

Spatial early warning signals in a lake manipulation

VINCE L. BUTITTA,^{1,†} STEPHEN R. CARPENTER,¹ LUKE C. LOKEN,^{1,2} MICHAEL L. PACE,³ AND EMILY H. STANLEY^{ID}¹

¹Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706 USA

²Wisconsin Water Science Center, U.S. Geological Survey, Middleton, Wisconsin 53562 USA

³Department of Environmental Sciences, University of Virginia, 291 McCormick Road, P.O. Box 400123, Charlottesville, Virginia 22904 USA

Citation: 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(10):e01941. 10.1002/ecs2.1941

Abstract. Rapid changes in state have been documented for many of Earth's ecosystems. Despite a growing toolbox of methods for detecting declining resilience or early warning indicators (EWIs) of ecosystem transitions, these methods have rarely been evaluated in whole-ecosystem trials using reference ecosystems. In this study, we experimentally tested EWIs of cyanobacteria blooms based on changes in the spatial structure of a lake. We induced a cyanobacteria bloom by adding nutrients to an experimental lake and mapped fine-resolution spatial patterning of cyanobacteria using a mobile sensor platform. Prior to the bloom, we detected theoretically predicted spatial EWIs based on variance and spatial autocorrelation, as well as a new index based on the extreme values. Changes in EWIs were not discernible in an unenriched reference lake. Despite the fluid environment of a lake where spatial heterogeneity driven by biological processes may be overwhelmed by physical mixing, spatial EWIs detected an approaching bloom suggesting the utility of spatial metrics for signaling ecological thresholds.

Key words: algal bloom; critical transition; early warning indicators; ecosystem experiment; regime shift; resilience; spatial analysis.

Received 20 June 2017; **accepted** 26 June 2017. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2017 Butitta et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: vincent.butitta@wisc.edu

INTRODUCTION

Ecosystem transitions can result in drastic changes in composition, structure, and internal processes (Scheffer et al. 2001, 2012). Desertification of grasslands (Kéfi et al. 2007), collapse of coral reefs (Hoegh-Guldberg et al. 2007), and blooms of harmful cyanobacteria in freshwaters (Scheffer et al. 1997) represent examples of notable state transitions. Models of transitions are often characterized by bifurcation points (or tipping points), in which a small perturbation causes the ecosystem to quickly and easily “tip” from one dynamical pattern to another (Lenton et al. 2008, Scheffer et al. 2009).

Recent work in ecology has explored how to identify when an ecosystem is at risk of undergoing a critical transition (Scheffer et al. 2009, 2012,

2015). Modeling suggests that there are common statistical characteristics of spatial or temporal data near a tipping point between alternative ecosystem states. Identifying these statistical characteristics—often referred to as early warning indicators (EWIs)—could make it possible to detect an approaching tipping point before it is crossed. Many EWIs assess an ecosystem's weakening attraction to its current state, which is represented by a decreasing ability to recover quickly after perturbations. Slower recovery rate of an ecosystem to a local equilibrium is referred to as critical slowing down and is the foundation of many EWIs (Wissel 1984, Dakos et al. 2011, Scheffer et al. 2015). Critical slowing down has been detected from changes in temporal dynamics in mesocosm experiments (Drake and Griffen 2010, Veraart et al. 2012, Dai et al. 2013) and in

whole-lake experiments (Carpenter et al. 2011, Pace et al. 2017). Simple spatially explicit models of critical transitions indicate that characteristics of spatial structure can also signal loss of resilience, and thus might be useful for early warnings (review by Scheffer et al. 2015). The mechanisms for spatial early warnings are diverse and are still active subjects of research. In many cases, appropriate spatial indicators are based on measures of variance, skewness, spatial autocorrelation, or patch size.

Although temporal and spatial EWIs may be fundamentally linked (Dakos et al. 2010), spatial analysis may sometimes be more powerful for assessing risk of critical transition (Guttal and Jayaprakash 2009, Dakos et al. 2010, Donangelo et al. 2010, Dai et al. 2013). Time series useful for detecting EWIs require unbroken series of frequent observations sustained for long periods of time. Existing time series that were collected for other purposes may not meet these requirements and thus can yield ambiguous results (Gsell et al. 2016). Spatial analysis at a few points in time (e.g., by remote sensing) may provide greater sensitivity at less cost than high-frequency time series.

While there are clear demonstrations of spatial EWI behavior drawn from theoretical examples (van Nes and Scheffer 2005, Guttal and Jayaprakash 2008, Carpenter and Brock 2010), and a handful from microcosm experiments (Drake and Griffen 2010, Dai et al. 2013), field experiments on spatial early warnings are rare (but see Carpenter et al. 2011, Cline et al. 2014, Ratajczak et al. 2016, Rindi et al. 2017). Physical processes that influence spatial patterning such as mixing or other homogenizing forces may limit detection of early warnings (Carpenter and Brock 2010, Dakos et al. 2010, Dai et al. 2013, Eby et al. 2017). For this reason, field studies exploring detection of EWIs under natural conditions are needed.

Lakes are a potentially useful ecosystem for evaluating spatial EWIs. Transitions of lakes to cyanobacterial bloom states, a common phenomenon of eutrophic lakes, can involve several types of critical transitions (Scheffer et al. 1997, 2000, Gragnani et al. 1999, Veraart et al. 2012, Batt et al. 2013). Many of these critical transitions could generate EWIs, and at least one model analysis has shown that this is the case (Batt et al. 2013). Spatial models of bloom formation

by cyanobacteria exhibit complex changes in spatial patterns that may generate spatial early warnings (Serizawa et al. 2008). Blooms are easily detected in surface waters with automated sensors capable of gathering high-frequency measurements. Time series from automated sensors successfully anticipated a cyanobacteria bloom in a whole-lake experiment (Pace et al. 2017). Cyanobacteria blooms are also of practical interest as they can create serious economic and human health problems (Dodds et al. 2009) as well as extensive alterations to aquatic ecosystems (Paerl et al. 2001). Their frequency and intensity are increasing in freshwaters globally—a trend that is expected to continue (O’Neil et al. 2011, Taranu et al. 2015).

Modeling studies cited above, especially the work of Serizawa et al. (2008), suggest that spatial patterns of cyanobacteria on lake surfaces may generate early warnings of blooms, but this phenomenon has yet to be tested under field conditions. Here, we induced a cyanobacteria bloom by adding nutrients to an experimental lake to investigate whether spatial early warnings are detectable prior to harmful cyanobacterial blooms. Cyanobacteria were mapped using a mobile sensor platform to measure the spatial structure of the cyanobacteria and attempt to detect early warnings of the bloom. We tested for increased spatial variance (Guttal and Jayaprakash 2009, Reinette et al. 2009), increased skewness (Guttal and Jayaprakash 2008), increased frequency of extreme events, and increased spatial autocorrelation (Dakos et al. 2010).

METHODS

In two consecutive years, we measured lake-wide spatial patterning of cyanobacteria using the FLAME platform (Crawford et al. 2015). To evaluate EWIs of a critical transition, in the first year we induced a cyanobacteria bloom through nutrient addition in an experimental lake while using a nearby unmanipulated lake as a reference ecosystem (Pace et al. 2017). During the second year, both lakes were left unmanipulated. Proposed detection methods for EWIs were compared between the manipulated and reference lakes to test for their ability to accurately detect statistical signals before the cyanobacteria bloom developed.

Lake description

Peter and Paul Lakes are small, oligotrophic lakes (Peter, 2.5 ha, 6 m, 19.6 m; and Paul, 1.7 ha, 3.9 m, 15 m, for surface area, mean, and max depth, respectively) located in the Northern Highlands Lake District in the Upper Peninsula of Michigan, USA (89°32' W, 46°13' N). These lakes have similar physical and chemical properties and are connected via a culvert with Paul Lake being upstream. Both lakes stratify soon after ice-off and remain stratified usually into November (for extensive lake descriptions, see Carpenter and Kitchell 1993).

In the first year, Peter Lake (hereafter “manipulated lake”) was fertilized daily starting on 1 June 2015 (day of year [DOY] 152) with a nutrient addition of 20 mg N·m⁻²·d⁻¹ and 3 mg P·m⁻²·d⁻¹ (molar N:P of 15:1) through the addition of H₃PO₄ and NH₄NO₃ until 29 June (DOY 180). The decision to stop nutrient additions required meeting four predefined criteria based on temporal changes in phycocyanin and chlorophyll concentrations indicative of early warning behavior of a critical transition to a persistent cyanobacteria bloom state (Pace et al. 2017). Nutrients uniformly mix within 1–2 d after fertilization based on prior studies (Cole and Pace 1998). No nutrient additions were made to Paul Lake (hereafter “reference lake”). In the second year (2016), neither lake received nutrient additions.

Field sampling

We mapped the surface water characteristics of both experimental lakes to identify changes in the spatial dynamics of cyanobacteria. In 2015, mapping occurred weekly from 4 June to 15 August (11 sample weeks). In 2016, when neither lake was fertilized, the lakes were mapped three times in early to mid-summer. In both years, mapping occurred between the hours of 07:00 and 12:00 (before the daily nutrient addition). We rotated the order that we sampled the lakes to avoid potential biases due to differences in time of day. Each individual lake sampling event was completed in approximately one hour.

The FLAME platform maps the spatial pattern of water characteristics. A boat-mounted sampling system continuously pumps surface water from the lake to a series of sensors while georeferencing each measurement (complete description of the FLAME platform in Crawford et al. 2015). For this study, the FLAME was mounted

on a small flat-bottomed boat propelled by an electric motor and was outfitted with a YSI EXO2 multi-parameter sonde (YSI 2015). We focused for this study on measures of phycocyanin (a pigment unique to cyanobacteria) and temperature. Phycocyanin fluorescence was measured using the optical EXO Total Algae PC Smart Sensor. The Total Algae PC Smart Sensor was calibrated with a rhodamine solution based on the manufacturer's recommendations. Phycocyanin concentrations are reported as µg/L; however, these concentrations should be considered as relative because we did not calibrate the sensor to actual phycocyanin nor blue-green algae concentrations. Geographic positions were measured using a Garmin echoMAP 50s (Garmin International, Olathe, Kansas, USA). Sensor data were collected continuously at 1 Hz and linked via timestamp to create spatially explicit data for each lake. Each sampling produced approximately 3500 measurements in the manipulated lake and 2000 in the reference lake. The measurements were distributed by following a gridded pattern across the entire lake surface to characterize spatial patterns over the extent of the lake (Fig. 1).

Statistical analysis

Phycocyanin concentration were transformed to log₁₀(x + 1) units for statistical analysis. Q-Q plots indicated that transformation improved fit to a normal distribution. Reported concentrations and ranges were back-transformed for ease of interpretation; lower bounds included negatives because the range of sensor output extends from slightly negative to positive values. We analyzed the statistical and spatial properties of phycocyanin to calculate proposed EWIs of a cyanobacterial bloom. Specifically, we were interested in estimates of spatial variance, spatial skewness, frequency of extreme events (as indicated by the shape parameter of the extreme value distribution or EVD-shape), and spatial autocorrelation. Based on models (Guttal and Jayaprakash 2009, Carpenter and Brock 2010, Dakos et al. 2010) and a laboratory experiment (Dai et al. 2013), we expected increases in spatial variance, skewness (in the positive direction), and spatial autocorrelation prior to the bloom. In addition, we expected the frequency of extreme values to increase as the manipulated lake approached a bloom. Extreme values were assessed using the shape parameter

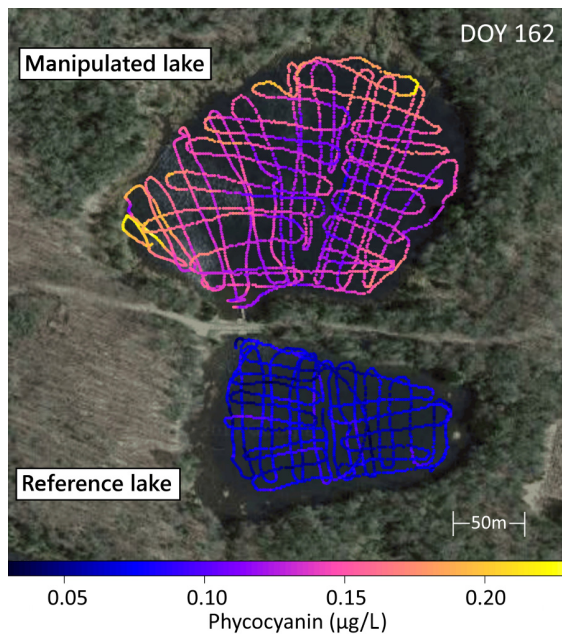


Fig. 1. A representative sampling day during the lake manipulation for both the manipulated lake ($N = 4169$) and reference lake ($N = 2422$). Each point represents a sampling location (sampling at 1 Hz), and the color of the point relates to the phycocyanin concentration.

of the generalized EVD (Gilleland and Katz 2016). This parameter increases with the frequency and magnitude of extreme events, assessed relative to the expectation from the normal distribution.

To check for spurious responses unrelated to a cyanobacteria bloom, we compared (1) statistical properties of cyanobacteria between the manipulated lake and reference lake, (2) years with and without fertilization in the manipulated lake, and (3) statistics for cyanobacteria to an abiotic variable, temperature. Temperature patterns should reflect physical processes that were not directly affected by nutrient addition nor biology. Thus, temperature provides an internal reference for abiotic effects on spatial pattern. Temperature was not transformed as it appeared to be normally distributed in Q-Q plots. The reference ecosystem tests the possibility that factors impinging on both lakes, such as weather, generated patterns we observed in the manipulated lake (Carpenter and Kitchell 1993).

High winds could potentially influence advective mixing of the lakes and thus the spatial structure of cyanobacteria. Comparisons between the

reference lake and the manipulated lake are likely minimally affected by differences in mixing given that they were sampled on the same day, are adjacent to each other, and are of similar size. However, to evaluate possible differences in wind between sampling dates, wind speeds from a nearby tower (3.2 km from the lakes) managed by the National Ecological Observatory Network (<http://www.neonscience.org>) were analyzed for high average wind speeds and gust speeds (average and maximum wind speed over 5-min windows) from a 4-h window that immediately preceded each day's sampling.

Data handling

All data are publicly accessible through the LTER data repository (Butitta et al. 2017). All statistical analyses were computed using R statistical software (R Core Team 2016). Aggregate statistics such as standard deviation (SD), median absolute deviation (MAD), and skewness were estimated across the spatial extent of the entire lake. Standard deviation and MAD were calculated using the "stats" package (R Core Team 2016). Skewness was calculated using the "moments" package (Komsta and Novomestky 2015). Extreme value distributions were fitted using the "extRemes" package in R using block maxima from bins of 16 consecutive data points (Gilleland and Katz 2016). Bin size is a compromise between precision of the block maxima and the number of bins for fitting the EVD. Extreme value distribution fits were based on an average of 200 bins for the manipulated lake and no <100 bins for the reference lake.

Non-parametric bootstraps of 1000 resamples were employed to calculate 99% confidence intervals for estimates of SD, MAD, skewness, and EVD-shape.

Semivariogram models and correlograms were used to evaluate changes in spatial structuring of individual lake variables. For both semivariogram and correlogram analysis, we used the geographic positions of point measurements. Semivariograms and correlograms were calculated at approximately 3-m intervals up to a distance of 60 m (approximately half the diameter of the manipulated lake). Model semivariograms were fit using fit.variogram function in the gstat package in R (Pebesma and Graeler 2016), using either an exponential or linear model (depending on goodness

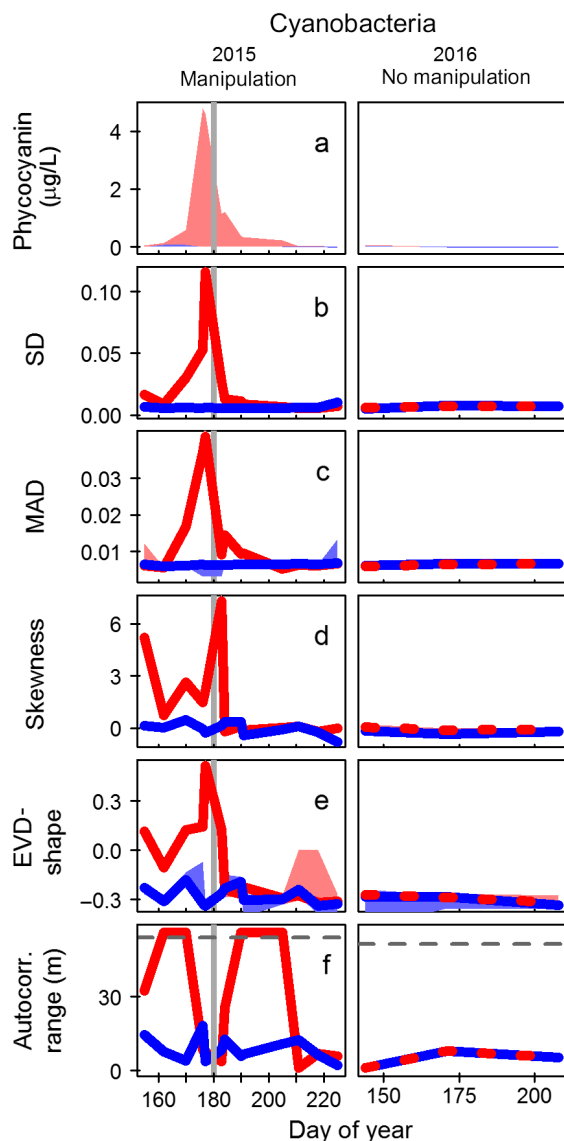


Fig. 2. Early warning statistics of cyanobacteria for manipulated and reference lakes during 2015 (left; with nutrient addition) and 2016 (right; no manipulation). For both the polygons and the lines, red and blue colors represent the manipulated and reference lake, respectively. Vertical gray lines represent the date nutrient addition stopped. Phycocyanin concentrations are displayed in the top panel (a). Lines are the following statistics based on phycocyanin: (b) standard deviation (SD), (c) median absolute deviation (MAD), (d) skewness, (e) shape parameter of the extreme value distribution (EVD-shape), and (f) autocorrelation range. Dotted gray line at 60 m in panel (f) represents the range of sample variograms, and estimated ranges

of fit) with weighting equal to $N_j/(\gamma(h_j)^2)$, where N_j is the number of observations in a distance class and $\gamma(h_j)$ is the estimated semivariance at distance class h_j . These models and parameterization were chosen because they consistently characterized sample semivariograms well and highly weight observations that are close in space. Correlograms were calculated using the `correlog` function in the “`ncf`” package in R (Bjornstad 2016). Standard deviations for correlograms (Figs. 4, 5) were calculated using 250 random resamples of 80% of observations from each sampling event. All reported error terms in the text are SDs.

RESULTS

We successfully initiated a cyanobacterial bloom during the experimental treatment (year 1) in the manipulated lake. Phycocyanin concentrations increased three orders of magnitude, reaching a peak lake-wide average of 4.8 µg/L on 25–26 of June (DOY 176–177; Fig. 2a). After nutrient additions stopped on 29 June (DOY 180), cyanobacteria concentrations steadily dropped until 30 July (DOY 211), after which they remained similar to the reference lake for the final three weeks of sampling. We used the date of peak phycocyanin concentration as the reference date for evaluating the spatial indicators, consistent with the interpretation of Pace et al. (2017). Phycocyanin concentrations in the reference lake (median ± 1 SD) were 0.0 µg/L (–0.02, 0.02) throughout both years of the study (Fig. 2a). In the second year, with no nutrient additions, the manipulated lake had consistently low phycocyanin concentrations, 0.0 µg/L (–0.07, 0.07). The manipulation that caused the cyanobacterial bloom allowed us to explore possible EWIs at a whole-lake areal scale.

Standard deviation and MAD of phycocyanin had similar temporal and within-treatment patterns. Standard deviation and MAD of phycocyanin concentrations were consistently low for the

(Fig. 2. *Continued*)

≥60 m were plotted at 60 m (lines jittered to see both). Polygons in panels (b–e) represent 99% confidence intervals computed from a non-parametric bootstrap. All estimates are based on 13 sampling events over 11 weeks in 2015 and three sampling events over a similar period in 2016.

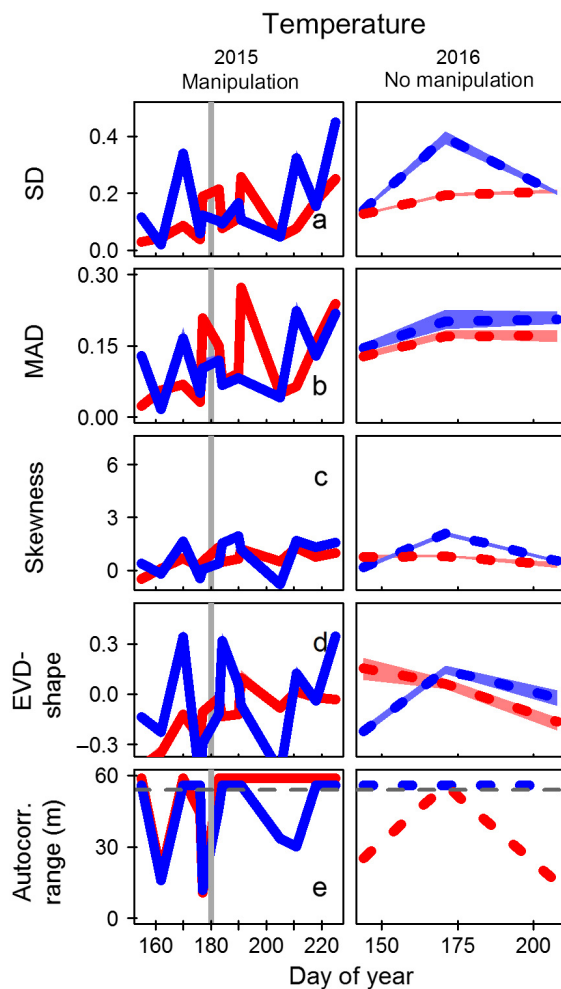


Fig. 3. Early warning statistics of temperature for manipulated and reference lakes during (2015) and after (2016) manipulation. For both the polygons and the lines, red and blue colors represent the manipulated and reference lake, respectively. Vertical gray lines represent the date nutrient addition stopped for reference. Lines are the following statistics based on temperature: (a) standard deviation (SD), (b) median absolute deviation (MAD), (c) skewness, (d) shape parameter of the extreme value distribution (EVD-shape), and (e) autocorrelation range. Polygons in panels (a–d) represent 99% confidence intervals computed from a non-parametric bootstrap. Dotted gray line at 60 m in panel (e) represents the range of sample variograms, and estimated ranges ≥ 60 m were plotted at 60 m. For 2015 data, all spatial temperature measurements were analyzed as deviations from a temperature probe mounted on a stationary central buoy to account for diel changes during the course of a sampling run (2016 data are not

reference lake during both years. In contrast, during nutrient additions in the manipulated lake, SD and MAD doubled at least one week prior to the cyanobacteria bloom (Fig. 2b, c). During nutrient addition, SD and MAD generally increased until nutrient additions halted, after which both quickly returned to low levels comparable to the reference lake. In the unfertilized year, SD and MAD in the manipulated lake remained low and were comparable to the reference lake. There were no early warnings of critical transitions nor discernible differences in the SD or MAD of temperature between the two lakes in either year (Fig. 3a, b).

Cyanobacteria displayed positively skewed spatial distribution before, during, and shortly after the bloom (Fig. 2d). During fertilization, increased skewness of cyanobacteria in the manipulated lake—however variable—was noticeably higher than in the reference lake at least one week prior to the bloom occurring. After nutrient additions halted, skewness in the manipulated lake decreased within a week to levels comparable to the reference lake and remained consistently low for the rest of the year. Skewness of cyanobacteria in the reference lake was consistently low during both years of the study. The skewness of temperature remained consistently low for both lakes which were indistinguishable from one another (Fig. 3c).

The shape parameter of the EVD was consistently higher for the manipulated lake compared to the reference lake leading up to the bloom, indicating a greater frequency and magnitude of extreme phycocyanin concentrations in the manipulated lake during enrichment. After halting nutrient additions, EVD-shape estimates returned to low levels comparable with the reference lake within a week (Fig. 2e). There was no difference in EVD-shape between the two lakes in the year with no cyanobacteria bloom. The EVD-shape of temperature was similar between the two lakes and showed no relationship to the cyanobacteria bloom (Fig. 3d).

Spatial autocorrelation in the reference lake was consistent and relatively weak throughout

(Fig. 3. *Continued*)

similarly corrected for lack of high-resolution buoy temperature measurements). All estimates are based on 13 sampling events over 11 weeks in 2015.

the study (mean autocorrelation distance = 8.2 ± 3.8 m). In the manipulated lake, semivariance models showed increased autocorrelation ranges during nutrient addition (mean = 33.2 ± 26 m) compared to baseline phycocyanin concentrations in 2016 (mean = 5.1 ± 3.6 m; range estimates larger than semivariogram fitting were rounded down to the sample semivariogram range of 60 m; Fig. 2f). Autocorrelation ranges were variable but generally higher during elevated phycocyanin levels. We detected no differences in autocorrelation between the two lakes in the non-manipulation year. This finding suggests that there is no inherent lake-specific difference between lakes in spatial patterning with respect to spatial autocorrelation. Also, analysis of autocorrelation of temperature showed no evidence of changes in the physical mixing between the two lakes in the first year that might be used to explain the changes observed in cyanobacteria (Fig. 3e).

Correlograms depicted detailed spatial patterns of cyanobacteria consistent with autocorrelation range estimates. During nutrient addition, we observed generally higher autocorrelation of cyanobacteria over a wide range of distances (10–60 m) in the manipulated lake compared to the reference lake (Fig. 4a). After phycocyanin concentrations in the manipulated lake returned to levels comparable to the reference lake, there were no noticeable differences in autocorrelation between the two lakes (Fig. 4b). Similarly, in the non-manipulation year, autocorrelation of cyanobacteria was indistinguishable between the two lakes (Fig. 4c). Correlogram characteristics of temperature were consistent between the two lakes and showed no relationship to the timing of cyanobacteria bloom (Fig. 5).

DISCUSSION

We detected spatial EWIs in the experimental lake before the onset of the cyanobacteria bloom. We observed changes in spatial variance, skewness, EVD-shape, and autocorrelation distance that were consistent with expected EWIs of critical transitions between alternative ecosystem states. On the other hand, autocorrelation distance was often at the maximum value and less useful as an early warning. Although the indicators differed in sensitivity to the approaching

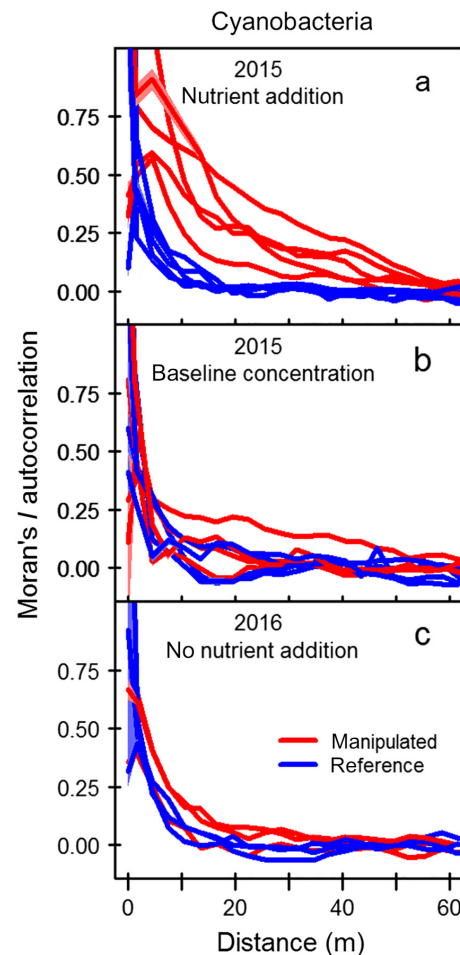


Fig. 4. Correlograms of phycocyanin for manipulated (red) and reference lake (blue) for each sampling date. Data were binned into distance classes of 3 m, and distance classes over 60 m were omitted. Correlation coefficients (y -axis) were calculated using Moran's I . The correlograms for both lakes are shown during the 2015 enrichment (top), baseline cyanobacteria concentrations after the bloom in 2015 (day of year 205–225; middle), and all dates in 2016 when there was no enrichment. Four dates (spanning two weeks) that immediately followed halting nutrient additions in 2015 were omitted from the middle panel as cyanobacteria concentrations remained elevated relative to the reference lake. Polygons represent one standard deviation around each estimate based on 250 random resamples of 80% of each sampling event.

bloom, these findings show that spatial EWIs could predict an impending regime shift, even in a dynamic fluid environment with patterns that could change within hours.

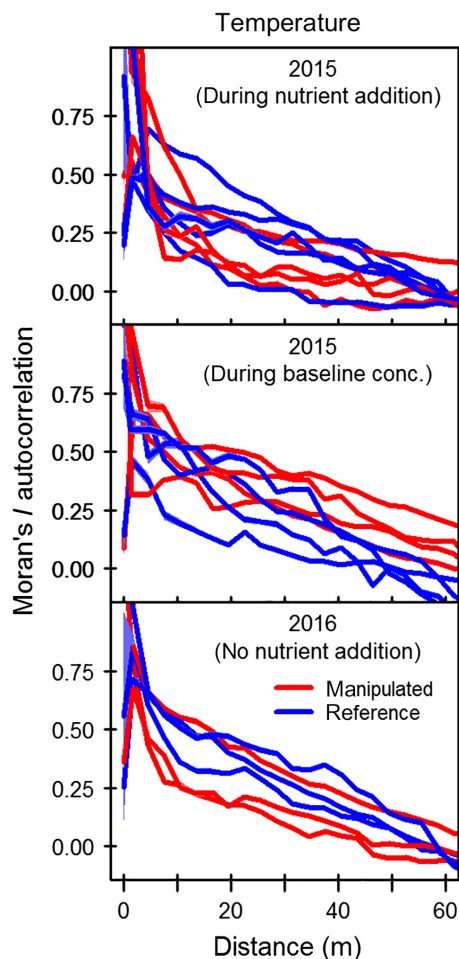


Fig. 5. Correlograms of temperature for manipulated (red) and reference lake (blue) for each sampling date. Data were binned into distance classes of 3 m, and distance classes over 60 m were omitted. Correlation coefficients (y -axis) were calculated using Moran's I . The correlograms for both lakes are shown during the 2015 enrichment (top), baseline cyanobacteria concentrations after the bloom in 2015 (day of year 205–225; middle), and all dates in 2016 when there was no enrichment (bottom). For 2015 data, all spatial temperature measurements were analyzed as deviations from a temperature probe mounted on a stationary central buoy to account for diel changes during the course of a sampling run. 2016 data are not similarly corrected due to lack of high-resolution buoy temperature measurements. Four dates (spanning two weeks) that immediately followed halting nutrient additions were omitted for direct comparison to Fig. 3. Polygons represent one standard deviation around each estimate based on 250 random resamples of 80% of each sampling event.

We found marked increases in spatial SD, MAD, and skewness of cyanobacteria in the manipulated lake as it approached the bloom (Fig. 2). In a spatially heterogeneous situation, exponential growth of cyanobacteria in patches could generate extremely high concentrations. We observed increases in the frequency of extreme events (EVD-shape) as the manipulated lake approached the bloom, likely reflecting these high and patchy cyanobacterial concentrations (Fig. 2). To our knowledge, this is the first study that shows the potential usefulness of the EVD as an EWI. The high rate of change between sampling dates of some statistics suggests a high sensitivity of the statistical indicators to changes in the spatial structure over a few days. Nonetheless, we observed no discernible differences in any of the EWI statistics in the reference lake in either year. Also, spatial statistics for temperature did not exhibit changes consistent with early warnings and remained similar for the manipulated and reference lakes. Lack of response in the reference lake suggests that responses in the manipulated lake were the result of enrichment rather than some regional factor, such as weather, that would have affected both lakes equally. Lack of spatial pattern in temperature suggests that responses of phycocyanin to enrichment were biological, or a combination of physical and biological processes.

Spatial autocorrelation, like temporal autocorrelation, is expected to increase near critical transitions (Dakos et al. 2010, Dai et al. 2013, Rindi et al. 2017). Correlograms during the period of enrichment showed that spatial autocorrelation of phycocyanin was higher in the manipulated lake than in the reference lake at nearly all spatial distances (Fig. 4). In contrast, correlograms of phycocyanin were similar in the manipulated and reference lakes during the unenriched period of 2015 and all samples from 2016. Correlograms of temperature were similar in both lakes in both years (Fig. 5). These results are consistent with expected responses near a tipping point (Dakos et al. 2010, Dai et al. 2013). In contrast, autocorrelation range was more ambiguous in relation to nutrient enrichment. Autocorrelation ranges of phycocyanin and temperature were frequently near the maximum discernible value (Figs. 2, 3). In this study, at least, autocorrelation range did not appear to provide consistent early warnings of the cyanobacterial bloom.

Interestingly, most of the EWI statistics were relatively higher when transitioning to the bloom compared to the shift back to low cyanobacteria concentrations. This was most notable in SD, MAD, and EVD-shape where the statistics returned to low levels (comparable to the reference lake) within days after halting nutrient inputs. In theoretical phytoplankton models, temporal EWIs can differ depending on the direction of transition between alternative states (Batt et al. 2013). Nutrient addition stopped prior to a critical transition to cycling blooms, but our results suggest an asymmetry of spatial EWIs similar to theory that are related to the direction of the transition. This suggests that our detection of early warnings is not merely a product of elevated phycocyanin concentrations, but is also related to whether the bloom is rising or falling. Thus, the indicators responded differently from phycocyanin concentration itself.

Spatial EWIs are likely influenced by many different factors, including diffusion/advection rates due to stochastic processes of wind and other mixing events, population or community interactions (e.g., clustered areas of high growth of cyanobacteria, trophic interactions), or lake-specific characteristics such as hydrology, surface shape, and bathymetry (van Nes and Scheffer 2005, Serizawa et al. 2008). These factors may cause differences among lakes and dates in the performance of early warning statistics. Therefore, multiple methods may provide diverse information, greater rigor, and more insight about characteristics of ecosystems near thresholds and the potential for critical transitions. While our results show that spatial statistics are promising tools for the study of developing blooms in lakes, further testing and comparisons on a wider variety of lake ecosystems are advisable.

The patterns suggestive of approaching thresholds in this study could potentially have been measured using remote sensing. The possibility of using remote sensing to detect changes in cyanobacteria at potentially relevant scales for EWIs is appealing (though currently limited by the availability to accurately differentiate cyanobacteria spectral properties). Future work should explore the usefulness of remote sensing to detect spatial EWIs in aquatic ecosystems.

This study is the first application of spatial indicators to detect impending blooms of

harmful cyanobacteria in lakes and addresses a growing call for testing the usefulness of early warnings approaches in ecosystems (Scheffer et al. 2009, Dakos et al. 2011, 2012). Surprisingly in the small lakes we considered, many spatial EWIs were detected under the manipulation despite the potential for physical mixing to homogenize conditions. We are far from a complete understanding of critical transitions in spatially structured ecosystems, and the findings presented here support the need for further tests of these ideas in the field.

ACKNOWLEDGMENTS

Stephen R. Carpenter, Michael L. Pace, Vince L. Butitta, and Emily H. Stanley designed the study, and Vince L. Butitta and Luke C. Loken collected the data. Vince L. Butitta and Stephen R. Carpenter performed the analysis. Vince L. Butitta wrote the first draft of the manuscript, and Stephen R. Carpenter, Michael L. Pace, Luke C. Loken, and Emily H. Stanley contributed significantly to revisions. The authors declare no conflict of interest with production or publication of this work. This work was supported by grants provided by the North Temperate Lakes Long Term Ecological Research (DEB-1440297), National Science Foundation (DEB-1144683, DEB-1144624), and Hildale Professorship Research Funds. The authors would like to thank Anders Uppgaard for helping collect and visualize the data and Patrick Dowd for also helping collect the data. The authors would also like to thank Cal Buelo, Grace Wilkinson, and Jason Kurtzweil for field support. Jon Cole contributed to design of the ecosystem experiment. The authors would also like to thank the Center for Limnology's Trout Lake Station and the University of Notre Dame's Environmental Research Center for the use of facilities. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Batt, R. D., W. A. Brock, S. R. Carpenter, J. J. Cole, M. L. Pace, and D. A. Seekell. 2013. Asymmetric response of early warning indicators of phytoplankton transition to and from cycles. *Theoretical Ecology* 6:285–293.
- Bjornstad, O. N. 2016. Package “ncf”: spatial nonparametric covariance functions. Pages 1–42. <https://CRAN.R-project.org/package=ncf>
- Butitta, V. L., S. R. Carpenter, L. C. Loken, M. L. Pace, and E. H. Stanley. 2017. Cascade project at North Temperate Lakes LTER – High-resolution spatial

- analysis of CASCADE lakes during experimental nutrient enrichment 2015–2016. Environmental Data Initiative. <https://doi.org/10.6073/pasta/403cc21eba48b801114801ea05c5c2fa>
- Carpenter, S. R., and W. A. Brock. 2010. Early warnings of regime shifts in spatial dynamics using the discrete Fourier transform. *Ecosphere* 1:10.
- Carpenter, S. R., and J. F. Kitchell, editors. 1993. *The trophic cascade in lakes*. Cambridge University Press, Melbourne, Victoria, Australia.
- Carpenter, S. R., et al. 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332: 1079–1082.
- Cline, T. J., D. A. Seekell, S. R. Carpenter, M. L. Pace, J. R. Hodgson, and J. F. Kitchell. 2014. Early warnings of regime shifts: evaluation of spatial indicators from a whole-ecosystem experiment. *Ecosphere* 5:1–13.
- Cole, J. J., and M. L. Pace. 1998. Hydrologic variability of small, northern Michigan lakes measured by the addition of tracers. *Ecosystems* 1:310–320.
- Crawford, J. T., L. C. Loken, N. J. Casson, C. Smith, A. G. Stone, and L. A. Winslow. 2015. High-speed limnology: using advanced sensors to investigate spatial variability in biogeochemistry and hydrology. *Environmental Science & Technology* 49: 442–450.
- Dai, L., K. S. Korolev, and J. Gore. 2013. Slower recovery in space before collapse of connected populations. *Nature* 496:355–358.
- Dakos, V., S. Kéfi, M. Rietkerk, E. H. van Nes, and M. Scheffer. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. *American Naturalist* 177:E153–E166.
- Dakos, V., E. H. Van Nes, P. D’Odorico, and M. Scheffer. 2012. Robustness of variance and autocorrelation as indicators of critical slowing down. *Ecology* 93:264–271.
- Dakos, V., E. H. van Nes, R. Donangelo, H. Fort, and M. Scheffer. 2010. Spatial correlation as leading indicator of catastrophic shifts. *Theoretical Ecology* 3:163–174.
- Dodds, W. K., W. W. Bouska, J. L. Eitzmann, T. J. Pilger, K. L. Pitts, A. J. Riley, J. T. Schloesser, and D. J. Thornbrugh. 2009. Eutrophication of U.S. freshwaters: analysis of potential economic damages. *Environmental Science & Technology* 43:12–19.
- Donangelo, R., H. Fort, V. Dakos, M. Scheffer, and E. H. Van Nes. 2010. Early warnings for catastrophic shifts in ecosystems: comparison between spatial and temporal indicators. *International Journal of Bifurcation and Chaos* 20:315–321.
- Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. *Nature* 467:456–459.
- Eby, S., A. Agrawal, S. Majumder, A. P. Dobson, and V. Guttal. 2017. Alternative stable states and spatial indicators of critical slowing down along a spatial gradient in a savanna ecosystem. *Global Ecology and Biogeography* 5:1–38.
- Gilleland, E., and R. W. Katz. 2016. Package “extRemes” extreme value analysis. *Journal of Statistical Software* 72:1–39.
- Gagnani, A., M. Scheffer, and S. Rinaldi. 1999. Top-down control of cyanobacteria: a theoretical analysis. *American Naturalist* 153:59–72.
- 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:E8089–E8095.
- Guttal, V., and C. Jayaprakash. 2008. Changing skewness: an early warning signal of regime shifts in ecosystems. *Ecology Letters* 11:450–460.
- Guttal, V., and C. Jayaprakash. 2009. Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems. *Theoretical Ecology* 2:3–12.
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Kéfi, S., M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. ElAich, and P. C. de Ruiter. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449:213–217.
- Komsta, L., and F. Novomestky. 2015. moments: moments, cumulants, skewness, kurtosis and related tests. Pages 1–15. <https://CRAN.R-project.org/package=moments>
- 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.
- O’Neil, J. M., T. W. Davis, M. A. Burford, and C. J. Gobler. 2011. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. *Harmful Algae* 14:313–334.
- 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.
- Paerl, H. W., R. S. Fulton, P. H. Moisander, and J. Dyble. 2001. Harmful freshwater algal blooms, with an emphasis on cyanobacteria. *Scientific World Journal* 1:76–113.
- Pebesma, E., and B. Graeler. 2016. Multivariate geostatistics in S: the gstat package. *Computers and Geosciences* 30:683–691.

- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ratajczak, Z., P. D'Odorico, J. B. Nippert, S. L. Collins, N. A. Brunsell, and S. Ravi. 2016. Changes in spatial variance during a grassland to shrubland state transition. *Journal of Ecology* 105:750–760.
- Reinette, B., 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.
- Rindi, L., M. D. Bello, L. Dai, J. Gore, and L. Benedetti-Cecchi. 2017. Direct observation of increasing recovery length before collapse of a marine benthic ecosystem. *Nature Ecology & Evolution* 1:153.
- 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. van Nes. 2015. Generic indicators of ecological resilience. *Annual Review of Ecology, Evolution, and Systematics* 46:145–167.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Scheffer, M., S. Rinaldi, and Y. A. Kuznetsov. 2000. Effects of fish on plankton dynamics: a theoretical analysis. *Canadian Journal of Fisheries and Aquatic Science* 57:1208–1219.
- Scheffer, M., S. Rinaldi, and L. R. Mur. 1997. On the dominance of filamentous blue-green algae in shallow lakes. *Ecology* 78:272–282.
- Scheffer, M., et al. 2012. Anticipating critical transitions. *Science* 338:344–348.
- Serizawa, H., T. Amemiya, and K. Itoh. 2008. Patchiness in a minimal nutrient-phytoplankton model. *Journal of Biosciences* 33:391–403.
- Taranu, Z. E., et al. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. *Ecology Letters* 18:375–384.
- Veraart, A. J., E. J. Faassen, V. Dakos, E. H. van Nes, M. Lürling, and M. Scheffer. 2012. Corrigendum: Recovery rates reflect distance to a tipping point in a living system. *Nature* 481:357–359.
- van Nes, E. H., and M. Scheffer. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* 86:1797–1807.
- Wissel, C. 1984. A universal law of the characteristic return time near thresholds. *Oecologia* 65:101–107.
- YSI. 2015. EXO user manual. YSI, Yellow Springs, Ohio, USA.