Indicators of regime shifts in ecological systems: what do we need to know and when do we need to know it?

INDICATORS OF REGIME SHIFTS IN ECOLOGICAL SYSTEMS: WHAT DO WE NEED TO KNOW AND WHEN DO WE NEED TO KNOW IT?

Raphael Contamin[1,2]

and

Aaron M. Ellison[1,3]

[1]Harvard University, Harvard Forest, 324 North Main Street, Petersham, Massachusetts, 01366, USA

[2]Permanent address for RC: ENS Ulm, 45 rue d'Ulm, 75005 Paris, FRANCE

[3]Author for correspondence: aellison@fas.harvard.edu

Abstract. Because novel ecological conditions can cause severe and long-lasting environmental damage with large economic costs, ecologists must identify possible environmental regime shifts and pro-actively guide ecosystem management. As an illustrative example, we apply six potential indicators of impending regime shifts to Carpenter and Brock's (2006) model of lake eutrophication and analyze whether or not they afford adequate advance warning to enable preventative interventions. Our initial analyses suggest that an indicator based on the high-frequency signal in the spectral density of the time-series provides the best advance warning of a regime shift, even when only incomplete information about underlying system drivers and processes is available. In light of this result, we explore two key factors associated with using indicators to prevent regime shifts. The first key factor is the amount of *inertia* in the system – how fast the system will react to a change in management, given that a manager can actually control relevant system drivers. If rapid, intensive management is possible, our analyses suggest that an indicator must provide at least 20 years advance warning to reduce the probability of a regime shift to < 5%. As time to, or intensity of, intervention is increased, the necessary amount of advance warning required to avoid a regime shift increases exponentially. The second key factor concerns the amount and type of variability intrinsic to the system, and the impact of this variability on the power of an indicator. Indicators are considered *powerful* if they detect an impending regime shift with adequate lead time for effective management intervention but not so far in advance that interventions are too costly or unnecessary. Intrinsic "noise" in the system obscures the "signal" provided by all indicators and therefore power of the indicators declines rapidly with increasing within- and between-year variability in measurable variables or parameters. Our results highlight the key role of human decisions in managing ecosystems and the importance of pro-active application of the precautionary principle to avoid regime shifts.

Key words: alternative stable states; hysteresis; lakes; management response; regime shift; simulation; spectral density; threshold; time-series.

INTRODUCTION

Ecologists, climatologists, and oceanographers recognize that biological and physical systems can undergo major reorganizations due to changes in underlying environmental conditions. Such "regime shifts" are of significant management concern because many of them have negative ecological impacts (*e.g.,* the shift from oligotrophic to eutrophic states in lakes), whereas others may be deliberately induced to attain specified management goals (*e.g.,* current practices in managing grazing lands or in accelerating ecological restoration). To date, most approaches to identifying regime shifts have been *post-hoc* – ecologists, climatologists, and statisticians examine historical time-series data of key ecosystem variables to determine whether or not a regime shift has already occurred. But managers – individuals who make decisions about ecosystem management or who implement those decisions - must have indicators that provide reliable advance warning of impending regime shifts. These indicators must provide enough lead time for implementation of management actions so that undesired regime shifts can be forestalled or the system can be moved into the desired regime. Recent research in this area is focused on developing prospective indicators of regime shifts, but these studies have not determined how much advance warning these indicators provide and whether it is enough time to actually direct an ecosystem into the desired regime. Here, we examine in detail how much advance warning six prospective indicators provide. We then explore two issues involved with using these indicators to manage a system subject to a regime shift. The first is what we call the *inertia* of the system: can progress towards a regime shift be slowed or stopped by a management intervention, or is the system too far gone? The answer depends on the relationship between how far in advance an indicator detects an impending regime shift and how quickly the system can respond to the intervention. Second, all processes are subject to *noise* – stochastic variance – that can obscure the *signal* of an impending regime shift. Are certain indicators better at identifying the relevant signal of an impending regime shift? We use shifts from oligotrophic to eutrophic regimes in modeled lakes as our example, but as we discuss at the end of the paper, our results can be generalized to a wide range of ecosystems.

BACKGROUND

The possibility that ecosystems can exist in alternative stable states was first illustrated using theoretical models (Holling 1973, May 1977). Predictions of these models, in which the parameters defining interactions between species remain constant but either the initial conditions or a strong perturbation to the system lead to alternative equilibrium points (May 1977, Beisner *et al.* 2003), have been demonstrated in a wide variety of ecosystems (Schröder *et al.* 2005). Climatologists and oceanographers also have recognized the existence of "regime shifts" – substantial, long-term reorganization of climate systems that result from directional changes in underlying environmental drivers and lead to new temporary or permanent equilibrium states (Easterling and Peterson 1995, Lazante 1996). Directional changes in environmental drivers also can lead to reorganization of ecological systems, and we now recognize regime shifts in a variety of ecosystems, including grasslands and rangelands, coral reefs, oceanic fisheries, and lakes (Steele 1998, Scheffer and Carpenter 2003, Walker and Meyers 2004, Litzow and Ciannelli 2007, deYoung *et al.* 2008).

Regime shifts often are caused by feedbacks among key environmental drivers (e.g., Carpenter and Brock 2006, Lawrence *et al.* 2007). Thus, processes that control the system after a regime shift has occurred may not necessarily be the same ones that controlled the system before the regime shift. Consequently, it can be difficult to reverse a regime shift. For example, an increase in the rate of phosphorus (P) recycling from lake sediments back into the water column occurs when the amount of P in solution reaches a certain threshold, rapidly shifting the lake from an oligotrophic to a eutrophic state (Carpenter and Cottingham 1997). A reduction in the amount of P after a regime shift may not lead the lake immediately to a shift back into an oligotrophic state (Carpenter *et al.* 1999) because P recycling no longer uniquely controls the new state of the system. Similarly, in rangeland systems, when shrub cover is low, grasslands can recover from overgrazing when grazers are removed. But when shrub cover is higher, grasslands cannot recover from overgrazing after grazers are removed because shrubs outcompete grasses (Anderies *et al.* 2002, Bestelmeyer *et al.* 2006). Transitions between grassland and shrubland states can be further controlled by frequency of fire, but the relative impact of competition (bottom-up effects) and grazing/predation (top-down effects) differ strongly in the different states (Anderies *et al.* 2002, Bestelmeyer *et al.* 2006).

Climatologists, oceanographers, and statisticians have focused on *post-hoc* identification of regime shifts in long time-series (Easterling and Peterson 1995, Lazante 1996, Solow and Beet 2005, Rodionov 2005a, 2005b), but such methods are of little use if a management goal is to avoid (or accelerate) a regime shift. Recent work with models of lake ecosystems suggests that increased variance of an evolving time-series may presage a regime shift from an oligotrophic to a eutrophic state (Brock and Carpenter 2006, Carpenter and Brock 2006). Indicators of regime shifts in atmospheric and oceanic (both physical and biological systems) include a change in the variance spectrum towards lower frequencies (Rodionov 2005c). van Nes and Scheffer (2007) identified a decreased rate of recovery from small perturbations as an indicator for regime shifts in models of aquatic macrophyte population dynamics; asymmetric competition between two or more species; effects of grazing pressure on populations; and phosphorus cycling in lakes. The development and use of any indicator should allow managers to anticipate regime shifts and manage systems accordingly, but it is not clear whether available indicators provide sufficient advance warning to managers who are working with relatively short time-series and incomplete information about the system of interest.

Our approach here is to explore potential methods to detect regime shifts when only partial knowledge of important underlying ecological processes is available, and then to use these methods to suggest conservative management strategies. We address these questions by applying several different indicators of an impending regime shift to an example system: Carpenter and Brock's (2006) model of lake eutrophication. We use this model because it has been used extensively to explore the possibility of detecting regime shifts (Brock and Carpenter 2006, Carpenter and Brock 2006).

Our approach differs from previously published economic and ecological approaches to detecting and managing regime shifts. Economists have tended to focus on the value of an ecosystem and have used cost-benefit analysis to determine the cost of a regime shift (for application of these economic models to ecological systems see Carpenter *et al.* 1999, Ludwig *et al.* 2003, Ludwig *et al.* 2005). Such a cost-benefit analysis results in a utility function for the ecosystem that depends on the state of the system and any additional inputs. Deterministic models are employed to determine the utility function that maximizes the economic value of the ecosystem. It is important to note that such an analysis expects managers to have a deterministic ecosystem model that describes the true dynamics of the system and allows for accurate forecasts of future states, including regime shifts. Such models are rarely available.

In contrast, ecological approaches have focused attention on detecting regime shifts given available data (Carpenter 2003, Keller *et al.* 2005). Recent approaches assume imperfect knowledge about the system and instead use simple models that approximate system dynamics (e.g., Carpenter and Brock 2006). These dynamic time-series models continually update parameter estimates as more knowledge accrues. Unfortunately, in models developed to date, parameter estimates become most reliable only *after* the threshold to a new regime has been crossed (Carpenter 2003).

The structure of this paper is as follows. First, we present a précis of Carpenter and Brock's (2006) lake model and the minor modifications that we made to it. Within this section, we also describe the different sources of stochasticity that contribute to variability in the model output. Second, we describe six indicators for impending regime shifts. Third, we illustrate the inertia of this system and discuss how far in advance an indicator must signal a regime shift for a management intervention to be effective. Fourth, we explore how differences in the types and magnitudes of variability in the system influence the power of each of the indicators and their ability to detect a regime shift. Finally, we discuss how managers could actually use these indicators to develop and implement realistic management plans.

THE LAKE MODEL

The basic model

Carpenter has developed a detailed model of ecosystem dynamics of lakes subject to phosphorus (P) input from non-point-source agricultural inputs (Carpenter 2003, Carpenter and

Brock 2006). Such chronic, long-term stressors are common features of many ecosystems, including forests subject to atmospheric deposition of nitrogen, sulfur, and heavy metals (*e.g.,* Gbondo-Tugbawa *et al.*, 2002, Holland *et al.* 2005, Vanarsdale *et al.* 2005) and estuaries and coastal waters that receive run-off from large rivers (*e.g.,* Rabalais *et al.* 2002). We focus here on a lake model because many underlying processes driving lake ecosystem dynamics are well understood (Carpenter 2003) and because indicators of regime shifts have been developed using lake models (Carpenter and Brock 2006, van Nes and Scheffer 2007).

But ecosystems are not impacted only by chronic, non-point-source stressors. Point-sources of pollutants (which may affect ecosystems acutely through single or intermittent discharges, or chronically through continuous operations of, *e.g.,* smelters or power plants) or targeted harvesting or grazing operations are examples of stressors for which continued operation could cause regime shifts but which are more tractably managed. Pipes can be shut off, herds can be moved, or fishing boats can be beached more readily than diffuse plumes of nitrogen moving through soil can be contained. Therefore, we modified Carpenter and Brock's (2006) model of lake ecosystems to include both types of stressors – non-point-source (*i.e.,* leaching of P from soil into water, as in the original model) and point-sources (*i.e.,* direct discharge into the water of P as industrial effluent) (Fig. 1). This addition allows our results to be generalized beyond agricultural systems.

The model we use is a system of three coupled stochastic differential equations for the density (g/m^2) of P in soil (*U*), lake water (*X*) and lake sediments (*M*):

$$\frac{dU}{dt} = F_a - cUH \qquad (1)$$

$$\frac{dX}{dt} = F_i + cUH(1+\varepsilon\frac{dW_1}{dt}) - (s+h)X + MR(X)(r+\sigma\frac{dW_2}{dt}) \qquad (2)$$

$$\frac{dM}{dt} = sX - bM - MR(X)(r+\sigma\frac{dW_2}{dt}) . \qquad (3)$$

The meaning and units of each variable and parameter in this model are given in Table 1.

The model is solved for successive summer seasons when the lake is stratified. The time-steps are one year (annual) for changes in *U* (phosphorus in soil) and 36 within-year increments for *X* (phosphorus in water) and *M* (phosphorus in lake sediments). The different time scales at which each of these processes occur are based both on current understanding of lake ecosystems and on consistency with Carpenter's coding of the model (*personal communication* from Steve Carpenter, May 2007). We followed Carpenter and Brock (2006) in assuming that the nutrients from the soil enter into the system once each year, prior to summer stratification of the lake. Equation 1 is solved on annual time steps, and this annual input is then distributed over all the within-year time-steps used to solve Eqns. 2 and 3. In contrast, recycling occurs continually throughout the year due to stochastic events driven by wind (Sorrano *et al.* 1997).

In Eqn. 1, F_a is the input rate of P to soil (from fertilizer use, dust deposition, or weathering). Equation 2 calculates the annual input of P into water, which comes from two primary sources. First is the non-point source leakage of P from soil into water, which is the product of soil P (*U*), the transfer coefficient from the soil into the lake (*c*), and two sources of variability, *H*, and $\varepsilon\frac{dW_1}{dt}$ (see *Sources of variability in the model*, below); throughout, we refer to the product $cUH(1+\varepsilon\frac{dW_1}{dt})$ as F_{soil}. Second are the additional inputs of P from industrial sources (F_i). Throughout, we refer to total P inputs, the sum of F_i and F_{soil}, as F_{total}. Loss of P from the water column occurs through sedimentation (s) and outflow (h). Equation 3 determines the amount of P in lake sediments as a function of sedimentation (s) and burial (b), and a recycling coefficient r. Recycling of P from sediment back into the water column acts as a third source of P input to the system and it is increases in P recycling that trigger the regime shift in the lake model (Carpenter 2003, Carpenter and Brock 2006). This recycling of P is represented by the recycling function $R(X)$:

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

where m is the value (2.4 g/m^2) at which recycling is half the maximum rate and the exponent q determines the slope of $R(X)$ near m (Carpenter *et al.* 1999). $R(X)$ ranges from 0 to 1, and $R(m)$ = 0.5.

In our initial simulations and numerical analyses, we used values for all the parameters estimated for Lake Mendota, Wisconsin, as provided in Table S1 of Carpenter and Brock (2006) (see also our Table 1). To determine how each of these parameters affects the behavior of different indicators of regime shifts, we suppressed or changed the values of one or more sources of variability in some of the simulations described below (by setting one or all of λ, ε, or σ equal to zero or to a value lower value than the defaults: see Table 1). All simulations and analysis were done using the R language (R Development Core Team 2007), version 2.4.

Figure 2 illustrates the behavior of this model subject to realistic increases in inputs of the two different sources of P. For both sources, we started the simulations at oligotrophic equilibrium, and with F_a = 0.3. In the first case we fixed F_a at 0.3 g/m^2 but increased F_i from 0 to 1.2 g/m^2 (Fig. 2A), which resulted in a total input of phosphorus (point-source + non-point source) of 1.5 g/m^2 by year 300 (Fig. 2B). In the second case we fixed F_i at 0 and we increased agricultural inputs F_a from 0.3 to 10 g/m^2 (Fig. 2A), which also led to an increase in F_{total} (= F_{soil} alone in this case) of 1.5 g/m^2 by year 300 (Fig. 2C). At these levels of total P inputs, the lake model shifted from an oligotrophic to a eutrophic state (*i.e.*, a regime shift occurred) sometime between simulated years 225 and 275 (dark grey vertical lines in Figs 2D and 2E). In both cases we dropped F_i or F_a to zero at year 300, shortly after the regime shift occurred.

As point-source input (F_i) increased (Fig. 2A), the total P in the water increased slowly at first and then the lake abruptly shifted to a eutrophic state (Fig. 2D). Turning off the point-source input resulted in a relatively rapid return to oligotrophic conditions (Fig. 2D). In contrast, a similar pattern of increase and then abrupt decrease in non-point source inputs of P to soil (F_a; Fig. 2A) was not paralleled by an abrupt decrease in total P inputs (Fig. 2C) because of the slow rate of transfer of P from soil to water. The shift from an oligotrophic regime to a eutrophic one was relatively rapid, but the time to reversal was lengthy (Fig. 2E) and controlled in part by the parameter c, the transfer coefficient of P from the soil into the lake. In both cases the new state of the lake system showed some resilience, as the regime shift was not reversed immediately. However, it took much more time to reverse a regime shift caused by non-point-source agricultural inputs F_a because the soil acted as a "sponge" and continued to release P to the lake long after inputs have stopped.

Sources of variability in the model

There are three sources of stochastic variability in the model. First, there is annual variance H in Eqn. 2 that describes the input of P from soil into water:

$$H = \exp(Z - \frac{\lambda^2}{2}) \tag{5}$$

where Z is a white noise process with mean = 0 and variance = λ^2. H generates a random lognormal variable with mean = 1. Second, there is within-year variation that depends on ε in Eqn. 2 (dW_1 is a white noise process with mean = 0 and variance = dt). Such variation could be caused by irregular rainfall events, for example. Third, frequent shocks to recycling because of wind events within the summer season are represented by $\sigma MR(X)\frac{dW_2}{dt}$ in Eqns. 2 and 3; dW_2 also is a white noise process with mean = 0 and variance = dt. Note that Z is independent of dW_1, and dW_2. These three sources of variability are illustrated schematically in Figure 3, which shows that the control parameters ε and σ have similar effects on within-year variability in concentration of phosphorus in the water column.

The key to understanding how a regime shift can occur in this system is to recognize processes occurring on three time scales (Brock and Carpenter 2006). The first is a very slow change in an exogenous driver or in a slowly changing system component, such as F_a or F_i in Equations 1 and 2 (see also Fig. 2). The second is a medium-speed change in the state variable subject to the regime shift, such as the concentration of P in the water column (X). The third is a fast change in X due to the white-noise processes Z, dW_1, or dW_2 (Table 1; Fig. 3).

Since the value of F_{soil} depends on λ and ε, the annual variance in X increases with inputs of phosphorus from soil. The parameter σ begins to affect the system once P recycling from the sediment into the water column begins. Therefore, if a regime shift is caused by an increase in agricultural inputs, an increase in the variance of X should precede a regime shift (Carpenter and Brock 2006). The parameter λ controls annual (between-year) variance, so ideally we would like to identify indicators that can differentiate within-year variance (*e.g.*, variance due to the control parameters ε and σ) from between-year variance due to λ. Such indicators also should allow us to detect the "signal" of an impending regime shift from the background "noise" of normal within-year and between-year variance.

INDICATORS OF REGIME SHIFTS

The lake model (Eqns. 1-3) is the result of decades of study and a deep understanding of lake biogeochemistry (Carpenter 2003). However, few ecosystems are as well understood, and most often we do not have a mechanistic understanding, let alone measurements, of all the underlying drivers determining an ecosystem's state. Rather, we are more likely to work with a simplified model of the system (Carpenter and Brock 2006). In monitoring lakes, we typically monitor inputs of P from industry (F_i) or soil (F_{soil}) annually or at regular within-year intervals. Annual concentration of P in the water (X) is estimated from samples taken throughout the year. From these observations, we can estimate change in water P as:

$$\frac{dX}{dt} = a_0 + (F_i + F_{\text{soil}}) - a_1 X \tag{6}$$

where a_0 and a_1 are parameters that represent the true but unknown processes for recycling of P from the sediment into the water column (a_0) and losses of P from the system (a_1). Total P input ($F_i + F_{\text{soil}} = F_{\text{total}}$) is assumed constant during the course of a year. This model is a dynamic linear model (DLM; Pole *et al.* 1994) that is upgraded annually (Brock and Carpenter 2006):

$$X_{[\text{DLM}],t} = X_{t-1}\exp(-a_{1_{t-1}}) + \frac{1+\exp(-a_{1_{t-1}})}{a_{1_{t-1}}} + (F_i + F_{\text{soil}}) + \frac{a_{0_{t-1}}(1-\exp(-a_{1_{t-1}}))}{a_{1_{t-1}}} \tag{7}$$

Using this model and the observed time series of F_{total} and X, one important goal is to develop clear indicators that will suggest a regime shift with ample time to respond. We explore the behavior of six such indicators (Table 2). Other indicators have been proposed but cannot be easily used in a management context. For example, indicators of resilience suggested by van Nes and Scheffer (2007) require experimental interventions, and an indicator based on Fisher Information is applicable only to systems that exhibit periodic time-series (Fath *et al.* 2003). Brock and Carpenter (2006) showed that the maximum eigenvalue of the variance-covariance matrix of their modeled system increases steeply prior to a regime shift. We also saw this behavior in our analysis of the lake model, but in order to use this indicator, a manager would need to have reliable within-year data on concentrations of P in sediments (M in Equations 2 and 3). Such data are rarely available in lake monitoring programs. Rodionov (2005a, 2005c) summarizes a number of other indicators used by climatologists that require amounts of data that are rarely available to ecologists or environmental managers.

The six indicators we used are listed in Table 2. The first two, SD and SD_{DLM}, are the standard deviation of the within-year values of P in the water column (X) around the mean of the model output (Eqn. 2) or around the prediction of the DLM (Eqn. 7), respectively (Carpenter and Brock 2006). Carpenter and Brock (2006) showed that because recycling of P from sediments to water increases before a regime shift, so does variability in the system due to σ (Fig. 3E, 3F), and so do SD and SD_{DLM}. SD_{DLM} also may be less susceptible to changes in between-year variability (λ).

The third indicator, SD_{rec}, is based on the fact that there is a predictably large shock to the system (excess P input) at the beginning of each year due to λ. Part of the within-year variation is caused by an adjustment of the system to this shock; if we assume that this adjustment is linear, linearize the within-year values of X, and then take the standard deviation around this linear model, we may be able to detect the signal due to the onset of recycling of P from sediments to the water column more clearly. In the equation for SD_{rec}, $X_{[rec],t}$ is the vector of linear fitted values for each year t. $X_{[rec],t}$ is calculated using the `lm` function in R to estimate X (the 36 within-year values of water-column P) as a function of time.

The SPEC indicator is based on the idea that within-year spikes (sharp increases followed by sharp decreases in a measured variable) in water-column P caused by recycling will, for some frequencies, result in an increase in spectral density of the time-series. That is, if there is no within-year variance in X, or if X increases or decreases smoothly within a given year, there will be no high-frequency signal to its time-series. However, when there are many spikes in X within a given year, a high-frequency periodic signal in the time-series may be detectable. Using the 36 within-year X values generated by the model, we estimated the maximum spectral density using the R function `spec` (in package `stats`). This may seem like a very approximate indicator, but like the other indicators, SPEC can be upgraded annually. It is also similar to other indicators predicated on the idea that new processes and regimes may change the variance spectrum of underlying time-series (Kleinen *et al.* 2003). Furthermore, the only assumption of this indicator is that recycling of P from sediments back into the water column occurs in bursts during the summer season; no additional data are required by a manager to determine the value of SPEC.

The a_0 indicator is simply based on the updated parameters in the DLM (Equations 6 and 7). When phosphorus recycling starts, there is a change in the processes that the DLM might be able to detect. Finally, X itself could be used as an indicator, because recycling causes spikes in the time-series of values of water-column P. We use this last indicator, X, as a "control" to see if the other indicators really improve the detection of regime shifts.

As P input increases, total water P (Fig. 4, top row) and all of the indicators (Fig. 4, rows 2-6) increase in value and variance after recycling of P from sediments to the water column starts (vertical grey lines in Fig. 4) but before the regime shift occurs at time ~ 245 in these simulations. The "signal" of the indicator is clearest when the only variability in the system is due to σ (Fig. 4, left column). As additional sources of variability are added, it is substantially more difficult to detect a "signal" within the annual variability of the indicators. Clearly, the variance in each indicator increases after recycling starts (Fig. 4, right column).

HOW SOON MUST A REGIME SHIFT BE DETECTED IN ORDER TO PREVENT IT?

Methods

Our first analysis asks if progress of a system towards a regime shift is irreversible (at least in the short term) or if it can be slowed or stopped (or accelerated) by a management intervention. The critical piece of information is the relationship between the lead time an indicator provides before a regime shift occurs and how quickly the system can respond to an intervention. As illustrated in the description of the model, the rate of response also may depend on the input source, here non-point source leakage of P from soil (F_{soil}) and point-source inputs of P (F_i) (Fig. 2, above).

To identify how far in advance any indicator must detect a regime shift so that a management intervention can successfully avert it, we used the same input schedules of P into soil (F_a) and directly into water (F_i) as we used to generate Fig. 2, above (parameters given in Table 1). We noted in the output when different levels of P were recycled from the lake sediments ($R(X)$ = 0.0001, 0.001, 0.01, and 0.1), and when the shift from an oligotrophic to a eutrophic regime occurred. We then altered the values of F_a and F_i (*i.e,* simulated a management response), and re-ran the simulation beginning at the year of the regime shift, and for each year preceding the regime shift. The number of years back that we restarted the system is called the *Delay*. It represents the (simulated) time an indicator gives a manager to attempt to prevent a regime shift.

Management responses depend on three parameters: (1) *Resp* – the number of years before any intervention (this represents, for example, the time it takes a manager to convince industry to stop P inputs into the lake); (2) *Base level* – the fraction of total (P) inputs that the manager cannot eliminate; and (3) *Nyears* – the number of years it takes to reach *Base level*. We simulated three different management responses. The first is a slow response that allows for high base level of P inputs: *Resp* = 10, *Base level* = 0.5, *Nyears* = 50. The second is an intermediate response that allows for a lower base level of P inputs: *Resp* = 5, *Base level* = 0.1, *Nyears* = 10. The third is a fast response that allows for no base level of P inputs: *Resp* = 0, *Base level* = 0.0, *Nyears* = 2. With these responses, we re-ran the simulations for 500 years for a range of *Delay* values. We determined whether a regime shift would still occur, and if it did, how long it would take to return the lake to the oligotrophic state following the different management interventions. We considered a regime shift to have occurred when the mean value of P in the water column exceeded 2.4 g/m^2, the concentration at which the rate of recycling $R(X)$ is 0.5 (*i.e.,* $X = m = 2.4$ g/m^2). We ran 200 replicate runs for each set of parameters: P input schedules (temporal trajectories of F_a and F_i), and the three management responses.

Results

If the increase in P input was entirely due to point-source effluent (F_i), the worst-case management intervention (slow management response, some base-level input allowed) prevented a regime shift if it was applied 30 years in advance (Fig 5A). In contrast, for non-point source inputs (F_a, F_{soil}), the best-case management intervention (rapid response, no allowable base-level of inputs) needed to have been applied at least 35 years in advance, and the worst-case intervention needed to have been applied at least 70 years in advance, to prevent the lake from shifting into a eutrophic state (Fig. 5B). For agricultural inputs, recycling of P from lake sediments to the water column reached 0.001 (0.1%) 60 years before the regime shift, and 0.01 (1%) 22 years before the regime shift was observed (Fig. 5B). Extrapolating this result to the "real world", where best-case interventions are unlikely, any indicator of a regime shift must detect a small recycling rate many decades in advance if regime shifts are to be avoided.

However, even if a regime shift cannot be prevented, intervention still may have utility. The mean recovery time of the system – how long it takes for the model system to return to an oligotrophic regime – is shorter when management intervention is applied sooner (Figs. 5C, 5D). This conclusion applies not only to lake eutrophication. The use of indicators for detection of regime shifts and triggering of management interventions will be most successful when a manager can quickly change a control variable (*i.e.,* small *management inertia*) and when there are no processes that will otherwise slow the response of the system; here, accumulation of P in the soil and its subsequent slow release (*i.e.,* small *system inertia*). Our analyses also assume a fixed linear schedule of change for F_i and F_a; that managers can measure and control these important input variables; and that their decisions to intervene depend strictly on preventing a regime shift. Variation in rates of change of inputs, the starting point of the system, stochastic noise, and constraints on decision-making all can influence the success of a monitoring or management plan. We discuss these in more detail in the last section of the paper, after we discuss the power of different types of indicators in the face of stochasticity in the system.

HOW POWERFUL ARE THE INDICATORS AT DETECTING IMPENDING REGIME SHIFTS?

Methods

When P begins to recycle from the sediments back into the water column, spikes of P in the water column become measurable. Thus, we hypothesized that by comparing the magnitude of spikes in water column P before and after P recycling had begun ($R(X) = 0.0001$), we could determine how powerful each of the indicators is at detecting a regime shift with different levels of variability from each of the three possible sources (λ, ε, and σ). An indicator is considered to be *powerful* if it detects an impending regime shift with sufficient lead time to allow for an effective management intervention, but not so far in advance that an intervention is not cost-effective. In particular, we suggest that if an indicator is powerful at identifying a regime shift, the spikes that occur in its time-series once P recycling starts and a regime shift is imminent should be much larger than the spikes that occurred earlier in the time series. Ideally, an indicator should pick up the potential for a regime shift far enough in advance for a management intervention to avoid (or minimize the probability of) a regime shift.

As before, we generated time-series of the lake system beginning at oligotrophic equilibrium and applied the same inputs of F_i and F_a. When F_a was held constant while F_i increased, only within-year recycling variability (controlled by σ) increased. In contrast, when F_a increased, between-year and within-year variability (controlled by λ and ε) also increased, and within-year recycling variability (controlled by σ) only increased after recycling started. For each input schedule, we varied λ, ε, and σ (Table 3), and for each combination, we ran 500 replicate simulations. For each input schedule of P and the combinations of variance parameters given in Table 3, we ask: (1) which indicator gives the best results with for the given set of parameters; (2) which indicator best detects the onset of recycling of P from the sediment back into the water column; and (3) which indicator is best able to isolate variability due to P recycling from the other sources of variability.

First, to determine the power of each indicator as a function of time-to-regime shift (=*Delay*), we constructed the vector of the difference between adjacent values in the indicator time series (the value at time $t + 1$ minus the value at time t), running from the onset of P recycling ($R(X) = 0.0001$) to the time-of-intervention *Delay* ($Delay \leq Year_{RS}$, the year in which the regime shift occurred). We called this vector SPIKE_1 and it contains the differences between adjacent indicator values; the maximum value of SPIKE_1 represents the highest spike in the indicator time-series. We then constructed a similar vector (called SPIKE_2) in the time-series of identical length running backwards from the onset of P recycling. Our measure of power is the log of the ratio of the maximum values of each of the two vectors:

$$\log\left(\frac{\max(\text{Spike}_1)}{\max(\text{Spike}_2)}\right), \qquad (8)$$

which basically represents how much higher the spikes in the indicator time series are after the onset of P recycling. If the magnitudes of the spikes are equivalent before and after the onset of recycling, Equation 8 = 0 and the indicator does not detect the upcoming regime shift (*i.e.,* its power is low). We compared the powers of the different indicators for each set of variance parameters in Table 3 by plotting the power (Eqn. 8) *vs. Delay*, and estimating the area under each curve using the R function `diffinv` in package `stats`. Higher values of power suggest that the indicator is able to discriminate the signal from the noise for each combination of parameters.

Second, as spikes in the time-series of concentration of P in the water column are much larger after P-recycling has started, we wanted to isolate those spikes that were "large enough" to correctly identify a regime shift. We use the algorithm in Box 1 to determine whether an indicator detects a regime shift. This approach is much closer to a year-to-year management approach than annual computation of the log of the ratio of the two vectors of spikes (Eqn. 8).

Box 1. Algorithm to determine whether an indicator detects a regime shift.

1. Record the values of the first twenty spikes in the time-series, and store in vector SPIKE.
2. For each subsequent year, determine if another spike occurs in the time-series.
3. If there is a spike, compare its value with SPIKE using different "filters". The filter uses the mean and standard deviation of the SPIKE to create a limit value:

$$LimitValue = \text{mean}(\text{SPIKE}) + \text{FAC} \times \text{SD}(\text{SPIKE}) \qquad (9)$$

where FAC is a coefficient that determines the sensitivity of the indicator.

4. If the spike of the year is above *LimitValue*, then the indicator detects a regime shift. Else, upgrade SPIKE (by using the new spike and the preceding 19 to create a new vector SPIKE) and return to step 2.

We ran this algorithm for each indicator, using a range of values for FAC (1 to 10 in increments of 0.5) to construct different filters. When the indicator detected a regime shift, we compared the year of detection ($Year_D$) with the year at which recycling of P from sediment to the water column actually began in the simulations ($Year_{REC}$) and with the year at which the regime shift actually occurred in the simulations ($Year_{RS}$) (note that $Delay = Year_{RS} - Year_D$, and is the time an indicator provides that can be used to prevent a regime shift from occurring).

We define two different types of error: α = the fraction of runs in which $Year_D > Year_{RS} - Delay$, and is the proportion of runs in which the detection occurs too late for an intervention to prevent a regime shift. In contrast, β = the fraction of runs in which $Year_D < Year_{REC}$, and is the proportion of runs that detected a regime shift too early, suggesting an intervention before it is needed to stop the regime shift. The remainder (1-[α + β]) is the fraction of runs that provide good detection of impending regime shifts ($Year_{REC} \leq Year_D < Year_{RS} - Delay$). Good detection implies adequate time to prevent a regime shift in a cost-effective manner.

We define the overall error rate as

$$Error = \text{percent}(\beta) + [5 \times \text{percent}(\alpha)] \tag{10}$$

This error rate weights α more than β because errors in α are false negatives, whereas errors in β are false positives. In this case, a false negative has more serious management consequences than a false positive. We used an arbitrary weighting factor of 5, but other weights could be used without qualitatively changing the results. By comparing values of *Error* as a function of *Delay* for each indicator and each filter, we can identify "optimal" filters and error values for each indicator across a range of parameters affecting variability in the system.

Results

When only F_a increased and when variance parameters were set at high levels (set number 6 in Table 3), all the indicators had higher power when the regime shift was imminent ($Delay \rightarrow 0$; Fig. 6). Power for all indicators approached 0 as *Delay* increased, but even when

Delay = 30, SD_{rec} and SPEC detected the upcoming regime shift (Fig. 6). For this combination of inputs and variability, SD and SD_{DLM} provided little gain in power relative to the time-series itself (X), and a_0 provided no indication of an impending regime shift at all (Fig. 6).

As we altered combinations of values of the variance parameters (Table 3), the rank order of the power of each indicator did not change, but the total power did (Fig. 7). With very low values for the parameters (Table 3, set 1), all indicators were poor (black bars in Fig. 7). Increasing the value of σ (variability in recycling) alone improved the power of all the indicators (dark grey bars in Fig. 7), but SPEC worked better, and X worked more poorly, than all the other indicators. The power of all the indicators decreased as the other variance parameters were increased (lighter grey and white bars in Fig. 7). Two indicators, SD_{rec} and SPEC were less responsive to increasing λ than the other indicators (Fig. 7), because *between-year* variance did not affect *within-year* patterns and did not alter the power of SPEC, which measures within-year spectral density. Since we purposely designed SD_{rec} not to respond to the shock at the beginning of each year, its lack of response to changes in λ was not surprising. The power of the other indicators declined as λ increased (Fig. 7). None of the indicators were particularly resistant to changes in ε, which is difficult to distinguish from variability due to σ (Fig. 3).

When F_a was held constant and increases in F_{total} were due entirely to F_i, the conclusions were qualitatively similar (data not shown). Overall power of all the indicators were better when F_i was the primary input source because F_a was lower and so there was less variability in the system due to ε and λ. Comparing the two different types of inputs, we note that if two different input sources can trigger a regime shift (*e.g.*, F_a and F_i), then detection of an upcoming regime shift will be more difficult if the input source (here F_a) that contributes most to the underlying variability is also the one that is increasing.

All indicators had lower values of total error (Eqn. 10) when a regime shift was imminent (low values of *Delay*), and errors increased with time to the regime shift (Fig. 8). The error rates paralleled the power of the indicators. SPEC and SD_{rec} had the lowest error values whereas a_0 and X had the highest error values. With increasing non-point-source inputs (F_a increasing, $F_i = 0$) and with realistic values for the variance parameters, SD_{rec} and SPEC could detect regime shifts with relatively low error (< 30%) up to 5 simulated years in advance (Fig. 8A). Alternatively, if non-point-source inputs are held constant and point-source inputs are increasing, these two indicators could reliably detect regime shifts up to 40 simulated years in advance (Fig. 8B).

The results that we show here used the FAC value that minimizes the error rate for each indicator. In a real management case, choosing the FAC value to use depends on the management goals: if a manager wants warning of a regime shift far in advance, the algorithm should be more sensitive, so FAC should be set relatively low. Because the examination of both the power and the detection ability (error rate) of the different indicators yielded similar conclusions, the detection algorithm (Box 1) could be used in a monitoring program to detect a regime shift for a given value of FAC. Thus, in the next section we discuss how one might effectively manage to prevent an impending regime shift.

AN ILLUSTRATIVE EXAMPLE: CAN PRO-ACTIVE MANAGEMENT AVOID A REGIME SHIFT?

Consider a situation where an oligotrophic lake is at equilibrium and is receiving only non-point-source agricultural inputs of P that leach slowly from the soil (as in the starting conditions of Carpenter and Brock's 2006 model). By comparing the amount of P in the water with data from other oligotrophic and eutrophic lakes, we can be confident that the lake has some lengthy but undetermined time to go before it crosses a threshold into a new nutrient regime. A new use is proposed for the lake: an industrial plant wants to discharge P into the lake, and a management plan is needed to allow increased inputs into the lake while avoiding an undesirable regime shift. The site manager is able only to monitor the amount of P in the lake and the agricultural (non-point-source) inputs of P into the lake, and to control only the proposed industrial inputs into the lake. Our results from the analyses presented in the preceding sections suggest the following simple management algorithm:

1. Allow linear increases in industrial inputs, calculate indicator values annually, and use the detection algorithm (Box 1) to detect when recycling of P from sediments into the water column begins.
2. Based on the input level when detection occurs, estimate the amount of total inputs (non-point-source + point-source) that will keep the lake far enough from the threshold so that a stochastic event (*e.g.,* an unanticipated spike in P inputs) will not trigger a regime shift.
3. Increase or decrease allowable point-source inputs in line with measured agricultural inputs to keep total inputs constant.

Our goal is not to find the best management strategy with a cost-benefit analysis. Rather, we first illustrate the effect of the time at which a regime shift is first detected on the risk of an actual regime shift. Second, we examine the influence of changing model parameters on the risk of triggering a regime shift. This sensitivity analysis allow us to determine the robustness of this management algorithm to changes in parameters and therefore to identify how altering a management "strategy" (*i.e.*, a set of adjustable parameters defined in the next paragraph) affects the final outcome. We don't show the results for total inputs into the lake, but these are correlated with the risk of regime shifts.

Methods

We ran 500-year simulations starting at oligotrophic equilibrium (initial $F_a = 0.3$; $\varepsilon = 0.01$; $\lambda = 0.35$), only agricultural inputs, and a linear increase in F_a that leads to a doubling of non-point-source P inputs in 40 years. We ran 500 replicate simulations and noted the proportion of replicates that led to a regime shift. We used the SPEC indicator, which had the best performance in detecting regime shifts across a broad range of conditions (see Figs. 6-8), and noted the percentage of regime shifts detected for each year prior to the regime shift.

For each set of simulations we defined two sets of parameters. *System parameters* are parameters that a manager cannot control. These system parameters include the variance parameters λ and ε and the non-point-source agricultural inputs F_a. Note that the initial value of F_a defines the distance of the system from its threshold. *Management parameters* are parameters that a manager can control. These management parameters are: (1) *Speed*, the rate at which total inputs can increase, and here is referenced to the time needed to double the initial P inputs into the system (the higher the value of *Speed*, the lower the increase in input rate of P); (2) the detection factor FAC used to calibrate the indicator (Eqn. 9 in Box 1); and (3) the *Best input*, which is the amount of allowable point-source P inputs set by the manager, relative to input levels when the impending regime shift is detected. We call a given set of management parameters a *management strategy*. Note that even though a manager cannot control the system parameters, knowledge of them can be used to alter management parameters and to improve the management strategy.

Results

When impending regime shifts were detected far in advance, the sensitivity of the algorithm could be decreased by modifying the management parameters so as to reduce the time from detection to potential regime shift ($Year_D$) without increasing the risk of regime shift. However, once $Year_D$ declined to ~ 60 simulated years prior to a regime shift, the percent of actual regime shifts that occurred began to increase exponentially (Fig. 9). By $Year_D$ ~ 30, the probability that a regime shift would occur approached 1 due to the inertia in the system.

Table 4 illustrates how changes in system parameters and management parameters altered the probability of a regime shift. The probability of runs resulting in regime shifts ranged from 1% to 69%, with higher numbers resulting from high input levels or lower sensitivity of the indicator. Increasing variability in the system (higher values of ε or λ) decreased the sensitivity of the indicator, made detection more difficult and led to higher probabilities of regime shifts. Larger values of these parameters also increased the risk that stochastic events could trigger regime shifts, even if they were detected well in advance. If a manager knows from past observations that these system parameters are high, s/he can keep point-source inputs lower to reduce the probability that a regime shift occurs (and reduce total inputs into the system). The crucial result is that detection algorithms need sufficient data to provide adequate warning of an impending regime shift: 20-30 simulated years seems to be the minimum we observed for any of our indicators.

The importance of process error and observation error

In reality, the true underlying processes determining regime states are stochastic (Equations 1-3) and generally unknown. Individual instances of the model reflect propagation of stochastic process variance, and final outcomes can vary greatly (and thus we illustrate probabilities of regime shifts over multiple runs in Figs. 5 and 9). Although we can simulate multiple instances of the generating equations and analytically determine the consequences of the propagation of process error through the model, managers and decision-makers are monitoring only a single realization of this process. And it is to this single realization that the detection algorithm (Box 1) would be applied. In different situations (or in different runs of the model), the realization of the process will also differ, but the algorithm should still work effectively. This is because managers are not trying to understand the underlying generating process itself, but rather they are trying to detect and respond to patterns emerging from a particular instance.

Observation error does not propagate through time in the model, but it may have more significant consequences in a management context because errors in observation may lead to erroneous assessment of the probability of a regime shift. Our model (Eqns. 1-3) does not incorporate observation error, but it is relatively straightforward to measure P content of water. In general, monitoring programs should measure variables with sufficient precision and accuracy so that the observation error is small, or at least is dominated by the process error.

DISCUSSION AND GENERAL CONCLUSIONS

Regime shifts occur in a wide range of ecological systems, including forests (e.g., Lawrence et al. 2007, Millar et al. 2007, deYoung *et al.* 2008), fisheries and other large marine ecosystems (e.g., Mantua 2004, Daskalov et al. 2007), and grasslands and rangelands (e.g., Anderies et al. 2002, Bestelmeyer 2006). A rapidly growing database of thresholds and regime shifts in ecological systems is described by Walker and Meyers (2004) and is maintained online by the Resilience Alliance.[1] Conceptual reviews identify two broad categories of regime shifts – ecosystems that cross thresholds because state variables have changed, or ecosystems that can occupy alternative stable states due to shifts in underlying system parameters (Beisner et al. 2003, Scheffer and Carpenter 2003). Our methods and analysis were developed for an example of the first type of regime shift, and should be generally applicable to systems of both types where new regimes are maintained by changes in state variables or other system drivers, and where alternative stable states characterized by fold bifurcations do not occur. However, there are also many examples in which alternative stable states can exist for the same set of underlying system parameters – systems in which fold bifurcations exist in phase-space (e.g., Petraitis and Latham 1999, Scheffer and Carpenter 2003, van Nes and Scheffer 2007, Carpenter et al. 2008).

Recent work suggests that such fold bifurcations are preceded by rising variance and spectral density increase (Carpenter et al. 2008), but the behavior of these indicators near critical points is not as smooth as we have found here, and other indicators may not work at all in these situations. In fact, how variance changes before, during, and after a regime shift is bound to differ in different ecosystems. For example, Kleinen *et al.* (2003) found that the variance spectrum shifted to lower frequencies and longer wavelengths near regime shifts in oceanic thermohaline circulation. Although our results along with others (*e.g.,* Kleinen *et al.* 2003, Rodionov 2005c, Carpenter and Brock 2006) suggest that properties of the variance spectrum can be useful as indicators of regime shifts, there is probably no one property that will work for all systems. Rather, if the emergent process has high frequency (such as P recycling in lakes),

[1] <http://www.resalliance.org/183.php>

then looking for indicators in the high frequency bands of the variance spectrum is likely to be fruitful. In contrast, if the emergent process has low frequency (such as in ocean circulation), then looking for indicators in the low frequency bands of the variance spectrum is more appropriate. Either way, a basic process model of how the system works is crucial. In the absence of detailed process information, management intervention should not wait for definitive proof of, or a single number that may presage, an impending regime shift. Rather, expeditious invocation of the precautionary principle in managing ecosystems seems prudent.

Our analysis illustrates that prospective indicators of regime shifts exist, but that when information about true processes driving the system are incomplete or when intensive management actions cannot be implemented rapidly, many years of advance warning are required to avert a regime shift. The lake model we used as our example is based on detailed, long-term study by a large number of investigators; the model accurately accounts for the processes causing regime shifts in north temperate lakes (Carpenter 2003, Carpenter and Brock 2006). However, most managers have neither the time nor the money to invest in decades of study by large groups of investigators to create a detailed model of a particular system. Encouragingly, our analysis shows that with only a basic understanding of a few core processes, managers still can identify indicators of impending regime shifts in lakes based on identifying feedbacks among system parameters that occur well before thresholds are crossed and regime shifts occur.

For the lake model, the indicator based on increases in the spectral density of the time series of P recycling is best at detecting impending regime shifts, but other indicators (Table 2) may be more effective for different ecosystems. The detection algorithm (Box 1) suggests a method to explore the effectiveness of the different algorithms, which in all cases should provide a high "signal" of feedbacks in the face of "noise" from other processes. But even if impending thresholds can be detected, prevention of regime shifts depends on the inertia of the system and the rapidity with which a manager can react and implement management actions. In our example of managing P inputs into a lake, we achieved good results because the management intervention could occur quickly (immediate adjustment in F_i). If the time to intervention increases, regime shifts may not be preventable even if managers can reliably detect thresholds well in advance. But even when inertial aspects of a system limit the ability to prevent a regime shift, it may still be important to intervene to reduce the hysteresis of the system so that it can return to its initial state more rapidly.

Another important consideration is the number of slow variables that interact to cause a regime shift. Management is easiest when only one slow variable causes the regime shift and when that variable can be controlled. But when several slow variables are involved, and some cannot be controlled (*e.g.*, F_a in our example) management may be more difficult. In our example, since the controllable slow variable (F_i) and the uncontrollable slow variable (F_a) had additive effects, their sum could be controlled simply by manipulating F_i. In other cases, such as when the slow variables are either non-interacting or interact in non-linear ways, such compensatory interventions may not be possible or successful.

Our work also suggests several additional avenues for future research in this area. Combining several indicators of regime shifts into a composite indicator may increase the signal-to-noise ratio in the analysis, thereby increasing the probability of detecting a true regime shift early and decreasing the probability of falsely detecting a regime shift. We also assessed only single year-to-year changes in indicator values (Box 1), but algorithms that consider multiple successive year-to-year changes may provide a mechanism for assessing the significance of observed changes in the system (Rodionov 2005b). Further assessment of the propagation of process error and the impact of observation errors of different magnitudes in the model, the application of the management algorithm, and in real situations would help to provide additional bounds on our ability to detect and respond to regime shifts. Finally we considered only linear increases in a single parameter that caused a regime shift, but in many cases multiple parameters will change nonlinearly, especially in the cases of fold bifurcations discussed above (and by Carpenter et al. 2008). Future work should also focus on identifying changes in indicators values that are caused by changes in multiple parameters – ideally ones that can be monitored easily and that are due to processes that may actually lead to regime shifts.

ACKNOWLEDGMENTS

We thank Steve Carpenter and Andy Solow for helpful discussions and answering repeated questions about their models and algorithms. David Foster made the initial observation that the original lake model considers only one kind of input and encouraged us to explore alternative (point-source) inputs in our model and analysis. The Harvard Forest lab discussion group gave us valuable feedback at various stages of this project. Brandon Bestelmeyer, Ben Bolker, Steve Carpenter, Elizabeth Farnsworth, David Foster, Clarisse Hart, and Subject Matter Editor Tom Hobbs provided incisive and valuable comments on the penultimate version of the manuscript. Our work was supported by an internship award to RC from ENS-ULM, and by NSF grant DEB 06-20443. This is a contribution of the Harvard Forest Long Term Ecological Research Site.

LITERATURE CITED

Anderies, J. M., M. A. Janssen, and B. H. Waker. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. Ecosystems **5**:23-44.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**:376-382.

Bennett, E. M., T. Reed-Andersen, J. N. Houser, J. R. Gabriel, and S. R. Carpenter. 1999. A phosphorus budget for the Lake Mendota watershed. Ecosystems **2**:69-75.

Bestelmeyer, B. T. 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. Restoration Ecology **14**:325-329.

Bestelmeyer, B. T., J. E. Herrick, J. R. Brown, D. A. Trujillo, and K. M. Havstad. 2004. Land management in the American southwest: a state-and-transition approach to ecosystem complexity. Environmental Management **34:**38-51.

Brock, W. A., and S. R. Carpenter. 2006. Variance as a leading indicator of regime shift in ecosystem services. Ecology and Society **11**:9.

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., and K. L. Cottingham. 1997. Reslience and restoration of lakes. Conservation Ecology **1**:2.

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

Carpenter, S. R., W. A. Brock, J. J. Cole, J. F. Kitchell, and M. L. Pace. 2008. Leading indicators of trophic cascades. Ecology Letters **11**:128-138.

Daskalov, G. M., A. N. Grishin, S. Rodionov, and V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Sciences, USA **104**:10518-10523.

deYoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner. 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends in Ecology and Evolution **23:**402-409.

Easterling, D. R., and T. C. Peterson. 1995. A new method for detecting undocumented discontinuities in climatological time series. International Journal of Climatology **15**:369-377.

Fath, B. D., H. Cabezas, and C. W. Pawloswki. 2003. Regime changes in ecological systems: an information theory approach. Journal of Theoretical Biology **222**:517-530.

Gbondo-Tugbawa, S. S., C. T. Driscoll, M. J. Mitchell, J. D. Aber, and G. E. Likens. 2002. A model to simulate the response of a northern hardwood forest ecosystem to changes in S deposition. Ecological Applications **12**:8-23.

Holland, E.A., B. H. Braswell, J Sulzman, and J.-F. Lamarque. 2005. Nitrogen deposition onto the United States and Western Europe: synthesis of observations and models. Ecological Applications **15**:38-57.

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

Keller, K., M. Hall, S. R. Kim, D. F. Bradford, and M. Oppenheimer. 2005. Avoiding dangerous anthropogenic interference with the climate system. Climatic Change **73**:227-238.

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

Lawrence, D., P. D'Odorico, L. Diekmann, M. DeLonge, R. Das, and J. Eaton. 2007. Ecological feedbacks following deforestation create the potential for a catastrophic ecosystem shift in tropical dry forest. Proceedings of the National Academy of Sciences, USA **104**:20696-20701.

Lazante, J. R. 1996. Resistant, robust and non-parametric techniques for the analysis of climate data: theory and examples, including applications to historical radiosonde station data. International Journal of Climatology **16**:1197-1226.

Litzow, M. A., and L. Ciannelli. 2007. Oscillating trophic control induces community reorganization in a marine ecosystem. Ecology Letters **10**:1124-1134.

Ludwig, D., W. A. Brock, and S. R. Carpenter. 2005. Uncertainty in discount models and environmental accounting. Ecology and Society **10**:article 13.

Ludwig, D., S. R. Carpenter, and W. A. Brock. 2003. Optimal phosphorus loading for a potentially eutrophic lake. Ecological Applications **13**:1135-1152.

Mantua, N. 2004. Methods for detecting regime shifts in large marine ecosystems: a review with approaches applied to North Pacific data. Progress in Oceanography **60**:165-182.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature **269**:471-477.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications **17**:2145-2151.

Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. Ecology **80**:429-442, 1999.

Pole A., M. West, and J. Harrison. 1994. Applied Bayesian forecasting and time series analysis. Chapman & Hall, New York, New York, USA.

R Development Core Team (2007). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rabalais, N. N., R. E. Turner, and W. J. Wiseman, Jr. 2002. Gulf of Mexico hypoxia, a.k.a. "The Dead Zone". Annual Review of Ecology and Systematics **33:**235-263.

Rodionov, S. N. 2005a. A brief overview of the regime shift detection methods. Pages 17-24 *in* V. Velikova, and N. Chipev, editors. Large-scale disturbances (regime shifts) and recovery in aquatic ecosystems: challenges for management toward sustainability. UNESCO-ROSTE/BAS Workshop on Regime Shifts, Varna, Bulgaria.

Rodionov, S. N. 2005b. A seqential algorithm for testing climate regime shifts. Geophysical Research Letters **31**:1-4.

Rodionov, S. N. 2005c. Detecting regime shifts in the mean and variance: methods and specific examples. Pages 68-72 *in* V. Velikova, and N. Chipev, editors. Large-scale disturbances (regime shifts) and recovery in aquatic ecosystems: challenges for management toward sustainability. UNESCO-ROSTE/BAS Workshop on Regime Shifts, Varna, Bulgaria.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution **18**:648-656.

Schröder, A., L. Persson, and A. M. de Roos. 2005. Direct experimental evidence for alternative stable states: a review. Oikos **110**:3-19.

Solow, A. R., and A. R. Beet. 2005. A test for a regime shift. Fisheries Oceanography **14**:236-240.

Soranno, P. A., S. R. Carpenter, and R. C. Lathrop. 1997. Internal phosphorus loading in Lake Mendota: response to external loads and weather. Canadian Journal of Fisheries and Aquatic Science **54:**1883-1893.

Steele, J. H. 1998. Regime shifts in marine ecosystems. Ecological Applications **8 (Supplement)**:S33-S36.

Vanarsdale, A., J. Weiss, G. Keeler, E. Miller, G. Boulet, R. Brulotte, and L. Poissant. 2005. Patterns of mercury deposition and concentration in northeastern North America (1996-2002). Ecotoxicology **14**:37-52.

van Nes, E. H., and M. Scheffer. 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. American Naturalist **168**:738-747.

Walker, B., and J. A. Meyers. 2004. Thresholds in ecological and social-ecological systems: a developing database. Ecology and Society **9**:3.

Table 1 – Parameters used in the basic model (after Carpenter and Brock 2006, with addition of F_i).

Symbol	Definition	Units	Nominal value	Source
b	Permanent burial rate of sediment P	y^{-1}	0.001	Carpenter (2003)
c	Transfer coefficient of P from soil to lake	y^{-1}	0.00115	Calculated from data of Bennett et al. (1999)
F_a	Net annual input of P to the watershed soil per unit lake area (weathering plus airborne input plus fertilizer application minus removal of phosphorus in harvest)	$g\ m^{-2}\ y^{-1}$	Variable	Bennett et al. (1999) estimated F_a=14.6
F_i	Net annual point-source input of P to the water per unit lake	$g\ m^{-2}\ y^{-1}$	Variable	
h	Outflow rate of P	y^{-1}	0.15	Carpenter (2003)
H	Annual variance in input of P from soil into water	unitless	$f(\lambda)$	
m	P density in the lake when recycling is half its maximum possible ($R(m) = 0.5$)	$g\ m^{-2}$	2.4	Carpenter (2003)
M	Concentration of P in lake sediments	$g\ m^{-2}$	Variable	

q	Parameter for steepness of $R(X)$ near m	unitless	8	Carpenter (2003)
r	Recycling coefficient of P from sediment to lake (= maximum recycling rate of P	g m^{-2} y^{-1}	0.019	Carpenter (2003)
$R(X)$	Recycling function (see Eqn. 4)	unitless	$f(X,m,q)$	
s	Sedimentation rate of P	g m^{-2} y^{-1}	0.7	Carpenter (2003)
U	Concentration of P in soil	g m^{-2}	Variable	
X	Concentration of P in lake	g m^{-2}	Variable	
λ	Standard deviation of annual P input	unitless	0.35	Carpenter (2003)
ε	Control parameter on within-year variance in P input	unitless	0.01	Carpenter (2003)
σ	Control parameter on recycling of P during the summer	unitless	0.01	Carpenter (2003)

Table 2. Six indicators of regime shifts. In each of these equations, **X** is the vector of 36 observed within-year values (indexed by *k*) of the concentration of P in the water column in year *t*.

Type of indicator	Name of indicator	Equation
Variance indicator	**SD**	$SD_t = \sqrt{\sum_{k=1}^{36} \frac{(X_{t,k} - \overline{\mathbf{X}_t})^2}{36}}$
	SD$_{\mathbf{DLM}}$	$SD_{[\mathrm{DLM}]t} = \sqrt{\sum_{k=1}^{36} \frac{(X_{t,k} - \overline{\mathbf{X}_{[\mathrm{DLM}]t}})^2}{36}}$
	SD$_{\mathbf{rec}}$	$SD_{[\mathrm{rec}],t} = \sqrt{\sum_{k=1}^{36} \frac{(X_{t,k} - \overline{\mathbf{X}_{[\mathrm{rec}](\mathrm{t}),k}})^2}{36}}$
Spectrum indicator	**SPEC**	$\mathrm{Spec}_t = \max(spec(X_{t,k \in 1:36}))$
DLM indicator	***A*$_{\mathbf{0}}$**	Upgraded parameter a_0 (from Eqns 6, 7)
“Control”	***X***	$X = \overline{\mathbf{X}_t}$

Table 3. Values of the three variance parameters used in the simulations to determine the power of each indicator listed in Table 1.

Set number	λ	ε	σ
1	0.01	0.001	0
2	0.01	0.001	0.01
3	0.01	0.01	0.01
4	0.10	0.001	0.01
5	0.35	0.001	0.01
6	0.35	0.01	0.01

Table 4. Results of the sensitivity analysis of varying system and management parameters on the probability that regime shifts occur. Values shown are means of 500 simulations for each set of parameters. The SPEC indicator was used to detect impending regime shifts. The percent of regime shifts that occurred in the model are those that occurred after simulated management intervention was applied as described in text.

Fixed parameters	Variable parameters: Relative	Variable parameters: Absolute	Percent of regime shifts	Conclusion
Initial F_a = 0.3; *Speed* = 40; FAC = 10; *Best Input* = 0.9	Low	$\lambda = 0.1$; $\varepsilon = 0.001$; $\sigma = 0.01$	1.2	Regime shifts are more difficult to detect and occur more frequently as variability in the system increases.
	Medium	$\lambda = 0.35$; $\varepsilon = 0.01$; $\sigma = 0.01$	21	
	High	$\lambda = 0.5$; $\varepsilon = 0.02$; $\sigma = 0.01$	53	
$\lambda = 0.35$; $\varepsilon = 0.01$; $\sigma = 0.01$	Low	Initial F_a = 0.2	10	The closer one is initially to the threshold, the harder
	Medium	Initial F_a = 0.3	23	

Speed = 40 FAC = 10 *Best Input* = 0.9	High	Initial F_a = 0.4	36	it will be for the indicator to detect the regime shift with ample warning (see Fig. 2)
λ = 0.35; ε = 0.01; σ = 0.01 Initial F_a = 0.3 FAC = 10 *Best Input* = 0.9	Low	*Speed* = 20	35	Allowing for a more rapid rate of new inputs gives less time for the indicator to detect the regime shift before it happens. Thus, the percent of regime shifts increases.
	Medium	*Speed* = 40	19	
	High	*Speed* = 60	18	
λ = 0.35; ε = 0.01; σ = 0.01	Low	FAC = 5	1.2	As the tuning coefficient increases, the detection
	Medium	FAC = 10	19	

Initial F_a = 0.3 *Speed* = 40 *Best Input* = 0.9	High	FAC = 20	67	rate declines and the probability of regime shift increases
λ = 0.35; ε = 0.01; σ = 0.01	Low	*Best Input* = 0.75	2	Higher allowable inputs is
	Medium	*Best Input* = 0.9	18	a special paramter It has

Initial F_a = 0.3 *Speed* = 40 FAC = 10				no effect on detection time, but it is critical because a high value means that management maintains the system close to its threshold.
	High	*Best Input* = 1.0	69	Consequently, after detecting the potential occurrence of a regime shift, there is an increased risk of a shift occurring due to small disruptive events.

Figure Legends

Figure 1. Schematic drawing of the basic model of a lake ecosystem (after Carpenter and Brock 2006), with additional point-source inputs of P ("Point-source P from industry"). Variables in parentheses correspond to variables in the model (Equations 1-3; Table 1).

Figure 2. Example of the behavior of the model (using basic parameter set described in Table 1) subject to realistic increases in point-source or non-point source inputs. **A** – simulated point-source (F_i in Eqn. 2) or non-point-source (F_a in Eqn. 1) inputs of phosphorus. **B** – total inputs ($F_{\text{total}} = F_a + F_i$) following increases in point-source inputs only. **C** – total inputs ($F_{\text{total}} = F_a + F_i$) following increases in non-point-source inputs only. **D** – total P in water column when point-source inputs are increased and then eliminated. **E** – total P in water column when non-point-source inputs are increased and then eliminated. In **B, C, D,** and **E**, the light-grey vertical line indicates the onset of observable recycling of P from lake sediments into the water column ($R(X) = 0.0001$), and the dark-grey vertical line indicates the shift from an oligotrophic to a eutrophic regime.

Figure 3. Effects of the three variance parameters (λ, ε, and σ) on time-series of concentration of P in the water column and its standard deviation. **A** - The parameter λ (here, $\lambda = 0.35$) controls annual variability in concentration of P in the water. **B** – The standard deviation in annual concentration of P in the water increases along with inputs of P from the soil (F_{soil}). **C** – The parameter ε controls within-year variability in concentration of P in the water (here, $\varepsilon = 0.01$). Note that in **A, B,** and **C** the *x*-axis (years) only ranges from 1-6

years as these figures simply illustrate the type of variability controlled by each of the three parameters. **D** – The within-year standard deviation of concentration of P in the water increases with inputs of P from soil (F_{soil}). **E** - The parameter σ controls summer variability in recycling of P from lake sediments into the water column (here, σ = 0.01). **F** – The standard deviation in concentration of P in the water column increases only after recycling of P from sediments into the water column reaches measurable levels ($R(X)$ = 0.0001; grey vertical line). For each of these runs, we used the base parameter values (Table 1). The only inputs of P to the system were from soil, and these inputs increased linearly through time (as in Fig. 2A up to simulated year 300).

Figure 4. Time series of concentration of P in the water column (top row) and the five indicators of regime shift (listed in Table 2) when the model was run only with noise due to recycling of P from sediment to the water column (σ = 0.01, λ = ε = 0.0; left column) or when the model was run with all sources of variability included (σ = 0.01, ε = 0.01, λ = 0.35; right column). The grey vertical line indicates when recycling of P from sediments into the water column reaches measurable levels ($R(X)$ = 0.0001). In all runs, the system shifted from oligotrophic to eutrophic regimes at ~ simulated year 250. When all sources of variation were included in the model (right column), the "signal-to-noise" ratio was large from the time that recycling of P begins, > 100 years before a regime shift. The "signal-to-noise" ratio is clearest for the SPEC indicator, which reliably signaled a regime shift ~40 years in advance.

Figure 5. Probability of a regime shift (top row) and average time to recovery ($N = 200$ simulation runs) from a eutrophic back to an oligotrophic regime (bottom row) as a function of time of three different management interventions when P inputs are due only to point-sources (left) or non-point-sources (right). Model parameters and input schedules as in Fig. 2. The three management interventions are slow (solid black line: 10 years from observable signal to response with a 50% reduction in P achieved after 50 years); intermediate (dashed black line: 5 years from observable signal to response with a 90% reduction in P achieved after 10 years); and rapid (dashed-dotted black line: immediate response with no allowable inputs 2 years after response). The grey vertical lines indicate when recycling of P from lake sediments into the water column = 0.0001 (dotted line); 0.001 (short-dashed line); 0.01 (long-dashed line); 0.1 (solid line). Note break on the vertical axis of panel **B**.

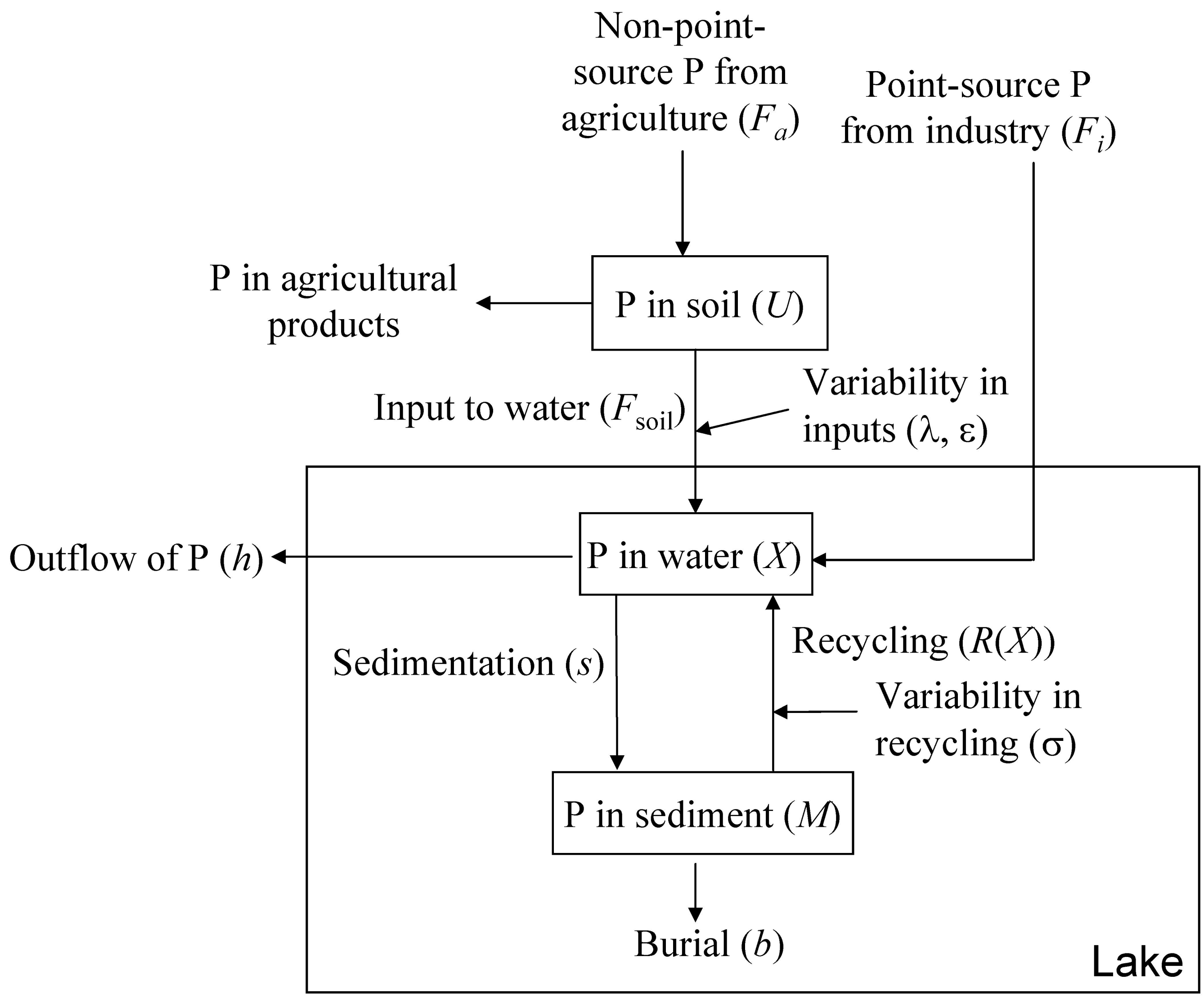
Figure 6. Power of each of the six indicators given in Table 2 as a function of time of management intervention (*Delay*) when all sources of noise are present in the model system (parameter set 6 of Table 3).

Figure 7. Total power of each of the six indicators given in Table 2 for all the parameter sets given in Table 3. Power of each indicator for each parameter set is calculated as the area under the Power *vs. Delay* curve (as illustrated in Fig. 6).

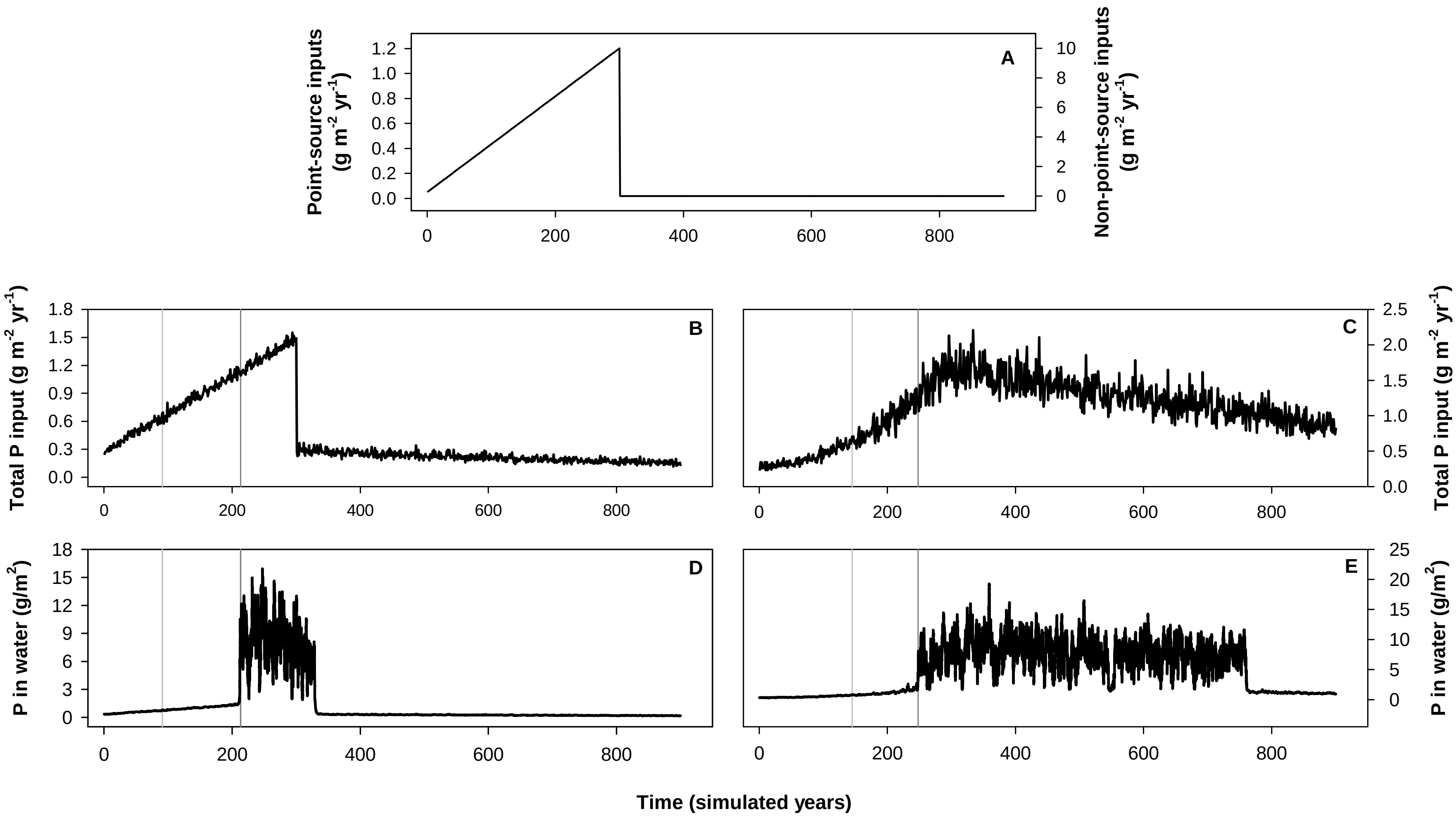
Figure 8. Error values (from Eqn. 10) for each of the six indicators given in Table 2 when all sources of variability were present in the model system (parameter set 6 of Table 3) and

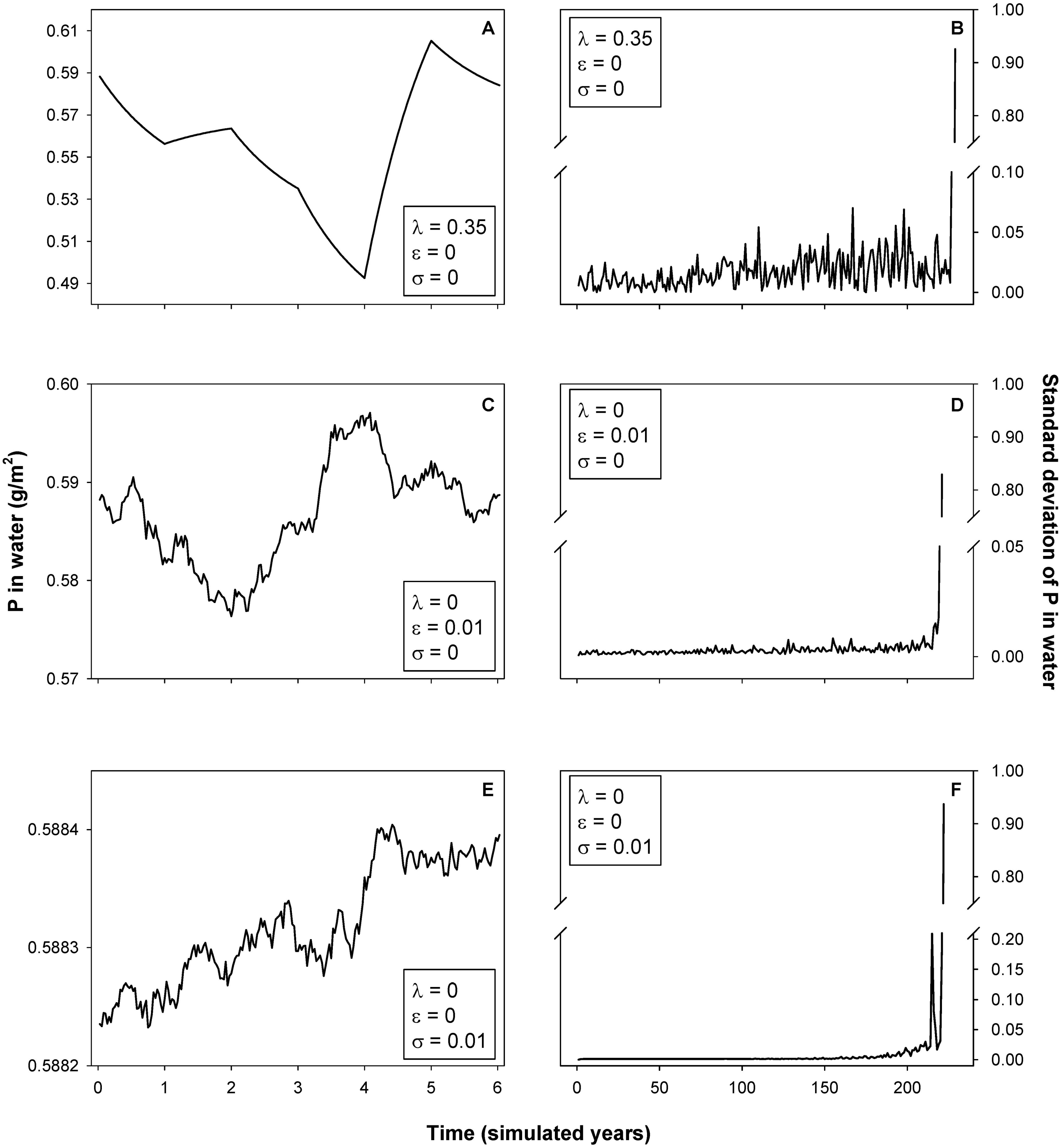
for the optimal level of FAC for each indicator. **A** – model run with only non-point-source inputs (F_a increasing linearly, $F_i = 0$, as in Fig. 2D,). **B** – model run with only point-source inputs increasing ($F_a = 0.3$; F_i increasing linearly as in Fig. 2C).

Figure 9. Probability that a regime shift occurs as a function of when it was detected. In the simulations used to generate these values, the system parameters were set at $\lambda = 0.35$, $\varepsilon = 0.01$, $\sigma = 0.01$, and initial $F_a = 0.3$. Point-source inputs (F_i) were allowed to increase linearly according to the management parameters *Speed* = 40 years to doubling total inputs ($F_{\text{total}} = F_i + F_a$) with the amount of allowable point-source inputs after management intervention *Best inputs* = 0.9. The tuning coefficient for the detection indicator FAC was set equal to 10. This parameter set was the "medium" parameter set of Table 4.

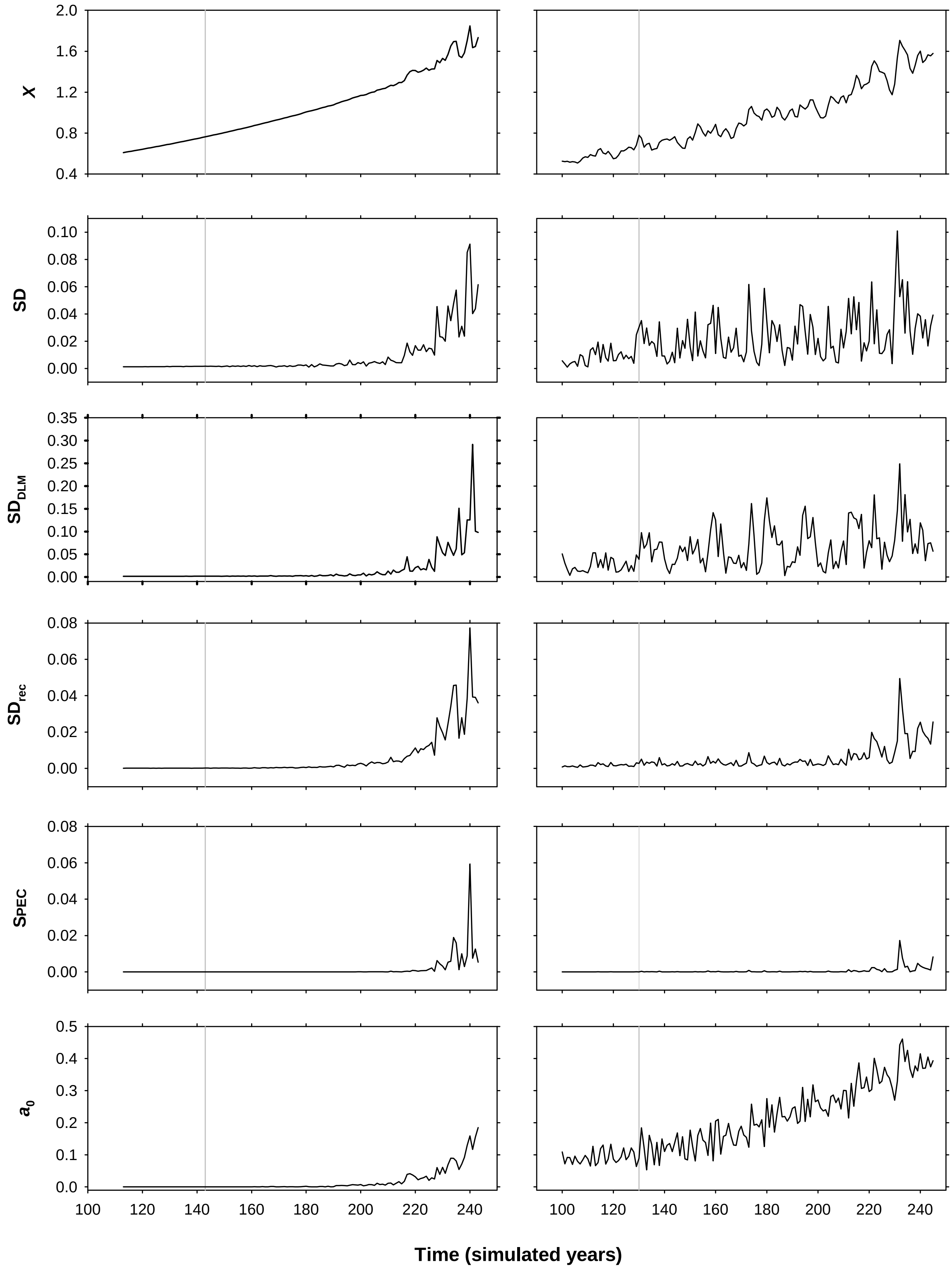


Non-point-source P from agriculture (F_a)
Point-source P from industry (F_i)
P in agricultural products
P in soil (U)
Input to water (F_{soil})
Variability in inputs (λ, ε)
Outflow of P (h)
P in water (X)
Sedimentation (s)
Recycling ($R(X)$)
Variability in recycling (σ)
P in sediment (M)
Burial (b)
Lake

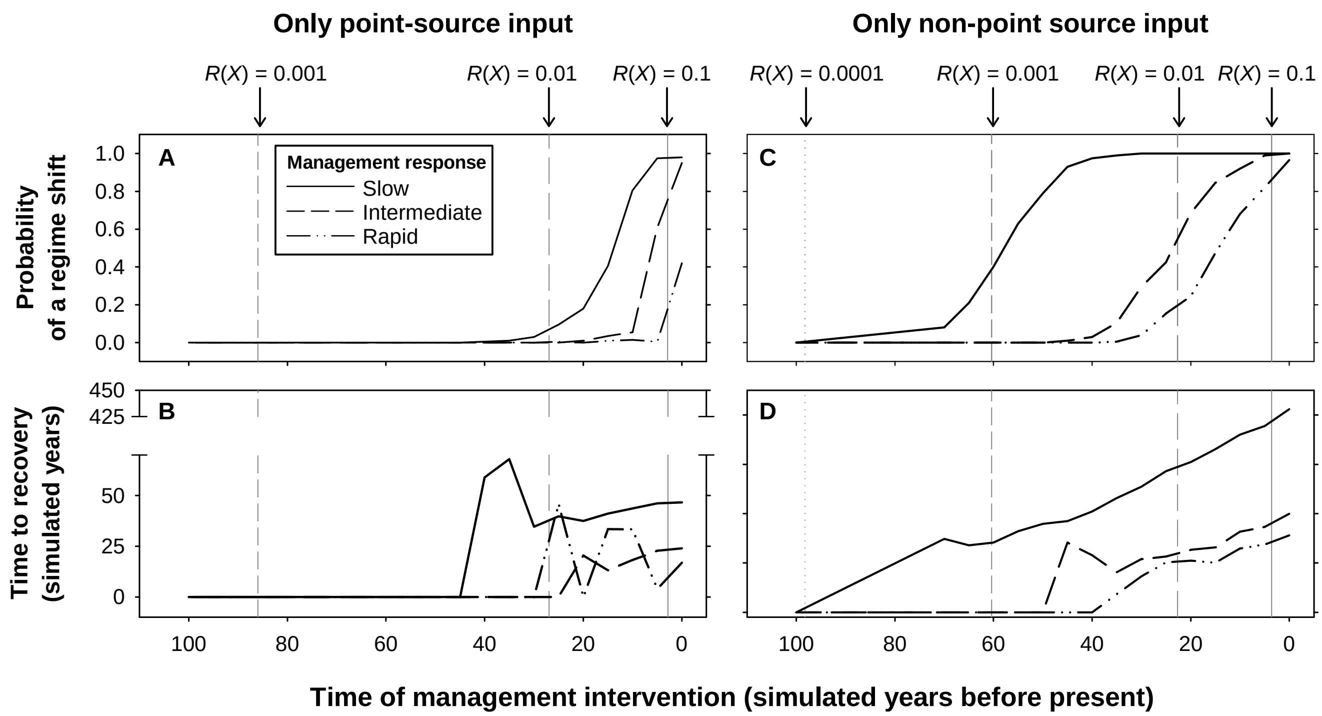

A
Point-source inputs (g m-2 yr-1)
Non-point-source inputs (g m-2 yr-1)
B
C
Total P input (g m-2 yr-1)
D
E
P in water (g/m2)
Time (simulated years)



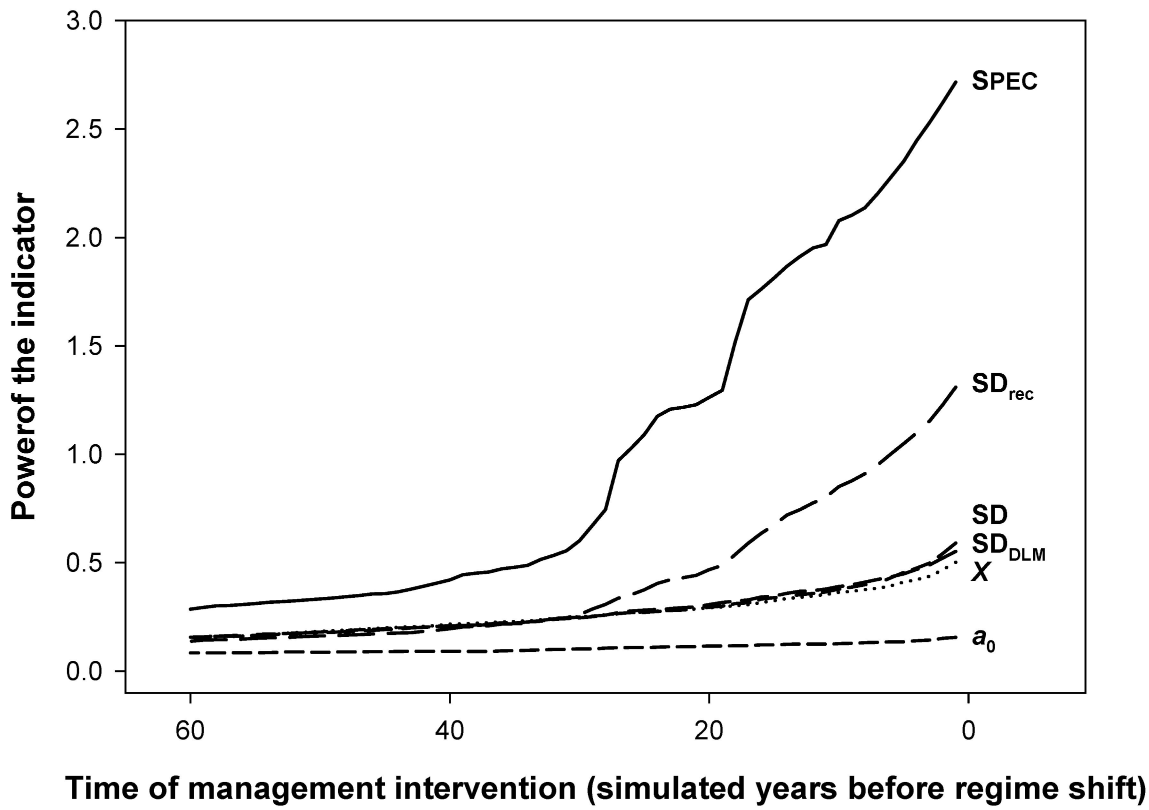
A
λ = 0.35
ε = 0
σ = 0
B
λ = 0.35
ε = 0
σ = 0
C
λ = 0
ε = 0.01
σ = 0
D
λ = 0
ε = 0.01
σ = 0
E
λ = 0
ε = 0
σ = 0.01
F
λ = 0
ε = 0
σ = 0.01
P in water (g/m²)
Standard deviation of P in water
Time (simulated years)
0.61
0.59
0.57
0.55
0.53
0.51
0.49
0.60
0.59
0.58
0.57
0.5884
0.5883
0.5882
1.00
0.90
0.80
0.10
0.05
0.00
0.20
0.15
0 1 2 3 4 5 6
0 50 100 150 200



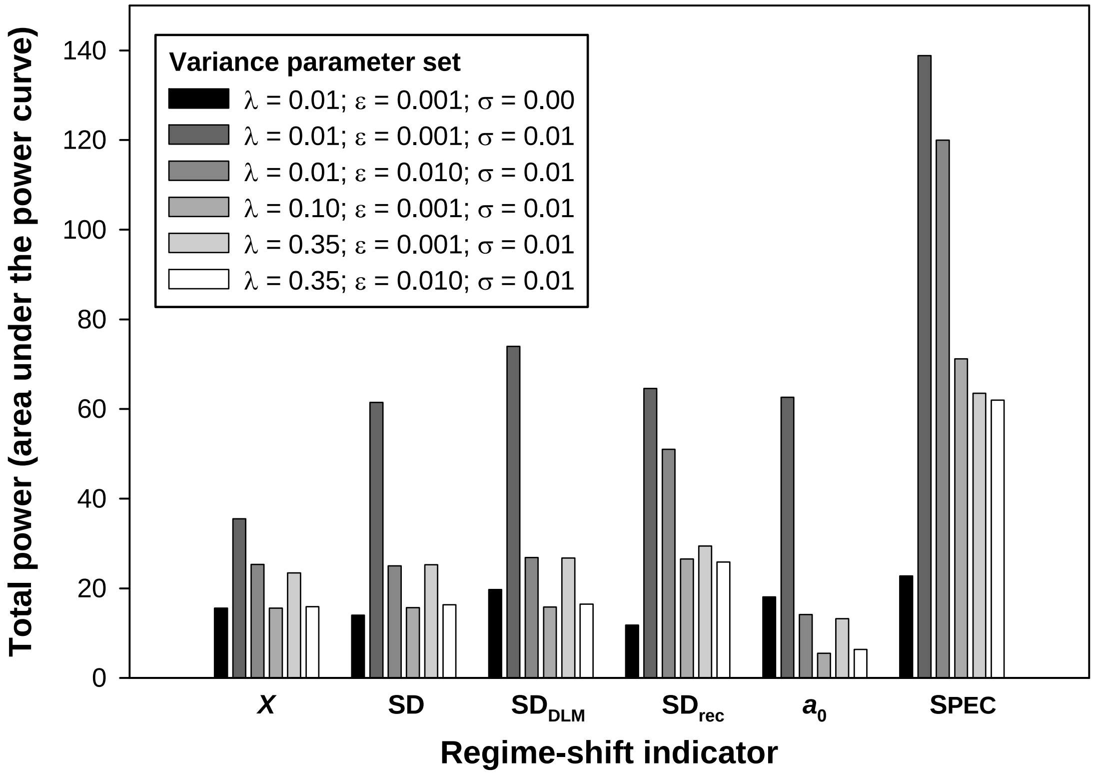
X
SD
SD_DLM
SD_rec
SPEC
a_0
Time (simulated years)



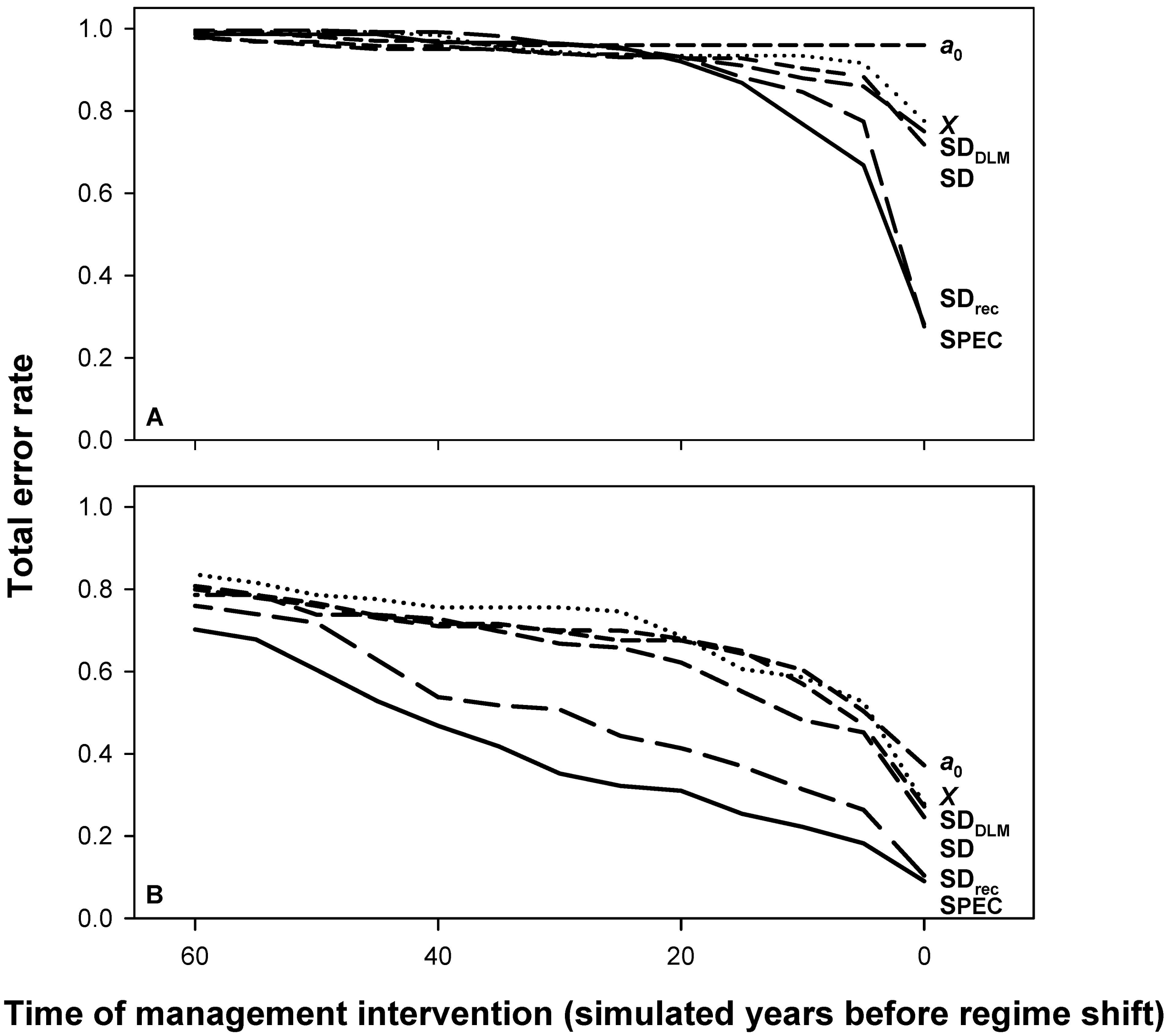
Only point-source input
Only non-point source input
R(X) = 0.001
R(X) = 0.01
R(X) = 0.1
R(X) = 0.0001
R(X) = 0.001
R(X) = 0.01
R(X) = 0.1
A
B
C
D
Management response
Slow
Intermediate
Rapid
Probability of a regime shift
Time to recovery (simulated years)
1.0
0.8
0.6
0.4
0.2
0.0
450
425
50
25
0
400
300
200
100
0
100
80
60
40
20
0
Time of management intervention (simulated years before present)



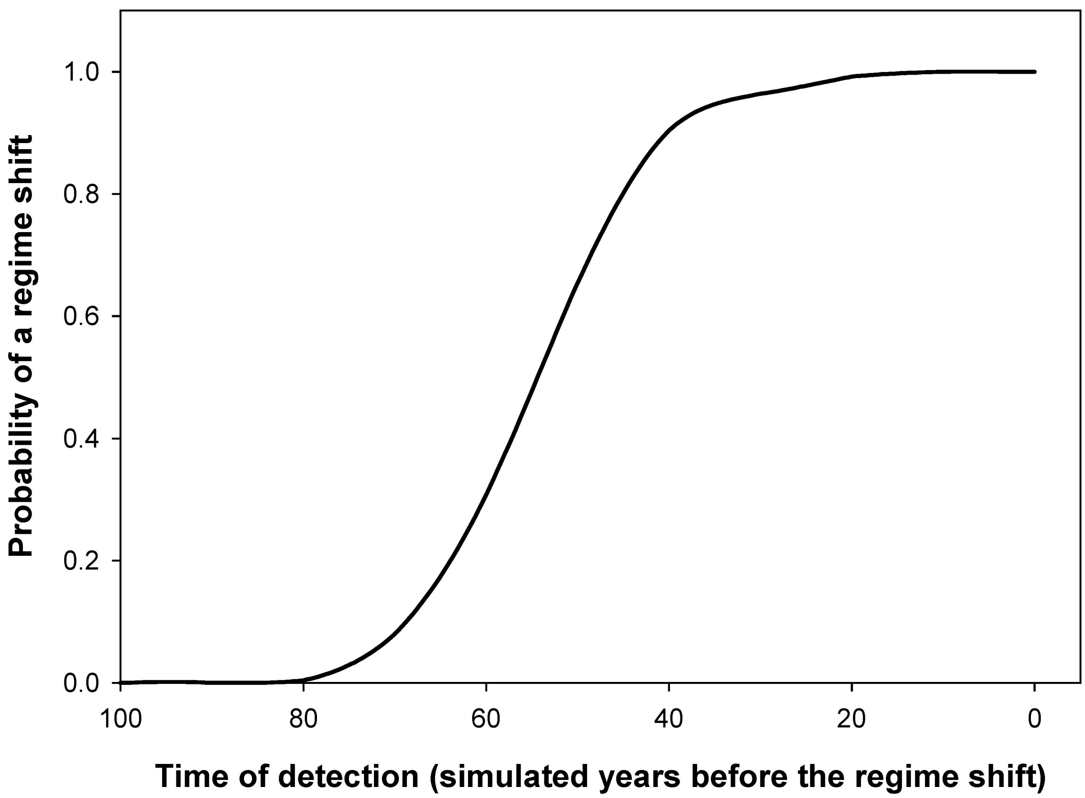
3.0
2.5
2.0
1.5
1.0
0.5
0.0
60
40
20
0
SPEC
SD_{rec}
SD
SD_{DLM}
X
a_0
Powerof the indicator
Time of management intervention (simulated years before regime shift)



Variance parameter set
λ = 0.01; ε = 0.001; σ = 0.00
λ = 0.01; ε = 0.001; σ = 0.01
λ = 0.01; ε = 0.010; σ = 0.01
λ = 0.10; ε = 0.001; σ = 0.01
λ = 0.35; ε = 0.001; σ = 0.01
λ = 0.35; ε = 0.010; σ = 0.01
Total power (area under the power curve)
0
20
40
60
80
100
120
140
X
SD
SD_DLM
SD_rec
a_0
SPEC
Regime-shift indicator



1.0
0.8
0.6
0.4
0.2
0.0
Total error rate
A
B
a0
X
SDDLM
SD
SDrec
SPEC
60
40
20
0
Time of management intervention (simulated years before regime shift)


Probability of a regime shift
0.0
0.2
0.4
0.6
0.8
1.0
100
80
60
40
20
0
Time of detection (simulated years before the regime shift)