Ecology Letters, (2006) **9**: 308–315 doi: 10.1111/j.1461-0248.2005.00877.x

LETTER

Rising variance: a leading indicator of ecological transition

S. R. Carpenter[1]* and W. A. Brock[2]
[1]*Center for Limnology, University of Wisconsin, Madison, WI, USA*
[2]*Department of Economics, University of Wisconsin, Madison, WI, USA*
**Correspondence: E-mail: srcarpen@wisc.edu*

Abstract

Regime shifts are substantial, long-lasting reorganizations of complex systems, such as ecosystems. Large ecosystem changes such as eutrophication, shifts among vegetation types, degradation of coral reefs and regional climate change often come as surprises because we lack leading indicators for regime shifts. Increases in variability of ecosystems have been suggested to foreshadow ecological regime shifts. However, it may be difficult to discern variability due to impending regime shift from that of exogenous drivers that affect the ecosystem. We addressed this problem using a model of lake eutrophication. Lakes are subject to fluctuations in recycling associated with regime shifts, as well as fluctuating nutrient inputs. Despite the complications of noisy inputs, increasing variability of lake-water phosphorus was discernible prior to the shift to eutrophic conditions. Simulations show that rising standard deviation (SD) could signal impending shifts about a decade in advance. The rising SD was detected by studying variability around predictions of a simple time-series model, and did not depend on detailed knowledge of the actual ecosystem dynamics.

Keywords

Alternate stable states, dynamic linear model, eutrophication, indicator, lake, regime shift, stationary distribution, stochastic differential equation, variance.

Ecology Letters (2006) 9: 308–315

INTRODUCTION

Regime shifts are substantial, long-term reorganizations of complex systems such as societies, ecosystems or climate (Steele 1998; Scheffer *et al.* 2001; National Research Council 2002; Carpenter 2003; Foley *et al.* 2003; Scheffer & van Nes 2004; Brock *et al.* 2006; Folke *et al.* 2005; Hsieh *et al.* 2005; Brock 2006). In ecology, some of the well-studied cases include eutrophication of lakes and coastal oceans, shifts among grassy and woodland cover types in rangelands, degradation of coral reefs and regional climate change (Scheffer *et al.* 2001; Folke *et al.* 2005). Feedbacks that control key system processes are different after a regime shift (Holling 1973). For example, in oligotrophic (clear water) lakes the concentrations of nutrients that affect primary production are controlled primarily by inputs from the watershed, whereas in eutrophic (turbid) lakes the concentrations of nutrients are driven by recycling within the lake as well as inputs (Carpenter 2003). Other kinds of feedback changes are known from regime shifts in other types of ecosystems (Scheffer *et al.* 2001; Carpenter 2003; Foley *et al.* 2003; Walker & Meyers 2004; Folke *et al.* 2005). Brock (2006) reviews social systems in which tipping points are found.

Regime shifts are difficult to study (Carpenter 2003; Scheffer & Carpenter 2003). They occur in large, spatially heterogeneous systems, and usually involve processes at more than one spatial scale. From the perspective of a human lifetime, regime shifts are infrequent events that may play out over many years, even though the change is rapid in comparison with routine ecological change. Regime shifts have multiple causes, so studies must track multiple variables simultaneously for long periods of time. Inference requires several lines of evidence, such as long-term observations or paleo-ecological data, comparisons of ecosystems across gradients of key drivers, models of various types and appropriately scaled experiments (Carpenter 2003). It takes considerable effort to build understanding of regime shifts.

Numerous models can potentially explain any particular regime shift, and it may be very difficult to discriminate among these models, particularly in early stages of an

© 2006 Blackwell Publishing Ltd/CNRS

investigation (Carpenter 2003). The kinds of evidence that are needed to understand a regime shift depend on the set of models that are believed to describe the regime shift. The appropriate evidence cannot be gathered without knowing the models, and the models cannot be assessed without the evidence. This circularity poses a challenge to researchers. It is important to design measurement programmes that could provide relevant evidence for a wide range of models, often over long periods of time and extensive spatial ranges.

Recently, however, researchers have noticed that the variability of system behaviour changes in advance of a regime shift (Kleinen *et al.* 2003; van Nes & Scheffer 2003; Brock *et al.* 2006; Oborny *et al.* 2005). These changes in variance may be discernible without detailed knowledge of the underlying ecosystem dynamics. Kleinen *et al.* showed that the variance spectra of an ocean–atmosphere model shifted to lower frequencies as the system approached a regime shift in the circulation of the North Atlantic ocean. van Nes & Scheffer (2003) showed that variability of an individual-based model of an aquatic macrophytes increased near thresholds between alternate attractors. Using a generalized model of spatial dynamics, Oborny *et al.* (2005) showed that spatial variance of terrestrial mosaics increased near the critical threshold for percolation. Brock *et al.* (2006) showed that rising variance near thresholds should be expected in a wide range of social and ecological systems with multiple attractors, including scientific paradigms, elections, monetary policy, lake eutrophication, fisheries collapse, ocean dynamics and climate change.

In general, the variance of temporal fluctuations in certain state variables increases and the variance spectra shifts towards longer wavelengths (lower frequencies) just before the regime shift occurs (Kleinen *et al.* 2003; Brock *et al.* 2006). The reasons for this behaviour seem general, and should apply to a wide range of plausible models of regime shifts (Horsthemke & Lefever 1984; Berglund & Gentz 2002a,b; Kleinen *et al.* 2003; Brock *et al.* 2006; Appendix S2). Therefore, increased variance may be an important clue of regime shifts even in cases where the appropriate model is unknown. Furthermore, increased variance may provide a leading indicator of regime shifts that can be used in ecosystem management. Regime shifts often have large ecological and economical consequences, e.g. losses of water quality, declining productivity of fish stocks or rangelands, or breakdowns of dryland agriculture. It would be useful to have advance warning of these changes so that managers have the opportunity to avoid them. Eutrophication, the regime shift studied in this paper, is a syndrome of aquatic ecosystems leading to blooms of nuisance (often toxic) algae, anoxic events, fish mortality and substantial economic losses (Carpenter 2003).

In practice, changes in variance due to impending regime shifts may be difficult to distinguish from other drivers of variance such as exogenous noise that affects the ecosystem. In lakes, for example, variance because of fluctuations in recycling (which may indicate a regime shift) may be difficult to discriminate from variance because of noisy nutrient inputs. Furthermore, the true model for ecosystem dynamics is unknown and inferences about changing variance must be drawn from approximate models. We addressed this problem using a model of lake eutrophication that includes both input noise and recycling noise. In addition to the complication introduced by input noise, the model has three state variables with distinctly different turnover times (Carpenter 2005). Thus the model is more realistic and complex than the one-dimensional systems examined in some previous work. Despite these complications, the regime shift to eutrophication could be detected years in advance by studying the standard deviation (SD) of phosphorus concentration in the water during summer stratification. Change in the SD could be detected by analysing time series of phosphorus in lake water using a simple empirical model that did not require detailed knowledge of the ecosystem dynamics.

METHODS

The model, which was modified slightly from previous papers (Carpenter *et al.* 1999; Carpenter 2003, 2005; Ludwig *et al.* 2003), is a system of stochastic differential equations (SDE) for phosphorus density (g m^{-2}) in soil (U), lake water (X) and surface sediment (M) (Fig. 1).

$$\frac{\mathrm{d}U}{\mathrm{d}t} = F - cUH, \tag{1}$$

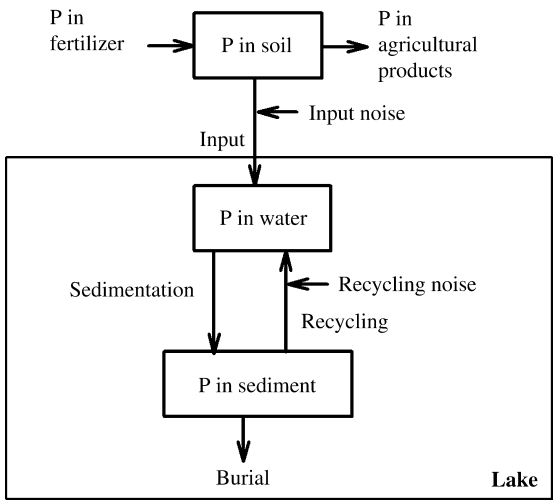

Figure 1 Phosphorus flows in the model.

© 2006 Blackwell Publishing Ltd/CNRS

$$\frac{\mathrm{d}X}{\mathrm{d}t} = cUH - (s+h)X + rMR(X) + \sigma MR(X)\frac{\mathrm{d}W}{\mathrm{d}t}, \tag{2}$$

$$\frac{\mathrm{d}M}{\mathrm{d}t} = sX - bM - rMR(X) - \sigma MR(X)\frac{\mathrm{d}W}{\mathrm{d}t}, \tag{3}$$

where F is the input rate of phosphorus to soil (e.g. from fertilizer use, dust deposition or weathering), c is a coefficient for transfer of soil phosphorus to the lake, H is noise for input to the lake (see below), s is sedimentation loss, h is hydrologic loss (outflow), r is a recycling coefficient, σ is the SD of recycling noise and b is the permanent burial rate of phosphorus in sediments; $\mathrm{d}W$ is a white noise process with mean zero and variance $\mathrm{d}t$. The recycling function $R(X)$ is

$$R(X) = \frac{X^q}{m^q + X^q}, \tag{4}$$

where m is the value of X at which recycling is half the maximum rate and the exponent q determines the slope of $R(X)$ near m (Carpenter *et al.* 1999). The annual load disturbance H is calculated within each year as the solution of the Ito SDE

$$\frac{\mathrm{d}H}{H} = \lambda \mathrm{d}Z \tag{5}$$

with initial condition $H_0 = 1$; $\mathrm{d}Z$ is a white noise process with mean zero and variance $\mathrm{d}t$ (independent of $\mathrm{d}W$). Using standard methods for Ito SDEs (Malliaris & Brock 1982), the solution of eqn 5 is obtained as

$$H_t = \exp\left[\lambda Z_t - \frac{t\lambda^2}{2}\right]. \tag{6}$$

Our numerical analyses use parameters estimated for Lake Mendota, Wisconsin (Table S1; Carpenter 2005). The model is solved for successive summer stratified seasons. We assume that the annual nutrient input enters prior to summer stratification. During the summer stratified season, recycling from sediments occurs in a series of stochastic events driven by wind (Soranno *et al.* 1997). Frequent shocks to recycling because of wind events within the summer season are represented by $\sigma MR(X)\mathrm{d}W/\mathrm{d}t$, where $\mathrm{d}W$ is a white noise process with mean zero and variance $\mathrm{d}t$ (Horsthemke & Lefever 1984). We set the scale parameter σ to 0.01, which produced variability in recycling similar to that observed by Soranno *et al.* (1997).

According to our hypothesis, the SD of water phosphorus (X) should increase prior to a regime shift. We used two approaches to estimate the SD. First, we computed stationary distributions of X (Horsthemke & Lefever 1984). Over a long period of time, the state variables approach a stationary distribution, just as a deterministic model would approach a stable point. While stationary distributions expose the causes of changes in the SD of X, stationary distributions may never be observed in ecosystems because the rate of convergence to the stationary distribution is not fast enough compared with the changes in slow variables such as soil or sediment phosphorus. To examine changes in the stationary distribution of X under conditions that might be observed in field studies, we simulated changes in a lake undergoing eutrophication, corresponding to changes that have been observed in many lakes (Carpenter 2003).

We computed the mean and SD for stationary distributions of water phosphorus by two methods: (i) the stationary probability densities obtained from Fokker–Planck equations presented by Horsthemke & Lefever (1984); and (ii) Monte Carlo simulation. Appendix S1 shows that these two methods give similar results. Because the Fokker–Planck expressions are not always computable due to overflow errors, we present Monte Carlo results here. For each estimate of the mean and SD, we simulated eqns 1–3 from each of 1000 different initial conditions for 1080 time steps (300 years with 36 time steps per year) using Ito calculus and the Euler method. The 1000 final values of X (one from each of the 1000 initial points) were used to calculate the mean and SD.

In addition to studying the stationary distributions, we examined changes in the SD during dynamic simulations. These come closer to the situation studied in the field, where ecosystems may be far from the stationary distribution. We used dynamic simulations to examine changes in the within-year SD of water phosphorus associated with transitions to eutrophy under non-equilibrium conditions. Simulations were computed with various schedules of phosphorus input to soil (F, eqn 1) for 300 years with 36 time steps per year, using Ito calculus and the Euler method.

In our simulations, as in ecosystems, changes in state variables are affected by proximity to the threshold as well as other factors such as input disturbances which may complicate the detection of threshold effects. Furthermore, the true processes generating the observed dynamics of the ecosystem will be unknown. Therefore, the analyst will work with an approximate model of the ecosystem, and attempt to use this model to discriminate the effects of input disturbances from other sources of variability that affect ecosystem dynamics. To analyse the lake simulations, we derived a simplified approximate model. It is reasonable to think that such a simplified model might be used by an analyst to estimate variability of lake phosphorus from observed time series.

Suppose the analyst believes that the true deterministic model for the lake can be approximated over a short period of time as

$$\frac{\mathrm{d}X}{\mathrm{d}t} = a_0 + L - a_1 X, \tag{7}$$

© 2006 Blackwell Publishing Ltd/CNRS

where a_0 and a_1 are functions of the actual but unknown parameters of the true but unknown ecosystem processes, and the time series of input L and water phosphorus X are measured. Equation 7 is a minimal empirical representation of phosphorus dynamics that depend on input (L), losses (a_1) and recycling (a_0) in a situation where X is the only state variable that is monitored. L is assumed constant over one annual time step. This situation is similar to many lake monitoring programmes that estimate annual values for L and X, where the annual mean estimate of X is based on many observations in the course of the year.

Over one time step the solution of eqn 7 from initial condition $X = X_0$ at $t = 0$ is

$$X_1 = X_0 e^{-a_1} + \frac{1 - e^{-a_1}}{a_1} L + \frac{a_0(1 - e^{-a_1})}{a_1}. \tag{8}$$

Dynamic linear models (DLMs) are among the statistical methods available for analysing time-series processes such as eqn 8 (Pole *et al.* 1994). In DLMs, the parameters can change slowly over time as new data are observed. Thus DLMs can adapt to gradual changes in the underlying ecosystem dynamics. In this situation, where ecosystem dynamics depend on slow change in unobserved variables (soil and sediment phosphorus), the DLM approach is reasonable (Pole *et al.* 1994; Cottingham *et al.* 2000; Carpenter 2003). Equation 8 converts to the following DLM:

$$X_t = [\, b_0 \quad b_P \quad b_L \,]_t \begin{bmatrix} 1 \\ X_{t-1} \\ L_t \end{bmatrix} + \omega_t, \tag{9}$$

$$[\, b_0 \quad b_P \quad b_L \,]_t = [\, b_0 \quad b_P \quad b_L \,]_{t-1} + v_t. \tag{10}$$

In eqns 9 and 10, ω and v are independent normally distributed observation and process errors respectively. The parameters b_0, b_P and b_L correspond to $a_0(1 - \exp(-a_1))/a_1$, $\exp(-a_1)$ and $(1 - \exp(-a_1))/a_1$ respectively. At each time step, parameter estimates are updated using measurements of L and X (Pole *et al.* 1994). Because of the regular updating driven by data, the parameters do not follow a random walk but instead move with trends in the data. The updating equations are well known (Pole *et al.* 1994) and will not be repeated here.

RESULTS

To illustrate the stationary distributions, we present an example in which stationary distributions were computed across a gradient of the loading coefficient, c (eqns 1 and 2). Manipulations of c are sometimes used as a control parameter by lake managers. Restorations of riparian vegetation to reduce c may mitigate eutrophication by decreasing phosphorus inputs, for example. We focus on the stationary distribution of water phosphorus (X) for a lake that has been oligotrophic for a long time. Monte Carlo simulations of the stationary distribution were initiated at the deterministic steady-state values of soil phosphorus (U) and sediment phosphorus (M) by setting the load disturbance λ to 0. We used the oligotrophic steady state for M if the system was bistable (otherwise the sole steady state of M was used). Simulations were initiated over a wide range of values of X. We present only the final values of X (Appendix S1).

Equilibria of phosphorus in the water vs. the loading coefficient, c, indicates alternate stable states, as known from previous studies of this model (Fig. 2a). At low c, there is only one equilibrium, an oligotrophic attractor. As c rises above roughly 0.00025, a eutrophic attractor appears, separated from the lower attractor by a repelling threshold. As c rises above roughly 0.0025, the lower oligotrophic attractor disappears. Similar behaviour occurs if the equilibria are plotted against other parameters, such as the recycling coefficient r or the more slowly changing variables,

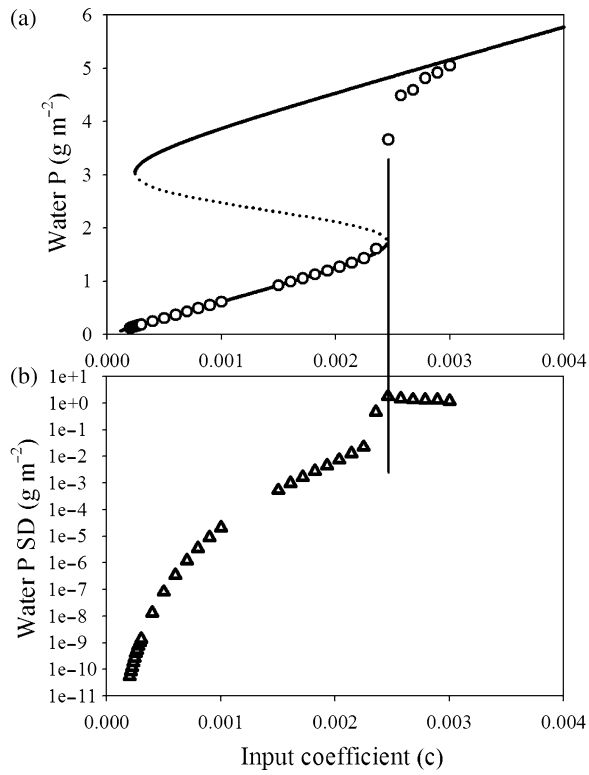

Figure 2 (a) Equilibria of water P vs. input coefficient (c). Stable equilibria are solid lines, unstable equilibria are the dotted line, and open circles are mean values of the stationary distribution from Monte Carlo simulation. Vertical solid line shows the relationship between the eutrophication threshold and the standard deviation. (b) Standard deviation of the stationary distribution versus input coefficient (c). Note log y-axis.

© 2006 Blackwell Publishing Ltd/CNRS

soil and sediment phosphorus. Appendix S1 shows that similar effects occur across a gradient of sediment phosphorus.

Mean values of the stationary distribution closely track the oligotrophic attractor for c less than *c.* 0.0023 (Fig. 2a). At higher levels of c, the mean values lie between the two attractors. The mean values gradually approach the upper eutrophic attractor as c rises to 0.003.

The SD of the stationary distribution of water phosphorus rises steadily as c passes through the shift to alternate stable states at $c = 0.00025$, until c reaches *c.* 0.0021 (Fig. 2b). Just below the c value where the lower oligotrophic attractor disappears, the SD increases sharply. The rise in SD between about $c = 0.0021$ and the transition point at $c = 0.0025$ could provide an advance warning that the system was approaching a regime shift.

Frequency distributions from Monte Carlo simulation illustrate the changes that occur near the transition point. At $c = 0.0021$, frequency is sharply clustered near the oligotrophic attractor, with a long tail to the right extending towards the eutrophic attractor (Fig. 3d). Near the transition point, frequency is spread broadly across the range of water phosphorus, with a peak slightly above the oligotrophic attractor (Fig. 3c). There is further spreading of the frequency distribution as c rises above the transition point (Fig. 3b). Finally, with $c = 0.0030$, frequencies seem to approach a bell-like distribution centred just below the eutrophic attractor (Fig. 3a).

Although the stable distribution is useful for exposing the underlying causes of the change in variability, it is not useful in practice because all of the dynamic variables (soil, sediment and water phosphorus) are changing at the same time. We used dynamic simulations to explore changes in variability of water phosphorus near the transition point. An example is presented in Fig. 4. We focus on the time period near the transition to eutrophy. The full 300-year simulation is presented in Fig. S1.

The upper, eutrophic attractor appears in year 101, and the lower oligotrophic attractor disappears in year 139 (Fig. 4). The lake shifts to the eutrophic state *c.* years 160–162.

Often, a field scientist will observe time series of a fast variable (such as water phosphorus), but will not know the slowly changing variables (in this case soil and sediment phosphorus) or the true ecosystem dynamics (eqns 1–6). In this situation, the analyst will often approximate ecosystem dynamics using a simplified model such as the one we derived in eqns 7–10. We calculated two measures of SD of water phosphorus. One is the within-year SD around the annual mean (within-year SD), and the other is the within-year SD around the prediction of the DLM (DLM SD). Uncertainty around both measures of SD is small. With 36 observations per year, the 95% CI around each SD ranges

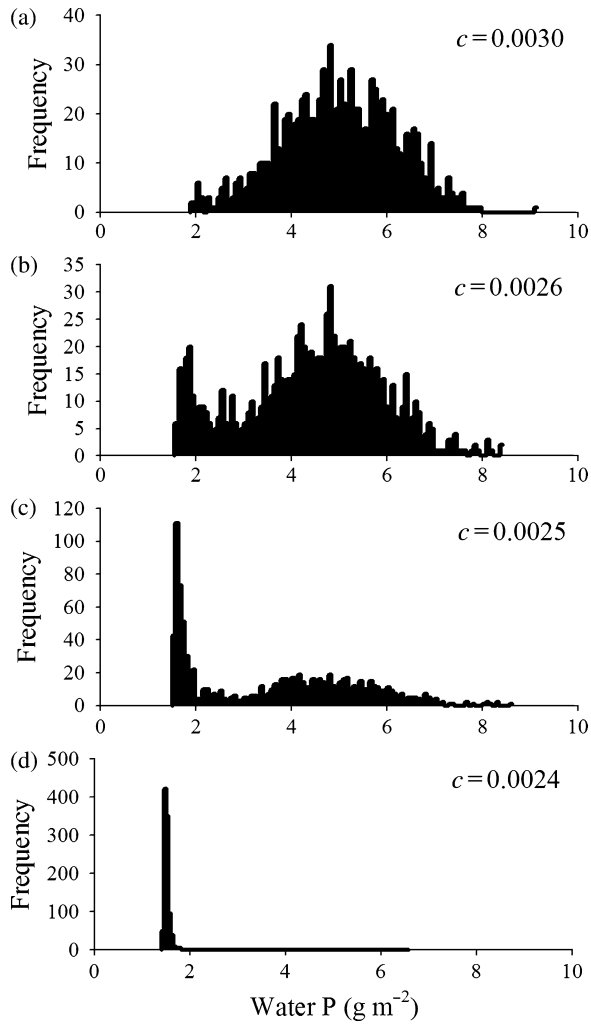

Figure 3 Stationary distributions of water phosphorus from Monte Carlo simulation at four values of the input coefficient (c) near the threshold for eutrophication at $c = 0.0025$.

from 0.81 to 1.29 times the estimated SD, a range that is too narrow to be plotted on Fig. 4.

The within-year SD rises, with fluctuations, over the course of the simulation (Fig. 4). The within-year SD represents the combined effects of varying phosphorus inputs to the lake and endogenous variance related to the regime shift. Variance of phosphorus inputs is rising through the simulation, because of rising soil phosphorus (Fig. S1) which increases mean input rate (cUH, eqn 2) as well as its variance (eqn 6). Despite the complicating effects of variable phosphorus inputs, there is some indication of regime shift effects in the within-year SD. The within-year SD shows unusual peaks in years 147, 152, 157 and 159, which could perhaps be taken as indicators of an impending transition.

The DLM SD provides a clearer indication of impending transition. The DLM accounts statistically for the fluctua-

© 2006 Blackwell Publishing Ltd/CNRS

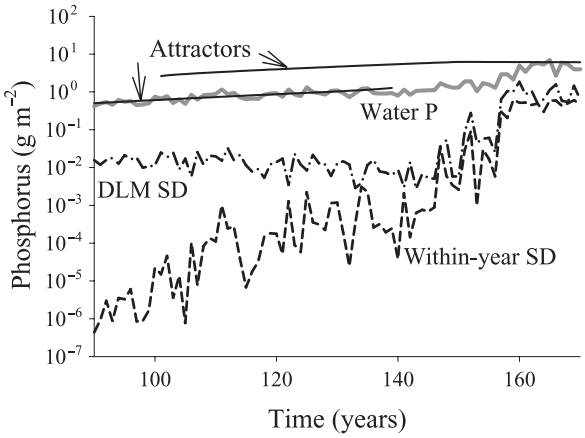

Figure 4 Simulated time series near a transition from the oligotrophic to the eutrophic state. Note log scale for the *y*-axis. Equilibria were computed for the sediment + water subsystem, assuming that changes in soil phosphorus are slow enough to make equilibria meaningful for the faster variables. Water P is the thick grey line, and the stable equilibria for water P are the thin black lines. The within-year standard deviation (SD) is shown by the dashed line, and the within-year SD around predictions of the dynamic linear model (DLM) is shown by the dash-dot line.

tions of phosphorus input to the lake (eqn 9). The SD around DLM projections therefore represents variability due to recycling, the key process in the regime shift. The DLM SD is generally declining until year 146, indicating lower variability around predictions of water phosphorus. However, after year 146 the DLM SD generally trends upwards. There are peaks in years 148 and 152 and a steady upward trend from years 155 to 160. These changes in the DLM SD provide an unambiguous signal of rising variability at least 10 years prior to the regime shift.

DISCUSSION

Variability of water phosphorus is a leading indicator of shifts between oligotrophic and eutrophic attractors in lakes. More specifically, the SD (or variance) of total phosphorus density in the water column within the period of summer stratification should increase as a lake approaches a transition from oligotrophic to eutrophic attractors. Persistent increases in variability of phytoplankton biomass are known from experimental eutrophication of lakes (Cottingham *et al.* 2000). Results presented here suggest that such increases in variability should be a general feature of lakes approaching a regime shift to eutrophication.

Previous work suggested that measures of phosphorus recycling rate could warn of threshold crossings 1 or 2 years in advance (Carpenter 2003). In contrast, the SD of water phosphorus appears to signal threshold crossings a decade or more in advance. This indicator may be a useful test for regime shifts in analyses of time-series data. In ecosystem management, the rising SD may provide an early warning. If heeded, such a warning could provide time to reduce phosphorus inputs and perhaps prevent a catastrophic loss of water quality.

An observer could detect the changes in SD without knowing the mechanisms of the regime shift. In our model, nature generates ecosystem dynamics using eqns 1–6 but the analyst needs only the water phosphorus time series and the simplified model of eqns 7–10 to estimate the SDs and compute the leading indicator of regime shift. This finding suggests that simple, empirical models for ecological time series could be used to develop indicators of potential regime shift for a wide variety of ecosystems. Of course, regular long-term observation of an ecosystem is essential to detect impending regime shifts. With more frequent measurements, the confidence intervals of estimated SDs become narrower, leading to more sensitive detection of changes in the SD. Approaches presented in this paper will become easier to apply as high-frequency long-term observations of ecosystems become more available (Porter *et al.* 2005).

In our model, as in real lakes, it is difficult to separate variability caused by proximity to the threshold from that caused by other sources of noise. We addressed this in simulations by using a DLM to filter out effects of input variability. Simulations show that the DLM improved the detection of changes in the SD prior to the transition. It is likely that research could identify better filters to improve detection of changes in variability for this particular system. Previous research has shown that the variance spectrum measured for system state variables shifts to lower frequencies and longer wavelengths as a threshold is approached (Kleinen *et al.* 2003). We focused on the SD instead, because ecological time series may often be adequate to estimate SDs but too sparse to estimate spectra. However, advances in ecosystem monitoring technology and statistical tools may increase the sensitivity of methods for detecting changes in variance of ecosystems.

If the increase in variance is due to trends in some unmeasured variable, then observations of increased variance could have nothing to do with impending regime shift. In this sense, the reliability of conclusions about impending regime shifts depends on observations of drivers that might affect variance of the focal state variable. In order to correct for such variables, one must know about them and observe them. Brock *et al.* (2006) comment on some of the model uncertainty and identification issues that arise in this context.

If the lake could be held near the threshold, the variance of water phosphorus would remain high for a long time. However, in reality other variables such as soil and sediment phosphorus are continually changing. The changes in these

© 2006 Blackwell Publishing Ltd/CNRS

slower variables affect the lead time of the indicator. The slower the changes in soil and sediment phosphorus, the longer the period of time that elevated variability is discernible prior to the transition. The stable distributions show that the SD of water phosphorus is high for a rather narrow range of c prior to the shift to eutrophy. Nevertheless, the simulations show that increases in the within-year SD of water phosphorus can be detected prior to the shift. Thus the relative speeds of interacting slow and fast variables is important for anticipating the regime shift in advance (Rinaldi & Scheffer 2000).

The mechanism that underlies the increasing variability near the threshold occurs in diverse physical, ecological and social systems (Brock *et al.* 2006). The mechanism depends on having two or more attractors which change slowly because they depend on a slowly changing variable, and a fast variable which relaxes quickly to equilibrium after small shocks (Rinaldi & Scheffer 2000). If the attractors change gradually so that a regime shift becomes more likely, the variance (or SD) of the fast variable will increase (Appendix S2). In the lake case, the slow dynamics of soil and sediment lead to gradual change in the attractors, while water phosphorus equilibrates rapidly after small shocks. As the system moves closer to the regime shift, the variance of water phosphorus rises.

Thus we expect that increased variability should occur prior to threshold transitions in many ecosystems. Increasing variability may provide a useful and general indicator of threshold transitions, even for systems with unknown dynamics. We have shown that variance around simple time-series models can be used to detect increases in variance as a complex system approaches a regime shift. This suggests a useful tool for studying or managing regime shifts in ecosystems, where the appropriate model structure and parameter estimates are often unknown or uncertain. On the contrary, the time window of increased variability will depend on details of the system dynamics and parameters. In particular, it depends on having relatively slow changes in the attractors combined with relatively rapid relaxation times of a fast variable. In some types of systems, increased variability may occur over a wide zone of conditions near a transition, while in other types of systems the zone of increased variability may be so narrow as to be useless for empirical purposes. Further study is needed to determine the types of systems and the ranges of conditions for which variability is a useful indicator of threshold transitions.

ACKNOWLEDGEMENTS

This paper is dedicated to the memory of Gerhard Petschel-Held. We thank C.S. Holling, Don Ludwig and Marten Scheffer for discussions of threshold transitions in stochastic ecosystems; Jon Chase, Jon Foley, Jon Norberg, Marten Scheffer, Craig Stow, Egbert van Nes and two anonymous referees for comments on the manuscript; and the Environmental Protection Agency and the National Science Foundation for support.

REFERENCES

Berglund, N. & Gentz, B. (2002a). A sample-paths approach to noise-induced synchronization: stochastic resonance in a double-well potential. *Ann. Appl. Probab.*, 12, 1419–1470.

Berglund, N. & Gentz, B. (2002b). Pathwise description of dynamic pitchfork bifurcations with additive noise. *Probab. Theory Related Fields*, 122, 341–388.

Brock, W.A. (2006). Tipping points, abrupt opinion changes, and punctuated policy change. In: *By Fits and Starts: A Punctuated Equilibrium Approach to Policy Change* (ed. Repetto, R.). Yale University Press, New Haven, CT (in press).

Brock, W.A., Carpenter, S.R. & Scheffer, M. (2006). Regime shifts, environmental signals, uncertainty and policy choice. In: *A Theoretical Framework for Analyzing Social-Ecological Systems* (eds Norberg, J. & Cumming, G.). Columbia University Press, New York, NY (in press).

Carpenter, S.R. (2003). *Regime Shifts in Lake Ecosystems: Pattern and Variation. Volume 15 in the Excellence in Ecology Series*. Ecology Institute, Oldendorf/Luhe, Germany.

Carpenter, S.R. (2005). Eutrophication of aquatic ecosystems: bistability and soil phosphorus. *Proc. Natl. Acad. Sci. USA*, 102, 10002–10005.

Carpenter, S.R., Ludwig, D. & Brock, W.A. (1999). Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.*, 9, 751–771.

Cottingham, K.L., Rusak, J.A. & Leavitt, P.R. (2000). Increased ecosystem variability and reduced predictability following fertilisation: evidence from paleolimnology. *Ecol. Lett.*, 3, 340–348.

Foley, J.A., Coe, M.T., Scheffer, M. & Wang, G. (2003). Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in Northern Africa. *Ecosystems*, 6, 524–539.

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. *et al.* (2005). Regime shifts, resilience and biodiversity in ecosystem management. *Annu. Rev. Ecol., Evol. Syst.*, 35, 557–581.

Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, 4, 1–23.

Horsthemke, W. & Lefever, R. (1984). *Noise-Induced Transitions*. Springer-Verlag, New York, NY.

Hsieh, C., Glaser, S.M., Lucas, A.J. & Sugihara, G. (2005). Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature*, 435, 336–340.

Kleinen, T., Held, H. & Petschel-Held, G. (2003). The potential role of spectral properties in detecting thresholds in the earth system: application to the thermohaline circulation. *Ocean Dyn.*, 53, 53–63.

Ludwig, D., Carpenter, S.R. & Brock, W.A. (2003). Optimal phosphorus loading for a potentially eutrophic lake. *Ecol. Appl.*, 13, 1135–1152.

Malliaris, A. & Brock, W. (1982). *Stochastic Methods in Economics and Finance*. North-Holland Publishers, Amsterdam.

© 2006 Blackwell Publishing Ltd/CNRS

National Research Council (2002). *Abrupt Climate Change: Inevitable Surprises*. National Academy Press, Washington, DC.

van Nes, E.H. & Scheffer, M. (2003). Alternative attractors may boost uncertainty and sensitivity in ecological models. *Ecol. Modell.*, 159, 117–124.

Oborny, B., Meszena, G. & Szabo, G. (2005). Dynamics of populations on the verge of extinction. *Oikos*, 109, 291–296.

Pole, A., West, M. & Harrison, J. (1994). *Applied Bayesian Forecasting and Time Series Analysis*. Chapman and Hall, New York, NY.

Porter, J., Arzberger, P., Hanson, P.C., Kratz, T.K., Gage, S., Williams, T. *et al.* (2005). Wireless sensor networks for ecology. *Bioscience*, 55, 561–572.

Rinaldi, S. & Scheffer, M. (2000). Geometric analysis of ecological models with slow and fast processes. *Ecosystems*, 3, 507–521.

Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.*, 12, 648–656.

Scheffer, M. & van Nes, E. (2004). Mechanisms for marine regime shifts: can we use lakes as microcosms for oceans? *Prog. Oceanogr.*, 60, 303–319.

Scheffer, M., Carpenter, S.R., Foley, J., Folke, C. & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Soranno, P.A., Carpenter, S.R. & Lathrop, R.C. (1997). Internal phosphorus loading in Lake Mendota: response to external loads and weather. *Can. J. Fish. Aquat. Sci.*, 54, 1883–1893.

Steele, J.H. (1998). Regime shifts in marine ecosystems. *Ecol. Appl.*, 8, S33–S36.

Walker, B. & Meyers, J.A. (2004). Thresholds in ecological and social-ecological systems: a developing database. *Ecol. Soc.*, 9, 3, Available at: http://www.ecologyandsociety.org/vol9/iss2/art3.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from http://www.Blackwell-Synergy.com:

Figure S1 The full 300-year simulation which is analysed in the main text.

Table S1 Model parameters, nominal values and sources of data.

Appendix S1 Stationary probability density.

Appendix S2 Heuristic explanation for the rise in variance near a regime shift.

Editor, Jonathan Chase
Manuscript received 4 October 2005
First decision made 5 November 2005
Manuscript accepted 21 November 2005

© 2006 Blackwell Publishing Ltd/CNRS

Copyright of Ecology Letters is the property of Blackwell Publishing Limited and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.