 1d). There was a brief increase in chlorophyll *a* concentrations between DOY 210 and 220, which coincided with an increase in phycocyanin (Fig. 1g), though not above the phycocyanin threshold, and a period of DO supersaturation (Fig. 1j); however, these conditions were not sustained. There was a moderate cyanobacterial bloom in Peter Lake in 2014 (Fig. 3), but only the phycocyanin threshold and not the chlorophyll *a* threshold was surpassed on DOY 210 (Fig. 1e, Table 3). There was synchrony in the dynamics of the three state variables between DOY 210–230, supporting the bloom status of the lake (Fig. 1h, k). The algal biomass during that period in Peter Lake was dominated by Cyanophyta and Cryptophyta, explaining the observed increase in phycocyanin. The largest bloom in Peter Lake occurred in 2015 and was dominated by cyanobacteria (*Anabaena* spp.; 93% of algal biomass on DOY 180; Fig. 3). The chlorophyll *a* bloom threshold was surpassed on DOY 173 and the phycocyanin threshold was surpassed on DOY 169 (Fig. 1f). The timing of the bloom in chlorophyll *a* coincided with the largest increase in phycocyanin (Fig. 1i) and DO supersaturation peaked at 130% (Fig. 1j).

The blooms in Tuesday Lake consistently occurred later in the sampling season than in Peter Lake (Figs. 1, 2). There was a moderate bloom in the later portion of the sampling period in 2013 in Tuesday Lake. Chlorophyll *a* concentrations surpassed the bloom threshold of 16.6 µg/L on DOY 208 (Fig. 2d, Table 3) and DO was supersaturated from DOY 211 to 240 (Fig. 2j). The bloom was a mix of dinoflagellates (*Glenodinium* spp.; 45% of algal biomass) and chrysophytes (*Ochromonas* spp.; 27% of algal biomass; Fig. 3). Consequently, there was little increase in phycocyanin (Fig. 2g), as the pigment is not produced by those groups of algae. There was a minor bloom in 2014 in Tuesday Lake with the maximum chlorophyll *a* concentration on DOY 172 briefly surpassing the bloom threshold (Fig. 2e). There was an elevation of phycocyanin above springtime concentrations (Fig. 2h), which surpassed the phycocyanin bloom threshold on DOY 231. This coincided with another period of chlorophyll *a* concentrations surpassing the bloom threshold. The algal biomass was dominated by chrysophyta near the chlorophyll *a* peak and haptophytes and cryptophyta (which contains phycocyanin) near the phycocyanin peak (Fig. 3). The largest bloom in either manipulated lake was a mix of *Anabaena* spp. (59% of algal biomass) and *Ochromonas* spp. (21% of algal biomass; Fig. 3) that occurred later in the sampling period in Tuesday Lake in 2015 (Fig. 2f). The chlorophyll *a* threshold was surpassed on DOY 221 and the phycocyanin threshold was surpassed on DOY 220 (Fig. 2i). There was strong synchrony in the dynamics of

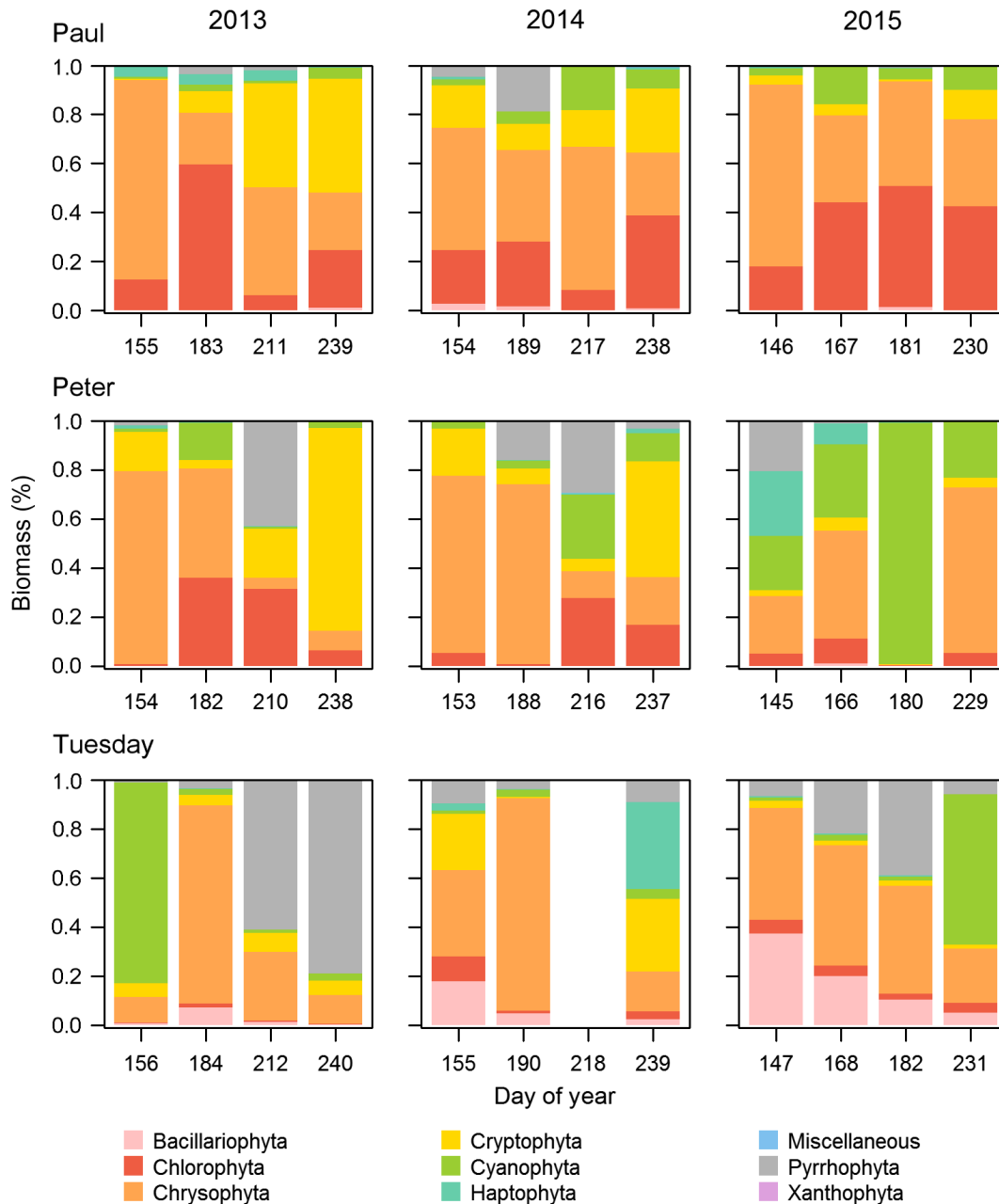


FIG. 3. Monthly algal taxa as a percentage of total biomass in each lake for each year. Data are missing in Tuesday Lake 2014 for day of the year (DOY) 218 due to a preservation error.

the state variables, including supersaturated DO during the bloom period (Fig. 2l).

Blooms can vary in strength due to external nutrient loading, water clarity (measured as water color), grazer biomass, ambient nutrient loading, and water temperature. Both drivers and algal dynamics varied among lakes and years. Among the experimental lakes, Tuesday Lake consistently had a higher water color than Peter Lake and water color decreased from 2013 to 2015 in all lakes (Fig. 5a). The biomass of the grazer *Daphnia*

declined in Peter and Tuesday Lakes from 2013 to 2015 as well but remained relatively constant in the reference lake (Fig. 5b). The cumulative external nutrient loading was lower in 2013 in both lakes compared to subsequent years (Figs. 1, 2). However, spring concentrations of TP, an indication of ambient nutrient loading, were low and consistent among lakes (Fig. 5c). Median water temperature was also consistent among lakes and years, although water temperature was less variable during the season in 2014 (Fig. 5d). Overall, differences in color



FIG. 4. Grab samples of the surface waters from Paul (left) and Peter (right) lakes on DOY 220 in 2014 illustrating the *Anabaena* spp. bloom in Peter Lake at that time.

and grazers are plausible explanations for differences among lakes and years in the blooms.

Alarm performance

Quickest detection alarms were tallied to assess the efficacy of the early warnings. In each lake year with an algal bloom, there was at least one resilience indicator with a pre-bloom alarm (Fig. 6, Table 3). Even though there was not a bloom in Peter Lake in 2013 (the bloom was approached but never achieved), alarms in both SD and AC occurred before the maximum chlorophyll *a* concentration was reached on DOY 211 (Table 3). For the smaller bloom in Peter Lake 2014 only SD gave pre-bloom alarms (Fig. 6). For the moderate bloom in Tuesday Lake 2013, there were pre-bloom alarms for one variable in SD and AC. The greatest number of pre-bloom alarms occurred in 2015 for both lakes. There were alarms for chlorophyll SD and AC, phycocyanin SD and AC, and $\text{DO}_{\% \text{sat}}$ AC before the onset of the bloom in Peter Lake and alarms for all indicators before the bloom in Tuesday Lake in 2015. A few alarms were observed when AC in Tuesday Lake was lower than AC in the reference lake (Appendix S1).

The number of days between the first alarm and the onset of a bloom was calculated to evaluate the timeliness of alarms. In general, the later in the season that the bloom occurred, the greater the number of days occurred between the first alarm and the bloom. The alarms in Tuesday Lake 2015, the bloom with the latest peak chlorophyll *a* concentration (DOY 240), triggered 46–57 d before the bloom onset, the earliest warning of a bloom detected in any lake-year (Table 3). The SD alarms for Peter Lake 2014 chlorophyll *a* and

phycocyanin also had a long lead-time, triggering 40 d before the onset of the bloom. The alarms in Peter Lake in 2015 were triggered much closer to the onset of the bloom, arriving only 1–10 d before the onset.

Eigenvalue estimates

Eigenvalues for phycocyanin time series approached or exceeded one in most lake years in the manipulated lakes (Fig. 7). In Peter Lake in 2013 there were early warning alarms from DOY 170–227 (Table 3, Fig. 6); although there was not an algal bloom, the eigenvalues for phycocyanin exceeded 1 on DOY 227 in Peter Lake 2013. There was a more substantial *Anabaena* bloom in Peter Lake in 2014 that was preceded by alarms in phycocyanin. The eigenvalues for Peter Lake 2014 phycocyanin briefly exceeded 1 early in the season (around DOY 150) and again surpassed 1 on DOY 212–217 consistent with a critical transition to algal dominance. In 2015 in Peter Lake, the eigenvalues for phycocyanin exceeded 1 from DOY 170–179, corresponding with the onset of the large cyanobacterial bloom.

The eigenvalues of phycocyanin time series briefly exceeded 1 in Tuesday Lake in 2013 around DOY 210, consistent with the first day of the bloom in that year (Table 3). In 2014, the eigenvalue of phycocyanin exceeded 1 in the early portion of the season (DOY 150) and remained less than 1 for the rest of the season, providing little evidence of a critical transition. In 2015, the eigenvalues were close to 1 throughout the first third of the season and exceeded 1 from approximately DOY 220–230. This pattern was consistent with the large bloom beginning on DOY 224.

TABLE 3. The timing of quickest detection alarms in the resilience indicators for each lake year.

State variable	DOY bloom	DOY max chl <i>a</i>	Standard deviation			Autocorrelation		
			DOY first alarm	No. alarms pre-bloom	No. alarms pre-max chl <i>a</i>	DOY first alarm	No. alarms pre-bloom	No. alarms pre-max chl <i>a</i>
Peter								
2013								
Chl <i>a</i>	n.a.	211	n.a.	n.a.	0	170	n.a.	5
Phyco	n.a.		171	n.a.	3	174	n.a.	1
DO			227	n.a.	0	n.a.	n.a.	n.a.
2014								
Chl <i>a</i>	n.a.	234	170	5	7	n.a.	n.a.	n.a.
Phyco	210		170	3	7	n.a.	n.a.	n.a.
DO			193	2	7	n.a.	n.a.	n.a.
2015								
Chl <i>a</i>	173	179	169	1	3	170	1	3
Phyco	169		166	1	4	163	1	2
DO			178	0	1	170	1	1
Tuesday								
2013								
Chl <i>a</i>	208	218	n.a.	n.a.	n.a.	172	1	1
Phyco	n.a.		204	1	3	246	0	0
DO			220	0	0	n.a.	n.a.	n.a.
2014								
Chl <i>a</i>	172	235	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Phyco	231		239	0	0	n.a.	n.a.	n.a.
DO			192	4	4	225	4	5
2015								
Chl <i>a</i>	221	240	192	1	4	170	1	2
Phyco	220		194	1	4	163	2	2
DO			188	5	10	170	5	5

Notes: The day of year (DOY) of the first alarm in the variable, alarms that occurred before surpassing the chlorophyll *a* (Chl *a*) bloom threshold or the phycocyanin (Phyco) bloom threshold, and before the peak of the bloom (maximum chlorophyll *a* concentration [max]) were tallied as indicators of the timing and efficacy of the various resilience indicator alarms. The boldface and italic DOY bloom is the beginning of the bloom in each lake year (see *Methods*). DOY 231 was selected as the bloom date for Tuesday 2014 due to the synchrony in all state variables at that time (see *Results*). DO, dissolved oxygen; n.a., not applicable.

The eigenvalues of phycocyanin time series in Paul Lake never exceeded 1; however, the eigenvalue was within one standard error of 1 at the end of 2013 and 2015 and on DOY 180 in 2014 (Fig. 7). The patterns in eigenvalues of chlorophyll *a* time series and periods where those eigenvalues exceed 1 corroborate the evidence of a critical transition in the manipulated lakes and a lack of a critical transition in the reference lake (see Appendix S1).

DISCUSSION

The statistical early warning indicators and quickest detection alarms were effective, reliable, and timely predictors of large algal blooms in the experimental lakes. With one exception, in all lakes and years when blooms occurred, the blooms were preceded by alarms in one or more resilience indicators. In the instance when no bloom occurred in an enriched lake (Peter Lake 2013), there were still alarms as the system slowly approached, but did not reach, bloom concentrations. The timing of first alarms ranged from as little as 8 d prior to blooms

in Peter Lake 2014 and 2015 to 61 d prior to the large bloom in Tuesday Lake 2015. There were more instances of pre-bloom alarms for SD than AC for the time-series variables, but for the total number of pre-bloom alarms (counting repeat alarms before the blooms) the two statistics were nearly equivalent (14 and 12 alarms across all lake years in SD and AC, respectively). Stronger blooms were associated with alarms in more of the time series variables prior to the bloom, while weaker blooms exhibited alarms in fewer variables.

In order to evaluate the reliability of the quickest detection alarms before the algal blooms, the number of state variables with pre-bloom alarms was compared to the magnitude of the subsequent algal bloom. Across the lakes and years, there was a general pattern of more variables with pre-bloom alarms when there were larger subsequent algal blooms (measured as the peak chlorophyll *a* concentration; Fig. 8). Similarly, the larger the subsequent algal bloom, a greater number of pre-bloom alarms occurred (Table 3). In general, AC alarms triggered before SD alarms when both occurred before a bloom in any lake year (Fig. 6).

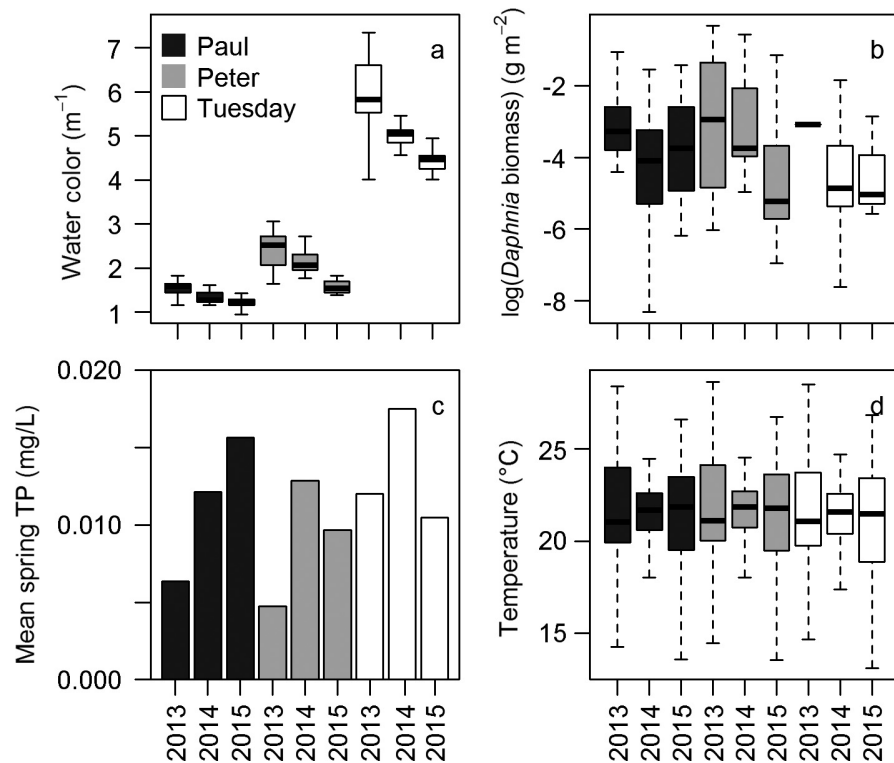


FIG. 5. Possible drivers of variability in bloom strength and timing among the lakes and years include (a) water color measured weekly in the epilimnion, (b) grazer biomass (g/m²) measured weekly, (c) background P loading measured as springtime total P (TP) concentrations, and (d) water temperature measured at a high frequency by the Hydrolab sensor. For the box plots, the middle line is the median, the box is the 25th and 75th percentile and the whiskers are the 5th and 95th percentiles.

There were instances, such as Peter Lake 2014, when alarms did not occur in both SD and AC prior to the onset of the bloom. Environmental variability, the rate at which a bloom is approached, and measurement error can contribute to the state variable dynamics and potentially cause false positives (alarms when a critical transition is not being approached) and false negatives (no alarms when approaching a critical transition). In the case of Peter Lake 2014, the critical transition was heralded by only SD alarms. Although we did not detect an alarm in AC, eigenvalues estimated by time-varying regression did approach and exceed one near the time of the bloom in Peter Lake 2014. The rolling window AC, which assumes stationarity over a 21-d window, failed to detect this shift. In four of the six lake years there was at least one false negative, or a lack of identification of an impending bloom for a resilience indicator in one variable.

The sensitivity of AC and SD alarms differed among the state variables. While alarms in chlorophyll *a* and phycocyanin occurred at similar times within a lake year, DO_{%sat} alarms often occurred at different times. As a byproduct of photosynthesis, DO_{%sat} varies with algal biomass. However, the continual equilibration with the atmosphere modifies the dynamics of DO_{%sat} and dampens the responsiveness of the variable. It is plausible that other variables commonly associated with water quality

(e.g., Secchi transparency or turbidity) would serve well as indicators. Batt et al. (2013b) found that directly measured variables such as pigments or chemical concentrations provided more sensitive resilience indicators than derived variables such as primary production and respiration. From the results of this study and Batt et al. (2013b), a general pattern in the utility of variables is emerging. Those variables that are a more direct measurement of the process tied to the critical transition appear to be more reliable indicators of resilience.

Historical information about manipulated and reference ecosystems is useful for interpreting early warning alarms. In order to evaluate the timing of the early warning alarms relative to the regime shift, the onset of a bloom was defined based on the probability of one sample exceeding the historic chlorophyll threshold out of 100 sampling days. The bloom criteria differed for Peter and Tuesday lakes due to their different historical concentrations of chlorophyll *a*. If the bloom criteria were established with no prior information about the lakes, the interpretation of the alarm timing would differ from the results presented here. However, it is important to note that the definition of a bloom does not change the occurrence of the alarms observed in this study, only the evaluation of the proximity of the alarm to surpassing the bloom threshold.

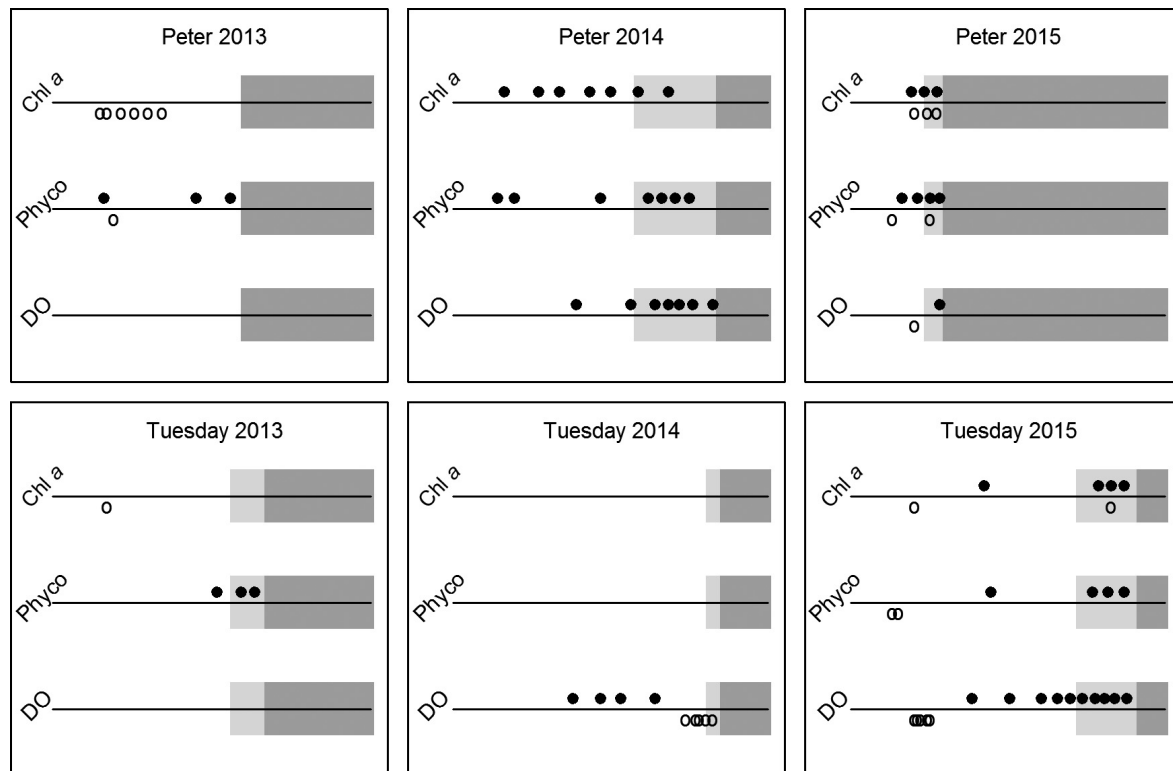


FIG. 6. Timeline of blooms and quickest detection alarms in all six lake-years for chlorophyll *a* (Chl *a*), phycocyanin (Phyco), and dissolved oxygen (DO). The light gray rectangle denotes the onset of bloom conditions and the dark gray rectangle is the period following the maximum chlorophyll concentration in the bloom. Standard deviation (SD) alarms are the solid circles above the timeline and autocorrelation (AC) alarms are the open circles below the timeline. The beginning of the timeline in each lake year is the first day of the rolling window calculation (e.g., DOY 150 in 2015 as monitoring began on DOY 129 and the rolling window length is 21 d).

Additionally, having a simultaneously measured reference lake to serve as the baseline state for calculating the S-R statistic may have improved the performance of the early warning alarms by accounting for variability due to weather and other factors not related to algal dynamics. In the absence of a simultaneously measured reference ecosystem, the baseline state could be estimated using historical data from the same system. Long-term ecological data provide valuable baselines for detecting abrupt changes and long-term trends in ecosystems (Bestelmeyer et al. 2011, Peters et al. 2013). It is plausible that long-term ecological data can provide a rigorous baseline for resilience indicators and this idea merits further empirical testing. Even in this experiment where historical data and a nearby reference lake were available, a few alarms suggest that the quickest detection method should be applied cautiously to time series data. Specifically, early warning indicator analysis is only appropriate when there is reason to believe a critical transition may occur and measurement frequency is sufficient relative to the rate of approach to the transition to quantify changes in resilience.

Regime shifts occur in a variety of ecosystems and in some cases are likely to be preceded by early warning

indicators similar to the alarms observed in this study. More work is needed to assess characteristics of indicators and sampling regimes that are appropriate for different ecosystem types and time scales. The intensity and rate of the driver pushing an ecosystem toward a critical transition and the duration of the driver influence the potential to detect and predict regime shifts (Ratajczak et al. 2017). Similarly, data need to be acquired at a rate that tracks the dynamics of both the driver and response in order to detect an impending transition.

Variability in drivers

Bloom strength varied substantially among the lakes and years, ranging from no bloom in Peter Lake 2013 (despite nutrient enrichment) to chlorophyll *a* concentrations greater than 70 $\mu\text{g/L}$ in Tuesday Lake 2015, 11 times greater than the lake's historical average. Additionally, there was variability in the timing of the blooms. For example, the blooms in Tuesday Lake 2013 and 2015 were delayed until the second half of the season whereas the bloom in Peter Lake 2015 occurred within 20 d of the start of nutrient additions. The blooms in the manipulated lakes in 2015 were also more

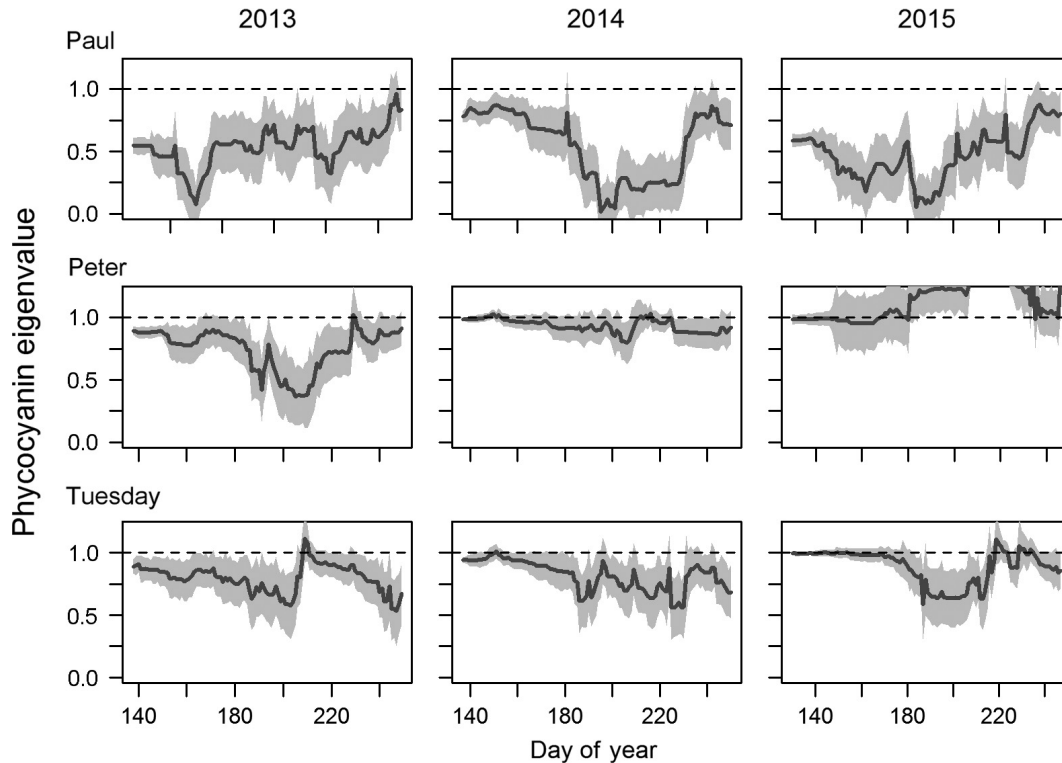


FIG. 7. Eigenvalues for the phycocyanin time series computed by time-varying autoregression for each lake year in the manipulated and reference lakes. The shaded bands are the bootstrapped standard error and the dashed line indicates the break between stable conditions (eigenvalues < 1) and unstable conditions (eigenvalues > 1).

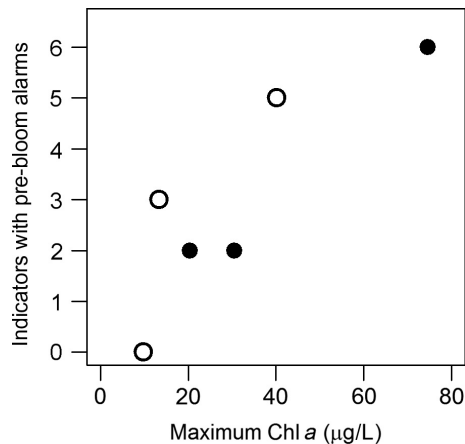


FIG. 8. The relationship between bloom magnitude (maximum chlorophyll concentration) and the number of variables with quickest detection alarms (both SD and AC) before the bloom occurred (Table 3). Open circles are the blooms in Peter Lake and solid circles are blooms in Tuesday Lake.

than double the chlorophyll *a* concentrations of blooms in 2013–2014. A number of factors could have contributed to the variability in bloom strength and timing including experimental nutrient loading, ambient loading, water color, temperature, and grazing.

Nutrient loading drove the shift toward blooms examined in this study. In the study lakes, ambient nutrient loading was low and was quickly exceeded by the experimental nutrient loading. The lower experimental nutrient loading in 2013 may have contributed to the lack of a bloom in Peter Lake, although the difference in annual P loading was $< 16\%$ among experimental years. The springtime phosphorus concentrations in the study lakes were similar to the concentrations in the reference lake, indicating that nutrient retention in the water column from year to year was unlikely. This supports the treatment of each lake year as an independent trial for the nutrient additions.

It is likely that other drivers may have moderated the response to nutrient loading. Water color was much higher in Tuesday Lake compared to Peter and Paul Lakes due to terrestrial inputs of colored dissolved organic matter (Wilkinson et al. 2013). Decreased light availability in Tuesday Lake could have contributed to the delayed blooms as algae had to overcome both nutrient and light limitations. There was also inter-annual variability in water color, as it decreased in all lakes across the three years. Inter-annual fluctuations in water color have been observed in these lakes previously (Pace and Cole 2002) and are likely caused by changes in external conditions. The biomass of a key zooplankton

grazer, *Daphnia* spp., also decreased in the experimental lakes over the three years. The combined influence of increased experimental nutrient loading, decreased water color, and decreased grazing pressure on phytoplankton of Peter and Tuesday Lakes in 2015 could explain the large blooms that occurred in that year. Temperature could also influence the timing and size of blooms, although it likely played a smaller role in this study as the median water temperature was the same in all lakes and years. However, the warming trajectory differed each year and could have interacted with the other variables and influenced the timing and size of the algal blooms.

Environmental variability at scales found in real ecosystems may interfere with statistical early warning signals (Perretti and Munch 2012, Boettiger et al. 2013, Dakos et al. 2015). Despite such variability, we were able to detect early warning signals before blooms occurred in these experimental lakes. Successful detection is attributable in part to the high frequency data collected for the express purpose of detecting approach to a specific regime shift, as well as the benchmark provided by the reference ecosystem. In contrast, happenstance data collected for another purpose may not detect changes in resilience indicators, even if major regime shifts occur (Gsell et al. 2016). Broader understanding of resilience indicators in natural ecosystems is likely to require increased high-frequency monitoring focused on likely transitions in stressed ecosystems, in conjunction with ongoing long-term observations and comparisons across ecosystems that exhibit a range of resilience characteristics.

Ecologists have proposed many theoretical ideas about the factors that increase or decrease the resilience and stability of ecosystems (Ives and Carpenter 2007, Donohue et al. 2016). These hypotheses can be evaluated using measurements of stability or resilience. Resilience indicators provide such metrics, and therefore offer a basis for comparing and classifying ecosystems with respect to resilience. Our study revealed clear differences in resilience among lakes and years. These differences suggest that the indicators could be used to evaluate hypotheses about causes for differences in resilience among contrasting ecosystems.

Management implications

Resilience indicators are supported by theory and increasingly by experiments, but are they useful to managers? To be useful a warning must be reliably detectable and occur far enough in advance to allow a response. In this study, strong blooms were signaled up to several weeks in advance. These advanced warnings would provide sufficient time for some, but not all management actions. For example, given warnings of a week or more managers could plausibly issue public alerts about health hazards, take direct action to curtail blooms by applying algaecides, shut off water intakes, or decrease point-source nutrient inputs. However, management actions to mitigate nonpoint runoff of nutrients may take years to

centuries to become effective and could not be implemented in the time frame of the warnings considered here (Hamilton 2012, Rissman and Carpenter 2015).

Our results indicate that managers could have more confidence in the alarms when a bigger bloom is forthcoming, as more alarms in a greater number of variables decrease the likelihood of misidentifying an impending bloom. The availability of a reference ecosystem is also helpful, but may not be possible in many cases. While the need to collect data at a high frequency (daily) to evaluate early warnings could be an impediment to implementing this detection system, the growing availability, reliability, and falling costs of sensors suggest monitoring for warnings of ecosystem regime shifts is increasingly feasible, especially in cases where protection of services (e.g., drinking water) is vital. Watershed management to prevent or limit algal blooms remains a critical best practice. Nonetheless, in lakes that are already degrading from excessive nutrient input, the resilience indicators may foreshadow blooms with enough advance warning to notify the public or intervene to prevent the bloom.

While the analysis of resilience indicators presented here is focused on early warnings of regime shifts within an ecosystem, the resilience indicators can also be used comparatively among ecosystems. In this multi-year, multi-ecosystem study, the resilience indicators correctly identified varying resilience across lakes and years. In management, differences in resilience could be used to classify ecosystems with respect to risk of regime shifts or guide the allocation of resources to prevent regime shifts in the most vulnerable ecosystems.

This study establishes that early warnings of declining resilience are evident in experimental lakes preceding strong phytoplankton blooms while weak changes give more ambiguous signals. These results are consistent with theory that loss of resilience near thresholds is associated with slower recovery from perturbations (Scheffer et al. 2015). The research suggests that resilience indicators may be valuable for comparative studies of ecosystems and analyses of long-term ecosystem change. Declining resilience should be a cause of concern for ecosystem managers. However, regime shifts often involve subtle changes in slowly changing variables, stochastic events, or other surprises. Thus many ecosystems changes are likely to occur without warning, which argues for research on thresholds and properties promoting resilience (Pace et al. 2015). Maintaining resilience of desired ecosystem states by avoiding dangerous levels of ecosystem stress (e.g., by reducing phosphorus loads in the case of lakes) may ultimately prove to be the most effective means of preventing unwanted shifts in ecosystems and loss of the services that ecosystems provide.

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LITERATURE CITED

- Ask, J., J. Karlsson, L. Persson, P. Ask, P. Byström, and M. Jansson. 2009. Terrestrial organic matter and light penetration: effects on bacterial and primary production in lakes. *Limnology and Oceanography* 54:2034–2040.
- Batt, R. D., W. A. Brock, S. R. Carpenter, J. J. Cole, M. L. Pace, and D. A. Seekell. 2013a. Asymmetric response of early warning indicators of phytoplankton transition to and from cycles. *Theoretical Ecology* 6:285–293.
- Batt, R. D., S. R. Carpenter, J. J. Cole, M. L. Pace, and R. A. Johnson. 2013b. Changes in ecosystem resilience detected in automated measures of ecosystem metabolism during a whole-lake experiment. *Proceedings of the National Academy of Sciences USA* 110:17398–17403.
- Bestelmeyer, B. T., et al. 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere* 2:1–26.
- Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences USA* 106:826–831.
- Boettiger, C., N. Ross, and A. Hastings. 2013. Early warning signals: the charted and uncharted territories. *Theoretical Ecology* 6:255–264.
- Box, G. E. P., and G. M. Jenkins. 1976. Time series analysis forecasting and control, Second edition. Holden-Day, San Francisco, California, USA.
- Brock, W. A., and S. R. Carpenter. 2010. Interacting regime shifts in ecosystems: implication for early warnings. *Ecological Monographs* 80:353–367.
- Butitta, V. L., S. R. Carpenter, L. C. Loken, M. L. Pace, and E. H. Stanley. 2017. Spatial early warning signals in a lake manipulation. *Ecosphere* 8:e01941. 10.1002/ecs2.1941
- Carlson, R. E. 1977. A trophic state index for lakes. *Limnology and Oceanography* 22:361–369.
- Carmichael, W. W., and G. L. Boyer. 2016. Health impacts from cyanobacteria harmful algae blooms: implications for the North American Great Lakes. *Harmful Algae* 54:194–212.
- Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. Ecology Institute, Oldendorf/Luhe, Germany.
- Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. *Ecology Letters* 9:311–318.
- Carpenter, S. R., W. A. Brock, J. J. Cole, and M. L. Pace. 2014. A new approach for rapid detection of nearby thresholds in ecosystem time series. *Oikos* 123:290–297.
- Carpenter, S. R., et al. 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079–1082.
- Contamin, R., and A. M. Ellison. 2009. Indicators of regime shifts in ecological systems: What do we need to know and when do we need to know it. *Ecological Applications* 19:799–816.
- Crépin, A., R. Biggs, S. Polasky, M. Troel, and A. de Zeeuw. 2012. Regime shifts and management. *Ecological Economics* 84:15–22.
- Cuthbert, I. D., and P. del Giorgio. 1992. Toward a standard method of measuring color in freshwater. *Limnology and Oceanography* 37:1319–1326.
- Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336:1175–1177.
- Dakos, V., S. R. Carpenter, E. H. van Nes, and M. Scheffer. 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B* 370:20130263.
- Dakos, V., M. Scheffer, E. H. van Nes, V. Brovkin, V. Petoukhov, and H. Held. 2008. Slowing down as an early warning signal for abrupt climate change. *Proceedings of the National Academy of Sciences USA* 105:14308–14312.
- Dakos, V., et al. 2012. Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. *PLoS ONE* 7(7):e41010.
- Donohue, I., et al. 2016. Navigating the complexity of ecological stability. *Ecology Letters* 19:1172–1185.
- Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467:456–459.
- Falconer, I. R. 1999. An overview of problems caused by toxic blue-green algae (cyanobacteria) in drinking and recreational water. *Environmental Toxicology* 14:5–12.
- Gsell, A. S., et al. 2016. Evaluating early warning indicators of critical transitions in natural aquatic ecosystems. *Proceedings of the National Academy of Sciences USA* 113:8089–8095.
- Guttal, V., and C. Jayaprakash. 2008. Changing skewness: an early warning signal of regime shifts in ecosystems. *Ecology Letters* 11:450–460.
- Hamilton, S. K. 2012. Biogeochemical time lags may delay responses of streams to ecological restoration. *Freshwater Biology* 57:43–57.
- van der Heide, T., E. H. van Nes, G. W. Geerling, A. J. P. Smolders, T. J. Bouma, and M. M. van Katwijk. 2007. Positive feedbacks in seagrass ecosystems – implications for success in conservation and restoration. *Ecosystems* 10:1311–1322.
- Holmes, E., E. Ward and K. Wills. 2015. MARSS: Multivariate autoregressive state space modeling, R package version 3.9, <http://CRAN.R-project.org/package=MARSS>
- Holm-Hansen, O. 1978. Chlorophyll a determination: improvements in methodology. *Oikos* 30:438–447.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hutchings, J. A., and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risks. *BioScience* 54:297–309.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
- Ives, A. R., and V. Dakos. 2012. Detecting dynamical changes in nonlinear time series using locally linear state-space models. *Ecosphere* 3:art58.
- Janssen, M. A., J. M. Anderies, and B. H. Walker. 2004. Robust strategies for managing rangelands with multiple stable attractors. *Journal of Environmental Economics and Management* 47:140–162.
- Kéfi, S., V. Dakos, M. Scheffer, E. H. Van Nes, and M. Rietkerk. 2013. Early warning signals also precede non-catastrophic transitions. *Oikos* 122:641–648.
- Kéfi, S., V. Guttal, W. A. Brock, S. R. Carpenter, A. M. Ellison, V. N. Livina, D. A. Seekell, M. Scheffer, E. H. van Nes, and

- V. Dakos. 2014. Early warning signals of ecological transitions: methods for spatial patterns. *PLoS ONE* 9:e92097.
- Kudela, R. M., et al. 2015. Harmful algal blooms: a scientific summary for policy makers. IOC/INF-1320 [Report]. IOC/ UNESCO, Paris, France.
- Lenton, T. M., H. Held, E. Kriegler, J. W. Hall, W. Lucht, S. Rahmstorf, and H. J. Schellnhuber. 2008. Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences USA* 105:1786–1793.
- McGlathery, K. J., M. A. Reidenbach, P. D'Odorico, S. Fagherazzi, M. L. Pace, and J. H. Porter. 2013. Nonlinear dynamics and alternative stable states in shallow coastal systems. *Oceanography* 26:220–231.
- Michalak, A. M. 2016. Study role of climate change in extreme threats to water quality. *Nature* 535:349–350.
- van Nes, E. H., and M. Scheffer. 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *American Naturalist* 169:738–747.
- Nyström, M., A. V. Norström, T. Blenckner, M. de la Torre-Castro, S. Eklö, C. Folke, R. S. Henrikösterblom, M. Thyreson Steneck, and M. Troell. 2012. Confronting feedbacks of degraded marine ecosystems. *Ecosystems* 15:695–710.
- Pace, M. L., R. D. Batt, C. D. Buelo, S. R. Carpenter, J. J. Cole, J. T. Kurtzweil, and G. M. Wilkinson. 2017. Reversal of a cyanobacterial bloom in response to early warnings. *Proceedings of the National Academy of Sciences USA* 114:352–357.
- Pace, M. L., S. R. Carpenter, and J. J. Cole. 2015. With and without warning: managing ecosystems in a changing world. *Frontiers in Ecology and Environment* 13:460–467.
- Pace, M. L., and J. J. Cole. 2002. Synchronous variation of dissolved organic carbon and color in lakes. *Limnology and Oceanography* 47:333–342.
- Perretti, C. T., and S. B. Munch. 2012. Regime shift indicators fail under noise levels commonly observed in ecological systems. *Ecological Applications* 22:1772–1779.
- Peters, D. P. C., et al. 2013. Long-term trends in ecological systems: a basis for understanding responses to global change. USDA ARS Technical Bulletin. USDA, Washington, D.C., USA.
- Pole, A., M. West, and J. Harrison. 1994. Page 409 Applied Bayesian forecasting and time series analysis. Chapman and Hall, New York, New York, USA.
- Polunchenko, A., and A. G. Tartakovsky. 2012. State of the art in sequential change-point detection. *Methodology and Computing in Applied Probability* 14:649–683.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ratajczak, Z., P. D'Odorico, S. L. Collins, B. Bestelmeyer, F. Isbell, and J. B. Nippert. 2017. The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. *Ecological Monographs* 87:198–218.
- Rengefors, K., S. Gustafsson, and A. Ståhl-Delbanco. 2004. Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profundal sediments. *Aquatic Microbial Ecology* 36:213–226.
- Rissman, A., and S. R. Carpenter. 2015. Progress on non-point pollution: barriers and opportunities. *Daedalus* 144 (3):35–47.
- Rocha, J., J. Yletyinen, R. Biggs, T. Blenckner, and G. Peterson. 2015. Marine regime shifts: drivers and impacts on ecosystems services. *Philosophical Transactions of the Royal Society B* 370:20130273.
- Scheffer, M. 2009. Critical transitions in nature and society. Princeton University Press, Princeton, New Jersey, USA.
- Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early warning signals for critical transitions. *Nature* 461:53–59.
- Scheffer, M., S. R. Carpenter, V. Dakos, and E. H. V. Nes. 2015. Generic indicators of ecological resilience: inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics* 46:145–167.
- Scheffer, M. J., and E. Jeppesen. 2007. Regime shifts in shallow lakes. *Ecosystems* 10:1–3.
- Scheffer, M., S. Rinaldi, and Y. Kuznetsov. 2000. Effects of fish on plankton dynamics: a theoretical analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1208–1219.
- Seekell, D. A., S. R. Carpenter, and M. L. Pace. 2011. Conditional heteroscedasticity as a leading indicator of ecological regime shifts. *American Naturalist* 178:442–451.
- Stauffer, R. E. 1990. Electrode pH error, seasonal epilimnetic pCO₂, and the recent acidification of the Maine lakes. *Water, Air, & Soil Pollution* 50:123–148.
- Veraart, A. J., E. J. Faassen, V. Dakos, E. H. van Nes, M. Lürling, and M. Scheffer. 2012. Recovery rates reflect distance to a tipping point in a living system. *Nature* 481:357–360.
- Wang, R., J. A. Dearing, P. G. Langdon, E. Zhang, X. Yang, V. Dakos, and M. Scheffer. 2012. Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature* 492:419–422.
- Wilkinson, G. M., J. J. Cole, and M. L. Pace. 2013. Terrestrial dominance of organic matter in north temperate lakes. *Global Biogeochemical Cycles* 27:43–51.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1286/full>

DATA AVAILABILITY

Data associated with this study are available from the LTER Network Data Portal:

<https://doi.org/10.6073/pasta/8d71e8d3fdec619807e5c05fa1b3eb13>,
<https://doi.org/10.6073/pasta/f2956422d5797c61fe6ceb15faa19f3b>,
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<https://doi.org/10.6073/pasta/364622a6632f857289f9abc6a99d3ae7>,
<https://doi.org/10.6073/pasta/6a658526e313dbcecb0331a1f343c01>,
<https://doi.org/10.6073/pasta/6fc6015c620056034512fde089d50c27>.